Taxonomy, ecology and fishery of Lake Victoria haplochromine trophic groups

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Based on ecological and morphological features, the 300 or more haplochromine cichlid species of Lake Victoria are classified into fifteen (sub)trophic groups. A key to the trophic groups, mainly based on external morphological characters, is presented. Of each trophic group a description is given comprising data on taxonomy, ecology and fishery. As far as possible data from the period before the Nile perch upsurge and from the present situation are compared. A list of described species classified into trophic groups is added.

Key words: ecology; fishery; *Haplochromis*; haplochromine cichlids; key; Lake Victoria; taxonomy; trophic groups.

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Contents

Introduction

Research in the early 1970s revealed that the haplochromine cichlids formed a substantial and underexploited protein resource in Lake Victoria. Based on bottom trawl surveys Kudhongania and Cordone (1974) estimated that 83% (564,000 metric tons) of the demersal ichthyomass in the lake consisted of these cichlids. The potential annual yield of haplochromine cichlids was estimated to be 200,000 metric tons, which to a large extent could be obtained from the relatively lightly fished deepwater areas (depth >20 m) of the lake. In 1976 a small scale industrial trawl fishery was started in the Mwanza area (Tanzania) of Lake Victoria. During the 1970s the haplochromine cichlids were also increasingly becoming the target of artisanal fishermen around the lake (Scully, 1975).

For fishery management the haplochromine cichlids constituted a problem because this group comprised over 250 species (van Oijen et al., 1981) with a wide ecological diversity. By catching in one haul up to 40 different species, varying in composition according to area and depth, fishing for haplochromines was an outstanding example of a multispecies fishery. Considering these species as a single unit was an unwarranted issue for fishery research and management. However, management of such a fishery at the species level would be unfeasible (Pauly, 1980). Moreover, identification of haplochromine species is generally a complex and time consuming affair (Barel et al., 1977; Basasibwaki, 1975; Greenwood, 1981). Using trophic groups (Greenwood, 1974; van Oijen et al., 1981) instead of species appeared a fair compromise, as it simplified the system while still allowing some important ecological conclusions on which fishery management could be based (Witte, 1981; Witte & Goudswaard, 1985).

Although researchers dealing with haplochromine cichlids can learn easily to distinguish the trophic groups, thus far no key to, nor a description of these groups has been made. In this paper a key to, and a short description of the trophic groups is presented. The description includes the fishery significance of the group as well as taxonomic and ecological data.

Since the upsurge of the Nile perch, *Lates niloticus** (Linnaeus, 1758), in Lake Victoria at the beginning of the 1980s, the haplochromine stock and its fishery have virtually disappeared. However, for the following reasons the information given in this paper is still thought relevant for researchers working on Lake Victoria:

a) The present and future situation in the lake can be better understood or better predicted when sufficient ecological data are available about the ecosystem prior to the Nile perch upsurge (e.g., the changes in the food web, Ligtvoet & Witte, in press; Ligtvoet et al., in prep);

b) Although the Nile perch affected the haplochromine cichlids in a major part of the lake, in certain habitats (e.g., shallow embayments and rocky littoral zones) they still are and may remain an important group (Witte, et al., in prep);

c) The current extremely high densities of the Nile perch may well be temporary.

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* Preliminary taxonomic investigations of *Lates* specimens from Lake Victoria failed to identify these fishes unambiguously as *L. niloticus* (Witte, pers. obs.). There remains the possibility that the *Lates* introduced into Lake Victoria belonged to other species, e.g., *L. macrophtalmus* Worthington, 1929 or *L. longispinis* (Worthinton, 1932), or that the species in the lake is a hybrid.

A decrease of these densities in the future might allow certain haplochromine species to increase in numbers.

d) The distinguished trophic groups may also be relevant for research on other cichlid lakes, of which the communities have many features in common with those of Lake Victoria (Fryer & Iles, 1972; Greenwood, 1973; Gwahaba, 1978; Lewis, 1981; Ribbink et al., 1983; Witte, 1984; Ribbink & Eccles, 1988).

Material, techniques and definitions

Data which are used for the provisional key and for the descriptions of the trophic groups are mainly based on the field research of the Haplochromis Ecology Survey Team (HEST), which operates since 1977 in the Tanzanian part (mainly Mwanza Gulf) of Lake Victoria. The collections of the Natural History Museum, London, and the papers of Greenwood (1974 and many papers republished in Greenwood, 1981) have also been an important source of information. However, many of the included data have not yet been published before.

For definitions of measurements and measuring techniques see Barel et al. (1977). Taxonomic features are compared with a so-called "generalized", viz. morphologically modal haplochromine cichlid as a reference. *Haplochromis elegans* Trewavas, 1933, an insectivorous species of Lake George (Uganda), featured as the model of such a "generalized" species (Barel et al., 1976; Anker, 1978, 1984, 1986, 1988, 1989).

A trophic group consists of species using the same food category. However, many species feed on several types of food. In these cases the dominant food category was taken as decisive of the trophic classification (Witte, 1981). Occasionally, when not enough data on food preference were available, morphological features were also used for classification.

One should bear in mind that although the following descriptions and data of the trophic groups hold to a large extent, there are several obvious constraints:

a) Species are known which, concerning diet and form features, are intermediate between trophic groups.

b) Form features are in fact not so much correlated with the food type itself, but with the way in which the food is collected from the environment (Barel, 1983; Barel, et al., 1989), e.g., molluscs can be wrenched from their shell or the shell can be crushed. When such information was available subtrophic groups were recognized (e.g., oral shellers and pharyngeal crushers). Often however, actual information about how food is obtained is lacking.

c) The form features of a species are not only determined by its feeding habits but also by other environmental and constructional factors and of course by historical factors (Barel et al., 1989).

d) Form features (and ecology) of juveniles and adults often differ. The form descriptions in this paper are based on adults only.

e) It is supposed that there are (were) still many unknown species in Lake Victoria. Such species may extend the presently known form ranges of trophic groups.

In the following descriptions we generally refer to the situation prior to the Nile perch upsurge in Lake Victoria. It should be realized however, that since the increase of the Nile perch many species not only decreased in numbers or even vanished from the catches, but also that considerable changes in the overall size (and also in other form features) of adult fish were observed (Witte & Witte-Maas, 1987). Moreover, occasionally ecological changes (e.g., in habitat preference, Witte & Witte-Maas, 1987; Goldschmidt et al., 1990; Wanink pers. comm., and in fecundity, Wanink in press) were observed.

Regarding water depth, three regions are recognized in Lake Victoria: littoral regions (0-6 m); sub-littoral regions (6-20 m) and deepwater regions (>20 m) (Greenwood, 1974). For a further description of the major habitats one is referred to Greenwood (op. cit.) and Van Oijen et al. (1981).

In a few cases informal names of as yet undescribed species have been used in this paper. These cheironyms are placed in quotation marks. A reference collection of these species has been deposited at the Nationaal Natuurhistorisch Museum, Leiden, The Netherlands.

Lake Victoria haplochromine cichlids in general

Taxonomy (fig. 1).— Size range of adults 5-25 cm standard length. One nostril on each side of the snout. The dorsal fin, comprising a spinous and a soft rayed part, is continuous. The lateral line is interrupted. From tilapiine cichlids, which share the foregoing characters, haplochromine cichlids are distinguished by the following features. *The scales on the flank and caudal peduncle are ctenoid (feel rough to the touch). Adult males have brightly coloured egg dummies on the anal fin*. The "tilapia mark" at the base of the dorsal fin, which characterizes the juveniles (up to 10 cm, Scully, 1975) of

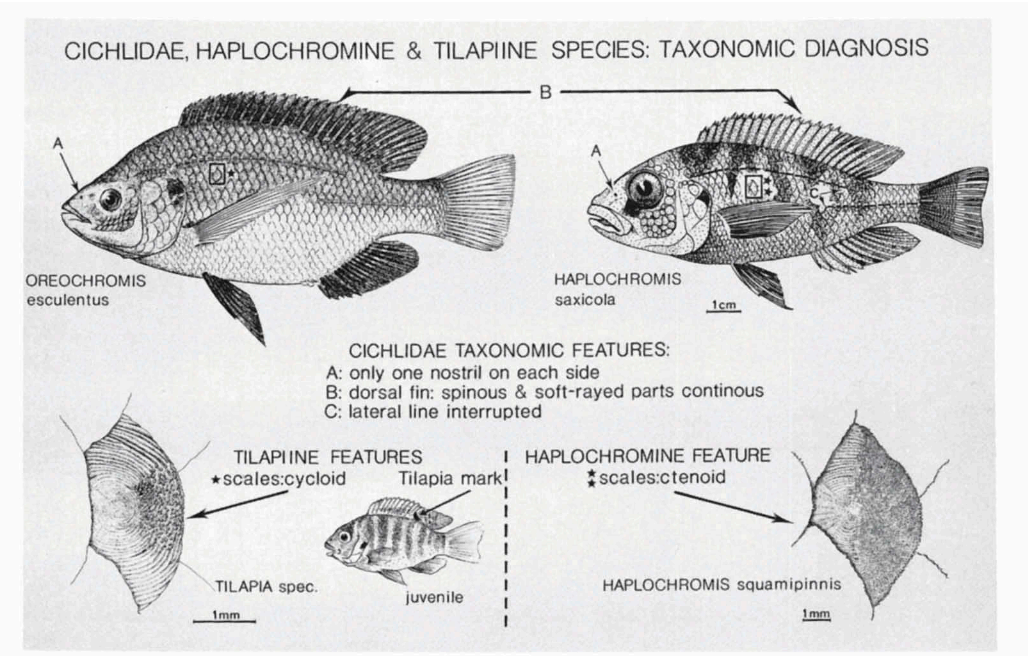

Fig. 1. External diagnosis of Cichlidae in general, and diagnostic comparison of tilapiine and haplochromine species.

the tilapiine cichlid species in Lake Victoria, is absent.

Ecology.— Originally haplochromine species occupied virtually all habitats of the lake (possibly with the exception of dense papyrus swamps). They fed on nearly all food sources in the lake; each species having a specific habitat (depth range, wind

Table 1. Trophic composition** of the haplochromine catches in the sublittoral area of the Mwanza Gulf. Figures calculated from 30 trawl-shots.

trophic groups	% occurrence of specimens per catch	mean % ± s.dev.
detritivores/phytoplanktivores	40.8-78.1	61.4 ± 10.5
zooplanktivores	11.4-53.3	30.4 ± 12.2
insectivores	0-7.8	3.1 ± 1.7
piscivores	0-2.3	0.7 ± 0.6
molluscivores	0-0.9	0.2 ± 0.3
paedophages	0-1.4	0.2 ± 0.3
prawn-eaters	0-0.9	0.1 ± 0.2
scale-eaters	*	*
parasite-eaters	*	*
unknown specimens	0-11.3	3.8 ± 2.9

* These trophic groups were rare in the catches and not present in the samples.

** Expressed as percentage of the total number of adult specimens in the samples (after Witte, 1981).

Table 2. Trophic composition of the haplochromine catches at stations A-J on a transect across the Mwanza Gulf (Witte, 1981). Figures represent the mean percentages** for the catches from February 1979 until February 1980. Mean percentages smaller than 1 are represented by " +".

	sand		mud							
Stations	A	B	C	D	E	F	G	H	I	J
Depth (in meters)	2-4	4-6	2-4	4-6	7-8	10-11	13-14	13-14	10-11	7-8
Trophic groups										
detrivores/phytoplanktivores	1	2	6*	7*	24*	65	80	84	85	75
zooplanktivores	2	8	1	3	25	31	13	10	11	22
insectivores	71	70	32*	21*	5*	1	3	4	3	1
piscivores	1	1	1	1	1	+	2	+	1	+
molluscivores	6	3	1	1	+	+	1	+	+	+
paedophages	+	+	+	-	+	+	+	+	-	+
prawn-eaters	-	-	-	-	-	+	+	+	+	-
scale-eaters	+	-	-	-	-	-	+	-	-	-
parasite-eaters	-	-	-	-	-	-	+	+	-	-
unknown specimens	20@	17@	4	3	1	2	3	2	1	2
detrivores/pytoplanktivores or insectivores			56	64	43					

* Figures based mainly on males. Females of the detrivores/phytoplanktivores and of insectivores often could not be distinguished from each other and therefore the percentages of these females are treated collectively at the bottom line of the table.

** Percentages were calculated with regard to the total number of adult specimens in a sample.

@ High percentages due to the fact that not all species of stations A & B could as yet be examined properly.

exposure etc.) and diet. The trophic group composition of the haplochromine communities differed between habitats (tables 1, 2). As far as is known, all species are female mouth-brooders. Fecundity, spawning areas, spawning periods and nursery grounds can be strikingly different among the species (see under separate trophic groups for details and references).

Fishery

Importance.— At the beginning of the 1970s haplochromines dominated the demersal fish stocks in all areas and all habitats of the lake (table 3). In the second half of the 1970s the haplochromine catches comprised 29-48% of the total fish catches in Lake Victoria (table 4). However, at present the catches are negligible.

Type of fishery.— Before the Nile perch upsurge the artisanal fishery on haplochromines was mainly carried out with gill nets (mesh size mainly 38-51 mm; cf. table 5; Scully, 1975), beach seines with a cod end mesh of 19-25 mm (Ligtvoet et al., 1988; pers. obs.) and mosquito seines with a cod end mesh of 8-13 mm (Marten, 1979). The latter were particularly used in the Kavirondo Gulf (Kenya). The trawl fishery in the Tanzanian part of the lake was performed with small bottom trawlers (10-15 m long; 80-170 hp) using nets with a 19 mm cod end mesh. The gill nets mainly retained specimens of 8 cm SL and longer (table 5). However, with the trawl nets and the beach seines specimens from 3.5 cm onwards could be caught in subtantial amounts (Witte & Goudswaard, 1985).

Table 3. Mean kilograms of haplochromine cichlids caught per hour of exploratory bottom trawling (38 mm cod end mesh) in Lake Victoria in 1969-1971. After Kudhongania & Cordone, 1974.

Depth in m	kg/hr	% of total catch
4-9	493.8	76.7
10-19	800.2	85.5
20-29	639.5	87.4
30-39	507.5	87.3
40-49	448.0	87.3
50-59	486.3	85.7
60-69	196.3	73.1
70-79	29.6	56.8

Table 4. Lake Victoria haplochromine catches (in metric tons) and percentage () contribution to the total weight of fish landed over the period 1975-1979. Compiled from data of CIFA, 1982 and 1988.

Year	Kenya	Tanzania	Uganda	Total
1975	4,626 (27.9)	16,148 (34.7)	1,690 (10.9)	22,464 (28.6)
1976	6,368 (34.1)	25,184 (49.8)	1,000 (9.0)	32,552 (40.5)
1977	6,255 (32.4)	36,158 (55.3)	1,560 (10.0)	43,973 (43.8)
1978	6,621 (27.8)	18,810 (40.4)	1,560 (10.0)	26,991 (31.4)
1979	6,599 (21.6)	21,760 (37.6)	1,550 (9.2)	29,909 (28.8)

Table 5. Particulars of haplochromine cichlid catches with commercial gill nets in all Tanzanian waters of Lake Victoria and for the Mwanza Gulf separately (). Basic data from Scully, 1975. Average fish weight in grammes calculated from average number and average weight per net. Standard length (SL) calculated as 75% of total length (TL).

Mesh size	Number per net	Weight per net in gr.	Average fish weight in gr.	Average TL in mm	Average SL in mm
38 mm	42.2 (47.2)	530 (480)	12.6 (10.2)	114.0 (109.0)	85.5 (81.8)
46 mm	20.9 (13.7)	703 (504)	33.6 (36.8)	123.7 (129.3)	92.8 (97.0)
51 mm	18.7 (12.6)	680 (365)	36.4 (28.9)	139.1 (131.4)	104.3 (98.6)

Exploitation.— Fishery on haplochromines was carried out in the littoral and sub-littoral zones of the lake, especially in the Tanzanian and Kenyan parts.

Yearly catches.— According to the official catch statistics the total yearly catches of the three riparian countries (Tanzania, Kenya and Uganda) over the period 1976-1979 varied from 22,464-43,973 metric tons (table 4).

