Taxonomical and ecological description of a species complex of zooplanktivorous and insectivorous cichlids from Lake Victoria

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Oijen, M.J.P. van & F. Witte. Taxonomical and ecological description of a species complex of zooplanktivorous and insectivorous cichlids from Lake Victoria.
Zool. Verh. Leiden 302, 15.ii.1996: 1-56, figs 1-64, tabs 1-15.— ISSN 0024-1652/ISBN 90-73239-44-3.

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Key words: Cichlidae; *Haplochromis*; zooplanktivores; insectivores; ecological segregation; intraspecific variation; ontogeny; sexual heterodonty; Nile perch; *Lates*; predation; habitat shift.

The zooplanktivorous *Haplochromis tanaos* spec. nov., and the morphologically very similar but insectivorous *Haplochromis thereuterion* spec. nov., from Lake Victoria (East Africa) are described and compared to *Haplochromis diplotaenia* Regan & Trewavas, 1928, a similar species which is known only from the holotype. Intraspecific variation is described for both new species. Ecological data of the new species are compared to those of known zooplanktivores and insectivores from the Mwanza Gulf area. Both new species disappeared concurrently with the Nile perch (*Lates*) upsurge early in the 1980's. The recent occurrence of individuals closely resembling the new species, in a different habitat close to the original one, is analysed.

Contents

Introduction

Although the existence of zooplanktivorous haplochromine species in Lake Victoria was still unknown twenty years ago (Greenwood, 1974), and explanations were sought to account for their absence in the lake (Greenwood, op. cit.; Fryer, 1977), publications of the *Haplochromis* Ecology Survey Team (HEST) have established that this trophic group was an important element in the aquatic ecosystem of Lake Victoria (van Oijen et al., 1981; Witte, 1981, 1984a; Witte-Maas & Witte, 1985; Witte & Witte-Maas, 1987; Goldschmidt et al., 1990; Goldschmidt & Witte, 1990, 1992; Witte & van Oijen, 1990). Zooplanktivores formed 30% of the number of individuals in trawl catches in the sublittoral waters of the Mwanza Gulf (Witte, 1981). Basic ecological data and data on intraspecific variation of five zooplanktivorous haplochromine species were presented in Witte & Witte-Maas (1987). Detailed research on distribution and food (Witte, 1984a; Goldschmidt et al., 1990), and on the reproductive strategies (Goldschmidt & Witte, 1990) of seven zooplanktivorous species occurring in the same area, made clear that these species, although morphologically very similar, are ecologically separated by three main characters, viz. substrate type, horizontal and vertical distribution, and type of food. Moreover, they were found to differ in breeding strategies.

The number of known zooplanktivorous *Haplochromis* species in Lake Victoria has greatly increased since 1981; according to Seehausen (1991) at least 24 species exist. Only six of these have been described taxonomically.

During the sampling program of HEST in the Mwanza Gulf (van Oijen et al., 1981; Witte, 1981: fig. 1) zooplanktivores were caught resembling *H. diplotaenia* Regan & Trewavas, 1928. This species is known only from the holotype, a female specimen preserved with a widely opened mouth and abducted suspensoria. The description of this species was not detailed enough to allow for a good comparison. For this reason, a redescription of the holotype is made (see below). Direct comparison of the above mentioned specimens with the holotype of *H. diplotaenia* showed that they are not conspecific, and subsequently the cheironym "double stripe" was adopted awaiting the present formal species description.

In the literature this cheironym was used for specimens occurring both over sand and near rocks. However, the present study reveals that these specimens represent two species which are similar in many morphological characters. One species occurs only over sand, the other is only found near rocks. Moreover, it seems that in the species restricted to sand bottoms two morphs can be distinguished, while in the rock-frequenting species an "island specific-variation" may be present. The new species are referred to as the "double stripe" complex.

Like many other haplochromine species from the Mwanza Gulf (Goldschmidt & Witte, 1990; van Oijen, 1991; Wanink, 1991; Witte et al., 1992a, b) both new species disappeared concurrently with the rise of the *Lates* population. However, at the end of 1993 some individuals greatly resembling specimens of the "double stripe" complex were caught over a mud bottom (Seehausen & Witte, 1994a; 1995). The taxonomic status of these specimens was investigated, and the significance of their appearance in terms of speciation was analysed.

Materials and techniques

Specimens of the new species were collected using three fishing techniques: 1) bottom trawling; 2) beach seining; 3) angling.

The majority of the specimens (over 300) of *H. tanaos* spec. nov. were collected in a bottom trawl over sand bottoms in Butimba Bay, one of the smaller bays at the eastern side of the Mwanza Gulf (fig. 1). Butimba Bay forms the eastern end of a transect across the Mwanza Gulf along which 11 stations (A-K) were defined (fig. 2) which were sampled almost monthly in the period from February 1979 till January 1980. From January 1980 till November 1981 only stations A-G were sampled frequently. Two substrate types are present in Butimba Bay, viz. soft organic mud at the northern half excluding the shore, and sand at the southern side and at a narrow strip along the northern margin (fig. 1). The southern margin of the bay mainly consists of rocks, whereas at the northern margin rocks and sandy beaches alternate. The eastern end, where the bottom is gently sloping, was covered by a vegetation of papyrus and reed. Both over sand and mud two stations were defined, one from 2-4 m and one from 4-6 m. Over these stations, tows with a duration of c. two minutes (and a length of about 170 m) were made. This was done with a trawl net with a 4.60 m headrope and a 15 mm streched mesh codend, which was operated from a 7 m long open boat powered by a 20 or 25 Hp outboard engine. To increase the number of smaller juveniles in the catches, from September 1979, when fishing over sand, a 5 mm stretched mesh codend was fixed over the 15 mm codend. Further details of the sampling stations at the transect are given by Witte (1981: table 1).

From rocks at the margins of Butimba Bay and Nyegezi Bay, and at a number of rocky islands in the Mwanza Gulf, fishes were caught using angling rods baited with earthworms. Bait was offered at a depth of 50-100 cm below the water surface. On sandy beaches in Butimba Bay and Nyegezi Bay, specimens of the new species were also collected from beach seine catches of local fishermen. Outside the Mwanza Gulf a few specimens were caught in bottom trawls of the research trawlers "Mdiria" and "Kiboko".

