The generic classification of the haplochromine cichlids of Lake Victoria, East Africa

M.J.P. van Oijen

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Key words: Cichlidae; *Haplochromis*; haplochromine cichlids; Lake Victoria; generic revision.
In chronologic order of publication, all papers dealing with the systematics of haplochromine cichlids of Lake Victoria are analysed with regard to the generic classification of the species. Taxonomists have disputed and changed the generic classification soon after cichlids from Lake Victoria were first described. At the turn of the century, different opinions among taxonomists working on Lake Victoria haplochromines were mainly based on the fact that they studied different material. The study of more extensive collections yielded the impression that differences between the species are gradual, rendering the delimitation of genera problematic. Recently, an attempt to use cladistic methods for the unravelling of the phylogeny of the haplochromines has resulted in a generic classification which most alpha-taxonomists working on the Lake Victoria super flock consider unworkable. Pending a more clear phylogenetic picture, a new definition of the genus *Haplochromis* is proposed in order to create at least temporary nomenclatoral stability.

Contents

Introduction

In the last two decades interest in the phylogeny of the African Cichlidae has greatly increased (Greenwood, 1979, 1980, 1983, 1984a + b, 1987, 1991, 1994; Lippitsch, 1989, 1990, 1991, 1992, 1993, 1995; McKay, 1991; Meyer, 1993; Meyer et al., 1990, 1991, 1994; Sage et al., 1984; Stiassny, 1981a + b, 1987, 1990, 1991; Sturmbauer & Meyer, 1992, 1993). Theories about the evolution of the East African cichlids have been developed based on research of many aspects of their biology (e.g.: molecular genetics, anatomy, physiology, functional morphology, ethology, and ecology). Amongst the East African cichlids, the haplochromines of Lake Victoria have become a focus of attention because their ecosystem has been irreversibly changed by the introduction of the Nile perch (*Lates niloticus*) (Barel et al., 1985, 1991; Kaufman, 1992; Witte et al., 1992a + b). As a result of direct predation and cascading effects on the food pyramid, many species must now be considered extinct (Witte et al., 1992a + b). To exchange

data and ideas it is important that there is agreement on the nomenclature of the species as well as their assigned genera. Among taxonomists dealing with the species of the Lake Victoria super flock Greenwood's revision of the genus *Haplochromis* (Greenwood, 1979, 1980) has met with much criticism (Coenen et al., 1984; Hoogerhoud, 1984; van Oijen, 1991; Snoeks, 1988, 1994; Snoeks et al., 1984, 1987, 1990; de Vos et al., 1990; Witte & Witte-Maas, 1987). The arguments brought forward by these taxonomists apparently have reached (or convinced) only a small number of researchers. Unfortunately, there has been little debate on this matter in the literature. Although Greenwood never answered the published criticism, he achieved his original goal by opening the debate. As stated (Greenwood, 1980), he primarily wanted to stimulate research on the phylogenetic classification of the haplochromine cichlids and he realised very well that his classification would be changed. Discussing the subject in a letter, Greenwood wrote me (21.ii.1992): "I don't feel, in any way, that my attempts at breaking up the genus are final, adequate, or without many loose ends." and, "I welcome the debate on the subject because both my "generic revisions" were targets, an attempt to open discussion and debate on a subject that all cichlid taxonomists since Regan have agreed is a serious problem of phylogeny not being reflected in cichlid taxonomy." At the moment there is great confusion in the application of the haplochromine nomenclature. Not only are there followers of the old and of the new generic classification, but various kinds of 'compromises' are developing. I feel that the nomenclatoral confusion resulting from Greenwood's revisions should be halted.

To place the present problem in a wider context, the use of genera in all papers dealing with the systematics of the haplochromine cichlids of Lake Victoria was analysed. In this paper all generic definitions used by taxonomists dealing with Lake Victoria haplochromines are cited in chronologic order. Definitions from papers written in French or German were translated in English. Where remarks were considered necessary in these citations, they are placed between square brackets. Underlined parts in definitions denote changes with respect to the chronologically immediately preceding definition of the genus concerned.

The term haplochromines is used as a collective one, denoting all cichlid species of the Lake Victoria basin (i.e. Lakes Victoria, Kioga, Edward, George, Nabugabo and Kivu) with a *Haplochromis* type of pharyngeal apophysis (i.e. all cichlids in the Lake Victoria basin of the tribe Haplochromini sensu Eccles & Trewavas, 1989).

The term Lake Victoria flock denotes the haplochromine cichlids occurring in Lake Victoria, and the Lake Victoria super flock is used for all haplochromine species from the Lake Victoria basin.

Historic account

Among the three great African Lakes, Lake Victoria, the source of the Nile, was the last to be discovered by Europeans. Not until thirty years after its discovery by John Hanning Speke in 1858, were the first fish specimens from Lake Victoria brought to Europe, by G.A. Fisher.

F. Hilgendorf (director of the Berlin Museum) was the first zoologist to examine and describe this collection. Among the 19 specimens, probably collected at the

shores of the southern (= "German") part of the lake, were eight specimens belonging to the Cichlidae (then known as Chromidae). Hilgendorf (1888) (erroneously) described two specimens as *Chromis niloticus* Linnaeus, 1758 (= *Oreochromis niloticus)* and placed the remaining six specimens in five new species. For the generic placement of the new species Hilgendorf followed Günther (1862) and Bleeker (1868).

Günther (1862) in his "Catalogue of the Fishes in the collection of the British Museum" in the family Chromidae recognized nineteen genera, among which were only three African ones. These African genera were defined as follows:

Chromis Cuvier, 1829; "Body compressed, oblong, covered with scales of moderate size; opercles scaly. Dorsal spines numerous, anal spines three. Teeth compressed, more or less lobate, in one series, behind which are other series containing immature teeth. Anterior prominences of the branchial arches short, thin, lamelliform, non-serrated. Dorsal fin not scaly. Intestines with numerous circumvolutions". [The genera *Tilapia* Smith, 1840; *Haligenes* Günther, 1859; and *Acara* Heckel, 1863 (part) were considered to be synonyms of *Chromis*].

Sarotherodon Rüppell, 1852 [synonym: *Coptodon* Gervais, 1853]: "Body compressed, oblong, covered with scales of moderate size; opercles scaleless. Dorsal spines numerous, anal spines three. Teeth compressed at the apex, in a single series, with a band of villiform teeth behind. Lateral line interrupted. Branchiostegals five."

Günther (1862: 273) added the remark that he had "serious doubts" as to the validity of this genus as "scales on the operculum are deciduous in all species of *Chromis*, and sometimes every trace of scales and of the cutis is lost on one side, whilst they are present on the other." Moreover, he considered tooth shape in the type species of *Sarotherodon (= Melanogenes macrocephalus* Bleeker, 1863) hardly different from that in certain *Chromis* species. *Sarotherodon* is not mentioned in Günther's (1880) general textbook on ichthyology: "An introduction to the study of fishes".

Hemichromis Peters, 1857 [synonym: *Chromichthys* Guichenot, 1859]: "Body oblong, covered with cycloid scales of moderate size. Dorsal spines numerous, anal spines three; base of soft dorsal naked; cheeks and opercles scaly. Mouth proctractile, teeth conical, in one or two series above, in one below. Anterior prominences of the first branchial arch short, compressed, horny, bicuspid. Branchiostegals five."

Bleeker (1868), describing new Chromidae from Madagascar, erected the genus *Paratilapia* which was characterized by an elongate body with large ctenoid scales; acutely pointed and curved conical teeth in three or four rows in both jaws; the teeth in the outer row much larger than those in the inner rows; 12 dorsal fin spines and 3 anal fin spines. Bleeker also gave the number of scale rows on operculum, interoperculum and cheek, and the shape of the lower pharyngeal element and the pharyngeal teeth. In the same paper Bleeker (1868) described the genus *Paretroplus*, which was never used for species from Lake Victoria. In contrast to Günther, Bleeker considered *Tilapia* Smith, 1840, a valid genus.

In 1878 Bleeker described the genus *Paracara*, which was synonymized with *Paratilapia* by Hilgendorf (1888) because he could not find any differences in Bleeker's definitions of the two genera.

Steindachner (1881) described the genus *Ptychochromis* for a species from Mada-

gascar which Bleeker had described in *Tilapia*. This generic name was never used for haplochromines.

When Hilgendorf received the cichlids from Lake Victoria six to eight "African" cichlid generic names were available. Four of the five new species of Hilgendorf exhibited characters that did not fit into these genera. Therefore he proposed the new subgenus *Chromis (Haplochromis)* for a new species named *obliquidens* (fig. 1), which was distinguishable from the real *Chromis* species because the crowns of its teeth were not notched.

Some characters of the specimens on which he based three new species, viz. *retrodens, cavifrons* and *longirostris,* did not quite fit in the genus *Paratilapia*; the new species all had more than twelve spines in the dorsal fin. For this reason Hilgendorf described these species under *(Paratilapia?)*. One of the new species, *(Paratilapia?) retrodens*, moreover differed by having a larger number of tooth rows; 9 in the upper and 8 in the lower jaw (3-4 in *Paratilapia* according to Bleeker's definition), and in its dentition. In both jaws, at the end of the tooth rows, a group of short, thick teeth was present. To solve this problem, Hilgendorf suggested that one could either 1) change the generic definition of *Paratilapia*, 2) create a new genus for *retrodens* (for which he suggested the name *Hoplotilapia*), or 3) "going to the other extreme", one could combine *Paratilapia* and *Hemichromis*. But although this would enlarge the range of dorsal fin spines, *Hemichromis* had only "1 or 2 tooth rows, and mostly cycloid scales". Because he already suggested the new genus name *Hoplotilapia*, it is likely that Hilgendorf preferred the second solution. However, he never executed his intention, stated at the end of his paper, to produce a more detailed description of the new species. That might have been the right opportunity to formally describe the genus *Hoplotilapia* and give a solution for *(Paratilapia?)*. His first paper on the Lake Victoria cichlids turned out to be also his last.

In 1893, Pfeffer proposed to restrict the genus *Chromis* to species with cycloid

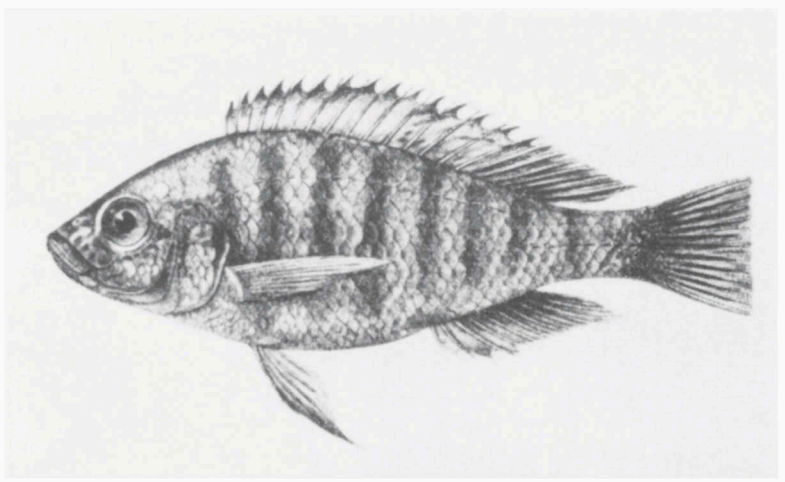


Fig. 1. A figure of the holotype of *Haplochromis obliquidens* Hilgendorf, 1888, the type species of *Haplochromis* was never published. This figure represents the lectotype of *Hemitilapia bayoni* Boulenger, 1908, a species synonymized with *Haplochromis obliquidens* by Regan (1922). From Boulenger, 1908, fig. 1.

scales on the body and large scales on the nuchal area. For species with ctenoid scales on the body and small nuchal scales, he described a new genus, *Ctenochromis*.

Steindachner in 1894, created the subgenus *Paratilapia (Pelmatochromis)* to accommodate species of *Paratilapia* with a soft, pillow shaped, papilla-bearing, mucous membrane situated rostral to the upper pharyngeal jaws (fig. 2).

Pfeffer (1896) used only three genera; *Chromis*, *Ctenochromis* and *Hemichromis*. His definitions were as follows:

Chromis: " Scales cycloid; spines of the dorsal fin numerous, of the anal usually 3 rarely 4. Outer row teeth with a major cusp and one or two minor cusps; several inner rows with small tricuspid teeth. Gill rakers thin, slender acutely tapering."

Ctenochromis, was defined as follows: " Like *Chromis*, but the scales on the largest part of the body ctenoid; but scales on head and neck and on the rostral parts of the body invariably cycloid." [*Ptychochromis* Steindachner was considered to be a synonym.]

Hemichromis: " Scales usually cycloid. Outer row teeth conical, as are the inner teeth when these are fully developed. A number of gill rakers at the end broadened into a hammer- or ax shape. "

On the basis of a single specimen from Bukoba, Pfeffer made a relatively extensive description of a new species from Lake Victoria which he named *Hemichromis serranus*. Pfeffer stated that no figure of the new species was added because it was only a preliminary description. However, he never published a more detailed description.

Hilgendorf's species *(Paratilapia?) retrodens*, *(P.?) cavifrons*, and *(P.?) longirostris* were also placed in *Hemichromis*. Pfeffer removed one of the two specimens on which the description of *Chromis nuchisquamulatus* Hilgendorf, 1888, was based from that species, and redescribed it as a new species: *Ctenochromis sauvagei*. The original species, *nuchisquamulatus*, was also placed in *Ctenochromis*. *Chromis (Haplochromis) obli-*

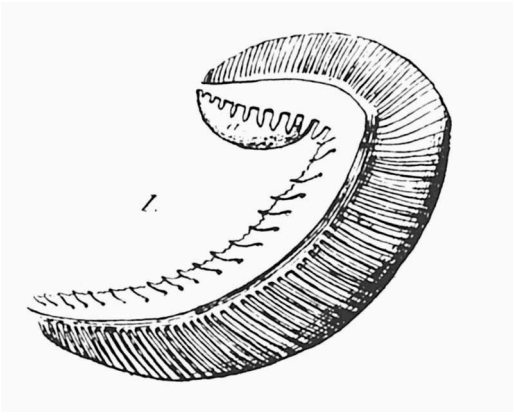


Fig. 2. First gill arch from left side of *Pelmatochromis lateralis* Boulenger, 1898. a = pillow shaped mucous membrane, the main distinguishing character for the (sub)genus *Pelmatochromis* Steindachner, 1894. From Pellegrin, 1904a, fig. 27.

quidens was not mentioned in this paper, but this species was listed as *Ctenochromis obliquidens* in a subsequent paper (Pfeffer, 1897).

In 1898 Boulenger, working in the British Museum (Natural History), London, published a list of African cichlids in which the species *retrodens*, *cavifrons* and *longirostris* were placed in *Paratilapia* (without question mark and not between brackets!). The species *nuchisquamulatus*, *sauvagei* and *obliquidens* were placed in the genus *Tilapia*. *Hemichromis serranus* was not mentioned.

An explanation for these generic changes was given in a next publication Boulenger (1898b). Boulenger had discovered that Günther, following Cuvier & Valenciennes (1829), erroneously had placed *Labrus niloticus* Linnaeus, 1758, in *Chromis*. The problem was that the definition of *Chromis*, was based on characters of *Sparus chromis*, a marine fish. Boulenger, therefore, proposed to place *niloticus* in *Tilapia* Smith, 1840, in the family named Cichlidae by Bleeker (1859). Bleeker's family Cychloidei apparently was derived from the tribus Cychlini (of the family Chromididae) of Bonaparte (1840).

In the first part of his revision of the Cichlidae, Boulenger mentioned nine genera of African cichlids. *Pelmatochromis*, until then a subgenus of *Paratilapia*, was raised to the generic level. Boulenger (1898b) defined the genus *Pelmatochomis* as follows: "Characters of *Paratilapia*, with the addition of a much developed cushion-like papillose pad of mucous membrane on each side of the palate, close to the upper part of branchial arches." The species *serranus*, just like *retrodens*, *cavifrons* and *longirostris*, was placed in *Paratilapia*. Boulenger's definition of *Paratilapia* was as follows: "Body short or more or less elongate, scales cycloid or ctenoid. Two or more series of conical teeth in the jaws. Maxillary exposed. Dorsal with 10 to 18 spines, anal with 3. Vertebrae 27-38 (13+14 in *P. pollenii*, 5+13 in *P. sacra*, 17+19 in *P. robusta*, 19+19 in *P. longiceps*)."

To the characters already in use Boulenger added the vertebrae number and the exposure of the maxilla.

In the second part of his revision of the Cichlidae, in which the number of African genera was raised to 19 (due to the examination of the Moore collection from Lake Tanganyika), Boulenger (1899) considered *Haplochromis* and *Ctenochromis* to be synonyms of *Tilapia*. Boulenger's definition of *Tilapia* was as follows: "Body short or moderately elongate; scales cycloid or ctenoid. Two or more series of small teeth in the jaws, all or greater part notched or bi- or tricuspid (fig. 3). Maxilla entirely concealed under the praeorbital when the mouth is closed, or a small part of its distal extremity exposed. Dorsal with 13 to 19 spines, anal with 3 or 4. Vertebrae 28-32 (14-17 + 13-16)."

Solely on the basis of the original descriptions, Boulenger placed *Tilapia sauvagei* and *T. obliquidens* in the synonymy of *T. nuchisquamulatus*.

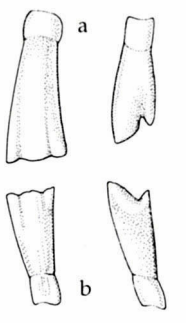


Fig. 3. Teeth of *Tilapia sparmanii* Smith, 1840. a. Two teeth of the upper jaw. b. Two teeth of the lower jaw. Redrawn from Smith, 1840, plate v.