Present status.— As a result of the Nile perch upsurge the haplochromines have almost completely vanished in the sub-littoral and deepwater regions of the Lake (Barel, et al., in press; Goudswaard & Ligtvoet, 1988; HEST, 1988; Hughes, 1986; Ogutu-Ohwayo, 1990; Okemwa, 1984; Wanink et al., 1988; Witte et al. in prep.).

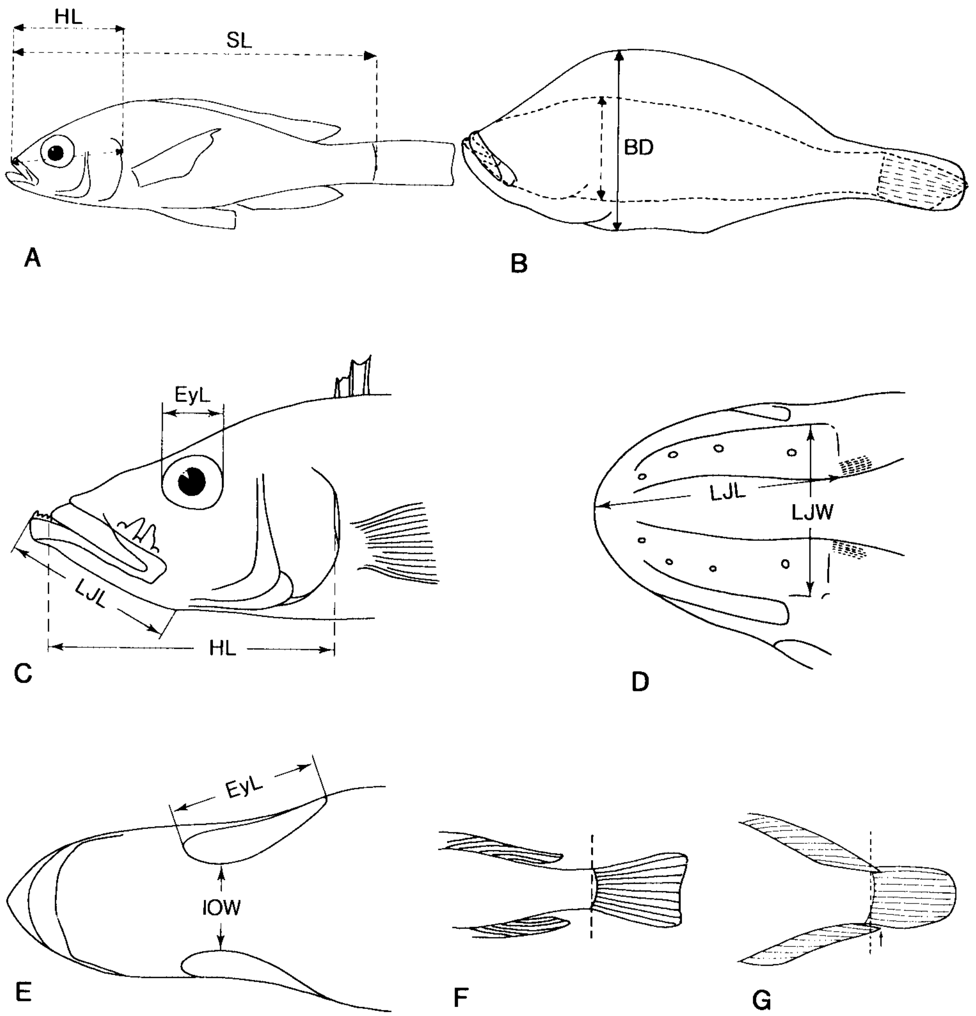

Fig. 2. External measurements used in the key to the trophic groups. For precise definitions of the measurements one is referred to Barel et al. (1977). BD= body depth; EyL= eye length; HL= head length; IOW= inter orbital width; LJL= lower jaw length; LJW= lower jaw width; SL= standard length.

However, signs of local overfishing in littoral and sub-littoral regions were already present at the end of the 1970s (Goudswaard, 1988; Goudswaard & Ligtvoet, 1988; Kukowski, 1978; Marten, 1979; Witte, 1981; Witte & Goudswaard, 1985, 1987).

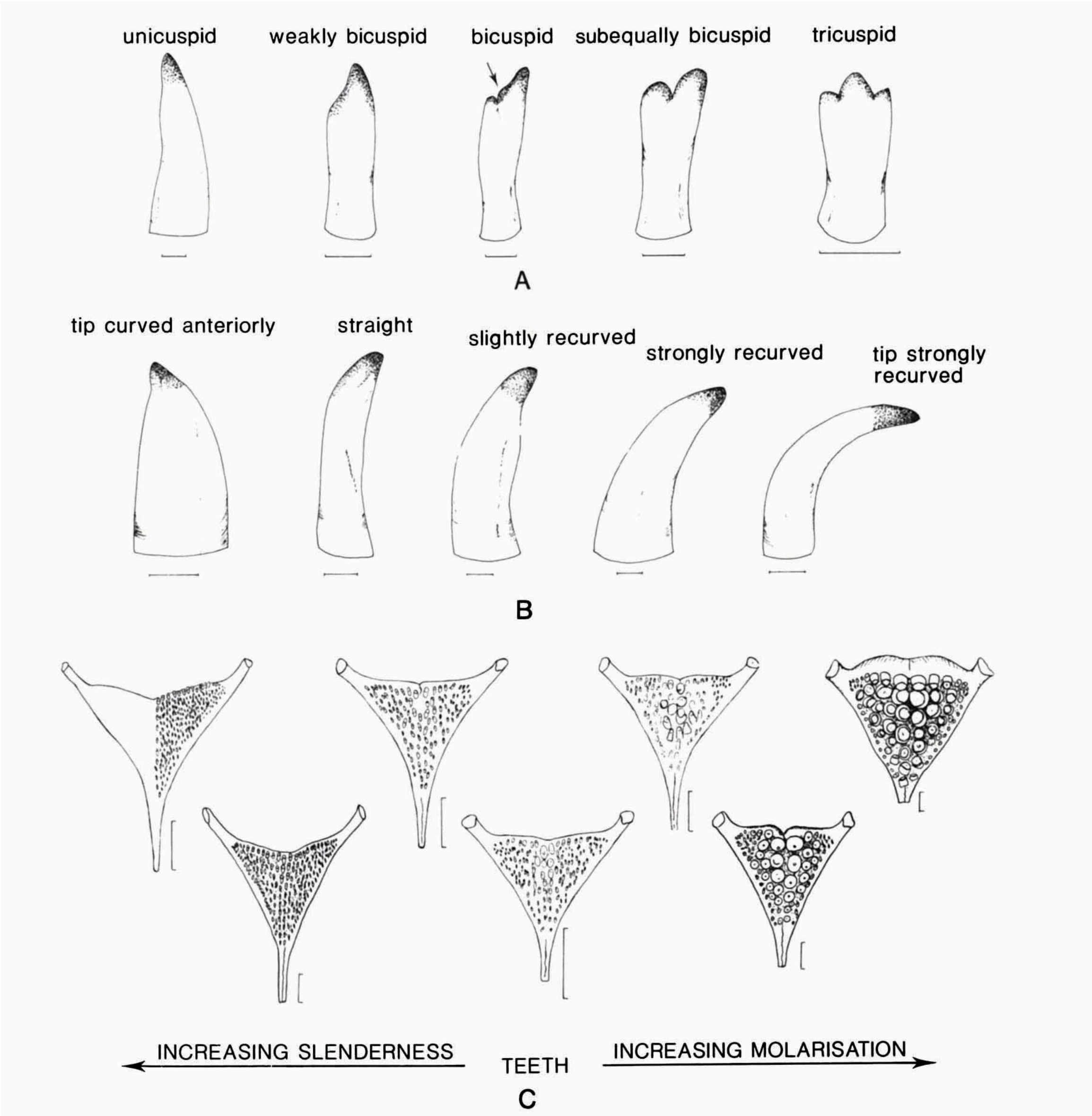

Fig. 3. Dental characters used in the key to the trophic groups. For an extensive description of the teeth see Barel et al. (1977). A. Labial view of outer teeth (scale = 0.2 mm). Arrow indicates a small flange. B. Lateral view of outer teeth (scale = 0.2 mm). C. Occlusal view of the lower pharyngeal jaw (scale = 2 mm).

Key to the trophic groups

1. Teeth in oral jaws well visible, recurved or straight, never anteriorly curved (fig. 3B) 2
- Teeth in oral jaws hardly visible, deeply embedded in tooth gum and/or anteriorly curved (fig. 14B, F); dorsal head profile often (slightly) concave; caudal part of the maxilla often (slightly) bullate (fig. 14E) .... **paedophages,** p. 35.
2. Lower jaw length (fig. 2C) more than 45% of head length; standard length (fig. 2A) generally more than 10 cm 3
- Lower jaw length less than 45% of head length; standard length generally less than 10 cm 4
3. Unicuspid and tricuspid teeth (fig.3A, 12C) in outer row of oral jaws; interorbital width smaller than eye length* (fig. 2E) .... **prawn-eaters,** p. 29

   * N. B. For this purpose eye length should not be measured as the bony orbit as defined in Barel et al. (1977) but between the ligamentous ring (fig. 2 C).
- Only acutely pointed unicuspid teeth in outer rows of the oral jaws; head length (fig. 2A) more than 36% of standard length; Interorbital width generally longer than eye length .... **piscivores s.s.,** p. 33; **crab-eater,** p. 31; **plant-eater** (*H. acidens*), p. 18
4. Body depth (fig. 2B) generally more than 38% of standard length; lower pharyngeal element hypertrophied; pharyngeal teeth molariform (fig.3C, 8D) .... **pharyngeal mollusc crushers** p. 20
- Body depth generally less than 38% of standard length; lower pharyngeal element not hypertrophied 5
5. Body depth less than 33% of standard length; caudal tip of dorsal and anal fin generally not reaching caudal fin origin (fig. 2F) 6
- Body depth more than 33% of standard length; caudal tip of dorsal and anal fin generally reaching caudal fin origin (fig. 2G) 7
6. Oral teeth closely set bicuspids with large flange (fig. 15D, E, 16B-D); three or more inner rows (fig. 15B, C, E) .... **scale-eater** (*H. welcommei*), p. 37; **parasite-eater** (*H. teunisrasi*), p. 38
- Oral teeth not closely set (fig. 10C, D); flange small (fig. 3A); one or two inner rows .... **zooplanktivores,** p. 24
7. Lower jaw length/width ratio less than 1.5 (fig. 5C) ....
- Lower jaw length/width ratio more than 1.5 (fig. 2D) 9
8. Oral teeth in outer row subequally bicuspid (fig. 3A, 5A), closely set (fig. 5E); inner teeth tricuspid, arranged in 3-7 rows (fig. 5E); scales on chest small and deeply embedded (fig. 5D) .... **epilithic algae grazers,** p. 15
- Oral teeth in outer rows recurved unicuspids (fig. 3A, 9F); inner teeth generally unicuspid, arranged in 3-9 rows (fig. 9B, D); scales on chest not deeply embedded .... **oral shellers,** p. 22
9. Oral teeth closely set and generally movably implanted; major cusp with a large flange, often obliquely truncated (fig. 6B, C, 16D); inner teeth arranged in 2-5 rows .... **epiphytic algae grazers,** p. 17 ; **parasite eater** (*H. cnester*), p 38
- Oral teeth not closely set; major cusp without or with a small flange (fig. 3A, 4B, 10C, D); inner teeth generally arranged in 1-3 rows .... **detritivores/phytoplanktivores** p. 12; **insectivores** p. 27; **phytoplanktivores** p. 14; **plant-eater** p. 18

Descriptions of the trophic groups
Detritivores/phytoplanktivores

Taxonomy

External features (fig. 4A).— Size range of adults 5-9 cm SL (reduced to 4-7 cm in the 1980s). Body shape mostly generalized; in a few species the dorsal head profile is concave above the eye.

Dentition (fig. 4B) — Outer teeth in oral jaws generally unequally bicuspid. Inner teeth in one or two, rarely in three rows.

Intestine.— Length 1.4-3.3 (mostly 1.7-2.8) times SL. Based on 51 specimens of 12 species. See Zihler (1982) for coiling types and intestinal weight length.

Species.— Thirteen or more species are known, of which three have been described (table 6).

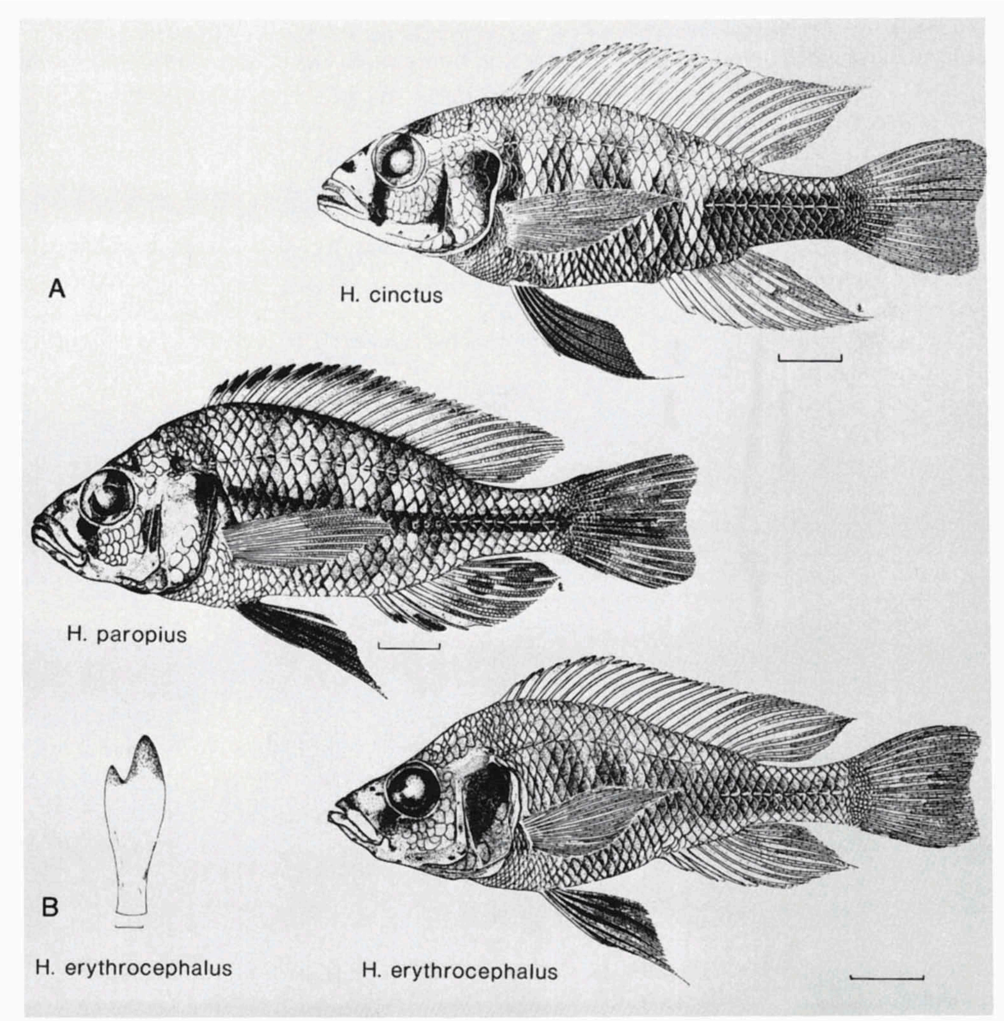

Fig. 4. Detritivorous/phytoplanktivorous haplochromines. A. Habitus (scale = 1 cm). B. Labial view of an outer tooth of *H. erythrocephalus* (scale = 0.2 mm).

Ecology

Distribution.— All areas of Lake Victoria. All Lake Victoria species are endemics.

Habitat.— Bottom dwelling species, over mud bottoms, from 2 to at least 30 m deep. Especially common in the sub-littoral and deepwater regions (tables 1,2).

Food.— Bottom debris and phytoplankton including diatoms, blue-green algae and few green algae; also insect larvae (mainly chironomids and *Chaoborus* Lichtenstein, 1800) and a little zooplankton.

Potential predators.— *Bagrus docmac* (Forskål, 1775), *Clarias gariepinus* (Burchell, 1822), *Schilbe mystus* (Linnaeus, 1762), *Protopterus aethiopicus* (Heckel, 1852), haplochromine piscivores, *Lates* in the 1980s.