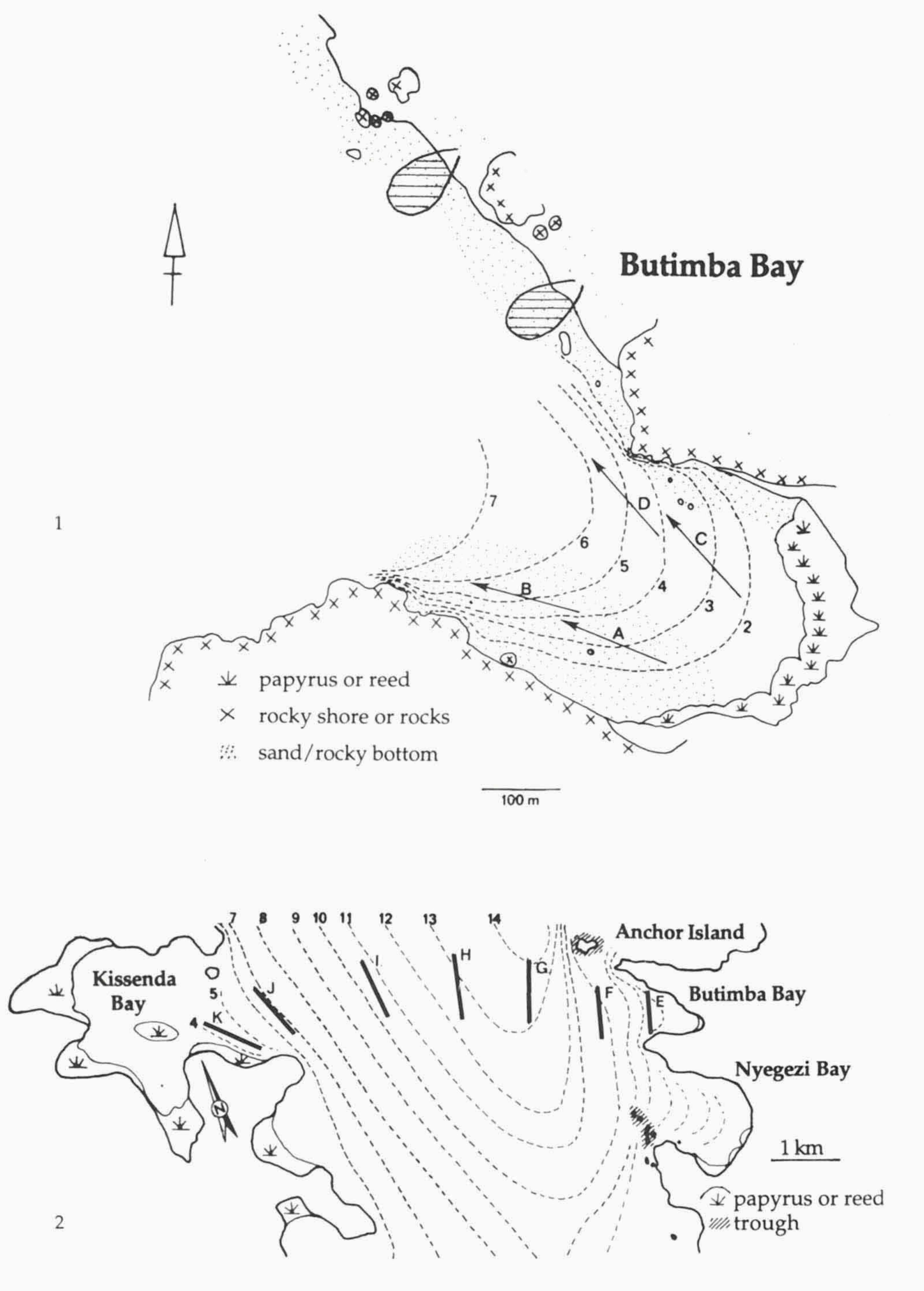
To speed up preservation, the dead specimens were cut in the ventral midline from the anus to the pelvic fin origin before storage in a solution of 10% formalin. After their arrival at the Nationaal Natuurhistorisch Museum in Leiden the specimens were transferred to ethanol 70%.

All specimens were measured to the nearest 0.1 mm. Specimens above 50 mm Standard Length were sexed and their gonad stage was recorded. Females were checked for brooding (i.e. for carrying eggs or larvae in their mouths). The gonads of a number of ripe females were removed and the size and number of eggs were recorded.

Stomach and gut contents of 69 specimens of 23-82 mm SL, from various localities and catch dates throughout the year were investigated with a binocular microscope. To trace possible changes in diet during the day, the gut was divided in four equal parts which were checked separately.

Terminology of skeletal elements follows Barel et al., 1976. Following the techniques described in Barel et al. (1977), Witte & Witte-Maas (1981), and van Oijen (1991) taxonomic measurements were taken from 90 specimens with a Standard Length of 50.3- 82.0 mm. For the Eye Length, instead of the distance of the bony orbit, the distance between the membranous ring was measured. Measurements of the premaxilla were made following Witte (1984b). For the description of scales and squamation the terminology of Lippitsch (1993) was used.

In the descriptions, shapes of skeletal elements are always given as compared to



Figs 1 & 2. Maps of Butimba Bay (fig. 1) and the Mwanza Gulf (fig. 2) with the localities where the trawl shots (stations A-K) and beach seine catches (hatched areas) were made. Isobaths in meters.

those of *Haplochromis elegans* Trewavas, 1933, a generalized *Haplochromis* species (Barel et al., 1976).

Statistics

The Spearman rank correlation test was used to examine whether taxonomical ratios, angular measurements and tooth counts were related with standard length. Males and females were treated separately. If a taxonomic ratio is significantly correlated with standard length it is concluded that allometric growth is involved in one (or both) of the elements measured.

The Wilcoxon (unpaired) test was used to test whether differences between taxonomic ratios, measurements and counts of the different groups (sexes and species) are significant. Generally only individuals of the same length classes were used for these tests. When only few data were available within a length class, and no significant correlation with standard length was found for the taxonomic measurement concerned, classes were added. Statistical calculations were done in STATGRAPHICS Plus Statistical Graphics System version 6.0.

Systematic part

Haplochromis diplotaenia Regan & Trewavas, 1928
(figs 3, 4, 58, tables 1 & 2)

Haplochromis diplotaenia Regan & Trewavas, 1928: 225.
'Haplochromis' diplotaenia; Greenwood, 1980: 13.

Material.— Holotype, ♀, 89.9 mm SL, BMNH 1928.6.2.44, Lake Victoria, Uganda, Sango Bay, M. Graham.

Diagnosis.— A small species with a slender body (27.8 % SL), a moderately large eye (EyL = 28.0 % HL), and two longitudinal bands of equal width on the body: a mid lateral band starting at a small distance from the gill cover and running uninterrupted to the caudal fin base, and a dorsal medial band starting slightly more rostrally and running caudad to a vertical through the anal fin origin. Preserved coloration: silvery white laterally and ventrally, grey dorsally.

Description.— Based on the holotype (the only known specimen). Although this specimen is in an exellent state of preservation, the slightly elevated head, the wide open mouth, the protruded upper jaw and the abducted suspensoria greatly hamper the recording of some taxonomic measurements. The description given below is partly presumptive as it is partly based on a radiograph of the head.

Habitus.— The holotype is moderately small, somewhat laterally compressed and slender. Dorsal head profile slightly curved, the ventral profile presumably almost straight. Presumably a moderately prominent premaxillary prominence. Premaxilla medially slightly expanded rostrad and slightly beaked. Eye moderately large. Dorsal eye margin almost touching the dorsal head profile. Due to the abduction of the suspensoria the eye seems rather elliptical. Pupil elliptical on the right side, ovoid on the left side. A small aphakic aperture rostral (and caudal?) to the lens. Presumably a gentle bend between the straight ventral profile of the lower jaw and the ventral head outline. Lower jaw possibly slightly prognathous. Rostral lower jaw outline slightly convex. Mental area with a sharp angle, no mental prominence. Mouth presumably moderately oblique. Vertical preopercular limb reclining caudad, the horizontal limb almost horizontal. Lateral line openings on head not enlarged.

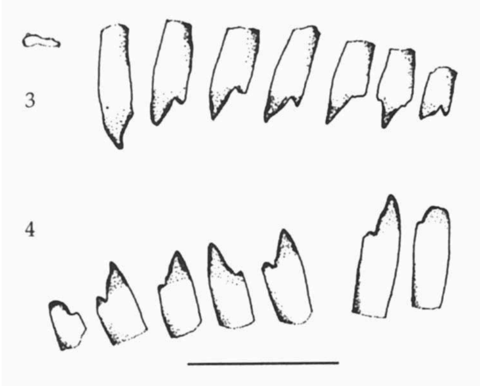
Fins.— Pectoral reaching slightly farther than the tip of pelvics, neither reaching origin of anal. Distance between pectoral and pelvics slightly more than width of pectoral fin base. Anal and dorsal fins just reaching second half of caudal peduncle. Caudal fin damaged; outline probably subtruncate, slightly emarginate.

Scales.— All scales on the head are cycloid. Operculum fully scaled except for a small area which partly covers the opercular blotch. Suboperculum scaled except for a thin ventral rim. Interoperculum scaled only on its caudal half (3-4 scales). Preoperculum scaleless. Cheek fully scaled. Postorbital column with two scale rows. Lachrymal scaleless. Occiput scaled, no distinct pattern recognizable on occiput or area in front of the dorsal fin. Scales on rostral part of dorsum very weakly ctenoid, caudal part of dorsum with ctenoid scales. Scales on flank and caudal peduncle ctenoid. Ventral chest scales relatively small and cycloid, lateral chest scales relatively small and weakly ctenoid. Size transition from chest scales to flank and belly scales gradual. No scales or scale sheath on dorsal or anal fins. Caudal fin scaled on its proximal half, the basal scales ctenoid, the distal ones cycloid. The distal scales are arranged in single rows between the rays.