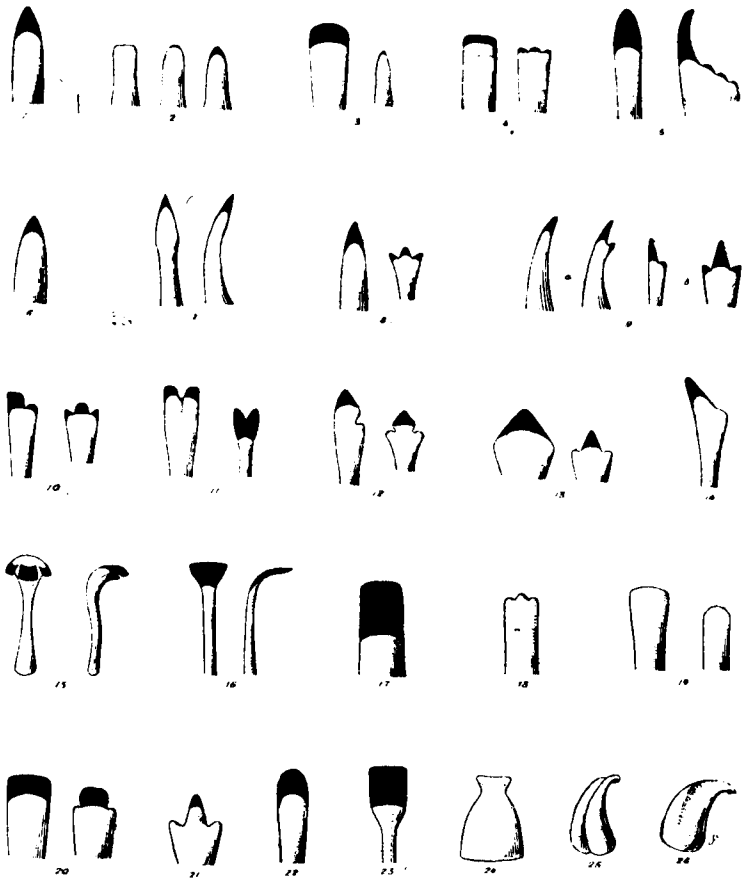


Fig. 20. – Dents maxillaires. 1, *Heros spurius* ; 2, *Cichlasoma heterodontus* (3 dents, série externe) ; 3, *Neetroplus Bocourti* (sér. ext., sér. int) ; 4, *Herotilapia multispinosa* (id.) ; 5, *Uaru amphiacanthoides* (face et profil) ; 6, *Hemichromis fasciatus* ; 7, *Bathybates ferox* (face et profil) ; 8, *Gephyrochromis Moorei* (sér. ext., sér. int.) ; 9, *Astatotilapia Livingstonei* (type) (*a* sér. ext., *b* sér. int.) ; 10, *Tilapia Dardennei* (sér. ext., sér int.) ; 11, *Ptychochromis oligacanthus* (id.) ; 12, *Oreochromis shiranus* (id.) ; 13, *Docimodus Johnstoni* (id.) ; 14, *Corematodus shiranus* ; 15, *Petrochromis polyodon* (face et profil) ; 16, *Chilochromis Duponti* (id) ; 17, *Steatocranus gibbiceps* (médiane, sér. ext.) ; 18, *Asprotilapia leptura* ; 19, *Paretroplus polyactis* (médiane et latérale) ; 20, *Etroplus suratensis* (sér. ext. méd. et latérale) ; 21, *Etroplus maculatus* ; 22, *Spathodus erythrodon* ; 23, *Eretmodus cyanostictus* ; 24, *Perissodus microlepis* ; 25, *Plecodus paradoxus* ; 26, *Xenochromis Hecqi*.

Fig. 4. Variation in tooth shape of cichlids. From Pellegrin, 1904a.

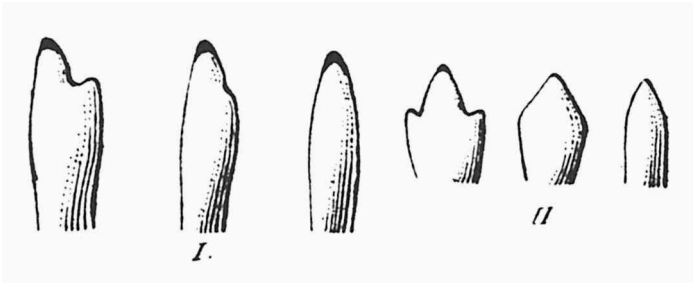


Fig. 5. Teeth of outer row (I) and inner row(II) of specimens of *Astatotilapia desfontainesi* (Lacépède, 1802). From Pellegrin, 1904a, fig. 39.

Boulenger (1902) erected the genus *Hemitilapia* for a new cichlid species from Lake Malawi (fig. 7). The genus was defined as follows: "Like *Tilapia* Smith, but jaws with moderately broad bands of slender club-shaped movable teeth, with slightly incurved crowns, those of the outer series larger, with the crown obliquely truncate and pointing forwards." Later on, two Lake Victoria species would be placed in this genus (see below; Boulenger, 1909 and Pellegrin, 1913).

In 1904 Pellegrin, working in the Muséum Nationale d'Histoire Naturelle, Paris, published a monograph on the family Cichlidae, which contained chapters on anatomy, reproduction, behaviour, food, and distribution. was the first to publish figures of the variation in oral tooth shape (fig. 4), oral and pharyngeal jaws, pharyngeal teeth, and gill rakers.

With regard to the classification of the Lake Victoria cichlids, Pellegrin (1904a) followed Boulenger (1898b, 1899). In his publication Pellegrin introduced the new genus *Astatotilapia* which in dentition was intermediate between *Tilapia* and *Paratilapia*. The species of *Astatotilapia* differed from the latter two genera because juveniles had bicuspid teeth in the outer row and tricuspids in the single inner row; all these teeth changed more or less completely in monocuspids in adult specimens (fig. 5). Besides this, the genus was characterized by few and short gill-rakers, large ctenoid scales, 14-16 dorsal fin spines, 3 anal spines, two lateral lines and an exposed maxilla.

Pellegrin (1904a) defined *Tilapia* as follows: "Body short or medium. Teeth small, compressed, all notched, more or less bi- or tricuspid, in two or more rows in both jaws, lateral teeth in the outer row exceptionally slightly conical. Maxilla exposed or hidden under the preorbital. Gill rakers short or medium sized (7-25). Scales cycloid or ctenoid, large (27-40), 13-19 spines in the dorsal, 3 (exceptionally 4) in the anal fin."

Paratilapia was defined as follows: "Body more or less elongate. Conical teeth in several series in both jaws. End of maxilla visible. Gill rakers either short or sometimes rather long (7-27). Scales cycloid or ctenoid, large or medium sized (28-68), 10-18 spines in the dorsal fin, 3 spines and 6-13 finrays in the anal fin."

Pellegrin added: "Certain forms very close to *Hemichromis*, others much more differentiated in the direction of the most important African genera *Pelmatochromis*, *Tilapia* etc."

In Pellegrin's generic definitions the number of gill rakers, the number of scales in a longitudinal series and the number of fin rays were added, but the number of vertebrae was not mentioned.

In an addendum Pellegrin gave the description of *Astatoreochromis alluaudi*, a

new species from Lake Victoria in a new genus which was characterized by the possession of four to six spines in the anal fin. Following his predecessors Pfeffer and Boulenger, Pellegrin (1904a) did not mention the subgenus *Chromis* (*Haplochromis*) Hilgendorf.

Later that year, Pellegrin (1904b + c) first published preliminary and thereafter slightly more detailed descriptions of three new cichlid species collected by Alluaud from the Kavirondo gulf of Lake Victoria. These species were placed in *Tilapia* and *Paratilapia*. With the more detailed descriptions, habitus figures of the new species were published, which are the first figures of Lake Victoria cichlids (see fig. 6).

When Boulenger received 800 specimens collected by Degen from Lake Victoria, his view that Lake Victoria had a relatively poor fish fauna changed completely. From this collection Boulenger (1906) described one new *Paratilapia* species, four new *Pelmatochromis* species, four new *Tilapia* species and six new species of *Haplochromis*. The subgenus *Chromis (Haplochromis)* was suddenly not only accepted by Boulenger, it was also raised to the generic level. In this publication no new definitions of the genera were given. However, in a footnote to the new species of *Paratilapia*, Boulenger remarked that "the very young *Paratilapia* and *Pelmatochromis* of Lake Victoria have more or less distinctly bi- or tricuspid teeth, rendering the distinction between these genera and *Haplochromis* or *Astatotilapia* just as difficult and unsatisfactory as is that between the latter and *Tilapia*."

Moreover, in a footnote to the new species *Haplochromis percoides*, Boulenger wrote that *Haplochromis* Hilgendorf, 1888, and *Ctenochromis* Pfeffer, 1893, have priority over *Astatotilapia* Pellegrin, 1904, and that *H. nuchisquamulatus*, which he (erroneously) considered the type species of both *Haplochromis* and *Ctenochromis*, was closely related to *H. desfontainesi* (Lacépède, 1802), the type species of *Astatotilapia*. The only defining remarks on *Haplochromis* were given in the same footnote. Boulenger stated that the teeth of *Haplochromis* are intermediate between *Paratilapia* and *Tilapia*, and that a considerable part of the maxilla in *Haplochromis* species is exposed when the mouth is closed.

Boulenger (1906) also described a new species in a new genus as *Platytaeniodus degeni* (fig. 7). *Platytaeniodus* was defined as follows: "Jaws with very broad bands of small conical teeth, the alveolar surface of the praemaxillaries widening towards the pharynx, the band of teeth in the upper jaw horseshoe-shaped, that in each row of the lower jaw not much longer than broad; a very small part of the maxilla exposed when the mouth is closed. Scales very feebly denticulate. Dorsal with 15 spines, anal with 3."

As part of his important publication, "The Fishes of the Nile", Boulenger (1907) again examined all known cichlid species from Lake Victoria. He borrowed "examples" of Pellegrin's material, and received photographs of Hilgendorf's types. Only the type of *Hemichromis serranus* Pfeffer, 1896, was not examined by Boulenger (nor by any of the subsequent ichthyologists studying the Lake Victoria haplochromines). The reinvestigation of all this material confirmed his earlier expressed doubt (Boulenger, 1901) on the possibility of separating genera on the basis of the number of cusps of the outer row teeth. Boulenger discovered that juveniles of some species have bi- or tricuspid teeth whereas adults of the same species have monocuspids. He

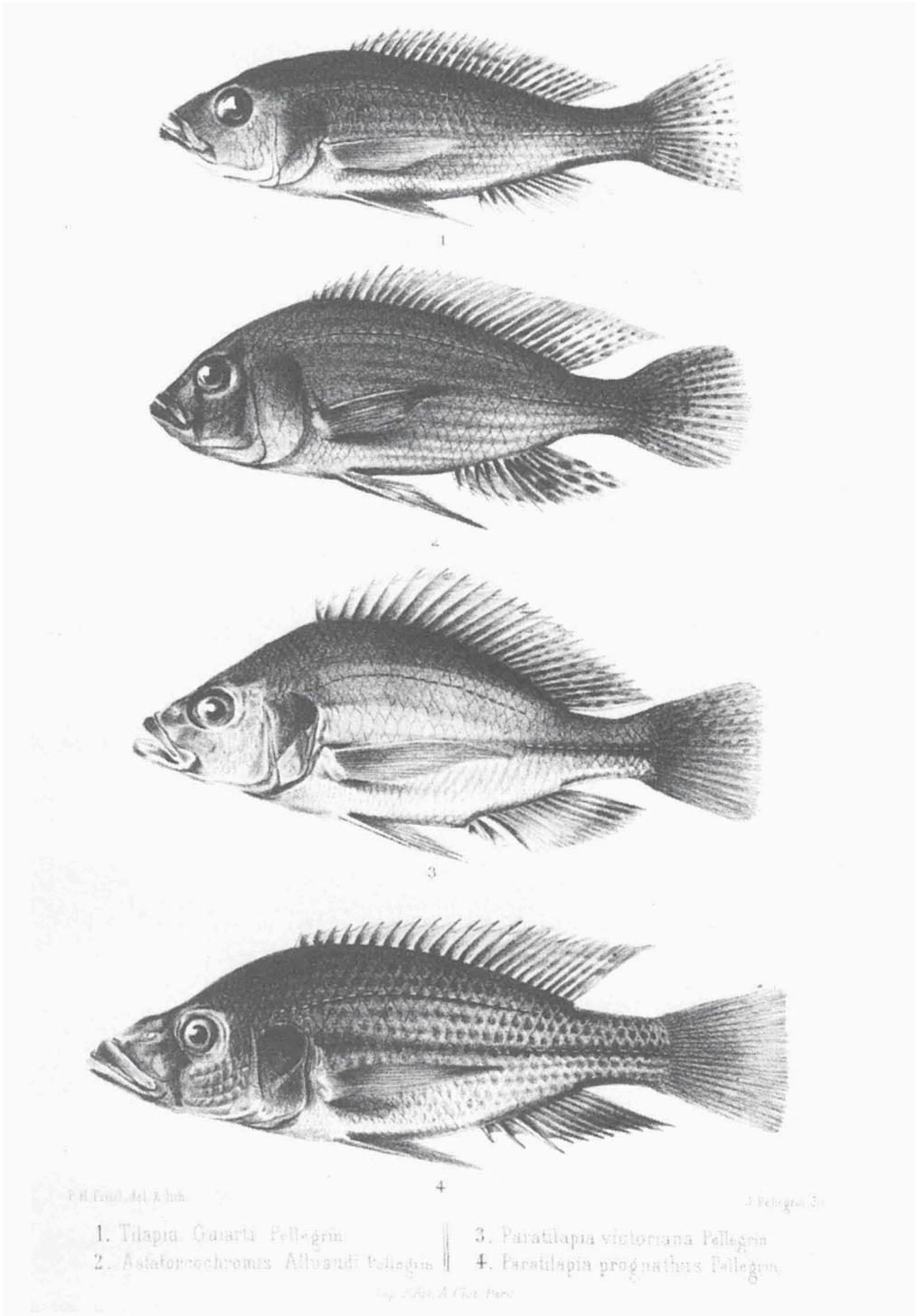
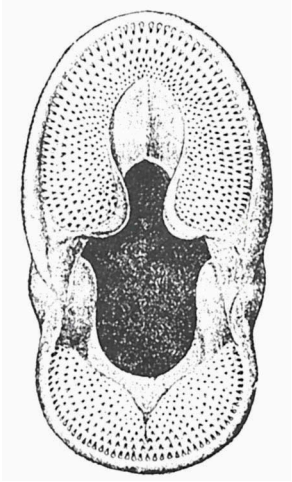


Fig. 6. The first cichlid fishes from Lake Victoria of which a figure was published. From Pellegrin 1904c, fig. 1.



Open mouth of *Platytæniodus degeni*.

Fig. 7. Oral dentition of *Platytaeniodus degeni* Boulenger, 1906. From Boulenger 1907, fig. 35.

wrote that the study of the "enormous collection" made by Degen had been "a bewildering one, specimens evidently of the same species showing every possible grade between the two extreme types of dentition according to age and even in individuals of the same size."

Although Boulenger stated that "the shape of the teeth is often a very unsafe guide for the determination of species", in the absence of other characters he "felt compelled to maintain the old generic divisions after modifying their definitions." He observed that "*Hemichromis* passes completely into *Paratilapia*, which leads, almost without gaps, to *Pelmatochromis* on the one hand, to *Haplochromis* on the other, the latter passing into *Tilapia*, which again merges into *Petrochromis*." Boulenger concluded: "These generic divisions are unsatisfactory, but they are the best I can suggest at present."

The 27 cichlid species from Lake Victoria were placed into five genera: *Tilapia* (4), *Paratilapia* (10), *Haplochromis* (7), *Pelmatochromis* (5) and *Platytaeniodus* (1). These genera were defined as follows:

Tilapia: "Teeth in three or more series, the outer bicuspid, the inner tricuspid. Maxillary bone entirely concealed under the praeorbital when the mouth is closed, or a very small portion of its distal extremity exposed. Body short or moderately elongate: scales cycloid or ctenoid; two lateral lines. Dorsal fin with 13 to 19 spines, anal with 3 or 4. Vertebrae 28 to 32 (14-17 + 13-15)."

Paratilapia: "Teeth in three or more series, the outer conical, unicuspid in the adult, sometimes bicuspid in the young, the others unicuspid or tricuspid. Maxillary bone exposed at the end when the mouth is closed. Body short or more or less elongate; scales usually ctenoid; two lateral lines. Dorsal fin with 10 to 18 spines, anal with 3. Vertebrae 27 to 38 (13-19 + 14-19)."

Haplochromis: "Teeth in two or more series, the outer conical or bicuspid, the inner usually tricuspid. Maxillary bone exposed at the end when the mouth is closed. Body short or moderately elongate; scales ctenoid; two lateral lines. Dorsal fin with

13 to 19 spines, anal with 3 to 6. The number of vertebrae 30 or 31, 15+16 in *H. desfontaines*, 14+16 in *H. alluaudi*, 14+17 in *H. ishmaeli*." [Boulenger considered *Ctenochromis*, *Astatotilapia* and *Astatoreochromis* synonyms of *Haplochromis*]. In an explanation to the genus Boulenger wrote: "The fishes of this genus are very perplexing in the variation of characters which have usually been regarded as of generic importance, such as the shape of the teeth and the number of anal spines. This state of things has given rise to much synonymy, and individuals of the same species have been referred to two genera. The outer teeth are always bicuspid and the inner tricuspid in young specimens, and often in females, whilst the outer and sometimes even the inner, are unicuspid in adult males, which, in the absence of series of specimens would be referred to *Paratilapia*."

Pelmatochromis: "Barely distinguishable from *Paratilapia* by the great development of a papillose pad on each side of the pharynx, between the gills, strongly projecting in front of the upper branch of the first branchial arch. The young of all the species described have bi- or tricuspid teeth in both jaws; some of the inner teeth may remain tricuspid in the adults, as frequently happens in the preceding genus".

The definition of *Platytaeniodus* did not differ from the first one given by Boulenger (1906). Because of the changes in the definitions of the genera, a number of species, three of which Boulenger had described only a year before, had to be placed in other genera. All described species were figured in a separate atlas.

From a collection made by Bayon on the Sesse Islands in the north-western part of Lake Victoria (and presented to the Genova Museum) Boulenger (1908) described a new species which he placed in *Hemitilapia*, a genus until then only known for Lake Malawi cichlids (fig. 8). This single specimen of *Hemitilapia bayoni*, was later on reidentified by Greenwood (1956b) and turned out to be *Haplochromis obliquidens*, a species Boulenger on the basis of "good photographs" [!] considered to be a synonym of *Haplochromis nuchisquamulatus*. Out of a second collection of Bayon from the Sesse Islands, Boulenger (1909) described two new species of *Paratilapia*.

On the basis of a second collection made by Alluaud, Pellegrin (1909a + b) again wrote two papers on the cichlids of Lake Victoria. The first was merely a list of species including a new variety and two new species. The new variety and the new species, one in the genus *Tilapia* and one in *Paratilapia*, were formally described in the second paper. Descriptions of all fishes from the second Alluaud collection, and

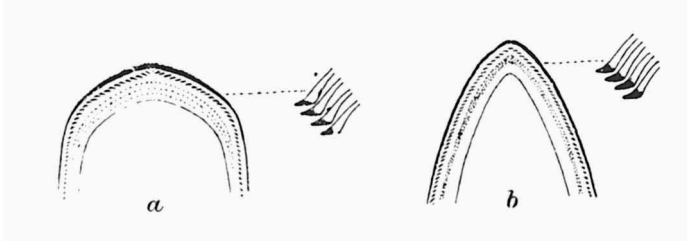


Fig. 8. Lower jaw dentition of *Hemitilapia*. a) *Hemitilapia bayoni* Boulenger, 1908. b) *Hemitilapia oxyrhynchus* Boulenger, 1902. From Boulenger, 1908, p. 7.

more detailed descriptions and figures of the new species were published the next year (Pellegrin, 1910). In his papers of 1909 as well as in this paper, which contains descriptions of 15 cichlid species, Pellegrin deviated from the classification of Boulenger (1907) who did not accept the genera *Astatotilapia* and *Astatoreochromis*. An explanation was given in two cases:

In the description of *Astatotilapia guiarti* Pellegrin, 1904, the author mentioned that in juveniles the outer teeth are clearly bicuspid, while the inner teeth are tricuspid. In one of the adult examples most teeth are conical, but in another specimen bi- and tricuspids dominate. He therefore concluded that tooth shape in *Astatotilapia* is variable.