Reproduction.— Egg size (mean major egg axis of five species): 2.4-3.1 mm. Fecundity (means of 4 species): 20.2-67.6 eggs. Fecundity positively correlated with standard length (Goldschmidt, 1989b; Goldschmidt & Goudswaard, 1989). Gonadosomatic index (means of two species): 4.8 and 6.1% (Goldschmidt, unpublished) Spawning period: most species are seasonal spawners; in the Mwanza area with peaks at the end of the rainy season and the beginning of the dry season; April-August (Goldschmidt, 1986; Goldschmidt in prep; Witte, 1981). Spawning areas: probably distributed over all habitats occupied by the group, although there are indications that some deepwater species move to shallower areas for breeding. Nurseries: juveniles (<4 cm SL) of at least one species (*H.* "nigrofasciatus") are known to concentrate in shallow bays (2-6 m).

Growth.— Most species used to reach a size of approximately 5-6 cm within a year (Witte, 1981, 1984). However, in the 1980s the growth rate in the first year retarded with 1-2 cm (Witte & Goudswaard, 1985, 1987).

Endoparasites in *H.* "nigrofasciatus" and *H.* "75".— *Eustrongylides* Jaegerskiold, 1909 (Nematoda); *Contracaecum* Raillet & Henry, 1912 (Nematoda), mean infection rate <<10%; dilepedid larvae (Cestoda), mean infection rate <10%; proteocephalid cestodes (Mbahinzireki, 1984).

Ectoparasites in *H.* "nigrofasciatus" and *H.* "75".— *Ergasilus lamellifer* Fryer, 1961 (Copepoda); *Lamproglena monodi* Capart, 1944 (Copepoda); *Lernaea cyprinacea* Linnaeus, 1761 (Copepoda), mean infection rate <<10% (Mbahinzireki, 1984).

Ecological importance.— Before the upsurge of the Nile perch one of the main groups converting organic debris and primary producers into fish (over 40% of demersal ichthyomass in the sub-littoral region, see below).

References.— Goldschmidt, 1986, 1989b; Goldschmidt & Goudswaard, 1989; Greenwood, 1974; Greenwood & Gee, 1969; van Oijen, et al. 1981; Witte, 1981, 1984; Witte & Goudswaard, 1985, 1987.

Fishery

Importance.— In the 1970s the most common trophic group among the haplochromines; mean percentage of total number of haplochromines >60% in the sublittoral regions over mud bottoms (tables 1, 2; Witte, 1981: Witte & Goudswaard, 1985); estimated percentage of total haplochromine biomass in these regions >50%. With haplochromines comprising approximately 80% of the demersal ichthyomass in Lake Victoria in the 1970s (table 3; Kudhongania & Cordone, 1974) this means that over 40% of the demersal fish biomass in the sub-littoral zone consisted of detritivorous haplochromines.

In the 1970s not a commonly preferred food fish, but accepted by certain social groups and preferred locally (e.g., Ukerewe Island), fresh, smoked and dried. Has been important for fishmeal production.

Type of fishery.— In the Mwanza Gulf and Speke Gulf mainly caught by bottom trawling (cod end mesh 19 mm). Larger specimens could be caught with gill nets (38 mm mesh; cf. table 5). In other areas of the lake probably some were caught with gill nets (38 mm mesh) and beach seines (8-25 mm mesh).

Mesh selectivity.— 50% retention length for a 25 mm cod end mesh is 6.0-6.5 cm SL (Witte & Goudswaard, unpublished).

Exploitation.— Especially in the 1970s in the Mwanza Gulf and the Speke Gulf and probably in other areas (no data on trophic group composition of artisanal catches available).

Present status.— Almost completely vanished as a result of the Nile perch upsurge but locally signs of overfishing were already apparent at the beginning of the 1980s (Witte & Goudswaard, 1985, 1987).

Phytoplanktivores

Taxonomy

External features.— Size range of adults 6-8 cm SL. Two species rather slender (BD< 33% of SL). No further special features.

Dentition.— Outer teeth in oral jaws bicuspid. Inner teeth in 1-3 rows.

Intestine.—Length 1.5-2.7 times SL. Based on seven specimens of two species.

Species.— Three as yet undescribed species are known.

Ecology

Distribution.— Thus far only known from the southern part of the lake (probably due to sampling bias). The three species are endemic to Lake Victoria.

Habitat.— Mainly pelagic species in waters with a depth range of at least 4-20 m (maximum depth not exactly known, because pelagic sampling was not carried out in water deeper than 20 m).

Food.— Phytoplankton, including blue-green algae (*Anabaena* Bory de St Vincent ex Bornet Flahult, 1866 and *Microcystis* Lemmerman, 1907), diatoms and green algae (Goldschmidt, 1986; Witte & Witte-Maas, unpublished).

Potential predators.— Probably mainly pelagic piscivores (e.g., haplochromines and *Schilbe mystus*) and birds, *Lates* in the 1980s.

Reproduction.— Data only known for one species (*H.* "kribensis"). Egg size (mean major egg axis): 3.5 mm. Mean fecundity: 22.2. Egg size as well as fecundity positively correlated with standard length (Goldschmidt, 1986; Goldschmidt & Goudswaard, 1989). Spawning period: throughout the year. Spawning areas: probably littoral regions. Nurseries: littoral regions in the southern half of the Mwanza Gulf (Goldschmidt, 1986).

Growth.— Unknown.

Parasites.— Unknown.

Ecological importance.— Converting primary production of the surface stratum (possibly including blue -green algae that are difficult to digest) into fish.

References.— Goldschmidt, 1986; Goldschmidt & Goudswaard, 1989; Witte, 1984, 1987.

Fishery

Importance.— Bycatch in dagaa (*Rastrineobola argentea* (Pellegrin, 1904)) light fishery, otherwise not important.

Present status.— Probably strongly diminished as a result of the Nile perch upsurge.

Algae grazers

All species feeding on sessile algae are collectively named algae grazers. A subdivision is made, based on the substratum from which the algae are collected. Epilithic algae grazers feed on algae growing on rocks, epiphytic algae grazers feed on algae growing on submerged vegetation.

A. Epilithic algae grazers

Taxonomy

External features (fig. 5B-D).— Size range of adults 5-12 cm SL. Lower jaw short and broad: length width/ratio 1.0-2.0 but mostly smaller than 1.5. No mandibular mental prominence (cf. fig. 12A,B), symphysis rounded. Retroarticular processes of lower jaw not interrupting ventral body outline and not touching each other (cf. fig. 10A,B). Scales on chest smaller and deeper embedded than those on ventral and ventro-lateral parts of the body, the size change is rather abrupt.

Dentition (fig. 5A,E).— *Oral teeth subequally bicuspid, closely set. Tricuspid inner teeth in 3-7 rows.* The space between outer row and inner tooth series is reduced and the inner row teeth are generally not much shorter than the outer teeth, thus providing a continuous scraping surface.

Intestine.— Length 3.0-4.5 times SL. Based on six specimens of two species. See Zihler (1982) for coiling types and intestinal weigth length.

Species.— At least three species are known. One species, *H. nigricans* (Boulenger, 1906), is described (table 6).

Ecology

Distribution.— Probably all areas of Lake Victoria with a rock habitat. All Lake Victoria species are endemics.

Habitat.— Occurring over rocks.

Food.— Epilithic algae, diatoms and some insects.

Potential predators.— Probably mainly birds (cormorants and gulls), otters, *Bagrus docmac* and to lesser extent haplochromine piscivores.

Reproduction.— Egg size (mean major egg axis) of *H. nigricans* and *H.* 'velvet black' are respectively 3.5 and 3.2 mm. Mean fecundity: 25 and 27 eggs(Goldschmidt & Goudswaard, 1989). Spawning period: probably spawning continuously throughout the year. Spawning areas and nurseries: along the rocks (Witte-Maas & Witte, unpublished).

Growth.— Unknown.

Parasites.— Unknown.

Ecological importance.— The major consumers of sessile algae on rocks. Probably an important food source for birds and otters which frequent the rocky habitat.

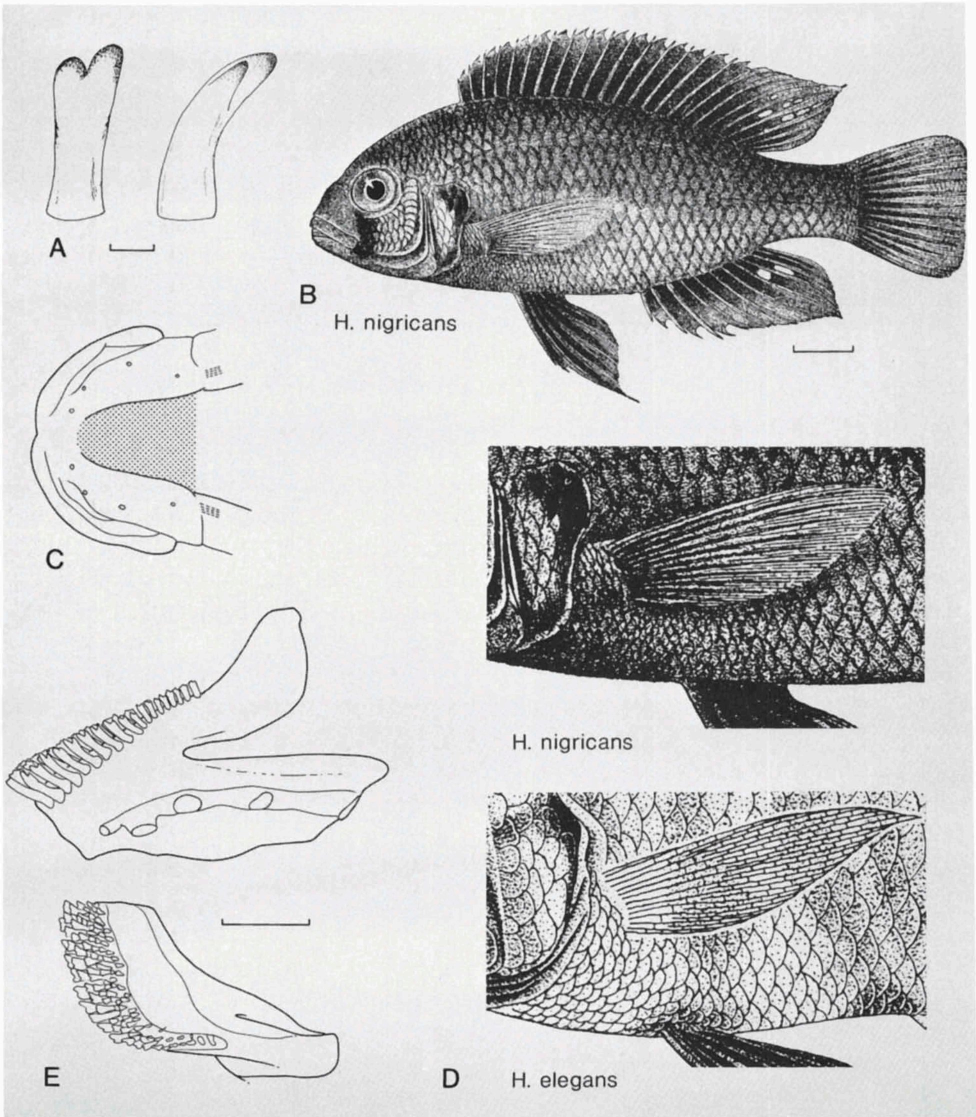

Fig. 5. Epilithic algae grazers. A. Labial and lateral view of an outer tooth of *H. nigricans* (scale = 0.2 mm). B. Habitus of *H. nigricans* (scale = 1 cm). C. Ventral view of lower jaw of *H. nigricans*. D. Scales on the chest of *H. elegans* (a generalized haplochromine cichlid of Lake George, Uganda) and *H. nigricans*. Note the difference in size of the scales. E. Lateral and occlusal view on the left dentary of *H. nigricans* (scale = 0.2 mm).

References.— Goldschmidt & Goudswaard, 1989; Greenwood, 1956a, 1974; van Oijen et al., 1981; Witte, 1984.

Fishery

Importance.— Not important in economic sense, but provides an easily obtainable protein source for people living near the lake. Used as bait fish in long line fishery. Could be valuable for aquarium fish trade.

Type of fishery.— Angling.

Present status.— Still common in 1990 and probably not much affected by the Nile perch (Bouton, pers. comm.; Witte, et al., in prep).

B. Epiphytic algae grazers

Taxonomy

External features (fig. 6A).— Size range of adults 6-9 cm SL. Body form generalized.

Dentition (fig. 6 B,C).— *Outer teeth closely set and movably implanted bicuspids,*

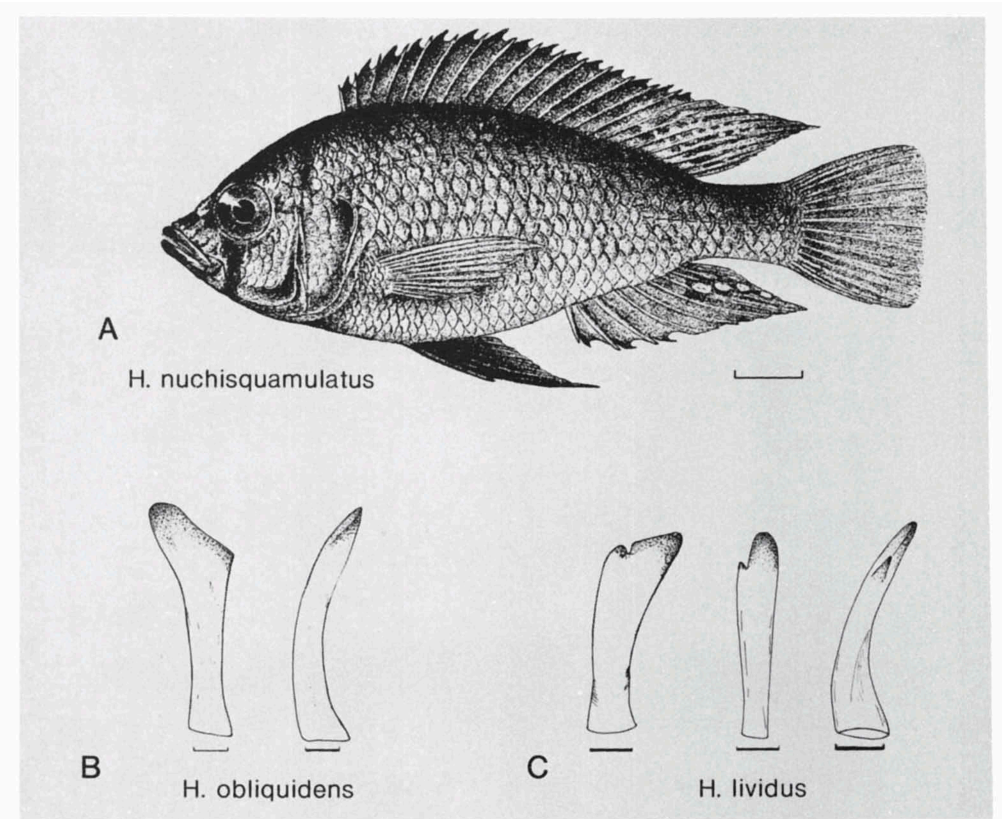

Fig.6. Epiphytic algae scrapers. A. Habitus of *H. nuchisquamulatus* (scale = 1 cm). B. Labial and lateral view of outer tooth of *H. obliquidens* (scale = 0.2 mm). C. Labial and lateral view of teeth of *H. lividus* (scale = 0.2 mm). The labial view is presented of teeth with an expanded and an unexpanded crown.

major cusp with a large flange, often obliquely truncated. In *H. obliquidens* Hilgendorf, 1888 the teeth are unicuspid and obliquely truncated. Generally 2-5 inner rows.

Intestine.— Length Unknown. See Zihler (1982) for coiling types and intestinal weigth length.

Species.— At least seven species are known, of which three have been described (table 6). The habitat of this group has not been sampled intensively by HEST, so more species might be present.

Ecology

Distribution.— All areas of Lake Victoria. Most of the species encountered in Lake Victoria are endemics. Exceptions are *H. obliquidens* and *H. nuchisquamulatus* (Hilgendorf, 1888) which were also collected in the Victoria Nile (Greenwood, 1956a).