Gill apparatus.— Nine gill-rakers on the lower part of the first gill-arch. The lowermost four reduced, the fifth bifid, and the remaining three simple, slightly compressed. The number of gill filaments could not be counted without damaging the specimen.

Viscera.— Intestines had been previously removed.

Oral teeth (figs 3 & 4).— Shape. In the upper jaw, the outer row teeth are nearly all weakly bicuspid, one unicuspid is present rostrally and a few weakly tricuspid teeth are found caudally. The major cusp of the bicuspid teeth bears a small flange. In the lower jaw, the rostral teeth are weakly bicuspid, laterally weakly bicuspids dominate over tricuspids and caudally tricuspids dominate. The outer teeth have both neck and crown somewhat compressed. The teeth are relatively small and slightly curved. Tooth size decreases caudad. Inner row teeth all relatively small, compressed, slightly curved, broadly shouldered, tricuspid.



Figs 3 & 4. *Haplochromis diplotaenia* Regan & Trewavas, 1928. Outer row teeth of oral jaws, rostrolateral view. Drawn in situ, therefore basal halves of teeth not visible. Fig. 3. Rostral teeth of left upper jaw. Fig. 4. Rostral teeth of right lower jaw. From holotype, BMNH 1928.6.2.44. Scale equals 1 mm.

— Dental arcade and toothband. Dental arcade rounded. There are two inner rows in both upper and lower jaw.

— Counts and setting. There are 55 teeth in the outer row of the upper jaw, and 45 teeth in the outer row of the lower jaw. Outer teeth of both jaws regularly set, widely set rostrally decreasing to closely set laterally and caudally.

— Implantation. Outer teeth in upper jaw erect rostrally to slightly recumbent caudally. Outer teeth in lower jaw somewhat procumbent rostrally to erect caudally. Inner teeth in upper jaw strongly recumbent, in lower jaw rostrally erect, laterally recumbent.

Coloration.— Live coloration unknown.

— Preserved coloration. Gill cover, a large central area of the cheek, the flank and the ventral half of the body silvery white. Towards the caudal peduncle, the dorsal part of the body and the rostral and dorsal parts of the head the silvery white turns light yellowish brown. Iris yellowish silver, darker dorsally. A moderately broad, continuous, mid lateral band running from the third flank scale caudal to the gill cover to the caudal fin. The band is continued on the distal third of this fin. A dorsal lateral band of equal width runs from the nape to the end of the upper part of the lateral line. Patches of a dorsal medial band are also present. The opercular blotch is rather vague. All fins yellowish hyaline.

Distribution.— *H. diplotaenia* is only known from Lake Victoria. The single known specimen was caught with a beam trawl in Sango Bay, Uganda.

Ecology.— Habitat unknown.

— Food. Unknown.

— Breeding and growth. The holotype is a ripe female. The eggs have an ovoid shape, with a length of 3.3 mm, and a width of 2.5 mm.

Resembling species.— Other micrognathic haplochromine species from Lake Victoria with two lateral bands, e.g. *Platytaeniodus degeni* Boulenger, 1906, *Hoplotilapia retrodens* (Hilgendorf, 1888), *Haplochromis sauvagei* (Pfeffer, 1896), *H. prodromus* (Trewavas, 1935), *H. granti* (Boulenger, 1906), and *H. plagiodon* Regan & Trewavas, 1928, all have a decurved dorsal head profile and a greater body depth. Moreover, most of these species, have the longitudinal bands crossed by vertical bands. For comparison with *H. tanaos* and *H. thereuterion*, see below.

The *Haplochromis* "double stripe" complex

Diagnosis.— Species of the *Haplochromis* "double stripe" complex are small, slender, laterally compressed micrognathic species (see Witte & Witte-Maas, 1987: 6). Dorsal head profile nearly straight or with a slight incurvation above the eye. Snout acute. Distinguishable from other slender species by the presence of two continuous longitudinal bands on the body. These bands may be difficult to distinguish in dark sexually active males. Males have a relatively higher number of unicuspid teeth in the outer row of both jaws when compared to females of a similar size. As there is no male specimen available of *H. diplotaenia* we do not know if sexual heterodonty is found in this species. For this reason *H. diplotaenia* as yet is not included in the *H.* "double stripe" complex.

Haplochromis tanaos spec. nov.

(figs 5-7, 9-24, 26-35, 53, 54, 60, 63, tables 3-6, 11-13, 15)

"Haplochromis" diplotaenia; van Oijen et al., 1981: 161, 169.

Haplochromis "double stripe" Barel, 1983: 419; Witte, 1984a: 159; Witte-Maas & Witte, 1985: 9; Witte, 1987, chapter 3: 8, 9; Goldschmidt et al., 1990: 344, 347; Witte & van Oijen, 1990: 25; Seehausen, 1991: 716, 718; Goldschmidt & Witte, 1992: 104; Witte et al., 1992b: 13, 26, 28; Barel, 1993: 356; Seehausen & Witte 1994a: 52; Seehausen, 1995: 195.
"*Haplochromis*" sp. "double stripe" Seehausen & Witte, 1995: 101.
?*Prognathochromis sp. aff. longirostris;* Selbrink, 1985: 65, 69; Seehausen, 1991: 718.

Material.— Holotype, ♂, 63.1 mm SL, RMNH 32544, Butimba Bay, sta. B, Mwanza Gulf, Lake Victoria, Tanzania. Paratypes 35 ♂♂ + 34 ♀♀. Paratypes collected by HEST from beach seine catches of local fishermen: 2 ♂♂, 62.8, 67.8 mm, RMNH 32525-26, 21.xi.1978, Nyegezi Bay; 2 ♂♂, 72.0-73.0 mm + 5 ♀♀, 66-73 mm, RMNH 32527-33, 24.xi.1978, Butimba Bay; 1 ♀, 60 mm, RMNH 32534, 20.iii.1979, Nyegezi Bay; 1 ♀, 72 mm, RMNH 32535, 5.v.1979, Nyegezi Bay; 1 ♀, 64.3 mm, RMNH 32536, 29.viii.1979, Nyegezi Bay. Paratypes collected by HEST with a bottom trawl: 1 ♂, 69.5 mm + 1 ♀, 72 mm, RMNH 32537-38, 21.xii.1977, Butimba Bay, sta. B; 1 ♂, 69.2 mm, 1 ♀, 69.8 mm, RMNH 32539-40, 28.viii.1978, Butimba Bay, sta. B; 1 ♀, 72 mm, RMNH 32541, 3.i.1979, Butimba Bay, sta. E; 1 ♂, 67 mm + 1 ♀, 72 mm, RMNH 32542-43, 27.iii.1979, Butimba Bay sta. A; 10 ♂♂, 54.0-68.7 mm, + 1 ♀, 64.1 mm, RMNH 32545-54, 25.iv.1979, Butimba Bay, sta. B; 1 ♂, 70.5 mm, RMNH 32555, 25.iv.1979, Butmba Bay; 2 ♂♂, 53,5, 59.0 mm, RMNH 32556-57, 24.v.1979, Butimba Bay, sta. B; 1 ♀, 70 mm, RMNH 32558, 27.ix.1979, Butimba Bay, sta. B; 1 ♂, 71 mm, RMNH 32559, 27.xi.1979, Butimba Bay, sta. B; 2 ♂♂, 57.8-70 mm + 2 ♀♀, 60.2-66.5 mm, RMNH 32560-63, 27.xii.1979, Butimba Bay, sta. B; 2 ♂♂, 55-58.8 mm + 1 ♀, 51.7 mm, RMNH 32567-69, 29.i.1980, Butimba Bay, sta. B; 1 ♀, 70 mm, RMNH 32564 13.iii.1980, Butimba Bay, sta. B; 3 ♂♂, 50.3-66.9 mm + 5 ♀♀ 54.2-61.0 mm, RMNH 32598-605, 15.iv.1980, Butimba Bay, sta. B; 4 ♂♂, 51.5-66.9 mm + 3 ♀♀, 50.9-61.2 mm, RMNH 32606-12, 16.v.1980, Butimba bay, sta. B; 2 ♀♀, 58.7-63 mm RMNH 32613-14, 16.v.1980, Butimba Bay, sta. B; 1 ♀, 52.2 mm, RMNH 32615, 18.vi.1980, Butimba bay, sta. B; 3 ♂♂, 64.2-68.2 mm + 2 ♀♀, 55.7-61.4 mm RMNH 32616-20, 13.viii.1980, Butimba Bay, sta. B.