Pellegrin defended his genus *Astatoreochromis* by stating that contrary to Boulenger (1907), he considered the occurrence of four anal spines in a few specimens of *H. desfontainesi* not a strong enough argument to suppress the genus.

Boulenger (1911), in a paper on a third collection made by Bayon, with over 3000 specimens the largest until then made in Lake Victoria, described four new species of *Paratilapia*, one new *Pelmatochromis* species, five new *Tilapia* species, and one species in a new genus: *Bayonia xenodonta* (fig. 9). Besides these four genera *Hemitilapia* and *Haplochromis* were used.

Bayonia was defined as follows: "Near *Hemitilapia*, but teeth much larger and fewer, in two series, the outer with very large compressed crowns, with long inner cusp directed inwards and very short or indistinct outer cusp, the inner minute and conical."

Preliminary descriptions of new species of *Paratilapia* (1), *Astatotilapia* (2) and *Hemitilapia* (1) from a new collection made by Alluaud and Jeannel were given in Pellegrin (1912a).

In Pellegrin's (1913), more extensive report on this collection, the new species

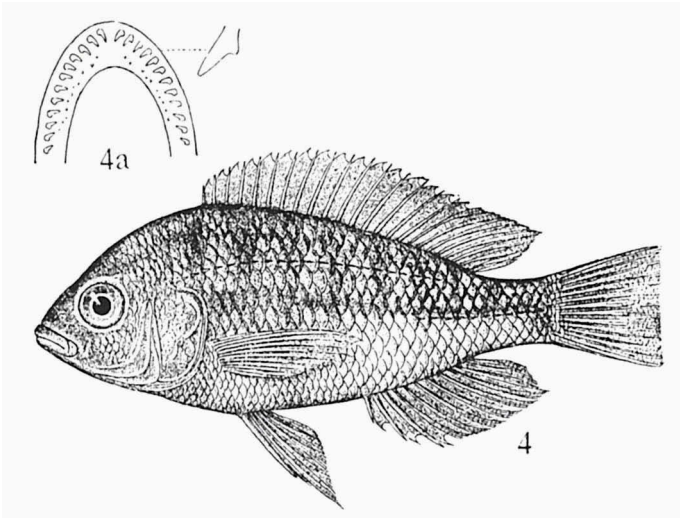


Fig. 9. Habitus and dentition of *Bayonia xenodonta* Boulenger, 1911. From Boulenger 1911, pl. II, fig. 4.

were figured. In this paper 34 cichlid species from Lake Victoria were distributed among *Paratilapia*, *Pelmatochromis*, *Astatotilapia* and *Tilapia*. Also mentioned were *Hemitilapia bayoni*, *H. materfamilias*, *Bayonia xenodonta*, *Platytaeniodus degeni* and *Astatoreochromis alluaudi*. The genus *Haplochromis* was not mentioned in this last paper of Pellegrin dealing with Lake Victoria cichlids, but in (1912b), in the species list preceding the descriptions, he indicated where his generic classification departed from that of Boulenger (1911).

In the description of *Astatotilapia guiarti* Pellegrin remarked that the specimen he examined (140 mm TL) had the outer teeth bicuspid and the inner ones tricuspid. According to Pellegrin this gave him all the more reason to place this species in *Astatotilapia* instead of in *Paratilapia* as was done by Boulenger (1907).

To *Astatotilapia jeanneli* (= *Platytaeniodus degeni*, see Greenwood, 1956a) he added: "This fish shows a certain similarity in shape and coloration with *Tilapia martini* Boulenger, 1906, but the tooth shape is different and the caudal peduncle is too short. The setting of the teeth in adult specimens indicates affinities with *Platytaeniodus degeni* Boulenger 1906. Once again an intermediate form which are so numerous in Lake Victoria!"

In the description of *Hemitilapia materfamilias* (= *Macropleurodus bicolor*, see Greenwood, 1956a), Pellegrin wrote: "This species, the third one known from this genus, approaches *Hemitilapia bayoni* Boulenger [= *Haplochromis obliquidens*, see Greenwood, 1956a] from Bugala, on the Sesse Island (Lake Victoria). It differs however, by its dentition (15-17 teeth on each side of the upper jaw, instead of 27-30), its more rounded dorsal head profile, its longer pectoral fin, and its shorter caudal peduncle" (fig. 10).

In the third volume of his monumental work, the "Catalogue of the Fresh Water Fishes of Africa", Boulenger (1915) stated in the introductory part to the family Cichlidae: "The classification of the very numerous African members of this family presents the greatest difficulties, and the division into genera, as here followed, is unsatisfactory and open to criticism, the dentition in certain species being subject to variation, according to age, or even of a purely individual nature."

The number of genera of African cichlids in this paper had climbed to 40. The Lake Victoria cichlids were distributed among 6 genera. Due to changed views, the larger number of new species, and an increased knowledge of the anatomy, the defi-

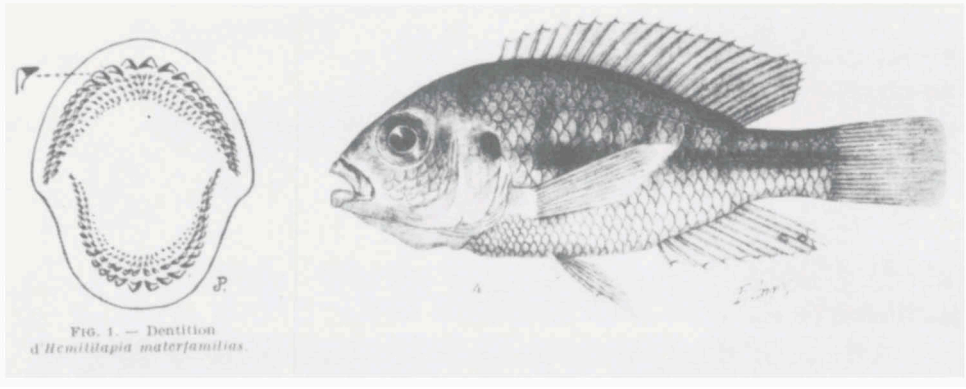


Fig. 10. Oral dentition and habitus of *Hemitilapia materfamilias* Pellegrin, 1912. From Pellegrin, 1912, fig. 1 & pl. V, fig 4.

nitions of these genera had been changed as follows:

Tilapia: "Body short or more or less elongate; scales cycloid or ctenoid; two incomplete lateral lines. Teeth in two or more series, the outer bicuspid*, the others tricuspid; maxillary usually more or less completely hidden under the praeorbital when the mouth is closed. Dorsal fin with 11 to 19 spines, anal with 3 or 4. Parietal and occipital crests strong, extending to between the orbit. Vertebrae 26-34. "(The asterisk referred to a footnote which added: "Occasionally conical or indistinctly bicuspid in a few species which are related to *T. nilotica* (*T. nigra, mossambica, natalensis, linelli, squamipinnis*). See also *Haplochromis*."

Haplochromis: "Body short or moderately elongate; scales ctenoid; two incomplete lateral lines. Teeth in 2 or more series, the outer conical or bicuspid, the inner usually tricuspid; maxillary bone exposed at the end when the mouth is closed. Dorsal fin with 13 to 19 spines, anal with 3 to 6. Vertebrae 28-32." To this Boulenger added: "Under this genus are grouped a number of allied species which vary to such an extend in their dentition that some specimens might be referred to *Tilapia* and others to *Paratilapia*." *Astatotilapia* and *Astatoreochromis* were still considered synonyms of *Haplochromis*.

Paratilapia: "Body short or more or less elongate; scales cycloid or ctenoid; two lateral lines both incomplete, or the upper nearly complete. Two or more series of teeth, the outer conical and sometimes caninelike in the adult, sometimes bicuspid in the young, the others unicuspid or tricuspid. Maxilla usually exposed when the mouth is closed. Dorsal with 10-18 spines anal with 3. Parietal and occipital crests strong, extending to between the orbit. Vertebrae 27-37."

Pelmatochromis: "Barely distinguishable from *Paratilapia* by the greater development of a papillose pad on each side of the pharynx, close to the upper part of the branchial arches, and appearing as a strong prominence in front of the latter when the gill cover is lifted up."

In the definition of *Platytaeniodus* only the number of dorsal fin spines was changed from 15 to 15-16.

Hemitilapia was defined as follows: "Body rather elongate, scales ctenoid. Jaws with moderately broad bands of slender, clubshaped, movable teeth, slightly incurved crowns, teeth of outer series larger, the oblique crown directed towards the symphysis. End of maxillary visible. Dorsal fin with 15-16, anal fin with 3 spines. Occipital and parietal crests strong, extending to between the orbits." This genus was not mentioned in Boulenger (1907).

The addition of anatomical characters of the neurocranium to the generic definitions was new. It makes clear that Boulenger had continued the preparation of a collection of skeletal specimens of cichlids. Boulenger (1907) gave figures of a whole skeleton and a neurocranium in dorsal view of *Tilapia nilotica*, but he did not use anatomical characters in defining cichlid genera.

Boulenger's (1915) remarks on the unsatisfying generic classification of the cichlids induced Regan to make cichlids an important subject of his research. To gain an insight into the anatomy of cichlids he made a large number of skeletal preparations. In 1920 Regan published the first part of his classification of the Cichlidae which deals with the genera from Lake Tanganyika. On the basis of the anatomy of the neurocranial apophysis, Regan divided the African cichlids into two groups. The group

where the apophysis was formed by the parasphenoid alone he named the *Tilapia* type; the other, where the apophysis was formed by the parasphenoid and the basioccipitals, was named the *Haplochromis* type (fig. 11). Regan noticed that each of the three largest genera of Boulenger (i.e. *Tilapia*, *Paratilapia* and *Haplochromis*) contained species of both types. According to Regan, the larger part of the species of these genera with an *Haplochromis* type apophysis could indeed be placed in the genus *Haplochromis*, making it the largest African genus. He wrote that for most of the genera it could be demonstrated that they were related either to *Tilapia* (e.g. *Paratilapia*, *Pelmatochromis* and *Hemitalapia*) or to *Haplochromis* (e.g. *Hemichromis*).

For his new definition of *Haplochromis*, besides the character of the neurocranial apophysis, Regan (1920) also used the external morphology: "Dorsal fin with 13-19 spines and 6-13 finrays, anal fin with 3, sometimes 4, spines and 6-12 finrays. Scales large, usually with denticles. Outer teeth bicuspid or conical, one or more series of small conical or tricuspid innerteeth. Lower pharyngeal jaw triangular; teeth slender, or rather stout, compressed or cylindrical, uni- or bicuspid, acute or blunt." In a footnote to the description of the genus *Haplochromis*, Regan gave very short descriptions of a number of new genera he considered closely related to *Haplochromis*. For cichlid species from Lake Victoria he suggested the following genera:

Lipochromis (type species *Pelmatochromis obesus* Boulenger, 1906); "lower jaw closing within the upper jaw."

Neochromis (type species *Tilapia simotes* Boulenger, 1911); "teeth small in bands, outer series not enlarged."

Cnestrostoma (type species *Paratilapia polyodon* Boulenger, 1909); "jaws with broad bands of conical teeth, outer series not enlarged."

Labrochromis (type species *Tilapia pallida* Boulenger, 1911); "pharyngeal jaws stout and blunt, articular surface of upper pharyngeal jaw nearly as broad as long, basioccipitals nearly touching each other behind the parasphenoid. "

Astatoreochromis (type species *A. alluaudi* Pellegrin, 1904); "4-6 anal spines, pharyngeal jaws large and blunt."

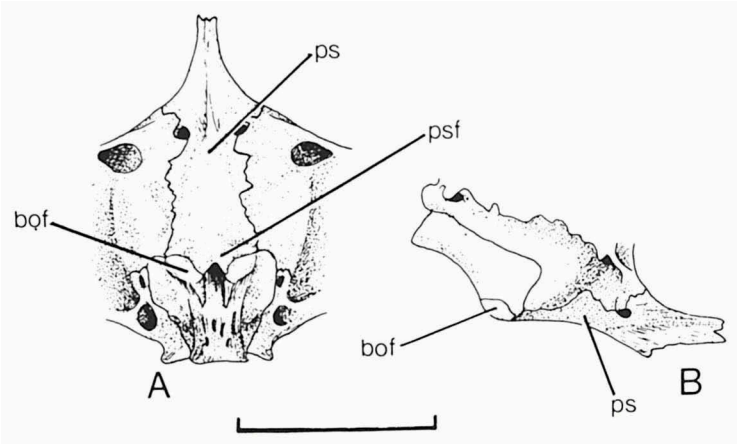


Fig. 11. Neurocranial apophysis of the *Haplochromis* type. *Haplochromis obliquidens*. Apophysis in A: ventral and B: right lateral views. Scale 5 mm. Legend: bof = articulation facet on basioccipital process: ps = parasphenoid: psf = articulation facet, or region, on parasphenoid. From Greenwood 1978, fig. 17.

Clinodon (type species *Hemitilapia bayoni* Boulenger, 1908 [= *Haplochromis obliquidens*, see Greenwood, 1956b]); "structure of *Haplochromis*, dentition of *Hemitilapia*." (This was the third time that the species *obliquidens* was placed in a separate genus.)

In dealing with Lake Nyassa cichlids, Regan (1921) modified the definition of *Haplochromis* as follows: "An outer series of bicuspid or conical teeth, decreasing in size posteriorly, and one or more inner series of smaller bicuspid or conical teeth, 2 to 6 series of scales on the cheek. Scales usually distinctly denticulate. Pharyngeal apophysis formed by parasphenoid in middle and basioccipital at sides. Third vertebra with inferior apophyses, which meet below."

Regan (1921) noted that the differences in the pharyngeal dentition were sometimes very striking. He therefore concluded: ..."that it is not desirable to regard the development of large, round, blunt pharyngeal teeth as warranting generic separation." Herewith Regan suppressed his genus *Labrochromis*, defined only a year before.

Regan (1921) also gave a redefinition of *Astatotilapia* (a genus never recognised by Boulenger): "Near *Haplochromis*, but posterior teeth of outer series of upper jaw increasing in size backwards. Teeth in 3 to 5 series, cuspidate or conical, those of the outer series of upper jaw sometimes bicuspid anteriorly, conical posteriorly; band of teeth in lower jaw crescentic. Middle teeth of lower pharyngeal somewhat enlarged. Dorsal XIII-XVII 8-11. Anal III 7-11. Scales 26 to 36."

Regan (1922) described 18 new Lake Victoria *Haplochromis* species and resurrected some that had been placed in synonymy by earlier authors. Still the number of species Regan recognised (50) hardly differed from that of Boulenger (1915) (46), because Regan synonymised a great number of species recognised by Boulenger.

In his introduction Regan (1922) stated that he had great difficulties with the classification of the Lake Victoria cichlids: "From what has been said above as to the evolution and relationships of the Cichlidae of Lake Victoria, it will be evident that I do not regard the classification here proposed as entirely satisfactory. A number of divergent species are placed in *Haplochromis* and a few extreme types are regarded as generically distinct, although the close relationship of each to a species of *Haplochromis* is obvious. At present I am not in a position to improve this arrangement."

Forty-six of the 50 species recognized by Regan were placed in *Haplochromis*, which was defined as follows: "Pharyngeal apophysis formed by parasphenoid in middle and basioccipital at sides. Scales ctenoid. Teeth in 2 or more series anteriorly, becoming a single series laterally, conical or compressed, unicuspid, or outer mostly bicuspid and inner tricuspid." Regan continued: "*Haplochromis obliquidens*, the type species, has a dentition unlike that of most of the species which have been placed in this genus, but the discovery of a species in L. Kivu (*H. astatodon*) some individuals of which have a typical *Ctenochromis* dentition, whilst others approximate to *H. obliquidens* makes it possible to regard this difference as only subgeneric and to still include species with conical or cuspidate teeth in *Haplochromis*." Re-examination by Greenwood (1979) of the Lake Kivu specimens on which Regan based this statement showed that two species were involved.

Within *Haplochromis*, Regan now distinguished 4 subgenera which were only

shown coupled with their respective species in the key.

These subgenera were defined as follows:

(*Neochromis* Regan): "Teeth slender, cuspidate, in 5 to 8 series, the inner well developed and not separated by a distinct inner space from the outermost." [2 species]

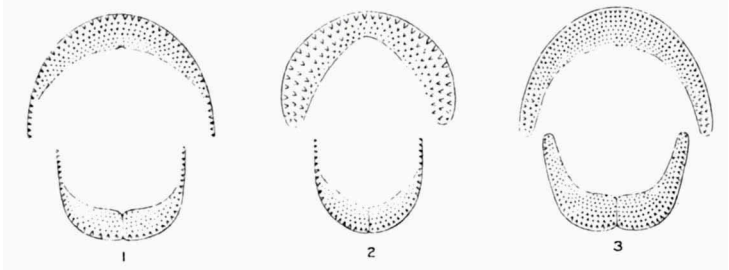
(*Ctenochromis* Pfeffer): "Outermost series of teeth conical or bicuspid, enlarged, separated by an interspace from the smaller inner teeth." [40 species]

(*Bayonia* Boulenger): "Outer teeth few and large, with long anterior cusps and indistinct posterior cusp." [1 species]

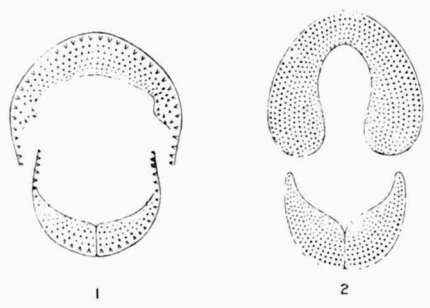
(*Haplochromis* Hilgendorf): "Teeth slender, distally expanded and compressed, outer oblique truncated." [1 species]

Besides *Haplochromis*, Regan recognized four other genera, all monotypic: *Astatoreochromis* Pellegrin, *Platytaeniodus* Boulenger, *Hoplotilapia* Hilgendorf and *Macropleurodus*; a new genus Regan erected for *Paratilapia bicolor* Boulenger, 1915. Except for *Astatoreochromis* these genera differed from *Haplochromis* mainly in the dentition of the oral jaws (fig. 12).

Macropleurodus was defined as follows: "Differs from *Haplochromis* in the dentition of the upper jaw, which has an outer series of enlarged teeth and several inner series of small teeth anteriorly and 3 or 4 series of enlarged teeth laterally, which are exposed as the mouth is shut."



Dentition of 1. *Haplochromis sauvagii*; 2. *Macropleurodus bicolor*; 3. *Hoplotilapia retrodens*.



Dentition of 1. *Haplochromis annectens*; 2. *Platytæniodus degeni*.

Fig. 12. Oral dentition of monotypic genera and related *Haplochromis* species which are all oral shelling moluscivores. From Regan 1922, figs 13 & 14.

In a footnote to the introduction Regan (1922) stated that he believed *Astatotilapia* [a genus he had redefined only a year before] could no longer be maintained as distinct from *Haplochromis* as "several of the Lake Victoria species have enlarged teeth at the end of the premaxillaries more or less developed and not at all constant."