Habitat.— Occurring in shallow littoral regions in the vicinity of emergent vegetation.

Food.— Mainly diatoms and some insects. Blue-green algae and green algae were also frequently encountered, but it is not known whether these are digested. Food is probably scraped from plant parts but also taken from the bottom (Greenwood, 1956a; Katunzi, 1980; Witte & Witte-Maas, unpublished). Large quantities of detritus were recorded for *H. obliquidens* (Katunzi, 1980).

Potential predators.— Piscivorous haplochromines, otters and birds. It is not known whether non-haplochromine piscivores frequent the particular habitat of the epiphytic algae scrapers.

Reproduction.— Spawning period: One species (*H. obliquidens*) probably breeds continuously (Katunzi, 1980). No information for the other species is available.

Growth.— Unknown.

Parasites.— Unknown.

Ecological importance.— Unknown.

References.— Greenwood, 1956a, 1974; Katunzi, 1980; Zihler, 1982.

Fishery

Importance.— Unknown.

Type of Fishery.— Possibly some gill netting (38 mm mesh; cf. table 5).

Present status.— Not precisely known, but like those of the rocky habitat, the fishes in the shallow littoral habitat with emergent vegetation are probably less affected by the Nile perch than the fishes in most other habitats.

Plant-eaters

Taxonomy

External features (fig. 7).— Size range of adults 7-13 cm SL. Of the two species in this group, *H. phytophagus* Greenwood, 1965 has a generalized appearance, while *H. acidens* Greenwood, 1967 has the features of a piscivore (lower jaw > 45% of HL).

Dentition.— *H. phytophagus* has bicuspid teeth with a relatively large flange on the outer rows in the oral jaws, *H. acidens* has long and slender unicuspids.

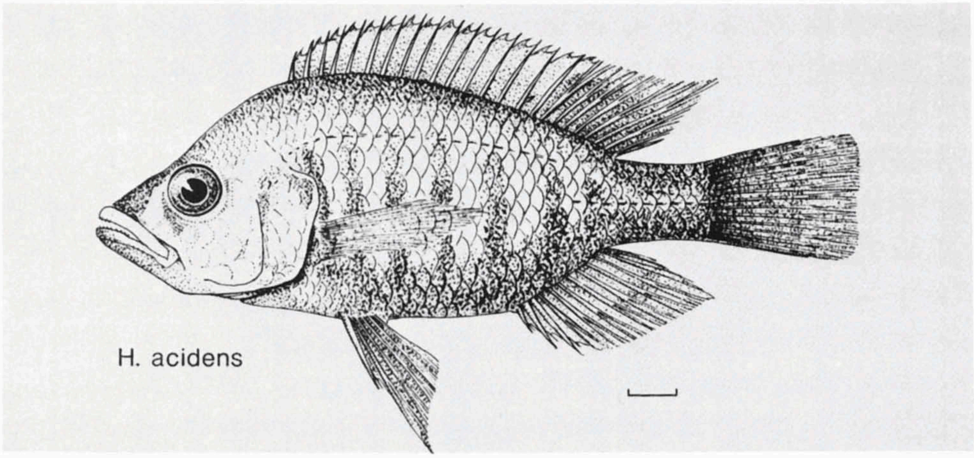

Fig. 7. Plant-eaters. Habitus of *H. acidens* (scale = 1 cm).

Intestines.— Length in *H. acidens* 1.5-2.0 times SL (Greenwood,1967).

Species.— Only two species known, both are described (table 6).

Ecology

Distribution.— Thus far only known from the northern part of Lake Victoria (Uganda and Kenya).

Habitat.— Shallow littoral regions with rooted aquatic plants.

Food.— Phanerogam tissue, together with epiphytic diatoms and algae. In *H. acidens* also insect remains and in one specimen some fish remains were found.

Potential predators.— Piscivorous haplochromines (especially on juveniles), otters and birds. It is not known whether non-haplochromine piscivores frequent the particular habitat of the plant-eaters.

Reproduction.— Unknown.

Growth.— Unknown.

Parasites.— Unknown.

Ecological importance.— Together with the introduced *Tilapia zillii* Gervais, 1848, the only fishes in Lake Victoria known to feed on macrophyta.

References.— Greenwood, 1965a, 1967, 1974.

Fishery

Importance.— Unimportant.

Type of fishery.— Possibly some gill netting (38-51 mm mesh; cf. table 5).

Present status.— Not precisely known, but like those of the rocky habitat, the fishes in the shallow littoral habitat with emergent vegetation are probably less affected by the Nile perch than the fishes in most other habitats.

Molluscivores

Molluscivores is a collective name for all species which feed on molluscs, both bivalves and gastropods. Based on feeding behaviour a subdivision is made: pharyngeal crushers crush the shell of their prey with their hypertrophied pharyngeal jaws; oral shellers/crushers wrench the flesh from the shell or crush the shell with their oral jaws.

A. Pharyngeal crushers

Taxonomy

External features (fig. 8A,B).— Size range of adults 6-18 cm SL (most species 9-13 cm). Deep bodied species (BD 34-46% of SL, mean >38%). In dorsal view, head tapering relatively strongly. One species, *Astatoreochromis alluaudi* Pellegrin, 1904, is easily identifiable, by its anal fin with four or more spinous rays, and its large number of anal spots (6-20) arranged in three or four horizontal rows.

Dentition (fig. 8C,D).— Outer teeth in oral jaws often relatively stout and unicuspid (blunt) but species with smaller bicuspid teeth are also known. Inner teeth in 1-3 rows. *Pharyngeal teeth molariform, pharyngeal jaws enlarged.* The degree of hypertrophy of pharyngeal teeth and jaws depends on the hardness of the shell of the snails which are eaten (Greenwood, 1965b; Hoogerhoud, 1986b, 1989; Witte et al., 1990)

Intestine.— Length 1.0-1.7 (mostly 1.3-1.4) times SL. Based on ten specimens of three species. See Zihler (1982) for coiling types and intestinal weigth length.

Species.— At least nine species are known, of which six have been described (table 6).

Ecology

Distribution.— All areas of Lake Victoria. With the exception of *A. alluaudi* all Lake Victoria species are endemics.

Habitat.— Bottom dwelling species, living at depths of 1-28 m over all substrate types.

Food.— The gastropod *Melanoides tuberculata* Muller, 1774 generally dominates the gut contents. *Bellamya unicolor* Olivier, 1804, the bivalve *Sphaerium stuhlmanni* Von Martens, 1897 and other molluscs may also be present; insect larvae (mainly chironomids?) are also frequently found.

Potential predators.— *Bagrus docmac* and *Clarias gariepinus*, *Protopterus aethiopicus*, haplochromine piscivores and *Schilbe mystus* (both probably too small to eat adults), birds and otters (in shallow waters), *Lates* in the 1980s.

Reproduction.— Egg size (mean major egg axis) of *A. alluaudi* and *H. teegelaari* Greenwood & Barel, 1978 2.9 and 3.2 mm respectively. Mean fecundity 169.6 and 86.7 eggs respectively (Goldschmidt & Goudswaard, 1989). Spawning period: In a number of species possibly throughout the year (Witte, 1981). Spawning areas: Probably in all habitats occupied by representatives of the group.

Growth.— Unknown.

Endoparasites in *H. ptistes* Greenwood & Barel, 1978 and *H. teegelaari*.— *Eustrongylides* larvae (Nematoda); *Contracaecum* larvae (Nematoda), infection rate <10%;

Allocreadium mazoenzis Beverley-Burton, 1962 (Trematoda) found exclusively on *H. teegelaari*, infection rate <<10% (Mbahinzireki, 1984, 1987).

Ectoparasites in *H. ptistes* and *H. teegelaari*.— *Ergasilus lamellifer* (Copepoda); *Lamproglena monodi* (Copepoda); *Lernea cyprinacea* (Copepoda), infection rate <<10%;

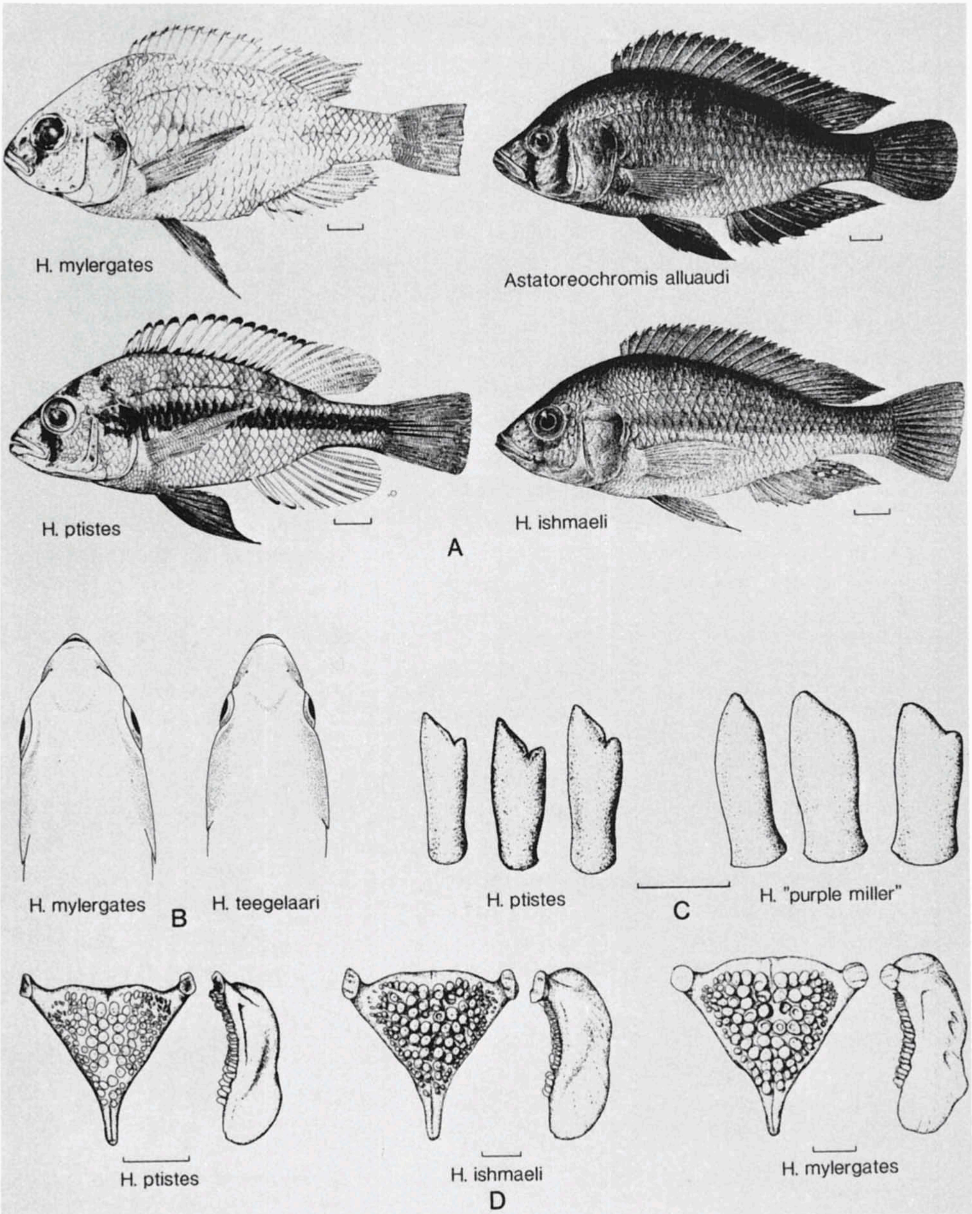

Fig. 8. Pharyngeal mollusc crushers. A. Habitus (scale = 1 cm). B. Dorsal view of the heads of *H. mylergates* and *H. teegelaari*. Note the strongly tapering head. C. Labial view of the outer teeth of *H. ptistes* and *H.* "purple miller" (scale = 0.5 mm). D. Occlusal and lateral view of lower pharyngeal jaws of *H. ptistes*, *H. ishmaeli* and *H. mylergates* (scale = 5 mm).

Dolops ranarum (Stuhlman, 1891) (Branchiura) one specimen found on a *H. teegelaari* (Mbahinzireki, 1984).

Ecological importance.— Before the upsurge of the Nile perch probably the main predators on *Melanoides tuberculata*, the most abundant gastropod in the lake. It is not known whether some of the littoral species play(ed) a role in controlling the abundance of schistosomiasis-transmitting molluscs.

References.— EAFRO, 1952, 1954; Greenwood, 1959a, 1960, 1965b, 1974; Goldschmidt & Goudswaard, 1989; Greenwood & Barel, 1978; Hoogerhoud, 1986a, 1986b, 1986c, 1987, 1989; Hoogerhoud & Witte, 1981; van Oijen et al., 1981; Mbahinzireki, 1984, 1987; Slootweg, 1986, 1987; Witte, 1981, 1984; Witte, et al. 1990; Zihler, 1982.

Fishery

Importance.— In the 1970s forming no more than 1% of the total number of haplochromines in the trawl catches (tables 1, 2). The percentage in gill net catches was probably somewhat higher due to the relatively large size of these fishes. Preferred to most other haplochromines because of their size.

Type of fishery.— Bottom trawling in the Mwanza Gulf and the Speke Gulf (cod end mesh 19 mm), gill netting (38-51 mm mesh; cf. table 5) and beach seining (8-25 mm mesh) in probably all areas of the lake.

Exploitation.— Especially in the 1970s in the Mwanza Gulf and the Speke Gulf, and probably in many other areas of the lake.

Present status.— With the exception of some species of the shallow littoral region this group has almost completely vanished as a result of the Nile perch upsurge. However, locally these relatively large haplochromines already showed signs of overfishing at the beginning of the 1980s (Goudswaard, 1988).

B. Oral shellers/crushers

Taxonomy

External features (fig. 9A).— Size range of adults 6-15 cm SL (most species 7-12 cm). Dorsal head profile often curved. *Lower jaw short and broad: length/width ratio generally 1.0 to 1.5.* No mandibular mental prominence; symphysis rounded. Retroarticular processes of lower jaw not interrupting ventral body outline and not touching each other (cf. fig. 10A,B).

Dentition (fig. 9B-F).— *Oral teeth generally stout, unicuspid, acutely pointed and (strongly) recurved.* Inner teeth mostly unicuspid in 3-9 rows. The outer teeth of *Macropleurodus bicolor* (Boulenger, 1906) are stout, obliquely truncated and have inwardly directed crowns.

Intestine.— Length 1.1-2.0 times SL. Based on 16 specimens of three species. See Zihler (1982) for coiling types and intestinal weigth length.

Species.— At least 12 species are known, of which eight have been described (table 6).

Ecology

Distribution.— All areas of Lake Victoria. All Lake Victoria species are endemics.

Habitat.— Bottom dwelling species. Mainly occurring over sand bottoms, from 1 to at least 32 m. More common in (sub-)littoral habitats less than 10 m deep.

Food.— Gastropods (mainly *Bellamya unicolor*?), bivalves and insect larvae.