Other material: 22 ♂♂, 60-74 mm, + 40 ♀♀, 62-76 mm, RMNH 32793, 24.xi.1978, beach seine, sta. II, Butimba Bay; 2 ♂♂, 68.1-70.8 mm + 5 ♀♀, 62.2-68.5 mm, RMNH 32794, 24.xi.1978, beach seine, sta. III, Butimba Bay; 1 ♂, 77.0 mm, RMNH 32795, 6.vi.1979, bottom trawl, West off Ukerewe Island; 1 ♂, 52.2 mm, RMNH 32796, 10.vi.1985, bottom trawl, Kamissa Bay; 2 ♀♀, 51.0-60.1 mm, RMNH 32797, 11.vi.1985, bottom trawl, Buchensi Bay; 1 ♂, 58.0 mm, RMNH 32798, 23.vi.1985, bottom trawl, Namirembe Bay; 1 ♀, 66.2 mm, RMNH 32799, 25.vi.1985, bottom trawl, Namirembe Bay; 1 ♀, 63.2 mm, RMNH 32800, 23.vi.1985, bottom trawl, Chicoga Bay; 1 ♂, 44.4 mm + 7♀♀, 48.0-62.8 mm, RMNH 32801, 7.viii.1985, bottom trawl, Bugongoro Bay, Kome Island; 1 ♂, 61.8 mm, 1 ♀, 58.2 mm + 4 juvs 53.0-55.5 mm, RMNH 32802, 6.viii.1978, beach seine, Kayenze Bay, Speke Gulf.

Etymology.— The name is derived from the Greek ταναοσ (elongate, slender), referring to the slender habitus of this species.

Diagnosis.— A small, slender, laterally compressed micrognathic species with a slightly curved dorsal head profile and a rather acute snout, distinguishable from most other such Lake Victoria haplochromines by the presence of two continuous longitudinal bands on the body. From *H. diplotaenia* it can be distinguished because the lips of *H. tanaos* are not thickened and its premaxilla is not expanded. For differences with *H. thereuterion*, see below.

Description. Based on 80 specimens with a Standard Length of 22-74 mm. Morphometric measurements were taken from 62 specimens of 50.3-73.0 mm standard length. Because males and females were found to differ in dentition and premaxilla shape it was believed, they might also differ in certain other head proportions. Therefore ranges, means and standard deviations of measurements of males and females were calculated separately.

Habitus (figs 5 & 62).— A small and slender, laterally compressed haplochromine

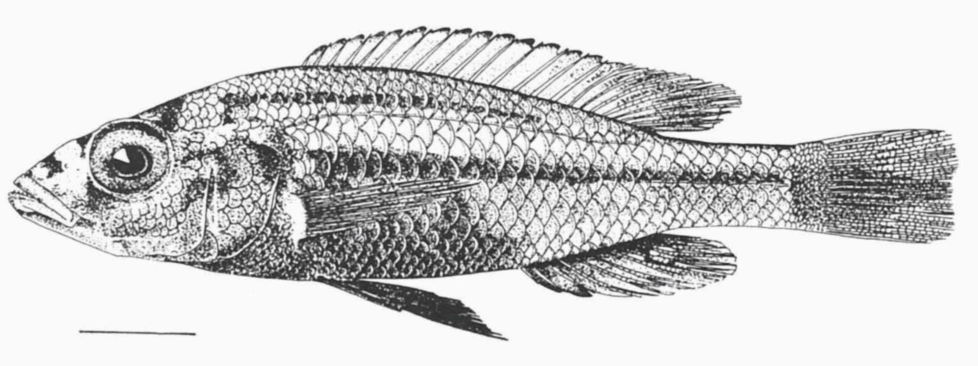
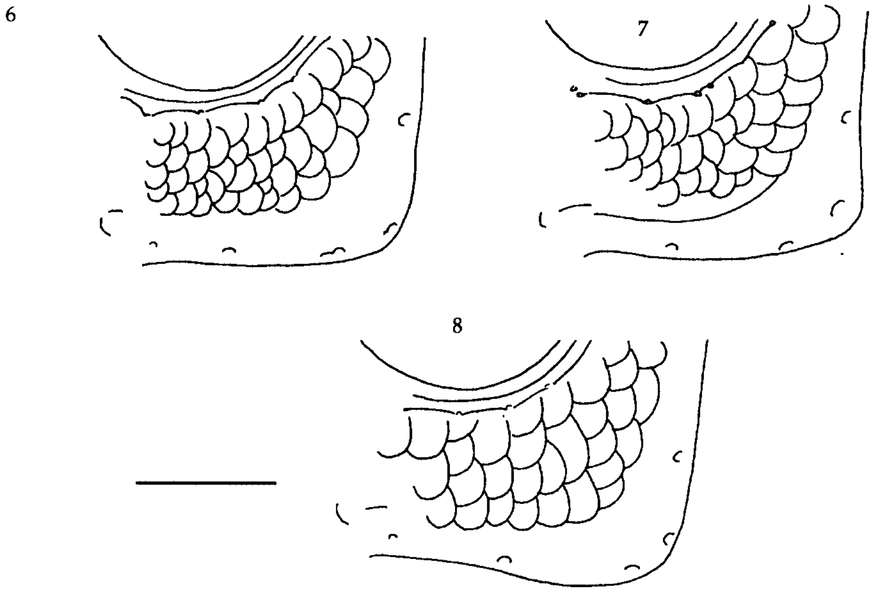


Fig. 5. *Haplochromis tanaos* spec. nov., ♂ paratype, RMNH 32600, scale equals 10 mm.

species with a rather acutely pointed snout and a terminal mouth. A larger part of the eyes is visible from a dorsal view than from a ventral view. Dorsal head profile slightly curved in the nape region but otherwise nearly straight. The premaxillary pedicel distinctly interrupting the profile in most specimens. Premaxilla not expanded medially. Upper lip not produced above the dorsal head profile. Exposed part of maxilla small, the posterior tip reaching a vertical just posterior to the anterior border of the pupil. Ventral outline of the head smoothly to sharply bent at the articulation process of the lower jaw. Sides of lower jaw slightly to moderately oblique. Lower jaw ventral outline almost straight. The slightly receding rostral outline of lower jaw straight or slightly convex with a smoothly rounded mental area, no mental prominence. Jaws isognathous or slightly prognathous. Lips not thickened. Dorsal eye margin almost touching the dorsal head profile or slightly protruding above it. Eye moderately large, circular. Pupil ovoid shaped. Small aphakic apertures rostral and caudal to the lens. Preopercular horizontal limb slightly declining, the vertical limb slightly reclining. The rostral part of the interoperculum is almost completely hidden under the preopercular horizontal limb. Lateral line canals on the preorbital relatively short and broad, the openings slightly enlarged in a few specimens.