New cichlid species of Lake Victoria cichlids described by Trewavas (1928), Regan & Trewavas (1928) and Regan (1929) were all placed in *Haplochromis* without any reference to the previously recognized subgenera.

Lohberger, from the Naturhistorisches Museum, Wien, in two papers (1929a + b), described five new cichlid species from Lake Victoria. Although he found only cycloid scales in one of them he placed all species in *Haplochromis*. A year later on, Lohberger (1930) removed *Pelmatochromis riponianus* Boulenger, 1911, from the synonymy of *Haplochromis cinereus* Boulenger, 1906, in which it was placed by Regan (1922). This action was triggered by problems in identifying a specimen from the NMW collection using Regan's (1922) key. The types of the species concerned were not examined. Lohberger (1930) used *Paratilapia* and *Pelmatochromis* as subgenera of *Haplochromis* in the captions to the figures (fig. 13) but not in the main text.

Borodin (1931, 1936) described the collection of A. Loveridge made in the great African lakes. Ten species from Lake Victoria were mentioned. One specimen was placed in *Callochromis*, a genus restricted to Lake Tanganyika, another was considered to be the first Lake Victoria representative of a new subspecies of a *Haplochromis* species until then known only from Lake Malawi, and a third specimen was placed in a subspecies of a *Tilapia* species known only from the Zaire river. In 1931 Borodin also described a new *Haplochromis* species from Lake Victoria.

Both Regan (1932) and Trewavas (1946) in their reactions on the papers of Borodin were indignant about the fact that someone without any experience with cichlids, "One of the most difficult groups for systematic research" (Regan 1932: 26), had

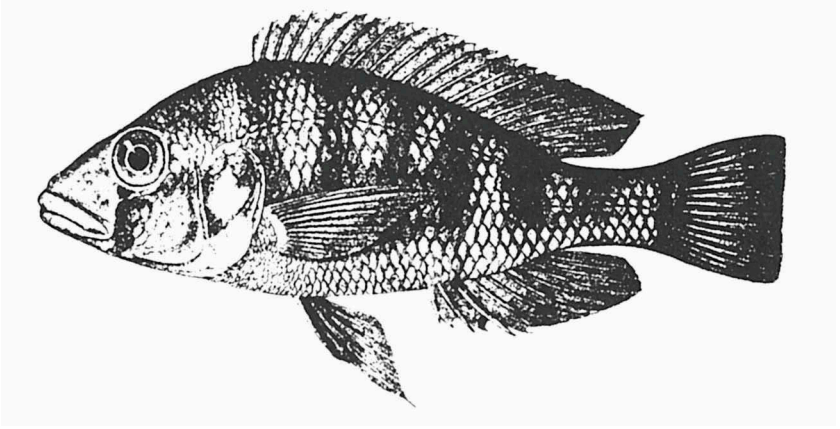


Fig. 13. *Haplochromis riponianus* Boulenger, 1911. From Lohberger, 1930.

dared to publish papers on cichlid taxonomy. Trewavas (1946) examined and re-identified Borodin's specimens.

Nichols & LaMonte (1938) described a haplochromine cichlid from Lake Victoria as a new species in the genus *Tilapia*. The superficial resemblance of the single specimen with *Tilapia inornata* Boulenger, 1908 (= *Copadichromis inornatus*) a Lake Malawi species, was apparently the reason for its generic placement (fig. 14).

These ichthyologists were the last to describe Lake Victoria haplochromines solely on the basis of preserved material. Subsequent species descriptions would all be made by persons who had been engaged in fieldwork on Lake Victoria and collected at least part of the material themselves. These fieldworkers saw the live coloration of the specimens and could observe the habitats in which the specimens were caught. Because more specimens were available to them, they obtained a better impression of intraspecific variability. Moreover, they were able to study gut contents and gather information of the food preferences of the species.

The species descriptions of Greenwood, the first ichthyologist involved in fieldwork on Lake Victoria, were quite different from preceding ones. They were characterized not only by the fact that the descriptions of the external morphology, gill rakers, oral and pharyngeal teeth and preserved coloration were much more detailed, but they also contained information on the ecology, e.g. habitat, breeding and food, and often, on live coloration.

Greenwood correlated food and feeding techniques (observed in the field or in tanks) with external morphological and dental characters. Based on food preferences and morphology he attempted to place all species in trophic groups (named ecological groups in his early papers). In eleven papers, Greenwood (1956-1978, reprinted in 1981), made a complete revision of the known haplochromine species of Lake Victoria to which he added 50 new ones of which 16 were co-authored with Gee and eight with Barel. In these revisionary papers the species were clustered in trophic groups.

After examining much new material (partly collected by himself) Greenwood (1956a) endorsed and redefined the monotypic genera *Platytaeniodus*, *Macropleurodus* and *Hoplotilapia* as follows;

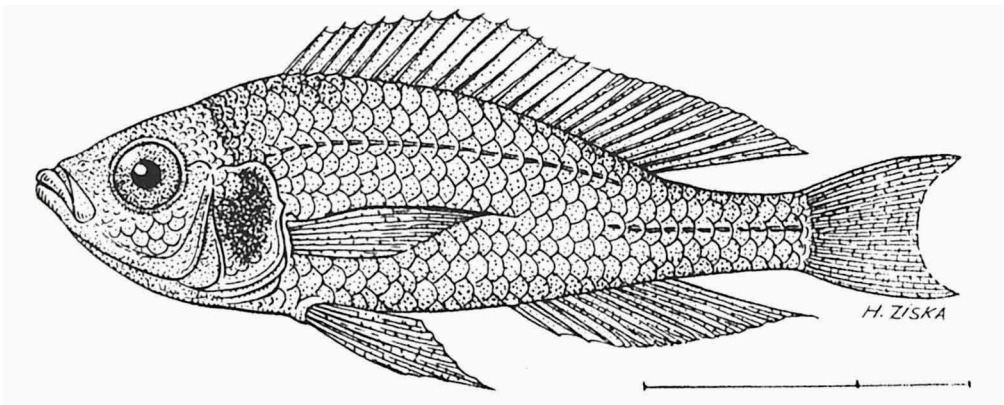


Fig. 14. Holotype of *Tilapia labriformis* Nichols & LaMonte, 1938. From Nichols & LaMonte, 1938, fig. 3.

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

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

Hoplotilapia: "Differing from *Haplochromis* as defined by Regan (1920 and 1922) in having broad bands of teeth in both jaws, well developed and usually of almost uniform breadth throughout or very slightly narrower posteriorly. Posterior teeth of the upper jaw enlarged and stout, those of the lower jaw slightly, if at all, enlarged, but the tooth-band continued posteriorly on to the steep ascending contour of the dentary. Lower jaw wide and flat, almost square in anterior outline, slightly shorter than the upper."

Because Greenwood examined specimens of a large size range, he discovered that both *Bayonia xenodonta* and *Hemitilapia materfamilias* should be considered to be synonyms of *Macropleurodus bicolor*. The subgenus *Bayonia*, named by Regan (1922) herewith had become superfluous. Greenwood placed *Astatotilapia jeanneli* in the synonymy of *Platytaeniodus degeni*. On the basis of anatomical studies Greenwood concluded that *Hoplotilapia* and *Platytaeniodus* are not closely related to any extant *Haplochromis* species. However, he found two *Haplochromis* species with a syncranial anatomy which he described as " leading to the syncranial type found in *Macropleurodus*."

On the basis of a single specimen Greenwood also described a new genus *Paralabidochromis* which was defined as follows: "Cichlid fishes of the *Haplochromis* group, but differing from that genus in having the anterior teeth in both jaws procurrent and disproportionally longer than the adjacent lateral teeth. Jaws narrowing at the symphysis; lips thickened." The type species of the genus was named *Paralabidochromis victoriae* Greenwood, 1956 (fig. 15).

In his paper on the *Haplochromis* species feeding principally on algae Greenwood (1956b), the type species of *Haplochromis, H. obliquidens*, was redescribed, and the affinities of this species with other algae-eating species were analysed. According to Greenwood (1956b: 226): "Tooth-form in *H. obliquidens* is unlike that of most species at present included in the genus *Haplochromis*. Yet three algal grazing species are

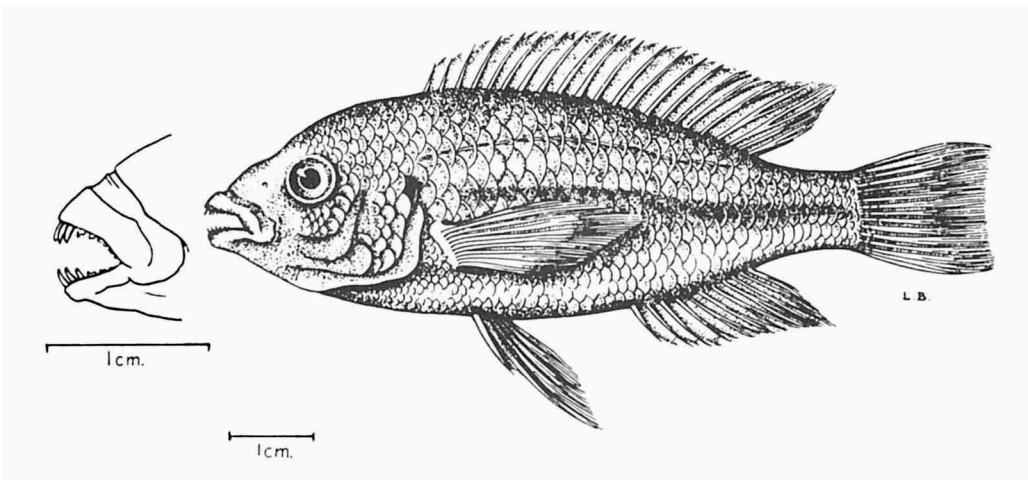


Fig. 15. Holotype of *Paralabidochromis victoriae* Greenwood, 1956. From Greenwood, 1956a.

known, which partly bridge this morphological gap. At the opposite extreme *H. nuchisquamulatus* exhibits incipient dental adaptation only slightly removed from a generalised *Haplochromis* type." Therefore, Greenwood (1956b: 231) concluded: "Thus the case for recognizing at least two subgenera of *Haplochromis* [*Ctenochromis* and *Haplochromis*] on the basis of dental morphology (Regan, 1920, 1922) is weakened. As was mentioned earlier, several ecologically defined groups, each comprising apparently related species, are known from Lake Victoria. In every case, the group shows certain morphological divergence from the generalized *Haplochromis* type, but no clear cut morphological gap has evolved which would allow for its formal recognition as a subgenus." Although, Greenwood considered the possibility to give a taxonomic status to a number of "nascent supra-specific groups which are more readily identified by ecological than morphological criteria", he had to abandon this idea because a clear morphological gap was lacking. Probably for this reason, Regan's subgenus *Neochromis*, except in the synonymy of *H. nigricans* (another species redescribed in this paper), was not mentioned.

All new species of haplochromine cichlids from lake Victoria described by Greenwood (et al.) (1957-1978) were placed in the genus *Haplochromis*.

The following remark of Greenwood (1957: 90) indicates that his larger collections did not always make defining the species easier: "The high intra-specific variability of *H. xenognathus* makes this species of particular interest when considering the evolution of monotypic cichlid genera. Some of the more aberrant specimens, if studied in isolation, might well be given a status equal with the monotypic genera recognized at present. Less extreme individuals, on the other hand, are not immediately distinguishable from *H. sauvagei*."

Astatoreochromis, the one monotypic genus not treated in Greenwood (1956a) was made the subject of a separate paper in 1959. Unlike the other monotypic genera

Astatoreochromis is not confined to Lake Victoria. Moreover, it does not differ from *Haplochromis* by characters of the oral dentition as do the other monotypic genera, but by the number of spines in the anal fin. According to Greenwood (1959a: 165, 166): "*Astatoreochromis* differs from *Haplochromis* only in having four or more spines in the anal fin. From other genera in the *Haplochromis* group with more than four anal spines, *Astatoreochromis* is distinguished by the absence of a marked antero-posterior differentiation in the form of the premaxillary teeth. In comparison with the *Haplochromis* of Lake Victoria, Edward, and Kachira, *Astatoreochromis* shows an increased ratio of spinous to branched rays in the dorsal and anal fins. From other *Haplochromis*-like genera in these lakes, *Astatoreochromis* differs both in having more anal fin spines and in the nature of its oral dentition."

For *Astatoreochromis alluaudi* Greenwood found the following additional characters which differ from *Haplochromis* spp.: the form of the pharyngeal apophysis, the shape of the caudal fin, the high number of ocelli of the anal fin of males, the slight sexual dimorphism in coloration, and the basic body colour. In all these characters *Astatoreochromis alluaudi* was found to resemble *H. vanderhorsti* Greenwood, 1954, from the Malagarasi river. Greenwood concluded that *Astatoreochromis* was closer related to such fluviatile species as *H. vanderhorsti* and *H. straeleni* than to the *Haplochromis* species of Lake Victoria.

On the basis of differences in the form of the pharyngeal bones and caudal fin length two subspecies of *Astatoreochromis* were recognized by Greenwood (1959a). These subspecies were invalidated by Greenwood (1965) because the differences of the pharyngeal elements seemed to be based on phenotypic plasticity.

In his revisions Greenwood often pointed to the difficulty of differentiating between phyletic relationship and parallel evolution (e.g. Greenwood, 1957: 95; 1959b: 204, 207; 1960: 252; 1962: 210). Yet in his species descriptions Greenwood always included a paragraph called "Affinities" in which the phyletic relationship of the species in question, based on morphological resemblance, was discussed. However, in the introduction of "The Haplochromine Fishes of the East African Lakes, a reprint of all his revision papers and the subsequent generic revision of the genus *Haplochromis*, Greenwood (1980: i) stated: "Whenever phrases with the word 'related' (or its derivatives or synonyms) are used in the descriptive papers, any implied phyletic relationship should be discounted. Rather, the words should be taken to mean 'resemblance' or 'similarity' in a strictly phenotypic sense."

Greenwood (1974) devoted a chapter to interrelationships of the species. Greenwood started by saying that the monophyletic origin of the species flock cannot be established. Then he stated (1974: 56): "the Victoria *Haplochromis* species present [...], an unusual picture of virtually complete morphological intergradation between the generalized and the specialized in any one adaptive radiation." After giving some examples of species groups which show gradation in morphological characters he continued: "The question now to be asked is whether all the constituent species of each gradal complex represent truly monophyletic lineages within the flock, or whether we are confronted with a web of parallelisms. Detailed studies of the species comprising the different radiations suggest that the latter explanation is the likely one." [The data on which this statement was based were not given.] Greenwood then

suggested that he must find combinations of apomorphic characters that will link together phyletic lineages within each grade. As "relatively few characters can be used to construct phylogenies" and meristic characters were found to be almost uniform throughout all species, Greenwood's interest concentrated on "cranial and dental characters which, on the whole, clearly show levels of specialisation and generalisation." In other words, characters related to the feeding apparatus were used, which are known to show various degrees of parallel evolution (Mayr, 1969; Fryer & Iles, 1972; Barel, 1984).

Although the approach in 1974 was said to be different, the outcome of Greenwood's new investigation of the phylogenetic relationships was largely similar to the views expressed in his descriptive papers. The greatest problem again was to differentiate between phyletic relationship and parallel evolution. For instance, when discussing relationships in the phytophagous species, Greenwood mentioned that the shape of the neurocranium and the lower jaw of *H. nigricans* (a rockscraper) approaches that of two insectivorous species living over hard substrates. Greenwood (1974: 66) interpreted the similarity in neurocranial- and lower jaw shape between *H. nigricans* and the two insectivores as parallelisms. However, the similarity in neurocranial shape of these two insectivores and a group of oral shelling molluscivores was considered as an indication of a phyletic relationship.

In the conclusion of the chapter on interrelationships of the Lake Victoria *Haplochromis* species, Greenwood (1974: 96) wrote "that despite the superficial impression of virtually complete morphological and adaptational intergradation amongst the species this partial phyletic analysis of the flock shows that a number of distinct groups are discernable". After naming some he continues "Each lineage is definable on the basis of shared morphological specialisations and on the whole, each is recognizable from its trophic peculiarities". (The possibility that species with similar food preferences and feeding techniques might have different phylogenies was not mentioned.) Greenwood suggested that if the least specialized members of the groups had been eliminated in the past, the groups would be recognizable as clearly as *Hoplotilapia* and *Platytaeniodus*. According to Greenwood (1974: 98) "we seem to have species aggregates which might be accorded higher rank". However, the least specialised members in fact were not eliminated, making it impossible to delimit these aggregates Greenwood realized that "the points were the 'generic' lines are to be drawn are by no means evident in case of a species flock". He also pointed at the probability that polychotomous rather than dichotomous branching could be basic in species flocks (fig. 16). Seeing no solution for the 'generic problem', Greenwood left the various lineages he discerned within "a single but almost certainly artificial genus".

As for the monotypic genera Greenwood concluded that "they are all clearly derived from *Haplochromis* ancestors." *Astatoreochromis* was thought to have originated from a stem distinct from that of all other Lake Victoria haplochromine cichlids. The morphological gap between *Hoplotilapia* and *Platytaeniodus* and the *Haplochromis* species, according to Greenwood, was a mystery in a "species flock where all structural grades are completely bridged by intermediate forms", but the generic status of *Macropleurodus* and *Paralabidochromis* was now said to be "questionable".