Potential predators.— *Bagrus docmac* and *Clarias gariepinus* (when these predators occur in the sandy littoral habitat), *Schilbe mystus* and haplochromine piscivores (both probably too small to eat most adults), otters and birds (which are common in

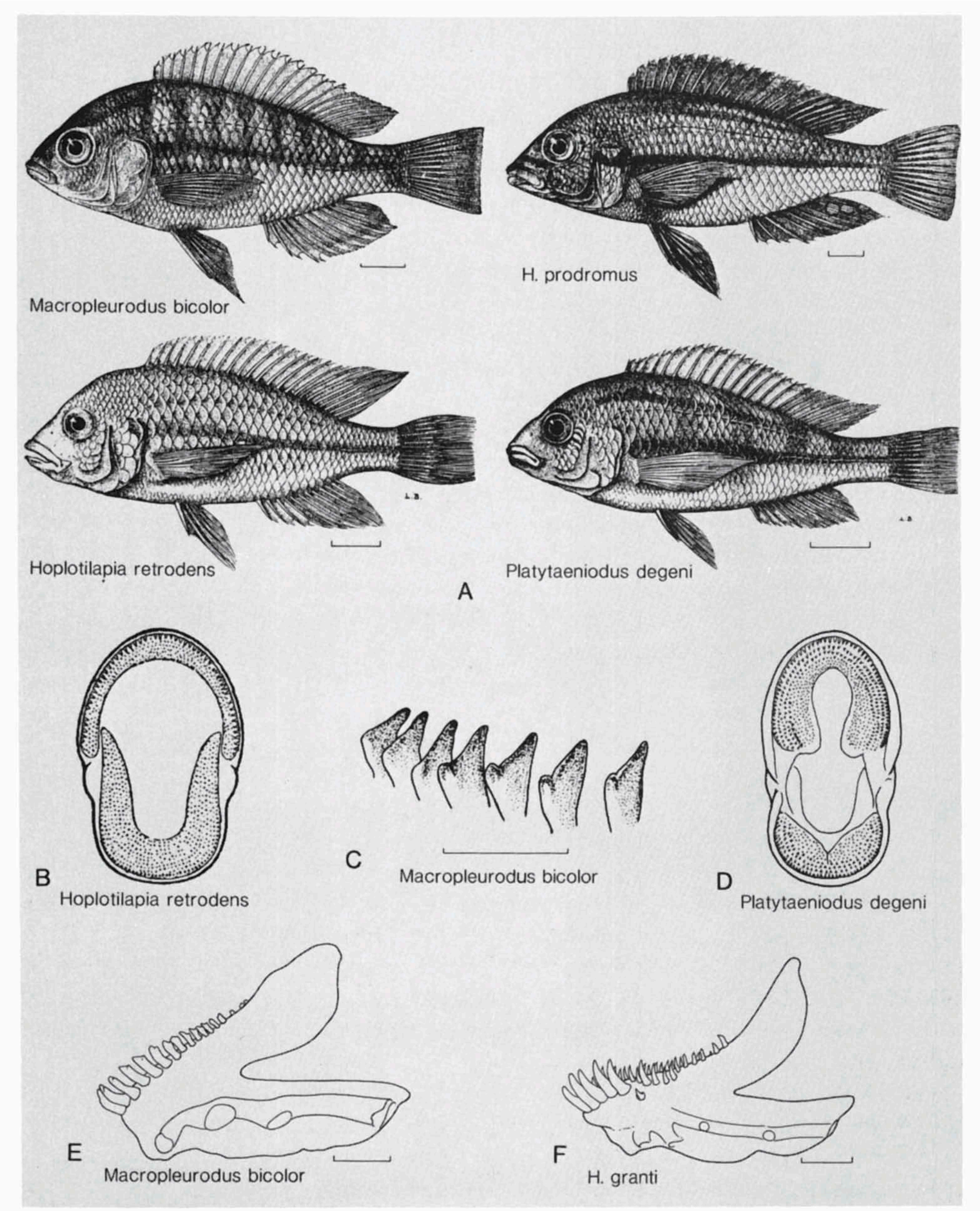

Fig. 9. Oral shelling/crushing molluscivores. A. Habitus (scale= 1 cm). B. Tooth-band of *Hoplotilapia retrodens*. C. Labial view of outer teeth of *Macropleurodus bicolor* (scale= 1 mm). D. Tooth-band of *Platyaeniodus degeni*. E,F. Lateral view of left dentary of *Macropleurodus bicolor* and *H. granti* (scale= 2 mm).

these habitats), *Lates* in the 1980s.

Reproduction.— Spawning period: probably continuous in many species.

Growth.— Unknown.

Parasites.— Unknown.

Ecological importance.— Before the upsurge of the the Nile perch probably the main mollusc consuming group in the shallow sandy habitats. It is not known whether some of these species play(ed) a role in controlling the abundance of schistosomiasis-transmitting molluscs.

References.— EAFRO, 1952, 1954; Greenwood, 1956b, 1957, 1959a, 1974; Katunzi, 1980, 1983; Slootweg, 1986, 1987; van Oijen et al., 1981; Witte, 1981, 1984; Zihler, 1982.

Fishery

Importance.— Over sand bottoms near Nafubo Island (Speke Gulf) and near Bukoba generally more than 5% of the total number of haplochromines in the trawl catch in the 1970s (in the former area even up to 25%, Witte & Goudswaaard, 1985, 1987). Because of their relatively large size, the percentage of the total weight was considerably higher. Rare in trawl shots over mud bottoms (<<1%; tables 1,2). Also relatively important in beach seine catches (which are preferrably made over sand bottoms) and probably in gill net catches. Preferred to most other haplochromines because of their larger size.

Type of fishery.— Bottom trawling especially in the Speke Gulf near Nafubo Island (cod end mesh 19 mm), gill netting (38-51 mm mesh; cf. table 5) and beach seining (8-25 mm mesh) probably in all areas of the lake.

Exploitation.— Especially in the 1970s in the Speke Gulf, and probably in many other areas of the lake.

Present status.— In many areas (e.g., Speke Gulf and Bukoba) strongly diminished as a result of the Nile perch upsurge but in the Mwanza area also due to the trawl fishery (Goudswaard, 1988). However, in very shallow sandy regions several species were still present in 1989 (Witte et al., in prep).

Zooplanktivores

Taxonomy

External features (fig. 10A,B).— Size range of adults 5-9 cm SL (reduced to 4-7 cm in the 1980s). *Generally slender bodied fishes (BD 27-35% of SL, mostly smaller than 33%).* Lower jaw slightly to rather oblique and slightly elongate (36-45%, generally over 40% of HL). Retroarticular processes of lower jaw generally interrupting ventral body outline. In non-expanded specimens the retroarticular processes of left and right articular lie closely to or against each other.

Dentition (fig. 10C,D).— Outer teeth in oral jaws generally unequally bicuspid, in a few species unicuspid. Inner teeth in one or two, rarely in three rows.

Intestine.— Length 0,9-2.1 (mostly1.1-1.7) times SL. Based on 52 specimens of 11 species. See Zihler (1982) for coiling types and intestinal weight length.

Species.— At least 21 species are known, of which eight have been described (table 6).

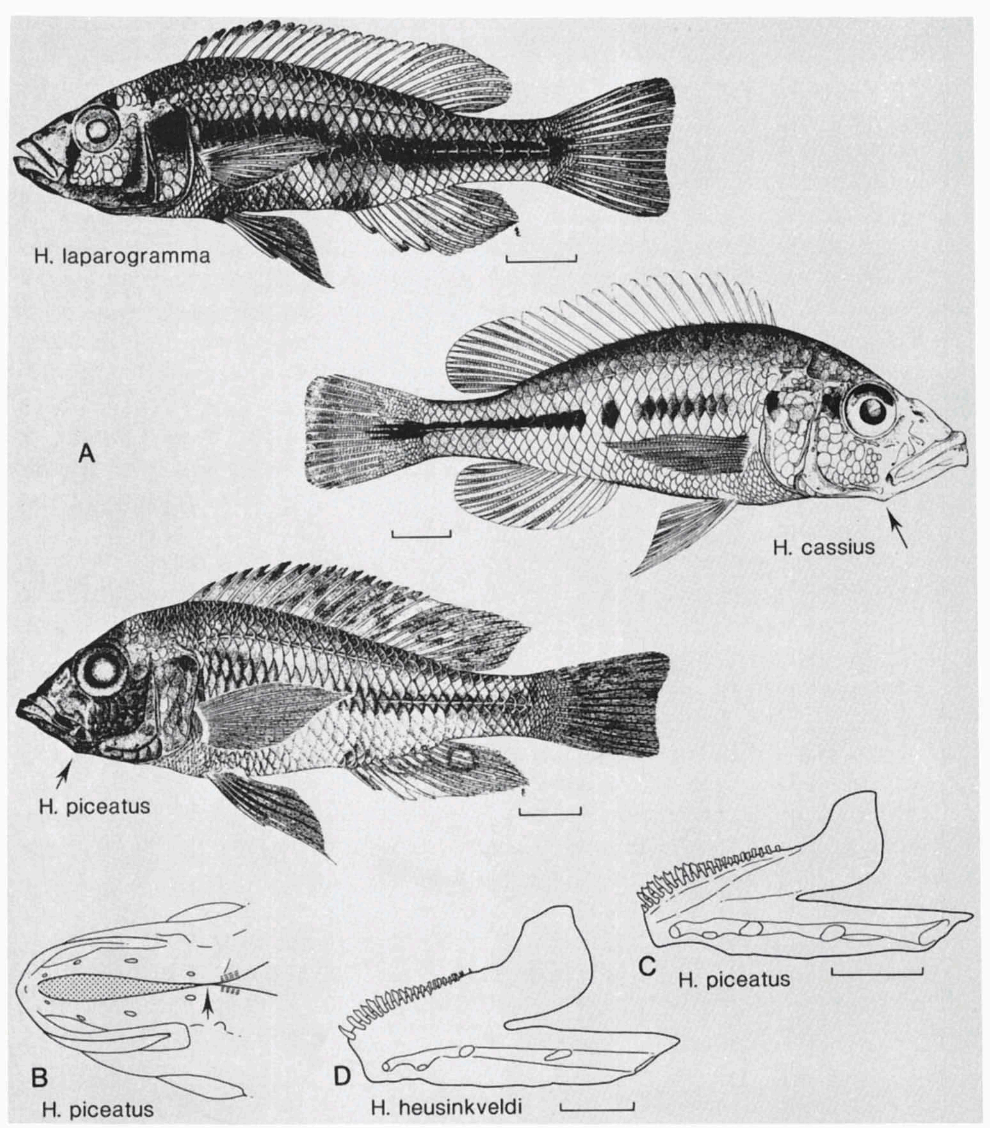

Fig. 10. Zooplanktivores. A. Habitus (scale = 1 cm). Arrows indicate retroarticular processes, interrupting the ventral body outline. B. Ventral view of lower jaw of *H. piceatus*. Arrow indicates retroarticular processes, touching each other. C,D. Lateral view of left dentary of *H. piceatus* and *H. heusinkveldi* (scale = 2 mm).

Ecology

Distribution.— All areas of Lake Victoria. All Lake Victoria species are endemics.

Habitat.— Occurring in littoral, sub-littoral and deepwater regions (up to at least 35 m depth); especially common in sub-littoral regions (table 2). Most species occur in the water column in areas with a mud bottom, one species (*H.* "double stripe") confined to sand and rocks, one species (*H. nyererei* Witte-Maas & Witte, 1985) confined to rocks. Most species are partly pelagic and migrate upward during the night.

Food.— In many species zooplankton (cycloid copepods, calanoid copepods and cladocerans) is the predominant prey category during the day, while *Chaoborus* larvae and pupae are the main food items during the night. To a lesser extent phytoplankton and chironomid larvae and pupae are included in the diet.

Potential predators.— *Bagrus docmac, Clarias gariepinus, Schilbe mystus*, haplochromine piscivores, birds, *Lates* in the 1980s.

Reproduction.— Egg size (mean major egg axis of six species): 3.1-3.6 mm. Fecundity (means of six species): 13.4-32.5 eggs. Fecundity and in a few cases egg size positively correlated with standard length (Goldschmidt & Goudswaard, 1989; Goldschmidt & Witte, 1990). Gonado-somatic index (means of 6 species) 3.9-5.7% (Goldschmidt & Witte, 1990). Spawning period: varies per species from distinctly seasonal to continuous, however most species show seasonality. In the Mwanza area spawning peaks occur mainly in the course of the dry season (May-October). Spawning areas: Several species have areas where sexually active males concentrate during the spawning period. The areas differ per species. The deepwater species *H. laparogramma* Greenwood & Gee, 1969 (living in water up to 35 m depth) migrates into shallower areas (e.g., Mwanza Gulf) for spawning (Goldschmidt & Witte, 1990). Nurseries: are known for several species, mainly in shallow bays.

Growth.— *H. piceatus* Greenwood & Gee, 1969 of the Mwanza area used to reach a size of approximately 5-6 cm within a year. However, in the 1980s growth rate in the first year of most species retarded with 1-2 cm (Witte & Witte-Maas, 1987).

Endoparasites in *H. heusinkveldi* Witte & Witte-Maas, 1987 and *H. pyrrhocephalus* Witte & Witte-Maas, 1987.— *Eustrongylides* larvae (Nematoda), mean infection rate <10%; *Contracaecum* (Nematoda); dilepedid larvae (Cestoda); proteocephalid cestodes, mean infection rate <<10% (Mbahinzireki, 1984).

Ectoparasites in *H. heusinkveldi* and *H. pyrrhocephalus*.— *Ergasilus lamellifer* (Copepoda); *Lamproglena monodi* (Copepoda); *Argulus africanus* Thiele, 1900 (Branchiura), mean infection rate <<10% (Mbahinzireki, 1984).

Ecological importance.— In the 1970s the most important predators on *Chaoborus* larvae and pupae when these emerged to the surface during the night.

References.— Galis, 1990; Galis & de Jong, 1986, 1988; Goldschmidt, 1986,1989a; Goldschmidt & Goudswaard, 1989; Goldschmidt & Witte 1990; Goldschmidt et al., 1990; Greenwood & Gee, 1969; Mbahinzireki, 1984; van Oijen et al. 1981; Witte, 1981, 1984, 1987; Witte et al., 1990; Witte & Witte-Maas, 1987; Witte-Maas & Witte, 1985.

Fishery

Importance.— In the 1970s the second most common trophic group among the haplochromines: mean percentage of total number of haplochromines in the sub-littoral regions generally >20% (tables 1, 2; Witte, 1981; Witte & Goudswaard, 1985, 1987); estimated percentage of total haplochromine biomass in these regions >20%. With haplochromines comprising approximately 80% of the total demersal ichthyomass in Lake Victoria in the 1970s (table 3; Kudhongania & Cordone, 1974) this means that over 16% of the demersal fish in the sub-littoral regions consisted of zooplanktivorous haplochromines. As the zooplanktivores are partly pelagic, this was still an underestimation of their actual biomass. In surface trawls (cod end mesh 5 mm) during the night the biomass of zooplanktivorous haplochromines was approximately three times as high as the biomass of *Rastrineobola argentea* (at night both taxa concentrate near the surface).

In the 1970s not a commonly preferred food fish, but accepted by certain social groups and preferred locally (e.g., Ukerewe Island) fresh, smoked and dried. Has been important for fishmeal production.

Type of fishery: Mainly bottom trawling in the Mwanza Gulf and Speke Gulf (cod end mesh 19 mm). The species are too slender to be caught substantially with gill nets with a mesh size of more than 25 mm. Bycatch in dagaa (*Rastrineobola argentea*) light fishery.

Mesh selectivity.— 50% retention length for a 25 mm cod end mesh is 7.0-7.5 cm SL (Witte & Goudswaard, unpublished).

Exploitation.— Especially in the 1970s in the Mwanza Gulf and the Speke Gulf.

Present status.— With exception of the rock frequenting *H. nyererei*, strongly diminished as a result of the Nile perch upsurge. As predicted by Witte & Goudswaard (1985), this group seems less affected by Nile perch predation than species of other trophic groups in the sub-littoral region. However, this only means that occasionally some specimens of some species are still caught (Wanink, in press; Wanink & Goudswaard, pers. comm.; Witte et al., in prep.).

Insectivores

Taxonomy

External features (fig. 11A).— Size range of adults 6-15 cm SL. Body shape mostly generalized, but a number of species with more specialized features are also known: e.g., one species, *H. chilotes* Boulenger, 1911, easily identifiable by its lobed lips.

Dentition (fig. 11B,C).— Outer teeth variable: bicuspids and unicuspids occur. Sometimes the teeth may be rather stout. In species with unicuspid teeth, the teeth generally are straight or slightly curved and not acutely pointed. In the latter case the medial teeth are often longer than the lateral ones. Inner teeth in 1-4, generally 2-3 rows. In some species the pharyngeal teeth are slightly to moderately enlarged.

Intestine.— Length 1.2-2.9 (mostly 1.6-2.3) times SL. Based on 36 specimens of nine species. See Zihler (1982) for coiling types and intestinal weigth length.

Species.— At least 29 species are known, of which eight have been described (table 6).

Ecology

Distribution.— All areas of Lake Victoria. Most Lake Victoria species are endemics. Exceptions are *H. nubilus* (Boulenger, 1906), which is also known from Lakes Nabugabo, Edward-George and Kyoga, (Greenwood, 1973) and *H. riponianus* Boulenger, 1911 and *H. saxicola* Greenwood, 1960 which possibly both occur in the Victoria Nile (Greenwood, 1960).

Habitat.— Representatives of this trophic group are found in all habitats of the lake.