Scales (figs 6, 7, 53, 54).— All scales on the head are cycloid. Operculum fully scaled except for a small area which partly covers the opercular blotch. Suboperculum scaled except for a thin ventral rim. Interoperculum scaled only on its caudal half (3-4 scales). Preoperculum scaleless. Squamation on cheek variable: The majority of the specimens have their cheeks fully scaled. A few specimens have the scales at the rostroventral corner rather deeply embedded. In a number of specimens this area (the rostral embayement of Lippitsch, 1993) is scaleless. The scaleless area may be extended caudad to include the entire ventral rim of the cheek. Postorbital column is variable: most specimens have a mixed row, but specimens with one or two scale rows are also found. Lachrymal scaleless. Occiput scaled, no distinct pattern recognizable on occiput or area in front of the dorsal fin. Scales on rostral part of dorsum cycloid or very weakly ctenoid, caudal part of dorsum with ctenoid scales. Scales on flank and caudal peduncle ctenoid. Ventral chest scales relatively small and cycloid, lateral chest scales relatively small and weakly ctenoid. Size transition from chest scales to flank and belly scales gradual. The scale between the pelvic fins slightly enlarged. No scales or scale sheaths on dorsal or anal fins. Caudal fin scaled on its proximal



Figs 6-8. Variation in squamation pattern on cheek. Figs 33 & 34. *Haplochromis tanaos* spec. nov. Fig. 6. Paratype RMNH 32666, ♂, 67 mm SL. Fig. 7. Paratype RMNH 32667, ♂, 68 mm SL. Fig. 8. *Haplochromis thereuterion* spec nov., paratype, RMNH 32640, ♂, 74 mm SL. Scale equals 5 mm.

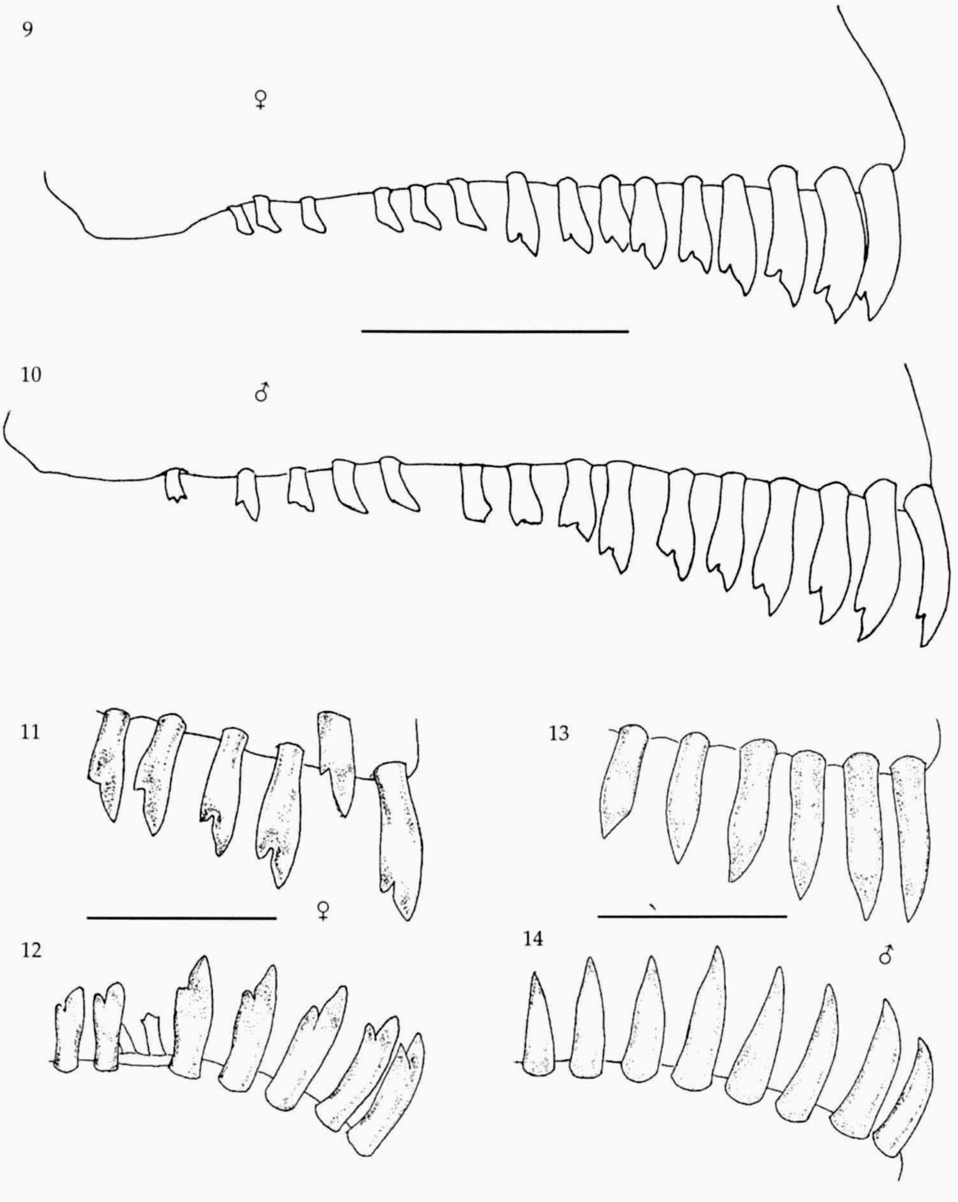
half, the basal scales ctenoid, the more elongate distal ones gradually becoming very weakly ctenoid to cycloid. The distal scales are arranged in single rows between the rays.

Fins.— Pectorals just reaching the anus. Pelvics in females just not reaching this point. Sexually active males have the first pelvic ray produced to reach the anal spines. Extension of dorsal and anal fin about equal, reaching the posterior half of the caudal peduncle. Pectoral fin base width equals the distance between pectoral and pelvic fins. Caudal fin outline (sub)truncate, slightly emarginate to straight caudally. In some specimens the ventral margin is slightly obliquely subtruncate.

Gill apparatus.— Eight to ten gill-rakers on the lower part of the first gill-arch; the lowermost two or three reduced, the remaing ones relatively small, compressed and usually simply tapering. The two rakers below the highest raker on the lower part may be bifid. The number of gill filaments on the lateral hemibranch of the first gill-arch ranges from 86 to 94 (n= 3)

Viscera.— Intestine length varies from 0.8-1.22 times the standard length (n= 30). Following the definitions of Zihler (1982) the arrangement of the digestive tract of adult *H. tanaos* is of type E.

Oral teeth (figs 9-14, 17-23).— Shape. In juveniles, the teeth of the outer row rostrally and laterally, are rather small, slighty compressed, unequally bicuspid; tricuspids are present only caudally. The major cusp of the bicuspid teeth sometimes has a small flange. All teeth are slightly to moderately curved. In adult specimens a remarkable difference in tooth shape occurs between males and females. In adult males the



Figs 9-14. *Haplochromis tanaos* spec. nov. Oral jaw teeth. Figs 9 & 10. Outer teeth of right premaxilla, lateral view. Figs 11 & 13. Rostral teeth of right premaxilla, rostro-lateral view. Figs 12 & 14. Rostral teeth of right lower jaw, lateral view. Fig. 9. RMNH 32670, juv ♀, 50 mm SL. Fig. 10. RMNH 32671, juv ♂, SL 52 mm. Figs 11 & 12. RMNH 32540, ♀, SL 69.8 mm. Fig. 13 & 14. RMNH 32528, ♂, SL 72 mm. Scale equals 1 mm.

bicuspid teeth are ontogenetically gradually replaced by unicuspids, starting with the anterior ones. Compared to males of a similar size, females have fewer unicuspid teeth in the outer row of both jaws (table 6). The largest males have only unicuspids in the outer rows of both jaws. The unicuspids are circular in cross section and acutely pointed. Tooth size gradually decreases posteriorly, however, caudal to the anterior 6-8 teeth a small difference in size is found. In males, even in specimens with bicuspids laterally, the posterior one to four teeth are often unicuspid and slightly larger than the preceeding ones. In females a unicuspid posterior tooth is only rarely found. Inner rows: all inner teeth are moderately curved tricuspids. In the rostral part of the jaws, the tricuspids have the middle cusp more elongated than the laterally placed tricuspids.

— Dental arcade and toothband. Dental arcade slightly acute in both jaws. Two inner rows in both jaws. Distance between outer row and first inner row larger than the distance between the inner rows.