In 1980, Greenwood published the results of a new investigation on the classifica-

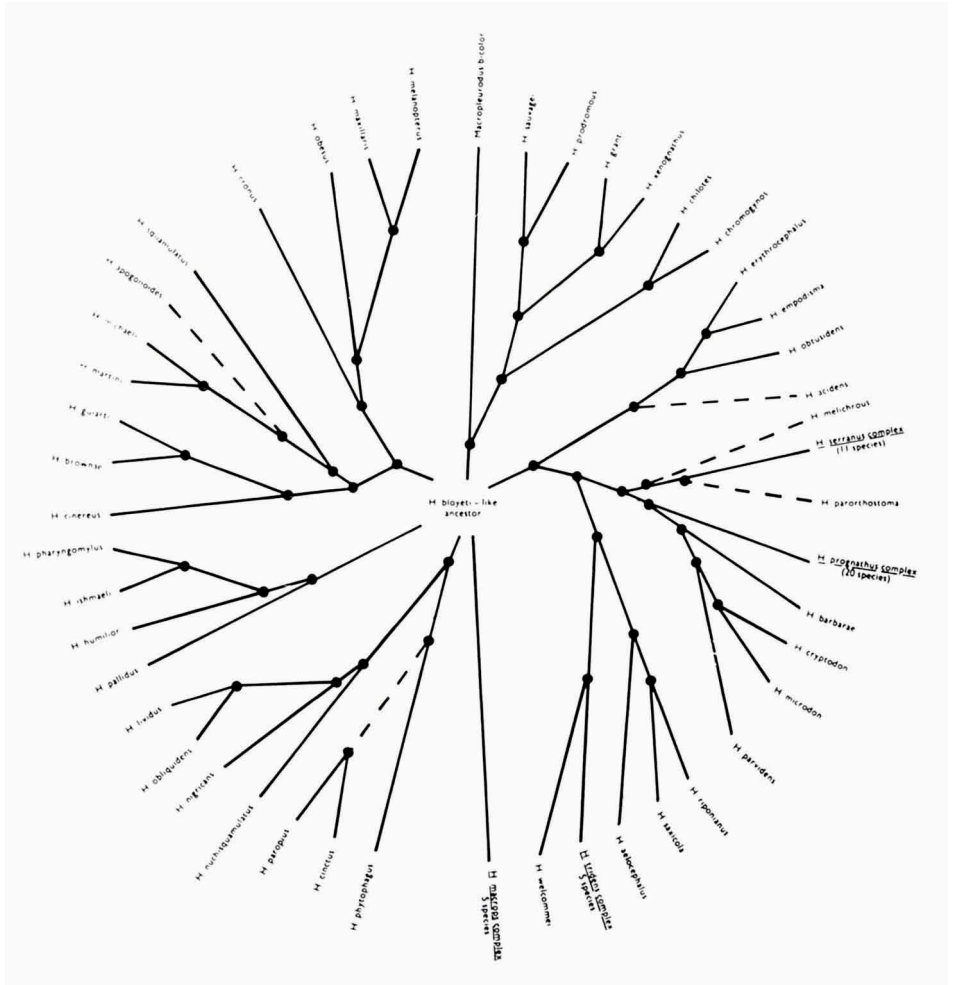


Fig. 16. The diagrammatic representation of the supposed relationships ("Greenwood's wheel") is not a real cladogram in which branching point are based on the possession of different apomorphic characters by the sister species, but "a tentative phylogenetic arrangement ... based on the assumed synapomorphy of various character states (particularly those of the neurocranium and the dentition)". The lineages are recognized on the basis of shared specialized characters. No shared specialisations were found that could link the lineages to common ancestral species. From Greenwood, 1974, fig. 70.

tion of the Lake Victoria haplochromine cichlids. This paper was part two of a generic revision of the genus *Haplochromis* for which some 290 species were examined. According to Greenwood, the large number of species, the wide distribution, and the large range of morphological and anatomical variation of *Haplochomis*, were indications that the genus as defined by Regan was polyphyletic.

Using a "basically Hennigian approach", Greenwood (1979) first investigated the fluviatile *Haplochromis* species. To distinguish genera the following characters were used; squamation, oral dentition, pharyngeal dentition and shape of the lower pharyngeal bone, neurocranial morphology, anal fin markings in male fishes, vertebrae number, anatomy of the caudal fin skeleton, number of dorsal and anal fin rays, and gill rakers.

The genus *Haplochromis* was defined mainly on apomorphic dental characters [italics are from Greenwood and denote apomorphies]: " 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. 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."* A further apomorphy was found in the anal fin markings: *"True ocellar egg dummies, usually 3 or 4 in a single row, are present in adult males."*

None of the investigated fluviatile haplochromine species possessed these apomorphies, and Greenwood restricted the genus *Haplochromis* to five lacustrine species, viz. two from Lake Victoria, and one from each of the lakes Nabugabo, Kivu, and Edward/George. The fluviatile haplochromine species were placed in eight genera two of which were new. *Astatotilapia* which had been synonymized with *Haplochromis* by Regan (1922) was also used. However, Greenwood did not succeed in defining *Astatotilapia* on the basis of apomorphic characters. Greenwood (1979: 284) remarked on the characters used for the description of this genus: "Apart from the ocellar anal fin markings, none of these characters can be considered derived, and the anal ocelli are an apomorhpic 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".

As a result of his investigation Greenwood postulated a polyphyletic origin of the Lake Malawi "*Haplochromis* group species". On the origin of the Lake Victoria haplochromines Greenwood (1979: 314) remarked: "Likewise, the assumed monophyly of the Lake Victoria *Haplochromis* species flock, Greenwood, 1974, must be thrown into doubt, because no characters have been found to support this concept."

In the introduction to the second part of his revision, Greenwood (1980) was rather critical towards his earlier (1974) attempt to resolve phyletic relationships within the Lake Victoria *Haplochromis* flock. Greenwood (1980: 3) considered it "quite inadequate, and in many respects even misleading when taxa from historically related Edward and Kivu are taken into account." This statement was based on the fact that Greenwood's re-examination of the lacustrine *Haplochromis* species in terms of plesiomorphic and apomorphic characters indicated that the haplochromines of Lake Victoria should be joined to those of Lakes Kioga, Edward, George and Kivu. Because he could not find apomorphies to separate the species of the various lakes he referred to them collectively as "the Lake Victoria super flock".

The only characters Greenwood (1980) could use to distinguish lineages were those concerning squamation, oral and pharyngeal dentition, shape of the oral and pharyngeal jaws, and neurocranial morphology. Some new definitions of neurocranial and premaxillary measurements were given. Based on the principal of commonality, the shape and proportions of jaw elements in *Astatotilapia* were taken to present

the plesiomorph condition amongst haplochromines. On the basis of apomorphic characters the haplochromine species of the super flock were divided into 20 lineages which were given generic status.

Greenwood (1980) placed nineteen lacustrine haplochromine species (ten from Lake Victoria) in *Astatotilapia* for which not a single synapomorphy could be found. Remarkably, Greenwood suggested a relationship for certain of these lacustrine *Astatotilapia* species with other genera on the basis of their diet.

Although Greenwood had only a few years before repeatedly referred to the problem of delimitating "supra generic groups", he now defined many lineages mainly on the basis of ranges of morphometric measurements, ranges of numbers of teeth and the measure of stoutness of the lower pharyngeal element (e.g. *Harpagochromis, Prognathochromis, Yssichromis, Gaurochromis, Labrochromis, Enterochromis).* This splitting of morphoclines by (supposed) differences in ranges of numerical characters would turn out to be a major cause of resistance against the new classification by those who actually had to use it (see below). "More substantial" characters were only found in elements of the oral jaws.

The following genera were distinguished within the Lake Victoria species super flock (only the apomorphic characters [printed in italics in Greenwood, 1980] are cited):

Harpagochromis: "*Haplochromines* [...] *reaching a large maximum adult size (146-200 mm SL); lower jaw long (43-61% of head length, modal range 47-54%). Neurocranium.*[...] *with a shallow otic region (40-44% neurocranial length cf 47-50% in the generalized type).*"

Prognathochromis: "Lower jaw long (41-62% head length, modal range 45-53%). Neurocranium elongate, slender and shallow, with a low, supraoccipital crest, Preorbital skull depth 18.6-23.% of neurocranial length (mode 21%), greatest orbital depth 22-28% (modal range 22-23%), depth of otic region 31-42% (no distinct mode), skull width 42-55% (modal range 47-50%) all expressed as ratios of neurocranial length."

Prognathochromis (Prognathochromis): *Prognathochromis* species with a "*Maximum orbital depth of the skull 22-25% neurocranial length (modal range 22-23%). Lateral ethmoid relatively narrow, its posterior face sloping backwards at an angle of 45-60° to the horizontal.*"

Prognathochromis (Tridontochromis): "Prognathochromis species in which *tricuspid teeth occur anteriorly and anterolaterally* (as well as posteriorly) *in the outer row of, generally, both jaws [...] The lachrymal bone (1st infraorbital) has, in 8 of the 9 species known, an enlarged ovoid to rectangular bullation occupying the greater part of the bone anterior to the first lateral line tubule, the bulla visible without dissection. The lower pharyngeal bone is narrow, its dentigerous surface having an anteroposteriorly attenuate appearance. The lower jaw is shallow, its lateral face having a pronounced upward and outward flare so that the alveolar surface is carried as a prominent shelf overhanging the body of the bone..*"

Yssichromis: "Shallow bodied, elongate haplochromines (body depth 23-30% SL, modal range 27-29%, caudal peduncle 17-25% of standard length, modal range 19-22%, its depth contained 1.7-2.1 times (modally 1.8-2.0) in its length, reaching a small maximum size (85-110 mm SL). Premaxilla *edentulous over the posterior 1/4 -1/3 of its dentigerous area.*"

Pyxichromis: "Haplochromines with a very oblique lower jaw (sloping upwards at 50°-70° to the horizontal), a sharply concave dorsal head profile, and the dorsal surface of the

snout virtually horizontal[...] The anatomy of the upper jaw is distinctive.."

Lipochromis: "Haplochromine fishes with a thick lipped, widely distensible and protractile mouth and small teeth deeply embedded in the oral mucosa (often invisible without dissection."

Lipochromis (Lipochromis): Characterized by the presence *"in the outer row, of stout uni- or bicuspid teeth whose crowns are inclined labially or laterally depending on their position in the jaw."*

Lipochromis (Cleptochromis): "The lower jaw at least anteriorly, closes within the upper, and has a boat-shaped dentary of the 'parvidens' type. The mouth is both markedly distensible and protractile."

Gaurochromis: "Outer teeth in both jaws (particular when compared with those in Labrochromis and Astatotilapia) finer, more compressed, shorter and closer set, with 44-82 (modal range 60-70) in the premaxillary outer row. Fishes <90 mm SL have unequally bicuspid teeth, *the crown barely broader than the neck."*

Gaurochromis (Gaurochromis): "Gaurochromis species with a slender, attenuated and fine lower pharyngeal bone with all or the majority of its teeth fine and compressed."

Gaurochromis (Mylacochromis): "Gaurochromis in which the lower pharyngeal bone is enlarged and stout, with at least the two median rows composed of enlarged and molariform teeth."

Labrochromis: "Haplochromines characterized by a massive hypertrophy of the pharyngeal mill (especially the lower pharyngeal bone and its dentition)

The lower pharyngeal bone is massive, relatively short and broad, the dentigerous surface concave, and the articular horns short and stout. Its dentition is composed almost entirely of stout molariform teeth. The apophysis for the upper pharyngeal bones is enlarged and stout, its expansive articular surface almost square in outline."

Enterochromis. "Haplochromines with a long coiled intestine that is at least 3 or 4 times longer than the standard length. "

Xistichromis: "Haplochromines with a much coiled intestine (ca. 3-4 times SL), *and broad bands (4-6 rows deep) of inner teeth anteriorly and anterolaterally in both jaws, narrowly, if at all separated from the outer tooth rows.* Neurocranium of the generalized type except that the *preorbital skull slopes more steeply and the supraoccipital crest is deeper and more pyramidical in shape. Teeth in the outer row of each jaw very close set (usually contiguous), movably implanted, tall, and slender but strong, showing only a slight antero-posterior decline in height and size."*

Neochromis: "Haplochromines with a very strongly decurved dorsal head profile (sloping at 70°-80° to the horizontal), a long much coiled intestine (ca. 3-4 times SL), broad bands of inner teeth anteriorly and anterolaterally in both jaws, not separated from the outer row, and equally or subequally bicuspid outer teeth. Neurocranium with a strongly decurved preorbital face, the ethmovomerine region almost vertically aligned. Dentary markedly foreshortened, deep and stout, its anterior margin strongly curved medially so that the anterior outline of the lower jaw is almost rectangular. The anguloarticular complex of the lower jaw is stout *with the anterior point of its anteroventral arm blunt or rectangular,* (never acute). *Premaxilla with noticeably inflated dentigerous arms, almost cylindrical in cross section, the alveolar surfaces broad."*

Psammochromis: "Neurocranium shallower in the otico-occipital region (40-46% neurocranial length). Dentary with a very distinctive form, each ramus noticeably inflated anteri-

orly and anterolaterally, this circumscribed swelling extending almost to the bone's ventral profile. Over this region (and slightly behind it) the narrow outer margin of the alveolar surface dips distinctly downwards so that the outer tooth row also has a ventral inflection."

Allochromis: "Teeth in the outer row of both jaws are close set and *have a very slender, tall and near cylindrical neck which expands abruptly into a compressed, bicuspid crown which is about twice as broad as the neck; the crown and upper third of the neck are strongly recurved and lie almost at right angles to the rest of the tooth. Both jaws have the teeth arranged in a broad almost crescentic band extending nearly to the posterior limits of the dentigerous surfaces involved."*

Ptyochromis: "Haplochromines with a lower jaw that is usually shorter than the upper. The slender teeth are very strongly recurved, those of the inner series arranged in a broad band across the anterior part of each jaw. "

Neurocranium with the preorbital face sloping fairly steeply (ca. 60°-70°, but 70°-75° in one species), its preorbital depth 30-33% of neurocranial length. Twenty-six to 56 teeth in the outer premaxillary row (modal range 40-44).

Dentary deep posteriorly but shallowing rapidly over the anterior two-thirds of its length, the lateral walls curving abruptly mediad from a level immediately below the alveolar surface. The outer margin of this surface, over its anterior half, dips downwards and slightly outwards so that the insertions of the outer row teeth lie below those of the inner series. Lower jaw length 22-38% of head length (modal range 34-35%)."

Paralabidochromis: "Haplochromines with a forceps-like dentition (lower teeth implanted procumbently). Neurocranium with a deep preorbital region (33-37% neurocranial length cf. *25-30%, modal range 26-27% in the generalized skull). Dentary foreshortened and deep. Profile of the symphysial region with a pronounced posteroventral slope giving the jaw a distinctly chinless appearance. Lower jaw length 30-49% head length (modal range 33-35%). Outer jaw teeth strong, slender, recurved and cylindrical in cross section, the crown somewhat compressed when bicuspid, otherwise cylindrical. Teeth anteriorly and anterolaterally in the lower jaw implanted procumbently[...]. Relatively few outer teeth in both jaws, ".*

Besides these genera which, except for *Allochromis*, were all represented by various species, the three monotypic genera were redefined.

Hoplotilapia: "The dentary has an almost square anterior outline, is very shallow over most of its length, is 'chinless'... Premaxilla with very strongly inflated dentigerous arms, the broad alveolar surface extending almost to their posterior tips, and virtually circular in cross section.

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

Platytaeniodus:"Teeth in the dentary are grouped into two broad pyriform patches, contiguous anteriorly. In the premaxilla the teeth are arranged in a broad, inverted U-shaped band, whose arms and base are of almost uniform width in fishes <100 mm SL, but in larger fishes the posterior parts of the arms are expanded medially so that they approach one another closely in the midline.

There are corresponding modifications to the shape of the premaxilla and dentary, the lat-

ter having a near-circular outline when viewed occlussally."

Macropleurodus: ..."the upper lip displaced laterally by the hypertrophied outer premaxillary teeth which, consequently, are exposed when the mouth is shut.

Teeth in the outer row of both jaws are stout, with an inwardly directed, strongly recurved major cusp (lying at almost right angles to the neck) and a greatly reduced minor cusp (often merely a slight protruberation on the crown). The minor cusp is vertical and, because of the extreme curvature of the major cusp, lies labially to the tip of that cusp. Fishes > 80 mm SL have, laterally on the premaxilla, one or more inner tooth rows composed of enlarged teeth morphologically similar to those of the outer series."

Discussion

Characters used in the definition of haplochromine genera

External characters mentioned in the earliest descriptions of haplochromine genera were: body shape (compressed, elongate, oblong); number of dorsal and anal spines; scale type (cycloid or ctenoid); scale size (small, moderate, large); squamation of cheek and gill cover. Dental characters which were used were: tooth shape (canine, monocuspid, bicuspid, or tricuspid); tooth size; number of tooth rows. Gill raker shape and size (short, medium sized, moderately long) was used as well. Later on the number of vertebrae and the exposure of the maxilla were added. Boulenger (1902) mentioned tooth curvature and the movability of the teeth. When specimens of larger size ranges became available, tooth shape in juveniles was also mentioned. The number of fin rays in dorsal and anal fin, and the number of scales in a longitudinal series were the next characters to be included. Boulenger (1915) added characters of the neurocranium (extension of the parietal and occipital crests). Regan (1921) defined two major groups of African cichlids on the structure of the neurocranial apophysis. Greenwood's generic definitions of the monotypic genera include details of tooth shape (adult and juvenile), shape of the dentigerous area and lower jaw shape. The generic diagnoses of the (sub)genera Greenwood (1979, 1980) made as a result of his generic revisions are almost as extensive as species descriptions. However, the differentiating characters (apomorphies), which really define his genera, are few and in one genus (*Astatotilapia*) they are even lacking.

From the review presented above it can be concluded that the generic definitions of the large African cichlid genera of the early taxonomists contained only few distinguishing characters. In Günther's (1862) definitions of *Sarotherodon* and *Hemichromis*, parts like "Lateral line interrupted.", "Branchiostegals five." and "Mouth protractile." might just as well have been omitted as they hold for all cichlid genera. Still the lateral line character was used by Boulenger in his generic definition till 1915. Some characters which proved not to be useful for distinguishing genera (i.e. gill-raker size and shape) were left out after some time, but others, like body shape, the number of vertebrae and exposure of the maxilla (the latter two introduced by Boulenger, 1898b), were retained until Regan (1922). The dorsal spine count was only supposed to be diagnostic when single specimens of only very few species of Lake Victoria were known. Pellegrin (1904a) discovered that the spine count of the anal fin was important in distinguishing *Astatoreochromis*, a fact never admitted by Boulen-

ger. The fin count of the anal and dorsal fin were also part of Regan's (1922) definition of *Haplochromis*. Of the remaining characters used in the generic definitions, scale size (little used) and scale shape were also of limited value as *Tilapia* and *Paratilapia*, as defined by Pellegrin and Boulenger, contained species with either type. The character which seemed most useful for separating the genera, the shape of the oral teeth, needed constant adjustment when new collections became available.

Until Greenwood's revisions, apart from the monotypic genera, the only generic name which was introduced especially for Lake Victoria cichlids was *Haplochromis*. Originally proposed by Hilgendorf (1888) as a subgenus of *Chromis* in the description of *Chromis (Haplochromis) obliquidens*, it was raised to the generic level by Boulenger (1906) to accommodate cichlid species from Lake Victoria with teeth intermediate between those of *Paratilapia* (outer rows with conical teeth) and *Tilapia* (outer rows with bicuspid teeth). In 1904, Pellegrin had named the genus *Astatotilapia* for all species in which the juveniles had bi- and tricuspid teeth and the adults had (mainly) conical monocuspid teeth. According to Boulenger (1906) *Haplochromis* had priority over *Astatotilapia*, but Pellegrin never used *Haplochromis*.

Genera in haplochromine taxonomy

To the cichlid taxonomists prior to Greenwood (1979, 1980), the definition of a genus probably was similar to that given in Mayr (1964: 283; 1969: 92) : "A genus is a systematic unit including one species or a group of species of presumably monophyletic origin, separated by a decided gap from other similar groups".