Food.— Insect larvae and pupae (e.g.,: *Chaoborus*; chironomids; *Povilla adusta* Navas, 1912) and adult insects together with many other items in various amounts (e.g.,: zooplankton; phytoplankton; detritus; molluscs; fish; prawns).

Potential predators.— Depending on habitat: *Bagrus docmac*, *Clarias gariepinus*, *Protopterus aethiopicus*, *Schilbe mystus*, haplochromine piscivores, birds and otters; the latter two especially in littoral regions, *Lates* in the 1980s.

Reproduction.— Egg size (mean major egg axis) in the rock frequenting species *H.* "rockpicker": 3.5 mm (Goldschmidt, 1989b). Spawning period: Varying from continuous to seasonal (Witte, 1981; Hoogerhoud et al., 1983).

Growth.— Unknown.

Endoparasites in *H. hiatus* Hoogerhoud & Witte, 1981 and *H. iris* Hoogerhoud & Witte, 1981.— *Eustrongylides* (Nematoda); *Contracaecum* (Nematoda), only in *H. hiatus*, mean infection rate <10%; proteocephalid cestodes, mean infection rate <<10%

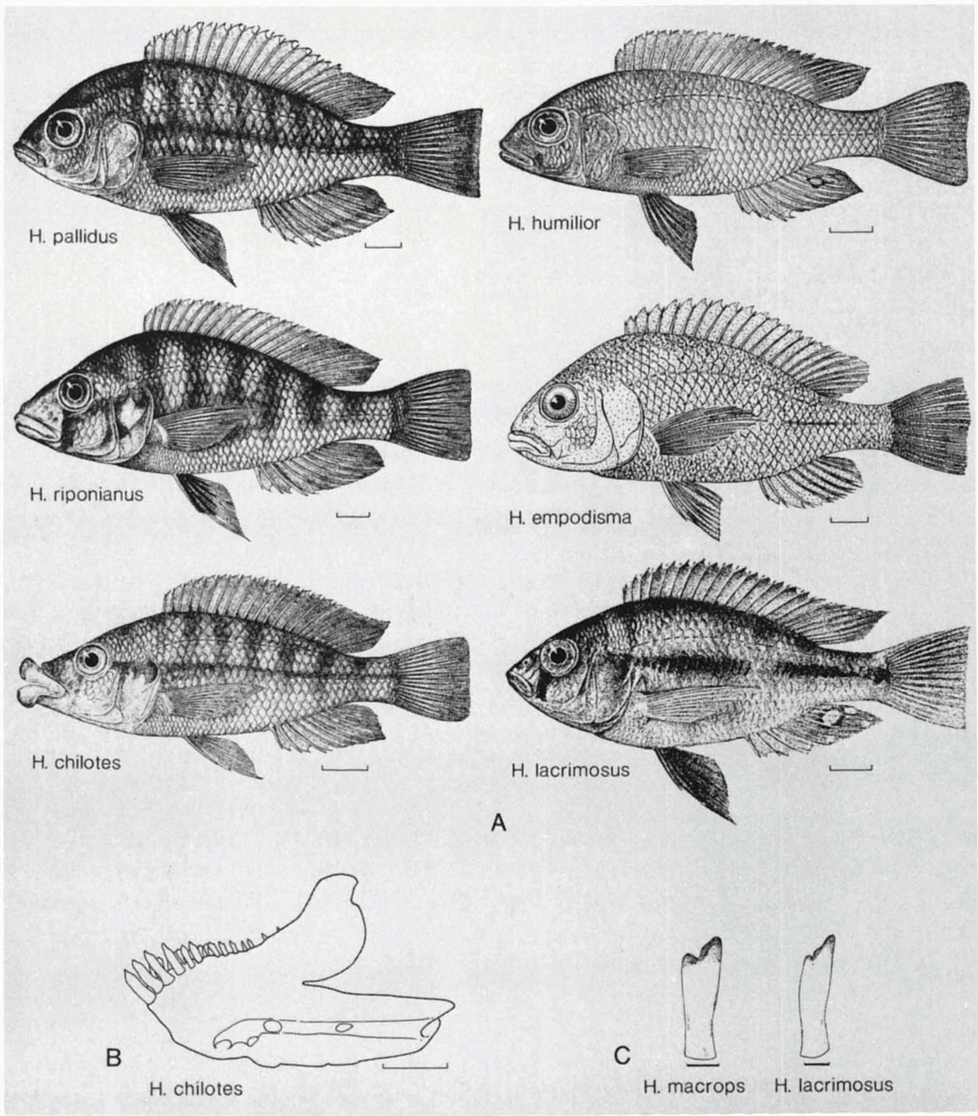

Fig. 11. Insectivores. A. Habitus (scale= 1 cm). B. Lateral view of left dentary of *H. chilotes*, a "specialized" insectivore (scale= 2mm). C. Labial view of outer teeth of *H. macrops* and *H. lacrimosus* (scale= 0.2 mm).

(Mbahinzireki, 1984).

Ectoparasites in *H. hiatus* and *H. iris*.— *Ergasilus lamellifer* (Copepoda); *Lamproglena monodi* (Copepoda); *Lernea cyprinacea* (Copepoda), mean infection rate <<10% (Mbahinzireki, 1984).

Ecological importance.— Before the upsurge of the Nile perch in sub-littoral regions the most important predators of chironomid and *Chaborus* larvae.

References.— Goldschmidt, 1989b; Greenwood, 1959b, 1960, 1962, 1965a, 1974; Hoogerhoud & Witte, 1981; Hoogerhoud et al., 1983; Mbahinzireki, 1984; v. Oijen et al., 1981; Welcomme, 1970; Witte, 1981.

Fishery

Importance.— Over mud bottoms in the sub-littoral regions of the Mwanza Gulf the mean number of insectivores (mainly of the "*empodisma*" group, viz. *H. iris* and *H. hiatus*) comprised 3.1% and 1.6% of the total haplochromine trawl catches in 1977-79 and 1982 respectively (tables 1,2; Witte, 1981; Witte & Goudswaard, 1985, 1987). Because of the relatively large size (7.5-13 cm SL) of these fishes, the mean percentage of biomass was approximately three times as high (4.8% in 1982; Witte & Goudswaard op. cit.). In gill nets used in the sub-littoral regions the contribution of this group was much higher (probably the most important group) due to the mesh sizes used (38-51 mm; table 5; Scully, 1975). With such mesh sizes the smaller detritivores and zooplanktivores were hardly caught.

In the littoral regions the mean number of insectivores may comprise between 20 and 70% (over sand bottoms) of the total number of haplochromines (table 2; Witte, 1981). Beside some large sized species also many smaller ones occur in these habitats. Because of their size, the fishes of the "*empodisma*" group were especially preferred to the other insectivorous haplochromines.

Type of fishery.— Depending on habitat. Bottom trawling (cod end mesh 19 mm) in the Mwanza Gulf and the Speke Gulf, gill netting (mesh size 38-51 mm) in sub-littoral regions and gill netting and beach seining (8-25 mm mesh) in the littoral regions especially over sand.

Exploitation.— Especially in the 1970s in many areas of the lake.

Present status.— The insectivores of the sub-littoral habitat have almost completely disappeared as a result of the Nile perch upsurge. Locally, at the beginning of the 1980s, they already showed signs of overfishing. The present status of the insectivores of the littoral region is not exactly known but, with exception of species in the very shallow waters and in the rocky habitat, they too are probably strongly affected by the Nile perch (Witte et al., in prep.)

Prawn-eaters

Taxonomy

External features (fig. 12A,D,E).— Size range of adults 9-12 cm SL. Except for *H. melichrous* Greenwood & Gee, 1969, moderately slender fishes (BD 29-35% of SL). All species have large eyes (EyL 25-35% of HL), the dorsal eye margin touching or extending above the dorsal head profile. Interorbital width less than eye length. Premaxillary expanded medially.

Dentition (fig. 12B,C).— Outer teeth in oral jaws generally consisting of a mixture of relatively small, acutely pointed unicuspid (and/or bicuspid) and tricuspid teeth. Inner teeth in 2-3 rows of mostly tricuspid teeth.

Intestine.— Length 0.8-1.4 (mostly 1.0-1.1) times SL. Based on 25 specimens of four species. See Zihler (1982) for coiling types and intestinal weight length.

Species.— At least 12 species are known, of which 11 are described (table 6).

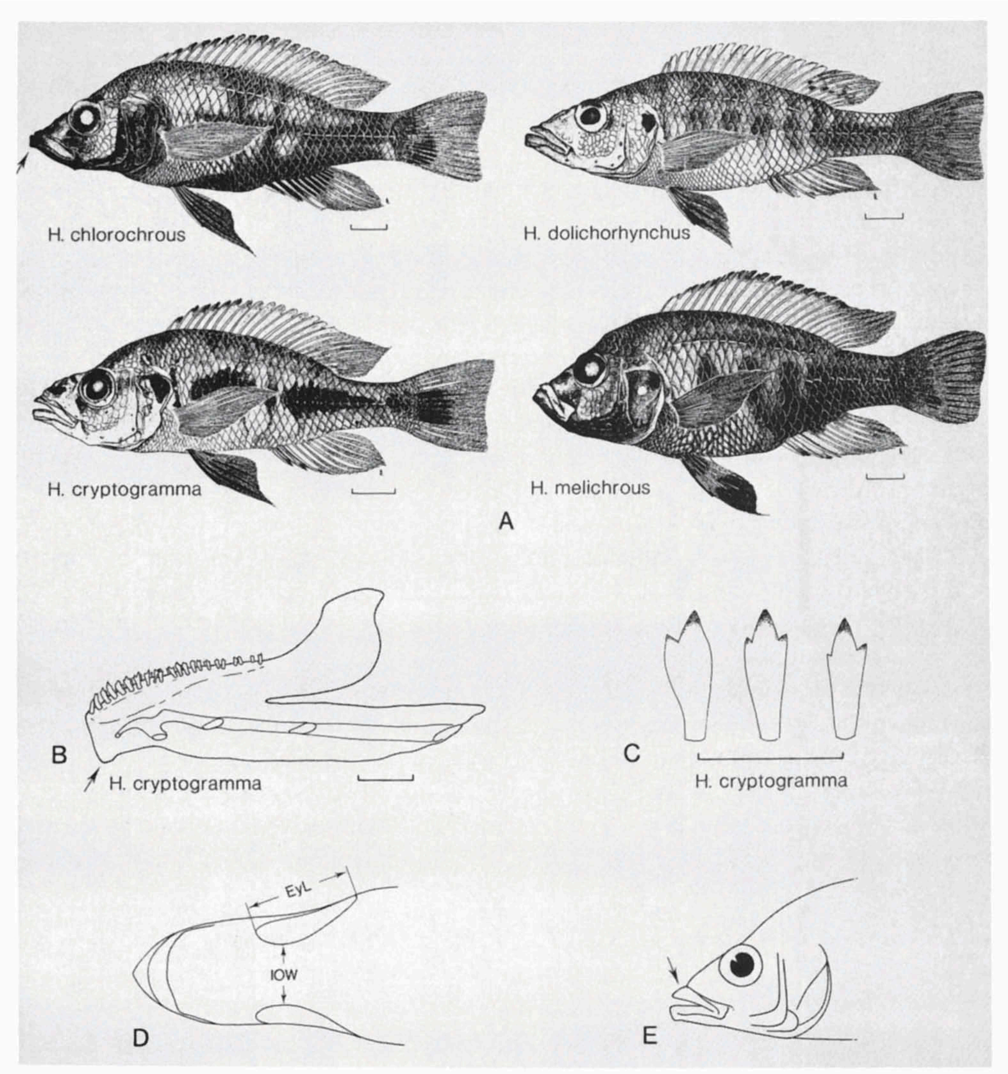

Fig. 12. Prawn-eaters. A. Habitus (scale = 1 cm). B. Lateral view of left dentary of *H. cryptogramma* (scale = 2 mm). C. Labial view of outer teeth of *H. cryptogramma* (scale = 0.5 mm). D. Dorsal view of the head of *H. tridens*. Note the narrow interorbital width. E. Lateral view of the head of *H. cryptogramma*. Arrow indicates the beaked premaxilla. Arrows in A and B indicate mandibular mental prominence.

Ecology

Distribution.— In all areas of Lake Victoria. All Lake Victoria species are endemics.

Habitat.— Over mud bottoms at depths between 6-30 m. Probably also in deeper water. Most species probably benthic, some species possibly also temporarily in mid water.

Food.— The prawn *Caridina nilotica* (Roux, 1833). Zooplankton may also form part of the diet.

Potential predators.— *Bagrus docmac, Clarias gariepinus, Schilbe mystus, Protopterus aethiopicus*, haplochromine piscivores, *Lates* in the 1980s.

Reproduction.— Data only known for one species (*H. crocopeplus* Greenwood & Barel, 1978). Egg size (mean major egg axis): 3.4 mm; mean fecundity: 81.7 eggs (Goldschmidt, unpublished). Spawning period: of most species probably seasonal.

Growth.— Unknown.

Parasites.— Unknown.

Ecological importance.— Before the upsurge of *Lates*, the haplochromine prawn-eating species were the only fishes in the lake which consumed prawns in large quantities.

References.— Greenwood, 1967, 1974; Greenwood & Gee, 1969; Greenwood & Barel, 1978; van Oijen et al., 1981; Witte, 1981.

Fishery

Importance.— Unimportant to fisheries because of low densities. In the trawl catches in the Mwanza Gulf and Speke Gulf in the 1970s this group comprised less than 1% of the total number of haplochromines (tables 1,2; Witte, 1981). Moreover, these fishes occurred mainly in the deeper (> 15 m) offshore parts of these areas where gill net fisheries were less intensive.

Present status.— Almost completely vanished as a result of the Nile perch upsurge.

Crab-eaters

Taxonomy

External features.— Size range of adults 14-16 cm SL. Body form of a typical piscivore; relatively slender body, large head, long lower jaw and deep cheek.

Dentition.— Outer teeth in oral jaw consisting of rather strong, moderately strongly recurved, acutely pointed unicuspids. Inner teeth in two or three rows.

Intestine.— Length 0.9-1.4 (mostly 1.2) times SL. Based on 30 specimens.

Species.— Only one species (*H.* "smoke"), still undescribed.

Ecology

Distribution.— *H.* "smoke" is endemic to Lake Victoria and until now only known from the Mwanza Gulf area.

Habitat.— Restricted to rocky outcrops and rocky islands, apparently living between boulders. Only caught with angling rod and fish traps at depths between 1 and 3 m.

Food.— The crab *Potamonautes niloticus* (Milne-Edwards, 1873), is an important food item. Beside crabs, juvenile haplochromine cichlids, prawns and insect larvae are also eaten (van Oijen, unpublished).

Potential predators.— *Bagrus docmac*, otters and birds.

Reproduction.— Spawning period: probably continuous.

Growth.— Unknown.

Parasites.— Unknown.

Ecological importance.— The only species in the lake known to feed regularly on crabs.

References.— Van Oijen et al., 1981, Witte, 1984.

Fishery

Importance.— Not important. Occasionally caught by anglers (see epilithic algae grazers).

Present status.— Although the rocky areas apparently have not been invaded by *Lates*, in a series of samples in 1989 and 1990 *H.* "smoke" was not present, while formerly it was not rare (Witte et al., in prep.).

Piscivores sensu lato

All species which feed on (parts of) fishes are collectively named piscivores s.l.. In this trophic group many subdivisions can be made based on predation techniques, prey size, prey species or prey parts (van Oijen, 1982). A group of species specialized in preying on eggs and embryos of haplochromine cichlids is collectively termed paedophages. Even more distinct from fish eating species is *H. welcommei* Greenwood, 1966, a species which feeds on scales of other haplochromine cichlids. Paedophages and scale eaters are treated as distinct trophic groups separate from the piscivores s.s.

Fishery

Importance.— Despite the high number of species, in all habitats examined the mean number of piscivores in the catches in the Mwanza Gulf (from 1977 on) rarely exceeded 1% (table 1, 2).

Because of the relatively large size of these fishes, the mean percentage of biomass was at least three times as high (Witte & Goudswaard, 1985, 1987). In gill nets the contribution of this group was probably higher, due to the mesh sizes used (38-51 mm), which hardly catch the smaller detritivores and zooplanktivores (table 5; Scully, 1975).