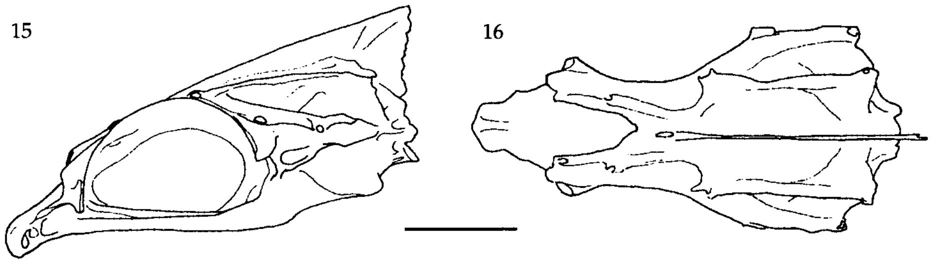
— Counts and setting. Adult specimens 64-73 mm SL have 42-45 teeth in the outer row of the upper jaw, 31-36 in the lower jaw. Outer row teeth are regularly set at a distance equal to or slightly less than the diameter of the toothbase. Outer row occupying 4/5 of the dentigerous arm. In two of the dissected lower jaws the most caudal tooth was separated by a distinct gap from the other teeth. In one case it was set relatively high on the coronoid process (fig. 23). Inner rows occupying c. 3/5 of the outer row length on the premaxilla and c. 3/4 of the outer row length on the mandible.

— Implantation. In upper jaw outer row teeth erect (medial teeth) to slightly recumbent (caudal teeth). In lower jaw outer row teeth are slightly procumbent (medially) to erect (caudally). All teeth are slightly suspensoriad inclined. Implantation of inner row teeth strongly recumbent.

Pharyngeal teeth.— Counts. About 32 teeth in the posterior row. Ten teeth in the two medial rows.

— Shape. Most pharyngeal teeth are of the bevelled type, relatively fine and acutely pointed; some medial teeth of the posterior row and some caudal teeth of the median row are slightly enlarged and hooked, with a blunt rostro-dorsad directed major cusp. Tooth size increasing from rostral to caudal and from lateral to medial.

— Neurocranium (figs 15 & 16). The neurocranium of *H. tanaos* is relatively slender, the otic region and the supraoccipital crest are both shallow. The ethmovomerine

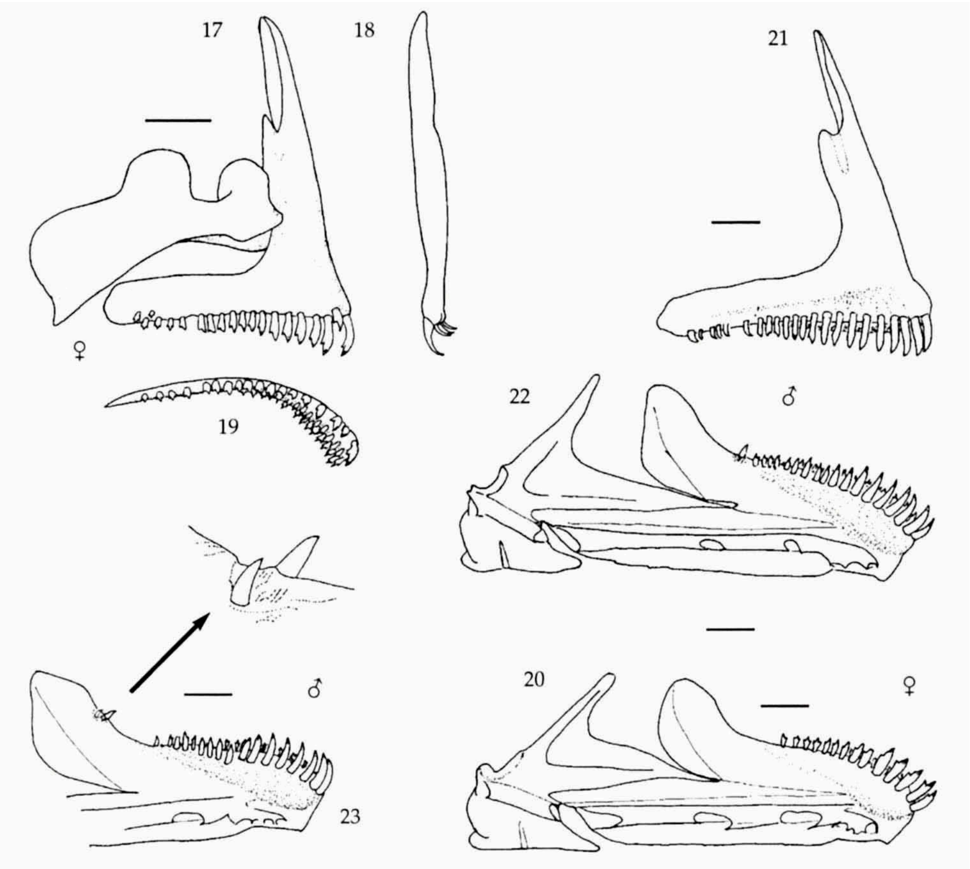


Figs 15 & 16. *Haplochromis tanaos* spec. nov., paratype, RMNH 32669, ♀, SL 71.1 mm, neurocranium. Fig. 15. Left lateral view. Fig. 16. Dorsal view. Scale equals 5 mm.

block is less decurved and slightly longer than that of *H. elegans*. The pharyngeal apophysis is situated relatively caudally, and the postorbital process is broadened.

— Oral jaws (figs 17-23). Premaxilla ascending arm longer than dentigerous arm, angle between the arms 75°-82° (n= 20). Ventral outline of the dentigerous arm slightly concave. Ventral part of the ascending arm very slightly expanded. There is a difference in the ratio of the Premaxillary Ascending Arm Length and the Dentigerous Arm Length of males and females. In males (n= 11) the ratio is 1.11-1.21 (mean± SD: 1.14±0.04). In females (n= 11) the range is 1.12-1.31 (mean±SD: 1.22±0.05). The different ratio seems a combined effect of a relatively longer ascending arm and a shorter dentigerous arm in females. Mandible relatively stout, with a rather steep coronoid process. The tooth bearing part is slightly less than half the jaw length. Especially rostrally, the tooth bearing part of the jaw is flaring outwards.

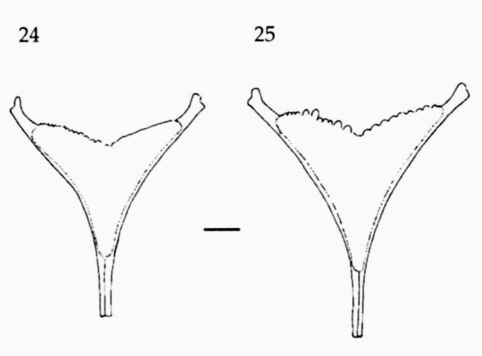
— Lower pharyngeal element (fig. 24). Lower pharyngeal element rather shallow, slightly longer than broad (length/width = 1.1). Dentigerous area slightly broader than



Figs 17-23. *Haplochromis tanaos* spec. nov. Oral jaws. Figs 17. Right premaxilla and maxilla, lateral view. Fig. 18. Medial view of ascending arm. Fig. 19. Occlusal view of dentigerous area. Fig. 21. Premaxilla, lateral view. Figs 20 & 22. Right lower jaw, lateral view. Fig. 23. Right dentary, lateral view, arrow points at detail of aberrant teeth at coronoid wing. Figs 17-20. RMNH 32540, ♀, 69.8 mm SL. Figs 21 & 22. RMNH 32528, ♂, 72 mm SL. Fig. 23. RMNH 32527, ♂, 73 mm SL. Scale equals 1 mm.

long (length/width = 0.87-0.94). The caudal margin of the element is concave.

— Vertebrae. The total number of vertebrae in 52 radiographed specimens was 29 (1), 30 (16), 31 (33) or 32 (2), comprising 13-14 abdominal and 16-18 caudal elements.