Boulenger (1898b) wrote about the "nearest affinities" of the family Cichlidae, but the relationships between the cichlid genera were not mentioned. Pellegrin (1904a) devoted an entire chapter to the affinities of the Cichlidae, but again only the interfamilial affinities were treated. In a discussion on the generic or specific value of morphological characters, only dental characters and the number of anal fin spines were considered of being valuable for the generic classification. In Pellegrin's (1904a) synopsis of cichlid genera of the world, they have been numbered in "the most likely sequence from a phylogenetic point of view." Pellegrin remarked that there are two parallel series, an American and an African one, and that it is not easy to arrange the genera in a linear series. However, he does not state on which characters he based his own sequence. Regan (1920), citing Boulenger's (1915) remark on the unsatisfactory classification of the African Cichlidae, stated that he, himself, undertook the study of this family in the hope of arriving at more precise definitions of the genera and a more natural arrangement. Because he thought that the cichlids of the three great African lakes had evolved separately, Regan treated them in separate publications. However, while he made clear that the *Haplochromis* species of Lake Malawi are a natural group which "may perhaps have evolved in the lake from a single ancestral form", he did not give them a separate generic status. Even though he defined a number of new genera which he considered closely related to *Haplochromis* (apparently only based on the shared neurocranial apophysis character), like his predecessors, Regan did not treat their intergeneric phylogenetic relationships.

The question of intergeneric relationships of the Lake Victoria haplochromines in a way was dealt with by Regan (1922) when he united nearly all of them in *Haploch-*

romis. Yet Regan found his own classification unsatisfactory.

The unravelling of the phylogenetic relationships within *Haplochromis* became a major research subject of Greenwood (1956-1994). Until 1974 Greenwood tried to establish lineages in the Lake Victoria *Haplochromis* species, which then was considered to be a monophyletic group (Greenwood, 1974). Later research based on cladistic principles indicated that the haplochromine species of Lakes Victoria, Edward, George, and Kivu had to be considered together and Greenwood (1979, 1980) embarked on a phylogenetic study of the Victoria-Edward-Kivu flock. To achieve this goal, he applied a cladistic analysis. Because he used a cladistic classification and followed the convention of Nelson (1972), he was obliged to create a large number of new genera and subgenera. Apparently he did not consider a Simpsonian classification (Charig, 1982), which might have been preferable for nomenclatoral stability.

We must accept, especially in the case of species flocks, that "no system of nomenclature can adequately express the complicated intergrading degrees of relationship" (Mayr, 1964: 102). For instance, if we would have to translate the cladogram of Lippitsch (1993: fig. 11; see fig. 17) into a classification, we would need at least eight hierarchical levels between the genus and the family level. The Linnean system of nomenclature is inadequate in this respect.

Special position of *Astatoreochromis*

Amongst the haplochromines of the Lake Victoria basin *Astatoreochromis* occupies a special place. It is the only genus which differs in characters which are not functionally related to the trophic apparatus. The species (*A. alluaudi*) has a wide distribution, occurring in several lakes of the Lake Victoria basin. Biochemical data (Sage et al., 1984; Verheyen et al., 1989; Meyer et al., 1990), and studies of the scale and squamation characters (Lippitsch, 1993) show that *Astatoreochromis* diverged from the rest of the haplochromines early in the history of the Lake Victoria basin and can be considered the sister group of the haplochromines. Therefore, it is omitted from the following part of the discussion.

Critical analysis of Greenwood's genera

The generic revision of the lacustrine *Haplochromis* species by Greenwood (1979, 1980) met serious criticism with researchers working on the alpha taxonomy of the species concerned (see table 1). New haplochromine species from Lake Kivu could not be placed in the genera as defined by Greenwood (Coenen et al., 1984; Snoeks, 1988, 1994; Snoeks et al., 1984, 1987, 1990; de Vos et al., 1990). Similar problems were encountered by researchers of the *Haplochromis* Ecology Survey Team (HEST), who described new haplochromine species from Lake Victoria (Hoogerhoud & Witte, 1981; Witte-Maas & Witte, 1985; Witte & Witte-Maas, 1987; van Oijen, 1991). The HEST taxonomists re-examined the material which Greenwood (1979, 1980) had used as basis for his definition of *Gaurochromis, Labrochromis, Enterochromis, Yssichromis, Psammochromis, Astatotilapia, Prognathochromis* and *Harpagochromis*.

Hoogerhoud (1984) analysed the insectivorous-molluscivorous haplochromine species placed by Greenwood (1980) in *Gaurochromis* and *Labrochromis*. After remeas-

Table 1. Of the 21 genera and subgenera made (*) or resurrected (o) by Greenwood (1980) nineteen have been critisised in literature, either because 1) species were known to bridge the gaps between genera, 2) because they were too narrowly defined, or 3) species were included that should be removed. The formerly monotypic genus *Paralabidochromis* was also critisised.

Genus	criticised by
*Allochromis**	
Astatotilapia°*	Greenwood, 1980; Coenen et al., 1984; Snoeks et al., 1987; Witte & Witte-Maas, 1987; Lippitsch, 1993; Meyer, 1993; Snoeks, 1994
*Enterochromis**	Coenen et al., 1984; Hoogerhoud, 1984
*Gaurochromis**	Hoogerhoud, 1984
*G. (Gaurochromis)**	Hoogerhoud, 1984
*G. (Mylacochromis)**	Hoogerhoud, 1984
Haplochromis°*	Snoeks, 1994
*Harpagochromis**	van Oijen, 1991; Lippitsch, 1993
Hoplotilapia	
Labrochromis°*	Coenen et al., 1984; Hoogerhoud, 1984; Lippitsch, 1993
Lipochromis°*	Eccles & Trewavas, 1989
*L. (Lipochromis)**	Lippitsch, 1993
*L. (Cleptochromis)**	Lippitsch, 1993; Snoeks, 1988, 1994
Macropleurodus	
Neochromis°*	Snoeks, 1994
Paralabidochromis	Lippitsch, 1993; Snoeks, 1994
Platytaeniodus	
*Prognathochromis**	van Oijen, 1991
*P. (Prognathochromis)**	
*P. (Tridontochromis)**	van Oijen, 1991
*Psammochromis**	Witte & Witte-Maas, 1987; Lippitsch, 1993; Snoeks, 1994
*Ptyochromis**	Snoeks, 1994
*Pyxichromis**	van Oijen, 1991; Lippitsch, 1993
*Yssichromis**	Witte & Witte-Maas, 1987; Snoeks, 1994
*Schubotzia**	
*Xistychromis**	Snoeks, 1994

uring all Greenwood's material he concluded that the subgenera *Gaurochromis (Gaurochromis)* and *Gaurochromis (Mylacochromis)*, which were based on the degree of stoutness of the lower pharyngeal bone and its dentition, are invalidated by two new species (*H. iris* and *H. hiatus*) which fully bridge the alleged subgeneric gap (figs 18 & 19). Further he demonstrated that *Gaurochromis* plus *Labrochromis* species can be placed in continuous morphoclines on the basis of different characters, including those supposedly defining the separate lineages (figs 20 & 21). The material used in the description of *Haplochromis humilior* Greenwood, 1960, was found to be polyspecific. Hoogerhoud suggested that the gap between *Gaurochromis* and *Enterochromis* might be bridged by the atypical material of *H. humilior* together with specimens of an undescribed species from the HEST collections (figs 22 & 23).

Witte & Witte-Maas (1987), in a paper describing the intraspecific variation of five zooplanktivorous species, analysed all data on the zooplanktivorous species placed by Greenwood (1980) in *Yssichromis* and *Astatotilapia*. According to Green-

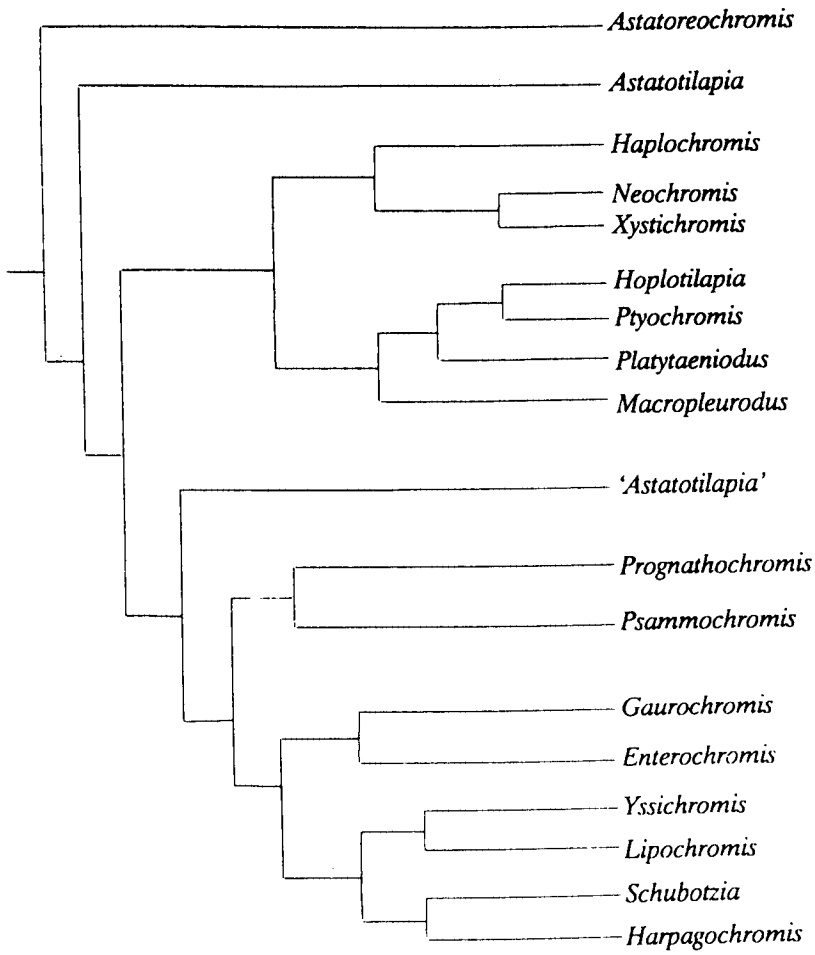


Fig. 17. Cladogram of haplochromine taxa based on scale and squamation characters. Adapted from Lippitsch, 1993, fig. 11.

wood (1980) the ranges for Body Depth, Caudal Peduncle Length and the extension of the teeth on the premaxilla of these two genera were separated by a gap. However, Witte & Witte-Maas (1987) discovered that when data from Greenwood & Gee (1969) are taken into account the gap between the genera is closed. New species described by Witte & Witte-Maas (1987) were also found to bridge the gap between these taxa (fig. 24). Moreover, Witte & Witte-Maas (1987) suggested that certain undescribed species would bridge the gap between *Yssichromis* and *Psammochromis*.

Van Oijen (1991) analysed the piscivorous species which Greenwood (1980), on the basis of four neurocranial measurements, placed in the new genera *Harpagochromis* and *Prognathochromis*. He found that it was impossible to place certain new piscivorous species unequivocally in either of these genera. After having measured all material used by Greenwood, van Oijen (1991: figs 7 & 8) could show that there is a

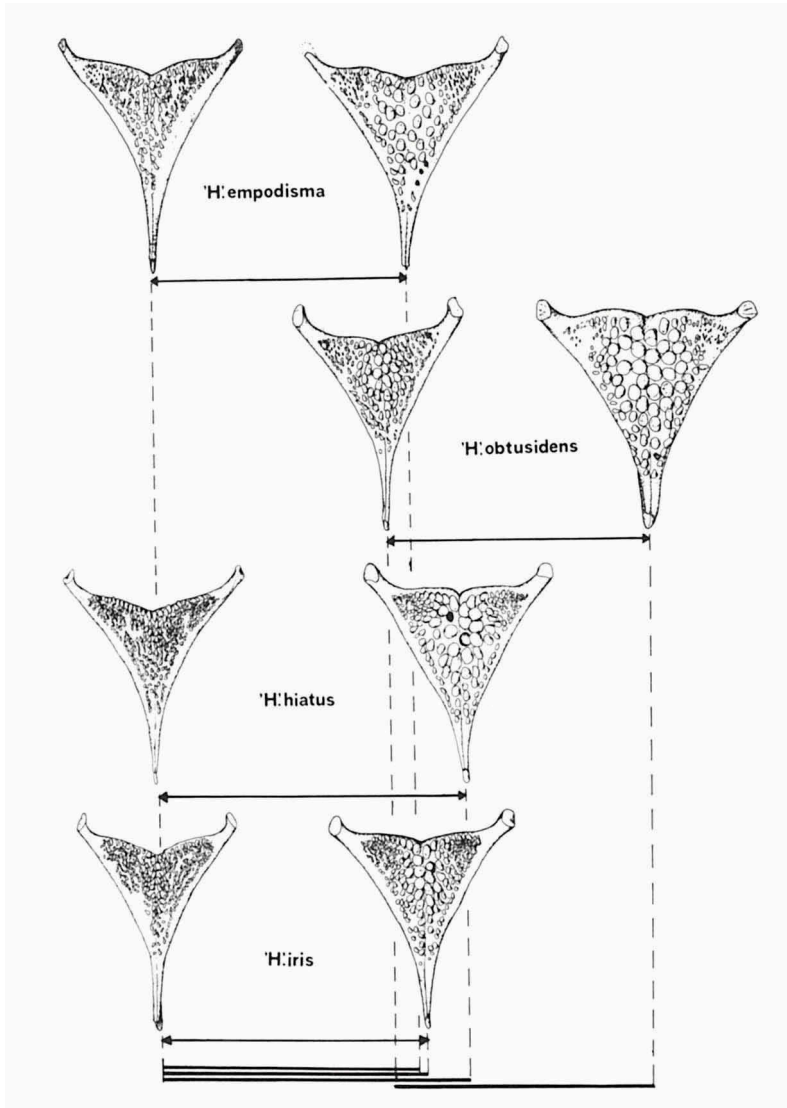


Fig. 18. Dorsal views of the lower pharyngeal element of the species the *Haplochromis empodisma* group (except *H. ptistes*). The stoutness of the bone and its dentition increases from left to right. From each of the four species two extreme elements are figured to show the morphological range within each species. In Greenwood (1980) *H. empodisma* was placed in *Gaurochromis (Gaurochromis)* and *H. obtusidens* was placed in *Gaurochromis (Mylacochromis)*. After Hoogerhoud & Witte, 1981, fig. 6.

considerable overlap between *Harpagochromis* and *Prognathochromis* in the ranges of all four measurements and concluded that separation of the two taxa on the bases of these measurements is impossible (figs 25 & 26)).

Re-examination of Greenwood's data has shown that it is not possible to separate *Gaurochromis* and *Labrochromis*, *Yssichromis* and *Astatotilapia*, and *Harpagochromis* and *Prognathochromis*. New species from Lake Victoria are known which bridge the gaps

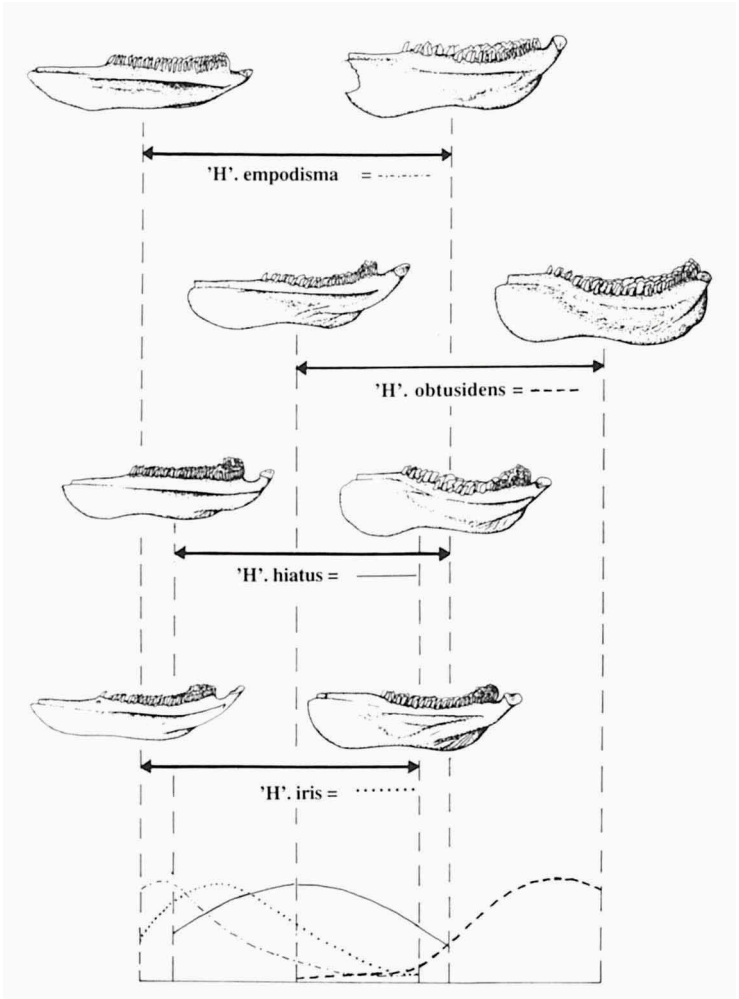


Fig. 19. Lateral views of the same lower pharyngeal elements as illustrated in fig. 18. The curves illustrate the approximate distribution of the various types of elements within each species. In Greenwood (1980) *Haplochromis empodisma* was placed in *Gaurochromis (Gaurochromis)* and *H. obtusidens* was placed in *Gaurochromis (Mylacochromis)*. After Hoogerhoud & Witte, 1981, fig. 7.

between *Gaurochromis* and *Enterochromis* (see Hoogerhoud, 1984) and *Yssichromis* and *Psammochromis* (see Witte & Witte-Maas, 1987). Haplochromine species from Lake Kivu were found to be intermediate between *Astatotilapia* and *Paralabidochromis*, and *Astatotilapia* and *Gaurochromis* (see Snoeks, 1994).

It is clear from the results of researchers who work with haplochromines on the alpha taxonomic level that most characters used by Greenwood to define his genera can be placed in continuous morphoclines. These morphoclines should not be arbitrarily split to define genera. Because many of Greenwood's new genera were judged impractical, the taxonomists working on Lakes Kivu and Victoria did not follow Greenwood's revision and placed their new species in *Haplochromis*.