Type of fishery.— Bottom trawling (cod end mesh 19 mm) in the Mwanza Gulf and the Speke Gulf, gill netting (mesh size 38-51 mm) probably in many sub-littoral regions of the lake and gill netting and beach seining (8-25 mm mesh) in the littoral regions.

Exploitation.— Especially in the 1970s, in many areas of the lake.

Present status.— The piscivores s.l. of the sub-littoral regions have almost completely vanished as a result of the Nile perch upsurge. Prior to that, however, in the Mwanza Gulf the piscivores were already seriously diminished by the trawl fishery with the 19 mm cod ends (Goudswaard, 1988; Witte, 1981; Witte & Goudswaard, 1985, 1987).

A. **Piscivores** sensu stricto

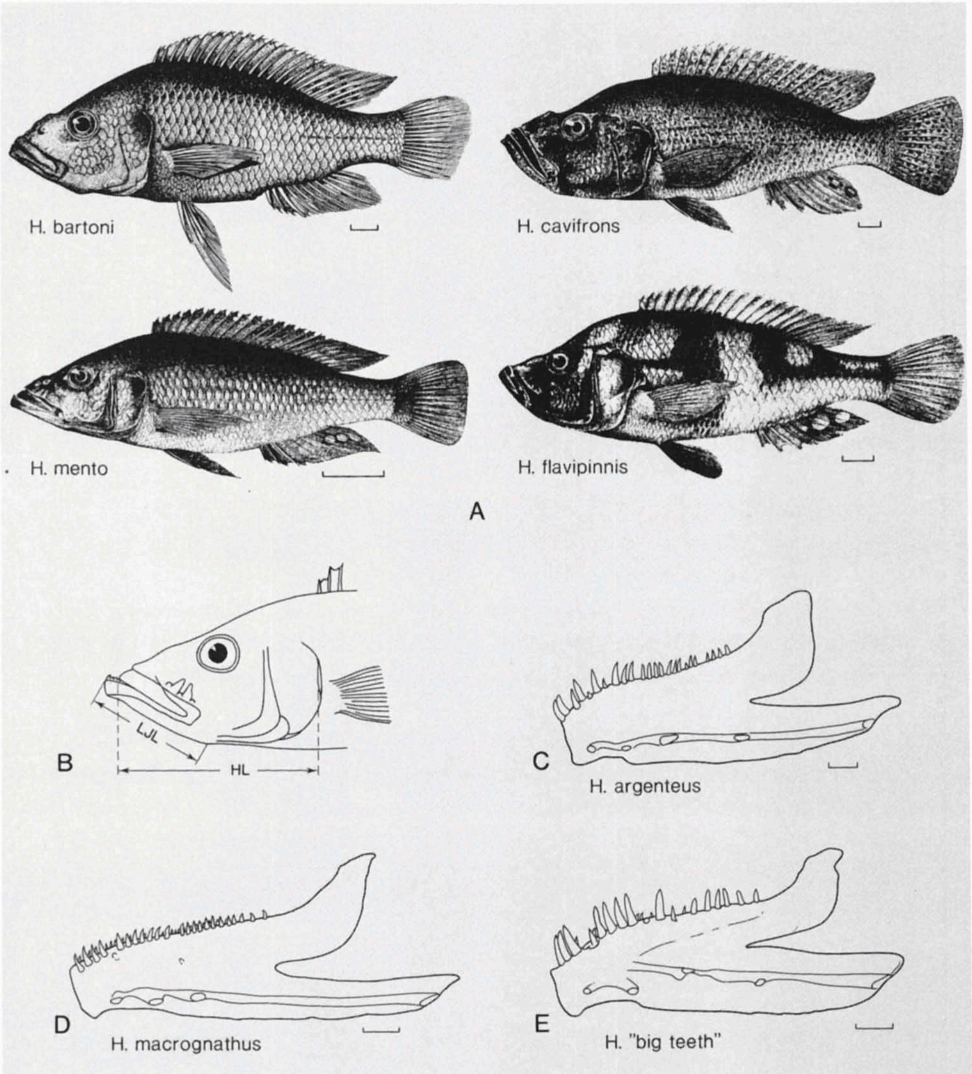

Fig. 13. Piscivores sensu stricto. A. Habitus (scale = 1 cm). B. Lateral view of the head of *H. macrognathus* indicating the long lower jaw length (LJL)/head length (HL) ratio. C,D,E. Lateral view of left dentary of *H. argenteus, H. macrognathus* and *H.* "bigteeth" (scale = 2 mm).

Taxonomy

External features (fig. 13A,B).— Size range of adults 8-25 cm SL (most species 10-16 cm). Body form very variable: deep bodied and slender bodied species are known, and compressed as well as broad bodied forms. These differences in body form probably reflect different predation techniques, e.g., ambush and pursuit hunting (van Oijen, 1982). All piscivorous species have relatively large heads (HL > 36% of SL) which accommodate long jaws (LJL > 45% of HL in all species, > 50% of HL in many species) and relatively deep cheeks. In many species the lower jaw extends beyond the upper jaw.

Dentition (fig. 13C-E).— A few species have a mixture of unicuspid teeth (dominating) and weakly bicuspid teeth in the oral jaws. However, most piscivores have only acutely pointed unicuspid teeth. Tooth size differs greatly between the species. Tooth curvature varies from almost straight to very strongly recurved. Tooth setting varies from relatively closely to widely set. Inner teeth generally in 2-3 rows, some species have 4-5 inner rows.

Intestine.— Length 0.8-2.0 (mostly 1.2-1.3) times SL. Based on 220 specimens of 26 species. See Zihler (1982) for coiling types and intestinal weight length.

Species.— At least 100 species are known, of which 42 have been described (table 6).

Ecology

Distribution.— Piscivores are found in all areas of Lake Victoria. All Lake Victoria species are endemics.

Habitat.— Over all substrate types from shallow littoral regions less than 1 m deep, to depths of 50 m in open waters. Pelagic species occupying the upper water layers are known from sheltered areas in bays with a depth of 2 m, as well as relatively open water with depths up to 15 m. Very few species occur in the rocky habitat.

Food.— Most species feed on haplochromine cichlids. The habitat restrictions of both piscivores and prey species probably result in predation on a limited number of species. A specialization on different prey-size is found. The relatively small species, because of their size are bound to prey on juvenile haplochromine cichlids (starting with immediately post-bucal specimens of 10 mm long), but larger species do not necessarily eat larger prey. Some of the largest species (20 cm) are specialized predators on juvenile haplochromine cichlids. About 10 species of haplochromine piscivores are specialized predators of *Rastrineobola argentea*. The only other non-cichlids eaten by haplochromine piscivores are small *Barbus* species like *B. radiatus profundus* Greenwood, 1970 (van Oijen, 1982).

Potential predators.— Depending on habitat: *Bagrus docmac, Clarias gariepinus, Protopterus aethiopicus*, haplochromine piscivores and *Schilbe mystus* (both probably too small to eat adults) otters (damaged fishes in gill nets indicate that otters prey by preference on large specimens), birds, *Lates* in the 1980s. The piscivorous species were amongst the first to disappear from the Mwanza Gulf once the Nile perch established itself in the area (Goudswaard, 1988; Witte et al., in prep.).

Reproduction.— Data known for one of the smaller (<10 cm SL) species *H. nanoserranus* Greenwood & Barel, 1978. Egg size (mean major egg axis): 3.4 mm.

Mean fecundity: 66.3 eggs (Goldschmidt unpublished). Spawning period: Littoral species probably continuous. Species from deeper, open water, seasonally. Nurseries: Juvenile piscivores were caught in shallow (< 2 m) water. Deepwater species probably move gradually out to their habitat as they grow.

Growth.— Unknown.

Endoparasites in *H. macrognathus* Regan, 1922.— *Eustrongilides* (Nematoda); *Contracaecum* (Nematoda), mean infection rate < 10% (Mbahinzireki, 1984).

Ectoparasites in *H. macrognathus*.— *Ergasilus lamellifer* (Copepoda); *Lamproglena monodi* (Copepoda); *Lernea cyprinacea* (Copepoda), mean infection rate <<10%; *Argulus africanus* infection rate <<10% (Mbahinzireki, 1984).

Ecological importance.— As predators of primary, secondary and tertiary consumers haplochromine piscivorous species, together with non-cichlid predators at the top of the food pyramid, may have played an important role in regulating densities of the smaller haplochromine cichlids before the Nile perch upsurge.

References.— Basasibwaki, 1973; Buruga, 1967; Greenwood, 1960, 1962, 1967, 1974; Greenwood & Barel, 1978; Greenwood & Gee, 1969; van Oijen, 1982, 1989; van Oijen et al., 1981; Witte, 1981, 1984; Zihler, 1982.

Fishery

See under piscivores s.l.

B. Paedophages

The paedophages of Lake Victoria can be subdivided into snout-engulfers, which suck eggs and larvae from the mouth of brooding females (Wilhelm, 1980a) and egg-snatchers which steal eggs from the substrate before they are taken into the mouth of the spawning female (Witte-Maas, 1981).

Taxonomy

External features (fig. 14A,E).— Size range of adults 6-17 cm SL (most species > 8 cm). Body form variable. Dorsal head profile slightly to distinctly concave. Maxilla often bullate. In some species the lower jaw is pointed, closes within the upper jaw and is narrow (length width/ratio 1.9-2.2). In the remaining group of species the length/width ratio may vary from 1.0-2.2.

Dentition (fig. 14B-D,F).— *Teeth (weakly bicuspids and unicuspids) of both jaws are deeply embedded in the oral mucosa. In a number of species the teeth of the lower jaw are curved anteriorly.* Inner teeth arranged in 1-2 (rarely 3) rows. In some species the teeth are hardly visible due to their small size.

NB: Two species have none of the above mentioned characters. The egg-snatcher, *H. barbarae* Greenwood, 1976, has generalized features. *H. cronus* Greenwood, 1976, which feeds on haplochromine larvae has stout unicuspid teeth which are not deeply embedded in the oral mucosa and a strongly curved dorsal head profile with a supra-orbital swelling.

Intestines.— Length 1.0-1.7 times SL Based on ten specimens of five species. See Zihler (1982) for coiling types and intestinal weigth length.

Species.— At least 24 species are known of which eight have been described (table 6).

Ecology

Distribution.— All areas of Lake Victoria. All Lake Victoria species are endemics.

Habitat.— Probably in all habitats of the lake where haplochromine cichlids are

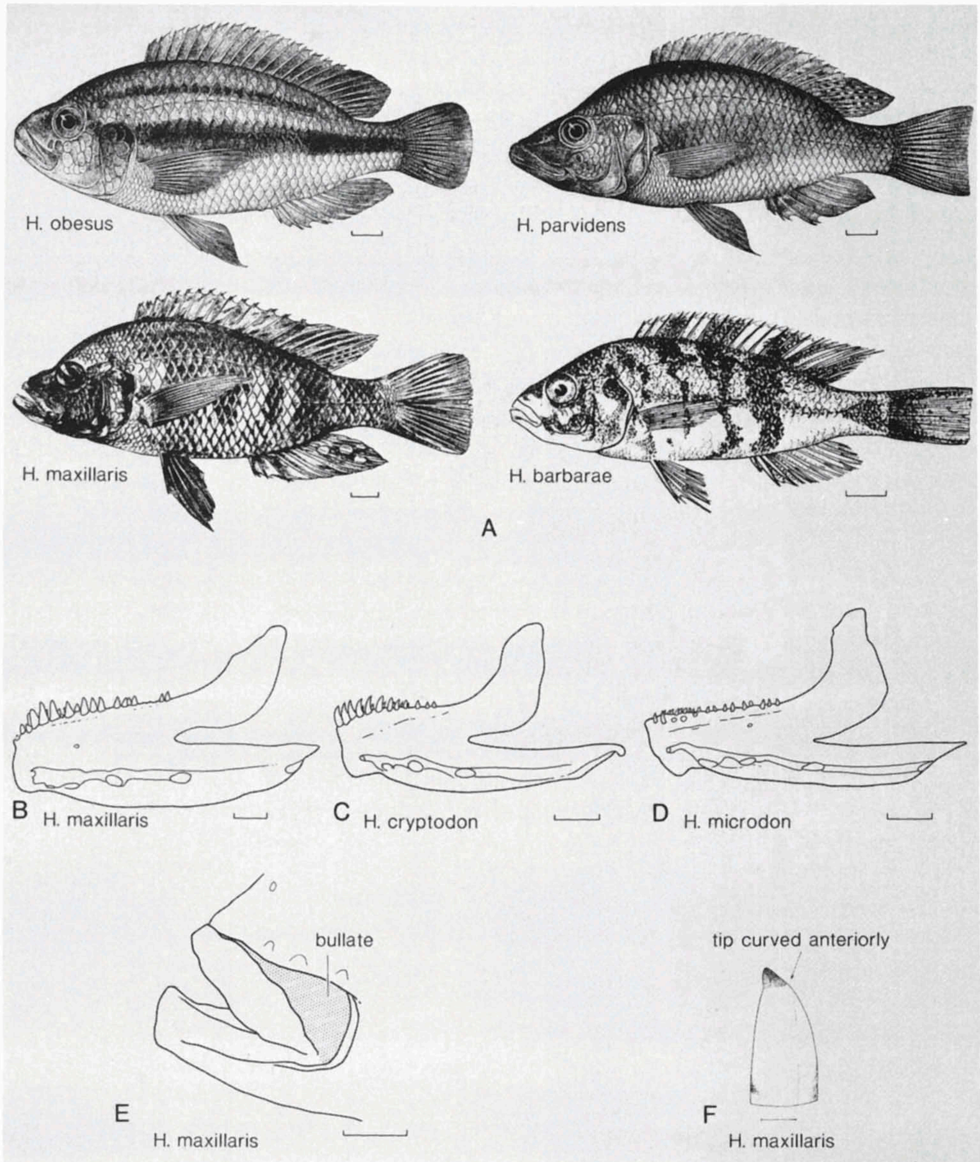

Fig. 14. Paedophages. A. Habitus (scale= 1 cm). B,C,D. Lateral view of left dentary of *H. maxillaris, H. cryptodon* and *H. microdon* (scale= 2 mm). E. Lateral view of oral jaws of *H. maxillaris* showing the bullate maxilla (scale= 5 mm). F. Lateral view of outer tooth (lower jaw) of *H. maxillaris* with anteriorly curved tip (scale= 0.2 mm).

present. One species is caught near the surface during the night.

Food.— Predominantly eggs and larvae of other haplochromine cichlids. Occasionally zooplankton, insect larvae and pupae, *Caridina nilotica*, detritus and algae (Greenwood, 1959, 1967, 1974; Wandera, 1984; Wilhelm, Witte & Witte-Maas, unpublished).

Potential predators.— See piscivores s. s.

Reproduction.— Spawning period: although extended over a long period of the year several species do show seasonal peaks in ripe gonads, mainly in the rainy months March to May (Wandera, 1984).

Growth.— Unknown.

Parasites.— Unknown.

References.— Greenwood, 1959b, 1967, 1974; Wandera, 1984; Wilhelm, 1980a, 1980b; Witte, 1981; Witte-Maas, 1981.

Fishery

See under piscivores s.l.