Figs 24 & 25. Outline drawings of lower pharyngeal elements, dorsal view. Fig. 24. *Haplochromis tanaos* spec. nov., paratype, RMNH 32528, ♂, SL 73 mm. Fig. 25. *Haplochromis thereuterion* spec. nov., paratype, RMNH 32624, ♂, SL 80.2 mm. Scale equals 1 mm.

Coloration.— In live quiescent males the basic colour is bluish-grey dorsally, and silvery white ventrally. The snout is greyish and the part of the head above the gill cover has a greyish blue sheen. The dorsal half of the cheek and gill cover are sooty, the ventral part of head silvery white. A relatively short and broad lachrymal stripe runs from the ventral eye margin to a line halfway between the ventral eye rim and the ventral margin of the lachrymal. The lachrymal stripe is extended on the iris. Above the eye it merges into the supraorbital stripe. A nape band, an opercular blotch and a vertical stripe rostral to the preopercular vertical limb are also present. Body bluish, darker grey blue dorsally and caudally. A mid lateral band, a dorsal lateral band and a (sometimes interrupted) dorsal medial band are present. Dorsal fin grey, lappets black. Dark red streaks may be present between the rays. Caudal fin dark grey proximally, grey with red margins distally. Anal dark red, except basally, caudally and around the egg dummies where it is dark grey. Usually only one, rather large, but relatively inconspicuously dull orange coloured egg dummy is present. Pectorals hyaline. Pelvics black. When becoming sexually active, males gradually become darker blue. Chest, belly and ventral part of head including the branchiostegal membrane turn black. The lachrymal stripe becomes broader and longer and the rostral extension of the opercular blotch almost merges into the preopercular stripe. In active males the entire ventral half of the body, from the mid lateral band to the ventral profile may become black. The dorsum becomes dark blue grey, while the area between the two longitudinal bands remains bluish. The snout and the dorsal head area remain light which is strongly contrasting to the markings in this area. The red streaks on the dorsal fin, red margins on the caudal fin and the red area on the anal fin become brighter. Two quiescent males (66.5 and 72 mm SL) had retained a juvenile coloration.

— Live coloration of females and juveniles. Females and juveniles have on the body a distinct, relatively thin mid lateral band, which is continuous between the gill cover and the caudal fin base. The caudal end of the band on the scaled caudal fin base is slightly broader. The dorsal lateral band on the dorsum is slightly less distinct. At the base of the dorsal fin a patchy dorsal medial band is present. In juveniles this band may be continued onto the caudal peduncle. Ventral side of head, chest and belly silvery white. In juveniles the entire dorsal surface of the head is rather uniformly greyish pigmented. The upper lip, the lip margins, and the mental area are also greyish. The area between the caudal eye margin and the distinct opercular blotch is weakly pigmented. On the body of some specimens very faint vertical bars are just visible. From c. 40 mm SL onwards juveniles have interorbital and nasal stripes, and a dark upper lip.

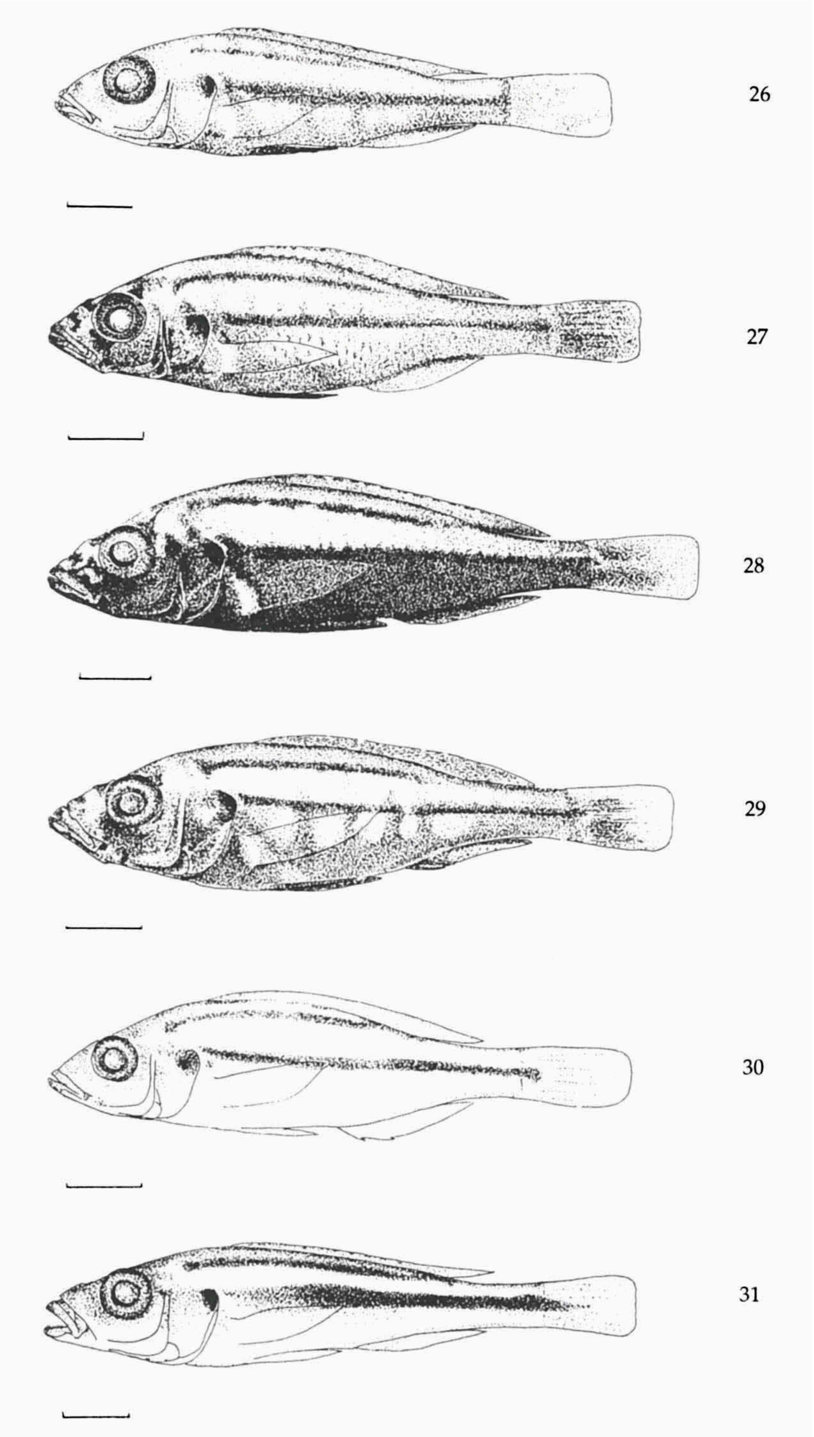
Amongst nearly one hundred examined female specimens, there was one (73 mm SL, quiescent) which had a dark "male" coloration including black pelvic fins.

— Preserved coloration of males (figs 26-29). There is a large variation in the overall darkness and distinctness of the head markings of the preserved specimens. All specimens have a continuous mid lateral band, a dorsal lateral band, and a dorsal medial band. The latter may be slightly interrupted. Relatively broad lachrymal, nasal, interorbital, and supraorbital stripes are present in most specimens, but are usually absent in spent males. In some specimens the starting point of the dorsal lateral line is an indistinct nape band. The lachrymal stripe often merges into a dark cheek. An opercular blotch is always present. Many males are very dark grey to nearly black below the mid lateral line. These specimens often have the lips a shade lighter and the snout area very light, strongly contrasting with the cheek and the nasal and orbital stripes. The dorsal parts of body and head are greyish. The caudal margin of the caudal fin may be ivory in some specimens. Lappets of dorsal fin black. Pectoral fins hyaline, and pelvics black. The membrane of the anal fin is very dark basally and along the caudal margin. Rostally and distally the membrane is light. In lighter males the membranes of the dorsal and caudal fins are light grey, lappets of dorsal black. Pectorals hyaline, pelvics black. Anal dark grey to black basally and along the caudal margin, remainder of fin membrane light grey. There are usually one or two egg dummies placed just rostral to the dark caudal margin. In quite a number of preserved specimens no egg dummies could be discerned. All males have a light area at the base of the pectoral fin. This area is more strongly contrasting in the darker males.