More general criticism on Greenwood's methodology was given by Eccles & Tre-

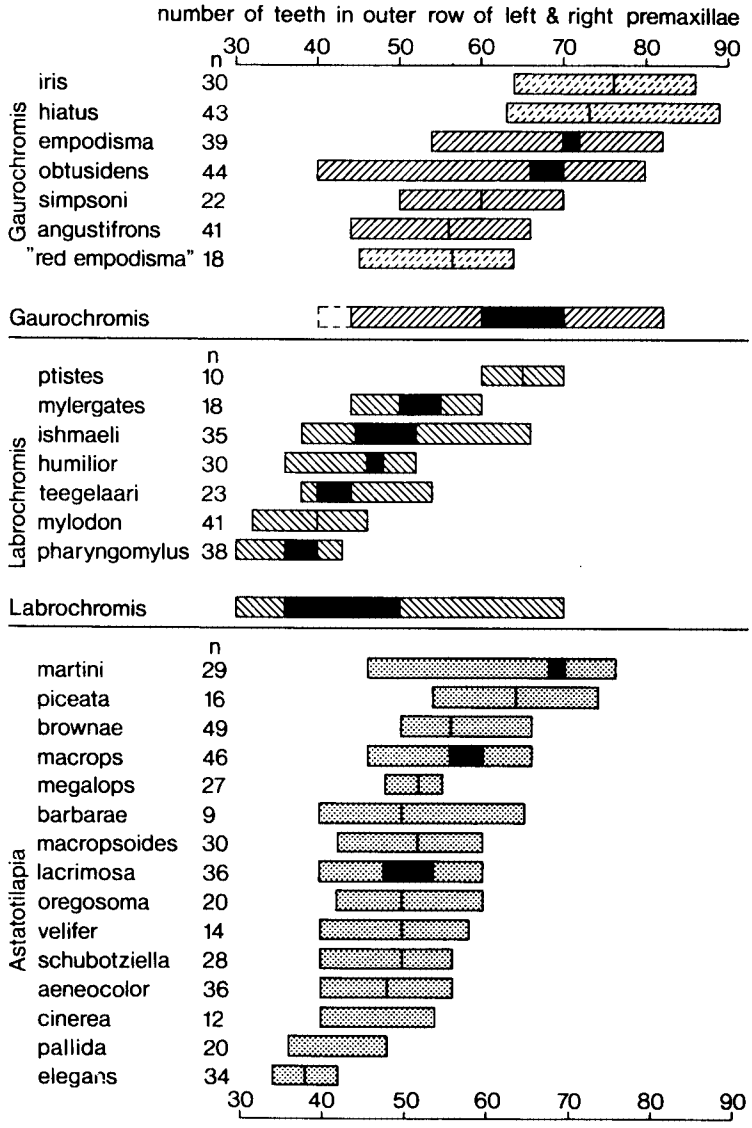


Fig. 20. Numbers of premaxillary outer row teeth (PORT). Ranges and means, modes or modal ranges of "*Labrochromis*", "*Gaurochromis*" and "*Astatotilapia*". Within the genera the species are arranged with the means or modal ranges of the PORT-counts increasing from bottom to top. Legend: n= the number of specimens on which the description is based; the shaded or hatched bars give the total range of PORT-counts: the black bars give the modal range and a line in the bar gives the mean or mode. Data for *G. iris*, *G. hiatus* and *G.* "red-*empodisma*" are from specimens in the collection Hoogerhoud. Other data compiled from Greenwood (1960, 1965 & 1974) and Greenwood & Barel (1978). The lower limit of the range given by Greenwood (1980) for *Gaurochromis* does not accord with the lower limit of one of its constituent species: according to Greenwood (1960) *Haplochromis obtusidens* has a minimum of 40 PORT. *H. iris*, *H. hiatus* and *H.* "red-*empodisma*" were not yet included in *Gaurochromis* by Greenwood (1980), but, according to his generic definitions would (partly) belong to this genus. From Hoogerhoud, 1984, fig. 3.

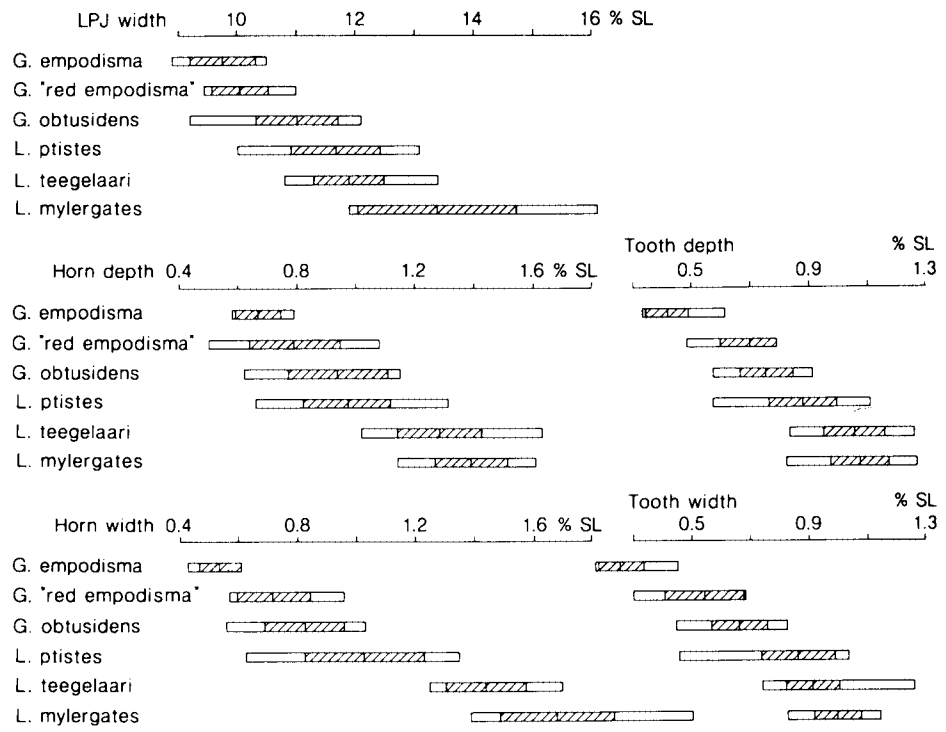


Fig. 21. Ranges (total bar), means (line in hatched part) and standard deviations (hatched) of main taxonomic characters (lower pharyngeal jaw width; horn width; horn depth; tooth depth; tooth width) of the lower pharyngeal element of pharyngeal crushing species placed by Greenwood (1980) in *Gaurochromis* and *Labrochromis*. (n= number of specimens). From Hoogerhoud, 1984, fig. 6.

wavas (1989). Taking as an example the paedophages, which occur both in Lake Malawi and in Lake Victoria, these authors repeated that close resemblances in trophic mechanisms should be regarded with caution in phylogenetics. This warning was already phrased differently by Barel (1984: 492), who after an extensive study of the relation between the form of the eye and the suspensorium in lacustrine cichlids concluded: ".. if there is in the morphology of cichlids a certain fixed trend to deal with a certain ecological demand, then the multiple intralacustrine origin of this trend is as likely as the interlacustrine one. Consequently, on the basis of morphological characters belonging to such a trend, no conclusions on intralacustrine relationship can be made". Sturmbauer & Meyer (1993: 764), after mapping morphological characters of 12 species of 12 genera of the Tanganyikan tribe Ectodini on phylogenies obtained by sequencing mtDNA, similarly concluded that "characters related to trophic specializations are prone to convergence." At least one of their discoveries, namely that intestinal prolongation in Lake Tanganyika cichlids may have evolved in different lineages, apparently also holds for Lake Victoria haplochromines (see Greenwood, 1980: 52). These two examples of possible convergent evolution are also mentioned by Fryer (1982), who expressed his doubts about the possibility to resolve the phylogeny of the super flock by applying a cladistic analysis.

One reason why Greenwood (1980) did not give a subgeneric rank to the lineages

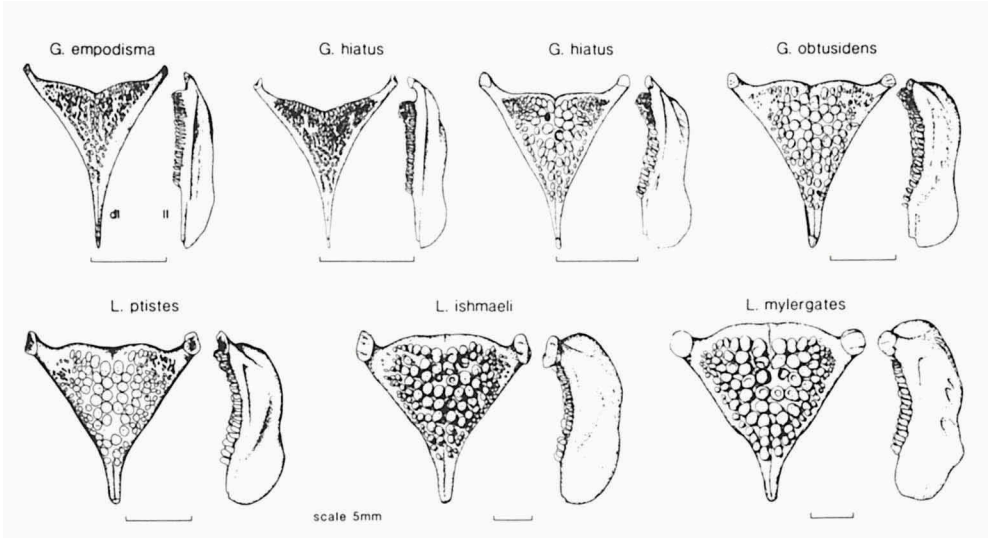


Fig. 22. Occlusal (dorsal) and lateral views of lower pharyngeal jaws (LPJ) of some *Gaurochromis* and *Labrochromis* species. Arrangement is according to degree of enlargement of the LPJ. To illustrate the continuity two (more or less) extreme specimens of *G. hiatus* have been figured. All LPJ's are drawn to the same LPJ length. From Hoogerhoud, 1984, fig. 7.

he distinguished was that he did not want to "imply a relationship that may not exist." Placing them as subgenera of *Haplochromis* would imply they all formed one monophyletic group and Greenwood did not find any morphological character to support this view. However, the outcome of subsequent investigations of the East African cichlids at the molecular level indicated that the haplochromine species from Lake Victoria, except *Astatoreochromis alluaudi*, are indeed a monophyletic group. (Meyer et al., 1990; Meyer, 1993; Van Rompaey et al., 1988; Sage et al., 1984; Verheyen, 1989; Verheyen et al., 1985, 1986, 1989). Although only species from Lake Victoria were examined, conclusions were drawn concerning the entire Lake Victoria super flock, thus including the species from the satellite lakes (e.g. Meyer, 1993; Meyer et al., 1991). The specimen of *Astatotilapia elegans* (an endemic species of Lakes Edward and George) mentioned in table 1 in Meyer et al. (1990) was clearly misidentified as it is said to be collected in the Mwanza Gulf of Lake Victoria. If indeed one specimen from Lake George had been included in the study of Meyer et al., it would still have been incorrect to draw conclusions about fishes from other lakes of which not even a single specimen was examined (i.e. Lakes Nabugabo and Kivu). Anyway, if important conclusions on the phylogeny of a very speciose flock are based on a relatively small number of species (14 species examined on a total of >300), the identity of the species must be established without any doubt.

Although the investigation of Meyer et al. (1990) made clear that morphologically very similar and highly specialized forms (*Macropleurodus* from Lake Victoria and *Chilotilapia* from Lake Malawi) are more closely related to generalized forms from their respective lakes than to each other, the relations within the Lake Victoria basin and within Lake Victoria were not solved. The molecular data could not test the validity of Greenwood's lineages. According to Meyer (1993: 280): "Phyletic relationships within the Victoria superflock [!] could not be established with certainty since

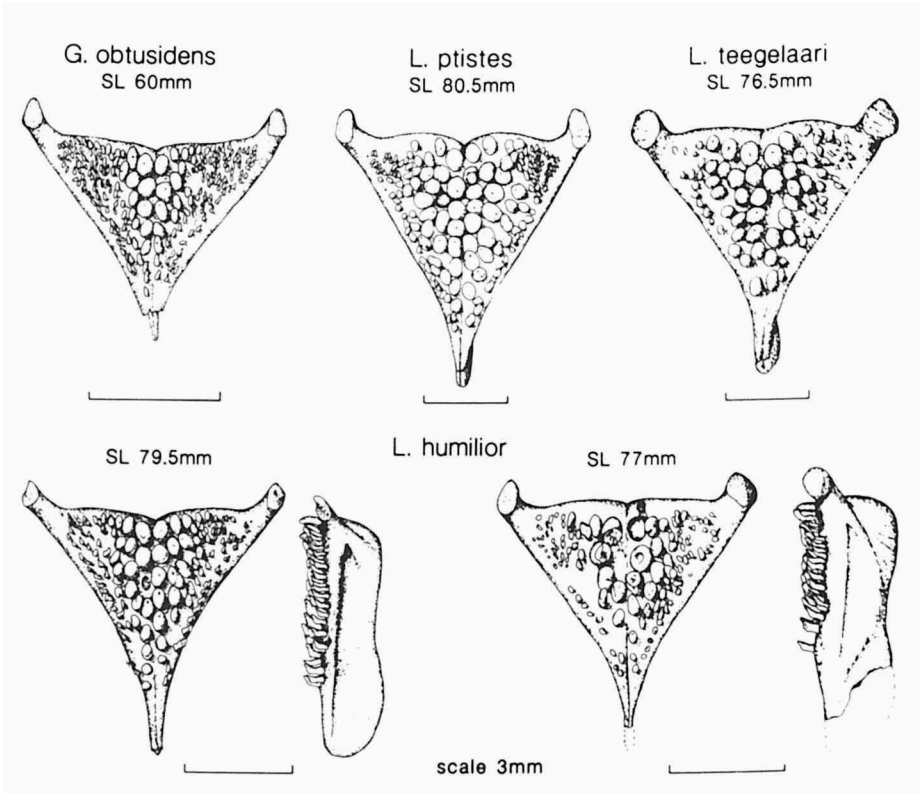


Fig. 23. Occlusal (dorsal) views of lower pharyngeal jaws of *Labrochromis teegelaari*, *L. ptistes* and *Gaurochromis obtusidens* and occlusal and lateral views of similarly sized *L. humilior* specimens. A new drawing of the specimen illustrated by Greenwood (1960) plus a modal specimen are given. From Hooogerhoud, 1984, fig. 8.

too little phylogenetic information was contained even in the most rapidly evolving portion of the mitochondrial genome". According to Greenwood (1994: 348), the question of monophyly versus polyphyly is still open, "particularly since the interspecific similarity of the mtDNA in the contemporary species is so great (Meyer et al., 1990) that had more than one closely related ancestral species been involved, their mtDNA could well then have been as similar as their descendants today".

As it is generally accepted that the accumulation of differences in nucleotides is largely a time dependent process (Avise, 1976; Thorpe, 1982; Verheyen et al., 1985), we have to accept that the species flock originated quite recently. On the one hand, uniformity in mtDNA structure does not really prove a monophyletic origin of this species group, but on the other hand it neither provides support for the hypothesis of a polyphyletic origin.

The molecular data (Meyer et al., 1991; Meyer, 1993) also indicated that the genus *Astatotilapia* as defined by Greenwood (1979, 1980) is a polyphyletic group. As this genus was only based on plesiomorph characters, Greenwood (1980) had already expressed his doubt about its monophyletic status. According to Lippitsch (1993: 937), based on scale and squamation characters, the fluviatile *Astatotilapia* species

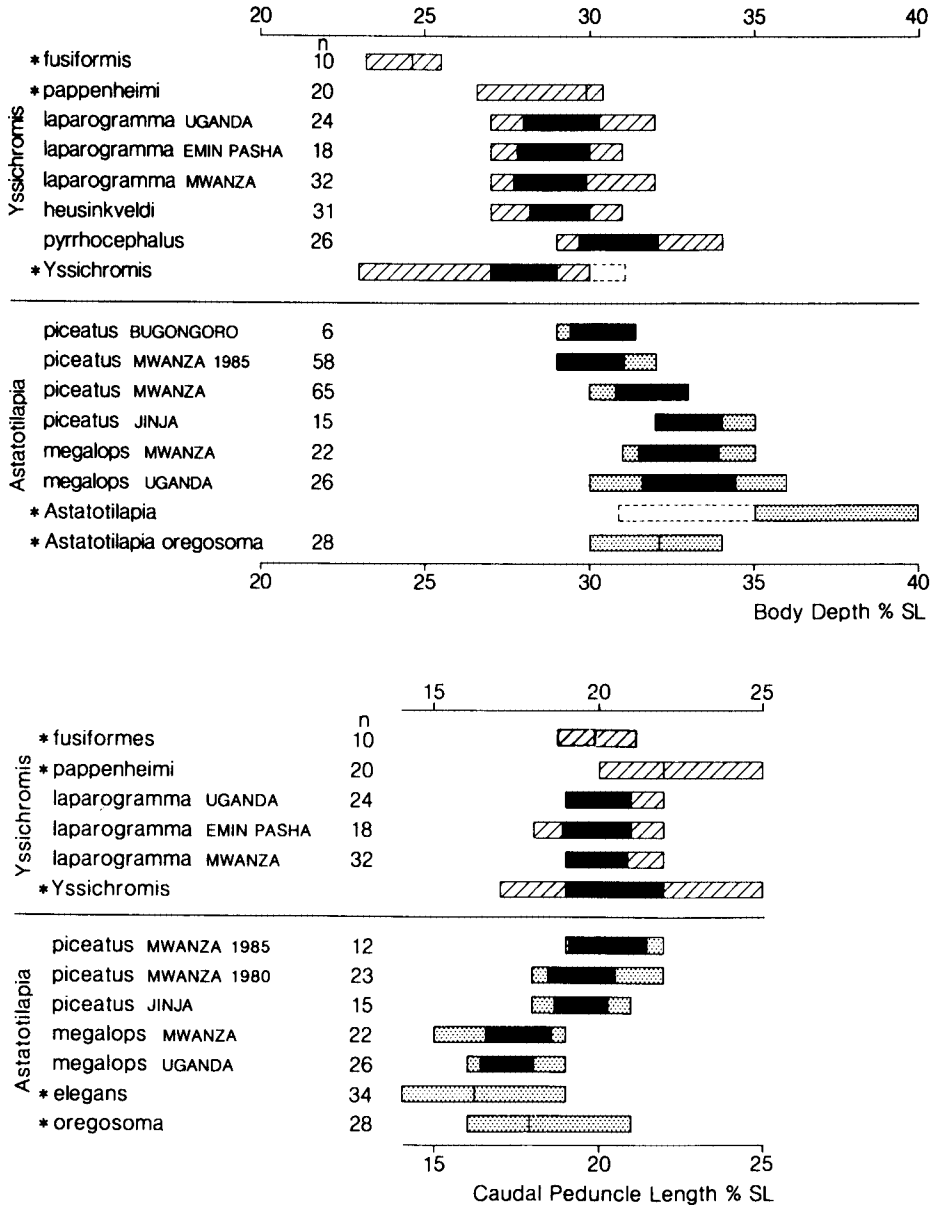


Fig. 24. Ranges and means or modal ranges of Body Depth/SL and Caudal Peduncle Length/SL ratios of *Yssichromis* and *Astatotilapia*. Legend: n= number of specimens on which data are based; asterisk indicates data compiled from Greenwood (1974, 1979, 1980) and Greenwood & Gee (1969); shaded and hatched bars give total ranges: black bars give modal ranges as given in Greenwood (1980) and mean ± standard deviation for other data; dashed lines indicate ranges which should be included in the range of the genus as presented in Greenwood (1980) according to Greenwoods measurements for Body Depth/SL of *H. laparogramma* and Caudal Peduncle Length/SL of *H. megalops* (Greenwood & Gee, 1969). From Witte & Witte-Maas, 1987, fig. 12.