C. Scale-eaters

Taxonomy

External features (fig. 15A).— Size range of adults 8-10 cm SL. Slender fishes (BD

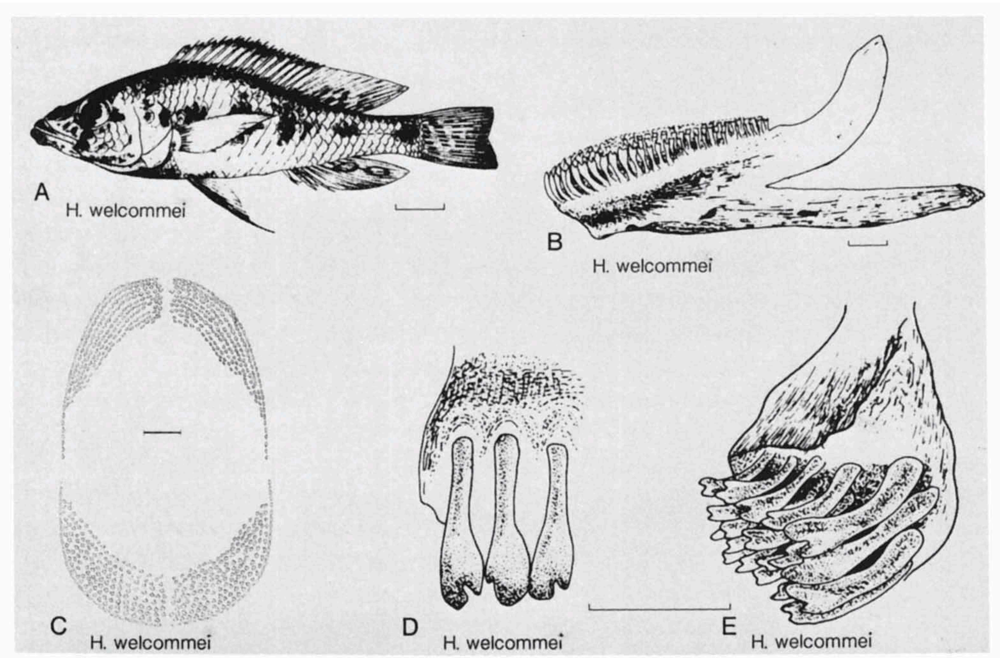

Fig. 15. Scale-eaters. A. Habitus of *H. welcommei* (scale = 1 cm). B. Lateral view of left dentary of *H. welcommei* (scale = 2 mm). C. Tooth band of *H. welcommei* (scale = 1 mm). D,E. labial view and lateral view of teeth in premaxilla of *H. welcommei* (scale = 1 mm).

30-33% of SL). Dorsal and anal fin do not reach caudal fin. Lips slightly thickened.

Dentition (fig. 15B-E).— *Movably implanted, characteristically shaped bicuspid teeth with expanded crowns. Inner teeth arranged in 6-11 rows.*

Intestine.— Length 2.3 times SL. Based on one specimen.

Species.— Only one described species, *H. welcommei*, is known (table 6).

Ecology

Distribution.— Probably all areas of Lake Victoria. *H. welcommei* is endemic to Lake Victoria.

Habitat.— A benthic species over mud, sand and rocky bottoms at depths of 1-18 m.

Food.— Mainly scales, diatoms and phanerogam tissue, occasionally insects (Greenwood, 1966; Witte & Witte-Maas, unpublished).

Potential predators.— *Bagrus domac, Clarias gariepinus, Schilbe mystus, Protopterus aethiopicus*, haplochromine piscivores, birds, otters, *Lates* in the 1980s.

Reproduction.— Nurseries: Juveniles were caught in littoral habitats.

Growth.— Unknown.

Parasites.— Unknown.

References.— Greenwood, 1966, 1974; Witte, 1981.

Fishery

See under piscivores s.l.

Parasite-eaters

Taxonomy

External features (fig. 16A).— Size range of adults 6-10 cm SL. One species, *H.*

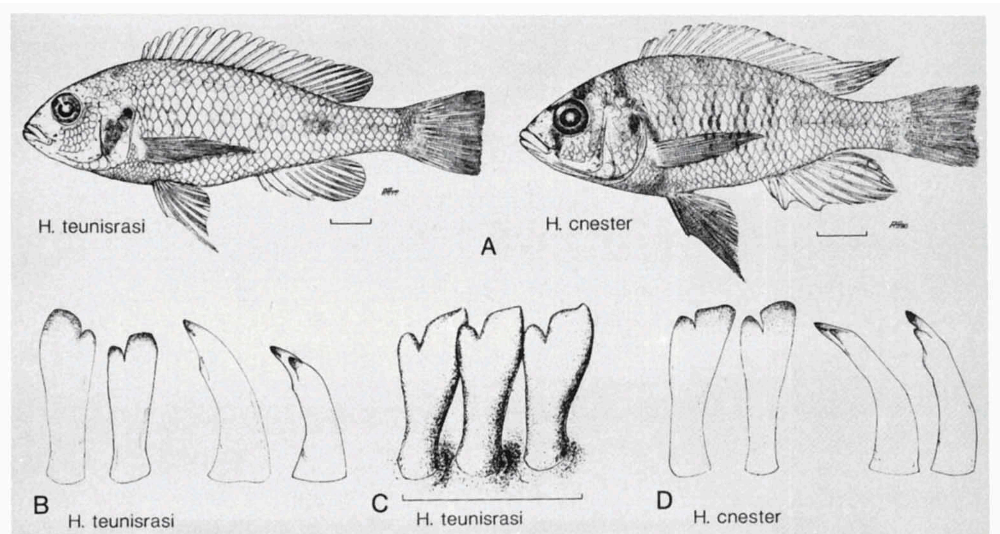

Fig. 16. Parasite-eaters. A. Habitus (scale = 1 cm). B,C,D. Labial view and lateral view of the outer teeth of *H. teunisrasi* and *H. cnester* (scale = 1 mm).

teunisrasi Witte & Witte-Maas, 1981, is slender (BD 30-35% of SL) with a relatively short and gently curved head. The other species, *H. cnester* Witte & Witte-Maas, 1981, has a generalized habitus.

Dentition (fig. 16B-D).— *Closely set unequally bicuspid teeth with an obliquely truncated major cusp.* Inner teeth in 2-4 rows.

Intestine.— Length 1.8-2.5 times SL. Based on nine specimens of two species.

Species.— Two described species are known (table 6).

Ecology

Distribution.— Until now only known from the Mwanza Gulf. The two species are endemic to Lake Victoria.

Habitat.— The species were caught over mud bottoms, at depths of 8-14 m.

Food.— Mainly carp lice (*Argulus* and *Dolops*) and leeches (*Helobdella* Blanchard, 1896), additionally small amounts of zooplankton and diatoms. It is supposed that these fishes obtain the parasites by cleaning other fish, probably mainly catfishes (Witte & Witte-Maas, 1981).

Potential predators.— *Bagrus docmac, Clarias gariepinus, Schilbe mystus, Protopterus aethiopicus,* and haplochromine piscivores, *Lates* in the 1980s. It is not known whether the parasite eaters are protected against predation because of their cleaning habits.

Reproduction.— Unknown.

Growth.— Unknown.

Parasites.— Unknown.

References.— van Oijen et al., 1981; Witte, 1981; Witte & Witte-Maas, 1981.

Fishery

Importance.— Because of very low densities, not important (tables 1,2).

Present status.— Unknown, but probably vanished due to the Nile perch upsurge.

Conclusions

Detailed ecological research in the Mwanza Gulf of Lake Victoria revealed that within trophic groups even highly similar species are ecologically segregated (Goldschmidt, 1986; Goldschmidt et al., 1989; Goldschmidt & Witte, 1989; Hoogerhoud et al., 1983; van Oijen, 1982; Witte, 1984). In spite of this it has been demonstrated in this paper that species belonging to a trophic group have more features in common than food alone. Most obvious are size ranges and habitat preferences. However, within trophic groups also similarities are found in reproductive strategies (e.g., detritivores, zooplanktivores) and for instance in parasites with which they are infected (e.g., dilepedid larvae on zooplanktivores). This is not so remarkable, as many of the forementioned features are directly or indirectly related to the food source the fishes use. On their turn certain features which are typical for trophic groups, such as size, habitat preference and migration patterns, influence the catchability of these fishes. Therefore the dramatic impact on haplochromines of both fishery and Nile perch predation differed strikingly for the trophic groups. Due to the small mesh sizes used, the trophic groups comprising larger species (e.g., piscivores, molluscivores) were the first to decline in the Mwanza Gulf after the trawl fishery started. The trophic groups which inhabit shallow littoral areas (e.g., algae grazers) are relatively little affected by the Nile perch. The reverse holds for the deepwater bottom dwellers, such as the prawn eaters (Witte et al., in prep).

Table 6. List of described haplochromine cichlid species of Lake Victoria. Morph.= morphologically; Ec.= ecologically.

Species	Remarks
Detritivores/phytoplanktivores	
Haplochromis cinctus Greenwood & Gee, 1969	
Haplochromis erythrocephalus Greenwood & Gee, 1969	
Haplochromis paropius Greenwood & Gee, 1969	
Epilithic algae grazers	
Haplochromis nigricans (Boulenger, 1906)	
Epiphytic algae grazers	
Haplochromis lividus Greenwood, 1956	
Haplochromis nuchisquamulatus (Hilgendorf, 1888)	
Haplochromis obliquidens Hilgendorf, 1888	
Plant-eaters	
Haplochromis acidens Greenwood, 1967	Morph.+ Ec. partly piscivore
Haplochromis phytophagus Greenwood, 1966	
Pharyngeal mollusc crushers	
Haplochromis ishmaeli Boulenger, 1906	
Haplochromis mylergates Greenwood & Barel, 1978	
Haplochromis pharyngomylus Regan, 1929	
Haplochromis ptistes Greenwood & Barel, 1978	
Haplochromis teegelaari Greenwood & Barel, 1978	
Astatoreochromis alluaudi Pellegrin, 1904	
Oral shelling/crushing molluscivores	
Haplochromis granti Boulenger, 1906	
Haplochromis plagiodon Regan & Trewavas, 1928	
Haplochromis prodromus Trewavas, 1935	
Haplochromis sauvagei (Pfeffer, 1894)	
Haplochromis xenognathus Greenwood, 1957	
Hoplotilapia retrodens Hilgendorf, 1888	
Macropleurodus bicolor (Boulenger, 1906)	Teeth aberrant, see text p. 22
Platytaeniodus degeni Boulenger, 1906	Ec. to a major extent detritivore
Zooplanktivores	
Haplochromis cassius Greenwood & Barel, 1978	Morph.+Ec.partly piscivore
Haplochromis fusiformis Greenwood & Gee, 1969	Classification based on Morph.
Haplochromis heusinkveldi Witte & Witte-Maas, 1987	
Haplochromis laparogramma Greenwood & Gee, 1969	
Haplochromis megalops Greenwood & Gee, 1969	
Haplochromis nyererei Witte-Maas & Witte, 1985	Body depth+teeth aberrant
Haplochromis piceatus Greenwood & Gee, 1969	
Haplochromis pyrrhocephalus Witte & Witte-Maas, 1987.	
Insectivores	
Haplochromis aelocephalus Greenwood, 1959	Morph. specialized

Haplochromis brownae Greenwood, 1962	
Haplochromis chilotes (Boulenger, 1911)	Morph. specialized, see text p. 27
Haplochromis chromogynos Greenwood, 1959	Morph. specialized
Haplochromis cinereus (Boulenger, 1906)	Morph. specialized
Haplochromis crassilabris Boulenger, 1906	
Haplochromis empodisma Greenwood, 1960	
Haplochromis hiatus Hoogerhoud & Witte, 1981	Morph.+Ec.partly molluscivore
Haplochromis humilior (Boulenger, 1911)	Morph.+Ec.partly molluscivore
Haplochromis iris Hoogerhoud & Witte, 1981	Morph.+Ec.partly molluscivore
Haplochromis lacrimosus (Boulenger, 1906)	
Haplochromis macrops (Boulenger, 1911)	
Haplochromis nubilus (Boulenger, 1906)	
Haplochromis obtusidens Trewavas, 1928	Morph.+Ec.partly molluscivore
Haplochromis pallidus (Boulenger, 1911)	
Haplochromis riponianus (Boulenger, 1911)	Morph.+Ec.partly molluscivore
Haplochromis saxicola Greenwood, 1960	
Haplochromis theliodon Greenwood, 1960	Morph. partly molluscivore
Prawn-eaters	
Haplochromis artaxerxes Greenwood, 1962	Only one specimen
Haplochromis chlorochrous Greenwood & Gee, 1969	
Haplochromis crocopeplus Greenwood & Barel, 1978	
Haplochromis cryptogramma Greenwood & Gee, 1969	
Haplochromis dolychorhynchus Greenwood & Gee, 1969	
Haplochromis eutaenia Regan & Trewavas, 1928	Only one specimen
Haplochromis melichrous Greenwood & Gee, 1969	
Haplochromis plutonius Greenwood & Barel, 1978	
Haplochromis sulphurius Greenwood & Barel, 1978	
Haplochromis tridens Regan & Trewavas, 1928	
Haplochromis tyrianthinus Greenwood & Gee, 1969	
Piscivores	
Haplochromis altigenis Regan, 1922	
Haplochromis apogonoides Greenwood, 1967	
Haplochromis arcanus Greenwood & Gee, 1969	
Haplochromis argenteus Regan, 1922	
Haplochromis bartoni Greenwood, 1962	
Haplochromis bayoni (Boulenger, 1909)	
Haplochromis boops Greenwood, 1967	
Haplochromis cavifrons (Hilgendorf, 1888)	
Haplochromis decticostma Greenwood & Gee, 1969	
Haplochromis dentex Regan, 1922	
Haplochromis dichrourus Regan, 19	
Haplochromis diplotaenia Regan & Trewavas, 1928	Only one specimen
Haplochromis estor Regan, 1929	
Haplochromis flavipinnis (Boulenger, 1906)	
Haplochromis gilberti Greenwood & Gee, 1969	
Haplochromis gowersi Trewavas, 1928	
Haplochromis guiarti (Pellegrin, 1904)	
Haplochromis longirostris (Hilgendorf, 1888)	
Haplochromis macrognathus Regan, 1922	
Haplochromis maculipinna (Pellegrin, 1912)	
Haplochromis mandibularis Greenwood, 1962	
Haplochromis martini (Boulenger, 1906)	
Haplochromis mento Regan, 1922	
Haplochromis michaeli Trewavas, 1928	
Haplochromis nanoserranus Greenwood & Barel, 1978	

Haplochromis nigrescens (Pellegrin, 1909)	Only one specimen
Haplochromis nyanzae Greenwood, 1962	
Haplochromis pachycephalus Greenwood, 1967	
Haplochromis paraguiarti Greenwood, 1967	
Haplochromis pellegrini Regan, 1922	
Haplochromis percoides Boulenger, 1906	
Haplochromis perrieri (Pellegrin, 1909)	
Haplochromis pitmani Fowler, 1936	
Haplochromis plagiostoma Regan, 1922	
Haplochromis prognathus (Pellegrin, 1904)	
Haplochromis pseudopellegrini Greenwood, 1967	
Haplochromis serranus (Pfeffer, 1896)	
Haplochromis spekii (Boulenger, 1906)	
Haplochromis squamulatus Regan, 1922	
Haplochromis thuragnathus Greenwood, 1967	
Haplochromis victorianus (Pellegrin, 1904)	
Haplochromis xenostoma Regan, 1922	
Paedophages	
Haplochromis barbarae Greenwood, 1967	Morph. insectivore, see p. 35
Haplochromis cronus Greenwood, 1959	Morph.+Ec. aberrant, see p. 35
Haplochromis cryptodon Greenwood, 1959	
Haplochromis maxillaris Trewavas, 1928	
Haplochromis melanopterus Trewavas, 1928	Only one specimen
Haplochromis microdon (Boulenger, 1906)	
Haplochromis obesus (Boulenger, 1906)	
Haplochromis parvidens (Boulenger, 1911)	
Scale-eater	
Haplochromis welcommei Greenwood, 1966	
Parasite-eaters	
Haplochromis cnester Witte & Witte-Maas, 1981	
Haplochromis teunisrasi Witte & Witte-Maas, 1981	
Unknown	
Haplochromis labriformis (Nichols & LaMonte, 1938)	Only one specimen
Haplochromis melanopus Regan, 1922	Only one specimen
Haplochromis niloticus Greenwood, 1960	
Haplochromis paraplagiostoma Greenwood & Gee, 1969	
Haplochromis parorthostoma Greenwood, 1967	
Paralabidochromis victoriae Greenwood, 1956	Only one specimen

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Errata

Cover and page 1:
for haplichromine *read* haplochromine

Page 7, table 2:
for detrivores/phytoplanktivores *read* detritivores/phytoplanktivores

Page 40, table 6: oral shelling/crushing molluscivores:
after *Haplochromis plagiodon* Regan & Trewavas, 1928 *insert* Teeth aberrant, see Greenwood, 1959b

Page 42, under Acknowledgements, first line:
insert Dr T. Goldschmidt

Page 42, under Acknowledgements, fifth line:
after Mr H. Heijn *insert* from the following sources: Barel et al. (1977), Greenwood (many papers republished in 1981), Hoogerhoud (1984), and Witte & Witte-Maas (1981)