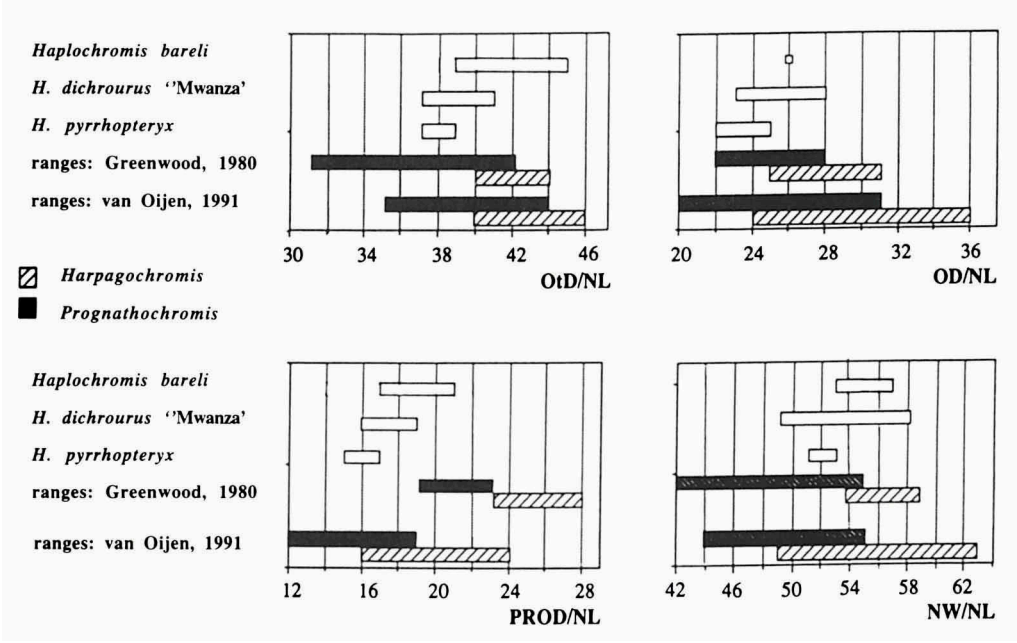


Fig. 25. Comparison of ranges of neurocranial measurements of species of *Harpagochromis* and *Prognathochromis*, as measured by Greenwood (1980) and by van Oijen on skeletal material from the BMNH collection (see van Oijen, 1991, table 1). Measurements of *Haplochromis bareli, H. dichrourus* "Mwanza" and *H. pyrrhopteryx*, from the Mwanza Gulf are by van Oijen, and have not been included in the ranges. Legend: OtD = Otic Depth, OD = Orbital Depth, PrOD = Preorbital Depth, NW = Neurocranial Width, NL = Neurocranial Length. From van Oijen, 1991, fig. 7.

obviously form a monophyletic group, whereas the lacustrine species classified with the same genus by Greenwood (1980) are only distantly related.

The monophyly of the Lake Victoria haplochromines was confirmed by a phylogenetic analysis of scale and squamation characters by Lippitsch (1993). After investigating about 190 cichlid species, she defined 96 characters with, in total, about 300 different character states. The plesiomorph state was assessed by using non-African cichlids, the African genera *Heterochromis* and *Tylochromis*, and by applying the commonality principle amongst most African taxa, but excluding *Tylochromis* and *Heterochromis*. Lippitsch concluded that the monophyletic origin of the Lake Victoria super flock (she examined species from Lakes Victoria, George, and Kivu) is backed by scale and squamation characters, but no synapomorphy was detected for all species. On the basis of scale characters it was possible to subdivide the Victoria flock and to interrelate the subdivisions. According to Lippitsch, many of Greenwood's genera can be recognized using scale characters, which indicates that they are phyletic entities. Thus, Lippitsch (1993: 942) concluded "Greenwood's phyletic classification (1979, 1980) of the haplochromine genera is essentially confirmed, and the availability of scale and squamation characters should make the practical use of this classification easier." However, the scale and squamation characters did not always confirm Greenwood's lineages; for instance, they indicated a possible diphyletic origin of

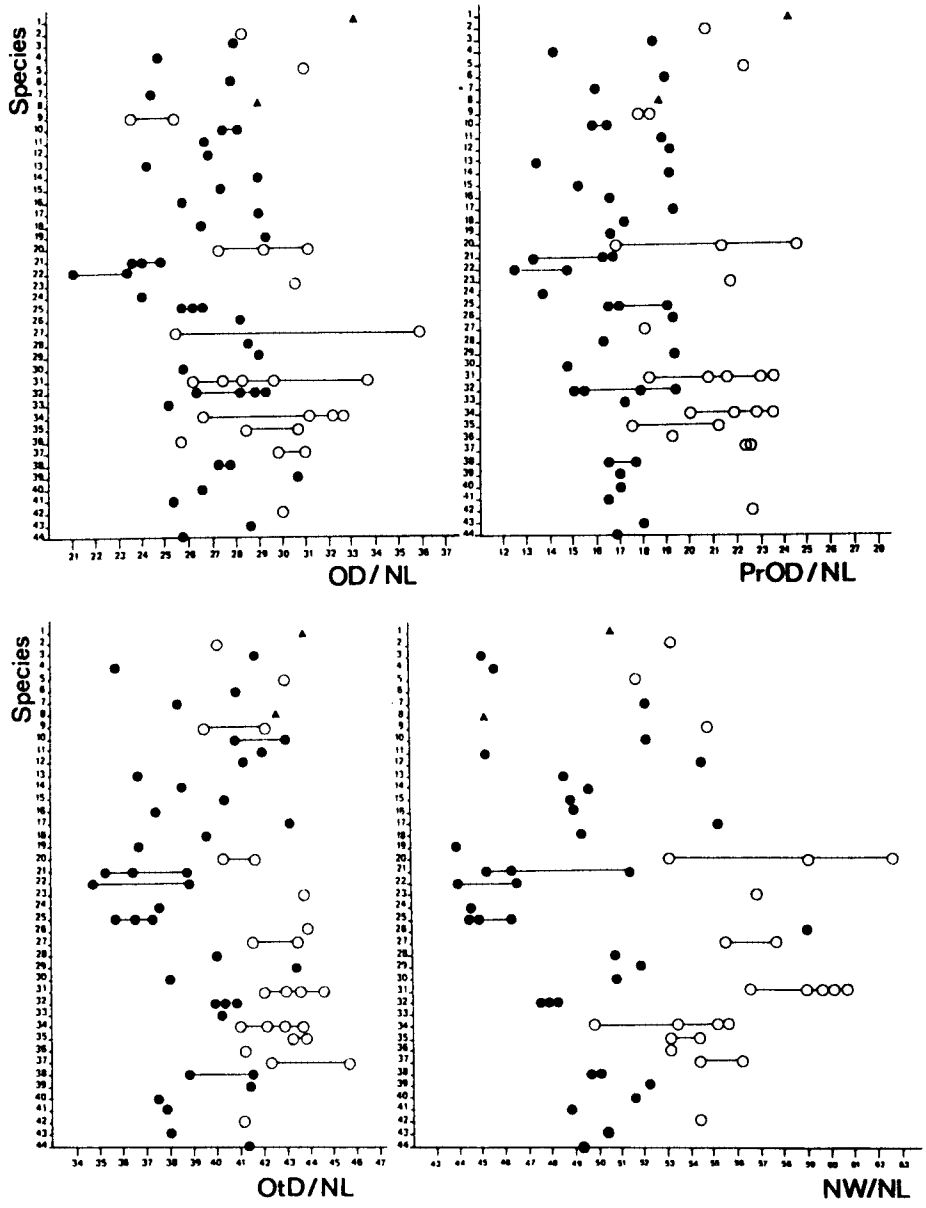


Fig. 26. Neurocranial measurements of species placed by Greenwood (1980) in *Harpagochromis*, *Prognathochromis* and *Psammochromis*, taken from neurocrania in the BM(NH) collection. Numbers on vertical axis refer to species listed by van Oijen, 1991, table 1. Legend: OD = Orbital Depth, PrOD = Preorbital Depth, OtD = Otic Depth, NW = Neurocranial Width, NL = Neurocranial Length. o = *Prognathochromis* (Greenwood, 1980), ● = *Harpagochromis* (Greenwood, 1980), ▲ = *Psammochromis* (Greenwood, 1980). From van Oijen, 1991, fig. 8.

Lipochromis, a possibility considered earlier by Greenwood (1959a) and hinted at by Eccles & Trewavas (1989).

As Lippitsch investigated only a few specimens of barely one-third of the described haplochromine species from Lake Victoria, one may wonder if all her conclusions are justified. For instance, the assertion that the two subgenera of *Prognathochromis* have five synapomorphies, is based on the examination of three specimens representing three species, while Greenwood based these subgenera on 24 and 9 species, respectively. According to Lippitsch, the genus *Harpagochromis* is characterized by two postorbital scale rows. Lippitsch (1993: 941) doubts the assignment of six species to *Harpagochromis* because, judging from figures accompanying species descriptions, they have only one postorbital scale row. However, figures of species placed in *Prognathochromis* with two postorbital scale rows can also be found in the literature, e.g. *Haplochromis dentex*, *H. gowersi* and *H. macrognathus* (Greenwood, 1962: figs 9, 13, 15).

According to Lippitsch (1993), similarity in granulation type will usually not be due to homoplasy. However, when there are no additional synapomorphies supporting monophyly for a group of taxa (e.g. *Astatotilapia*, *Enterochromis* and *Gaurochromis*), the granulation type is not considered to be decisive. Still the suggestion that scale and squamation characters are useful for phylogenetic research seems worth investigating, but many more haplochromine species of Lake Victoria will have to be examined for these characters before conclusions can be drawn about their phylogenetic relations.

Greenwood's genera in recent literature

From a screening of recent literature it seems that the generic names introduced by Greenwood (1980) are used mostly by researchers who are not directly involved in research on the haplochromines of Lake Victoria, but who as a matter of principle incorporate the latest systematic revision when they cite literature sources (e.g. Aerts et al., 1987; Strauss, 1984; Kornfield, 1991; Liem & Kaufman, 1984; Lowe-McConnell, 1987; Yamaoka, 1991). Among the researchers working on the molecular level, there is a division between Americans and Europeans; the former follow Greenwood (1980) and the latter, referring to the work of Hoogerhoud (1984), use the nomenclature prior to Greenwood's revision.

In aquarium literature, there was a hesitation to follow the revision. Referring to Greenwood's own remarks on the artificiality of some of his smaller genera, and to the fact that Greenwood did not use behavioural or coloration characters, and emphasizing the "far reaching consequences for nomenclature", Loiselle (1986: 140) used Greenwood's genera only as subgenera. This "solution" was adopted in other articles (Seegers, 1987; Seehausen, 1990), but alternatives were used as well. In some publications Greenwood's (1980) genera were not mentioned at all (e.g. Seehausen, 1991, 1994; Seehausen & Witte, 1994a + b), while in others the genera were adopted (e.g. Selbrink, 1985; Kimer, 1994). Kaufman & Ochumba (1993) followed Greenwood (1980) for described taxa, but placed taxa described since 1980 in: "Haplochromis". Recently, yet another nomenclature has been adopted. Because "the definitions and limitations of many genera proved unworkable with many of the new species ", Seehausen (1995a: 191; 1995b: 216) and Seehausen & Witte (1995: 99) used "Haplochromis" for all species, followed by the Greenwood's (1980) generic name, in parenthe-

sis. However, most taxonomists working with species from the Lake Victoria basin who are familiar with the intra-specific variation of the species and the morphoclines of which many of them are part, have rejected Greenwood's (1980) genera as insufficiently defined or as impossible to maintain. Therefore, the genera were not accepted by van Oijen et al. (1987) in the Checklist of Freshwater Fishes of Africa (CLOFFA).

A proposal to stabilize nomenclature

Until now morphological investigations have failed to give us a clear picture of the phylogenetic relationships among the Lake Victoria haplochromines. In the case of this very young species flock, molecular data have not (yet) elucidated the problems substantially. However, there are at least indications from both morphological (scale and squamation) characters (Lippitsch, 1993) and molecular data (Sage et al., 1984; Meyer et al., 1990) that the Lake Victoria (super) flock is a monophyletic group.

With the present state of knowledge of the systematics of the Lake Victoria haplochromines, with so many new species still being discovered (in littoral habitats where Nile perch did not penetrate, see Kaufman & Ochumba, 1993; Seehausen, 1995a) and described, and new approaches for the phyletic analysis of the cichlids being initiated, the kind of classification we need is a practical system of reference (cf. Charig, 1982). It would be wiser to adopt a conservative nomenclature than to change the classification with every new discovery. If we would unite all Lake Victoria haplochromines into a single genus, we would give it back its broad collective character (cf. Mayr, 1964; Rosen & Bailey, 1963).

As the present generic nomenclature of the haplochromine cichlids of the Lake Victoria super flock is untenable both from a theoretical and a practical standpoint, I propose, as at least a temporary solution, to unite all lacustrine haplochromines in one genus. For reasons of priority the generic name *Haplochromis* is the most appropriate one to be used. The following definition of *Haplochromis* may be used:

Lacustrine, maternal mouthbrooding Cichlidae naturally occurring in the Lake Victoria basin, with a *Haplochromis* type of pharyngeal apophysis, i. e. with the basioccipital contributing to the articulation facet for the upper pharyngeal bones as well as to the support of that cranial facet (Greenwood, 1978). The teeth of the outer row of the oral jaws are unicuspid, bicuspid or tricuspid. In many species a mixture of these types is found. When tricuspids are present they are usually most numerous in the caudal part of the jaws. Teeth of the 1-11 inner rows are unicuspid and/or tricuspid, exceptionally bicuspid, usually of a smaller size than the outer row teeth. The pharyngeal jaws may vary from thin and slender to massive and strong. Pharyngeal teeth vary from slender to molariform and from pronounced to bevelled or hooked (Barel et al., 1977). Usually there is a distinct sexual dimorphism in coloration; the males being the more colourful sex. On the anal fin of males 1-9 distinct egg dummies are present. The anal fin with 3 spines.

For molecular characters see Verheyen et al. (1985) and Meyer et al. (1990).

The monotypic genera

Although the monotypic genera *Hoplotilapia*, *Platytaeniodus* and *Macropleurodus* are separated by clear morphological gaps from the other known haplochromine

species from Lake Victoria, it should be realized that these gaps concern only characters related to the feeding apparatus. In all aspects of external morphology, coloration and reproduction the species do not differ from other Lake Victoria haplochromines. Regan (1920), while discussing the status of the nominal genera *Hoplotilapia*, *Platytaeniodus* and *Macropleurodus*, stated that "the close relationship of each to a species of *Haplochromis* is obvious". Greenwood (1974: 103), who erected the monotypic *Paralabidochromis* for a single specimen in 1959, found the generic status of both *Macropleurodus* and *Paralabidochromis* "questionable". Clearly, even in these genera the size of the morphological gap was not convincing.

Verheyen et al. (1985: 474), in a study of allozyme variation in ten haplochromine species concluded: " Even monotypic genera, such as *Hoplotilapia retrodens* and *Macropleurodus bicolor*, are essentially indistinguishable from members of *Haplochromis*. This similarity parallels that observed by Sage et al. (1984)". Van Rompaey et al. (1988: 514), examining general protein patterns of *Hoplotilapia retrodens*, *Macropleurodus bicolor* and eight species of *Haplochromis*, stated: " It is very remarkable that the correlation between molluscivorous species and electrophoretic pattern also transcends generic bounderies". Verheyen et al. (1988) on the basis of an analysis of eye lens proteins of seven species, concluded once more that *Hoplotilapia retrodens* and *Macropleurodus bicolor* are essentially indistinguishable from members of *Haplochromis*. Meyer et al. (1990) also do not mention differences between these monotypic genera and the other haplochromine species. Meyer et al. (1990: 553) stated that their "result weakens the hypothesis that similarly specialized species from different lakes are more closely related to each other than to the morphological generalists from the same lake". The morphologically convergent *Macropleurodus* from Lake Victoria and *Chilotilapia* from Lake Malawi, that served to support the notion of polyphyly (Greenwood, 1983), were represented in the study of Meyer et al. (1990) and confirmed their conclusions concerning monophyly.

As the so-called monotypic genera differ from the other haplochromines of Lake Victoria only in characters related to the trophic apparatus, I propose to treat these nominal taxa as subgenera of the redefined genus *Haplochromis*.

The (sub)generic names introduced by Greenwood (1980) could be used in the same way, thus as subgenera of *Haplochromis*. However, many objections have been brought forward against these taxa, and as their monophyly is far from being established, their use as subgenera should be discouraged. However, an exception should be made for the monotypic *Allochromis* Greenwood, 1980. As the differences between *A. welcommei* and *Haplochromis* species in morphology of the teeth and especially in dental pattern, are comparable to those between the other monotypic genera and *Haplochromis*, I propose to use *Allochromis* as a subgenus of *Haplochromis*.

Conclusion

The haplochromine cichlids from Lake Victoria form a group of closely related fishes (Greenwood, 1974, 1979, 1980; Lippitsch, 1993; Meyer et al, 1990; Sage et al., 1984; Verheyen et al., 1985). The species can be divided over 15 (sub)trophic groups (Witte & van Oijen, 1990). They all have a unique combination of habitat and food

preferences and feeding techniques, the extremes of which may be very different. Nevertheless, the Lake Victoria haplochromines are morphologically relatively similar (Greenwood, 1974; Barel et al., 1977). When taxonomists attempt to make subdivisions in this large group of species on the basis of the general facies, there is a large amount of agreement (Hoogerhoud, 1984). However, it turns out to be impossible to delimit the groups, as there are numerous intergradations between them. The combination of the geological history of the Lake Victoria basin and the evolutionary potential of the haplochromines, suggests that adaptation to changing habitats has taken place several times. It has been shown that the adaptation to similar environmental conditions by cichlids in different lakes has resulted in the development of remarkably similar structures (Barel, 1984; Greenwood, 1983; Stiassny, 1981b). The result of adaptation of closely related species in the same lake basin, possibly even in the same lake (e.g. like in Lake Barombi Mbo, see Schllewen et al,. 1994), would be even more strikingly similar. Periods of (near) extinction and rapid speciation have interchanged (episodic evolution: Ribbink, 1994) resulting in a complex pattern of adaptations. Seen in this light, any attempt to unravel the phylogenetic relationship of the Lake Victoria haplochromines is bound to get stuck in the web of evolution. Greenwood (1979, 1980) is to be commended as he saw it as a scientific challenge to make a start with the unravelling of this evolutionary plot. However, placed in the context of later research (Verheijen, 1989; Lippitsch, 1993; Meyer et al., 1990; Meyer, 1993; Sage et al., 1984), which indicates a monophyletic origin of the Lake Victoria haplochromines, Greenwood's (1979, 1980) attempt to make a phyletic classification of the genus *Haplochromis* has failed. His research did not yield data to justify the splitting of *Haplochromis*.

In order to end the nomenclatoral confusion at the generic level concerning the haplochromines of the Lake Victoria basin, a new definition of *Haplochromis* is proposed. The monotypic nominal genera *Hoplotilapia*, *Macropleurodus* and *Platytaeniodus* are provisionally given subgeneric status. Although it seems unlikely that the full phylogenetic history, if ever unravelled, can be translated into nomenclature, the research on the phylogeny of the haplochromines of Lake Victoria should continue.

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Index to genera which were used for haplochromine cichlids from Lake Victoria and the authors who described haplochromine cichlid species from Lake Victoria