Preserved coloration of females and juveniles (figs 30 & 31).— Head darker grey brown dorsally, whitish laterally. Dorsal part of cheek and gill cover sooty greyish. Body above dorsal lateral band dark greyish brown, between the mid lateral and dorsal lateral band greyish, and below the mid lateral band ivory white.

Sexual dimorphism.— Apart from differences in dentition and the ratio of Premaxillary Ascending Arm Length and Dentigerous Arm Length described above, a number of differences were found between the morphometric measurements of similarly sized males and females (see tables 3, 4). It is remarkable that these differences are only apparent in the two size classes above 60 mm SL, i.e. in mature specimens in which also the difference in tooth shape is developed. Compared to males of the same length class, females above 60 mm SL have a higher ratio for LJL/LJW and lower ratios for SnW/HL and LaW/HL. Only in the length class 60-69 mm, females have higher ratios for CPL/SL, SnL/SnW and LJW/HL. Only in the length class 70-73 mm, females have higher ratios for HL/SL, PoW/LaW and LJL/HL. Males have a higher ratio for EyD/HL for the total length range (table 13).

Significant correlations between Standard Length and other taxonomic measurements (table 15). In males a negative correlation with Standard Length was found for the ratios Body Depth/SL (p= 0.0039), Caudal Peduncle Length/SL (p= 0.0004) and



Figs 26-31. *Haplochromis tanaos* spec. nov. Patterns of markings in adult specimens. Fig. 26. Quiescent ♂. Fig. 27. Starting ♂. Fig. 28. Sexually active ♂. Fig. 29. Spent ♂. Fig. 30. Quiescent ♀. Fig. 31. Female, brooding eggs. Scale equals 10 mm.

Interorbital Width/HL (p= 0.0160). A positive correlation with Standard Length was found for the ratios Snout Length/HL (p= 0.0106), Lower Jaw length/HL (p= 0.0183), Lower JawWidth/HL (p= 0.0024) and Upper Jaw Length/HL (p= 0.0001).

In females a negative correlation with Standard Length was found for the ratios Body Depth/SL (p= 0.0438), Caudal Peduncle Length/SL (p= 0.0022) and Lachrymal Width/HL (p= 0.0006). A positive correlation with Standard Length was found for the ratios Head Length/SL (p=0.0005), Snout Length/HL (p= 0.0006), SnL/SnW (p= 0.0002), Preorbital Depth/HL (p= 0.0156), Lower Jaw Length/HL (p= 0.0001) and Upper Jaw Length/HL (p= 0.0025).

Intraspecific variation.— 1) Amongst the specimens of *H. tanaos* two groups differing in head shape can be distinguished (figs 53 & 54). One group is characterized by a "smooth" head, the outline of the head being only slightly and gently interrupted by the premaxillary pedicel and the articular process of the lower jaw (fig. 53), the other group has a more "angular" head (fig. 54). In specimens of the latter group the premaxillary pedicel prominence, and the articular process of the lower jaw are more distinctly angular, the lower jaw is slightly more oblique, and the lower jaw sides are more oblique and slightly broader. Specimens of the latter group also seem to have a smaller Body Depth. In Butimba Bay the "angular head" group is restricted to the northern (more exposed) side (fig. 1). Specimens with an "angular" facies were also found in beach seine catches made at the northern shores of Nyegezi Bay, in Kayenze Bay and in trawl catches in Buchensi Bay and Namirembe Bay (fig. 32). Both in Nyegezi Bay and Namirembe Bay specimens with a "smooth" facies were caught as well. Male specimens with an "angular" facies were only caught in Butimba Bay and Kayenze Bay. As the males of the two groups did not differ in coloration we conclude

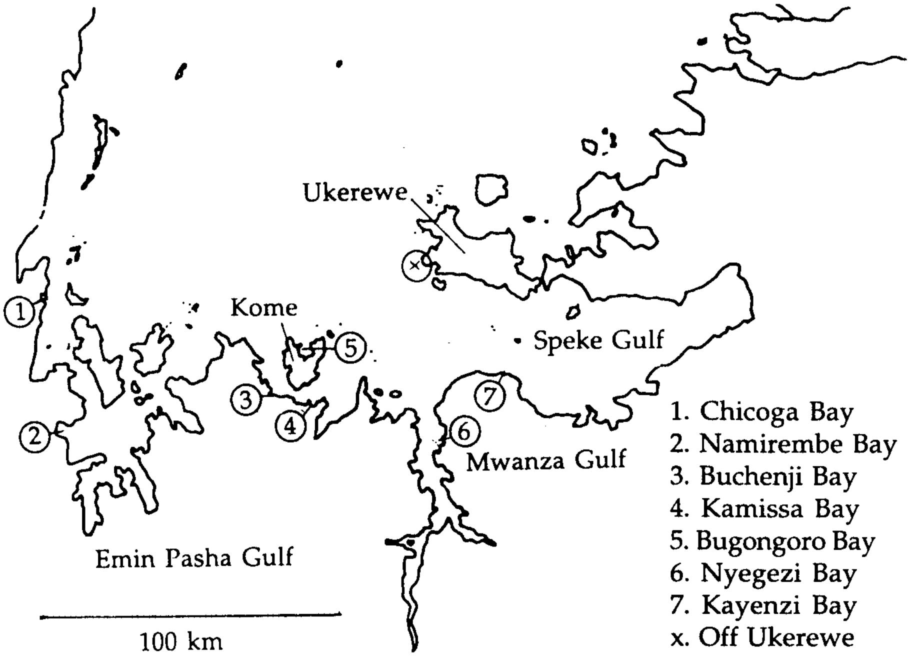


Fig. 32. Southern part of Lake Victoria with catch localities of *Haplochromis tanaos* spec. nov.

that they belong to one species. However, the possibility that they are sibling species cannot be excluded. If they belong to one species, the occurrence of morphologically different groups in different habitats could be an example of eco-phenotypic variation (Witte & Witte-Maas, 1987). If the differences in head shape are induced by ecological parameters, the fact that the two distinct forms are found in separate areas in one small bay could be taken as an indication that the fishes show very little horizontal migration.

2) Eight specimens (three ripe females, and four juveniles) caught in a bottom trawl over a sandy bottom in Bugongoro Bay, Kome Island, resemble *H. tanaos* in habitus and preserved coloration, but differ in proportional measurements. Unfortunately the live coloration of these specimens was not recorded.

3) A ripe male, 77 mm SL, caught in open water west off Ukerewe Island did show an aberrant coloration: it was much lighter than the specimens from Butimba Bay. The entire ventral side of head and body was bright white except for the belly which was sooty ventrally. It had a distinct mid lateral band and a fainter dorsal lateral band. A distinct but short lachrymal stripe was extended on and above the eye. Pectoral fins hyaline, pelvics black. Anal hyaline with a red flush and two yellow egg dummies. No dark area at the fin bases and along the caudal margin. Caudal fin hyaline with a dark red caudal half.

The specimen also differs in a number of morphometric measurements: compared to slightly smaller males, the snout is broader, the eye is smaller, the cheek is deeper, and both the upper jaw and the premaxillary ascending arm are longer. As the general facies, the dentition and aspects of its coloration are very much like that of *H. tanaos*, the specimen is only tentatively identified as belonging to this species.

Distribution.— *H. tanaos* is only known from Lake Victoria and it was caught only in the southern half of the lake (fig. 32).

Ecology.— Occurrence. In the period from 1977-1981 *H. tanaos* was a common species at the research transect across the Mwanza Gulf. However, concurrently with the explosive increase of the Nile perch population in the Mwanza Gulf it has disappeared from the catches (Witte et al., 1992b, but see below).

— Habitat. *H. tanaos* was almost exclusively caught in relatively sheltered areas with a sandy substrate (exceptionally with a peaty substrate; Namirembe Bay). These sandy areas did not exceed a depth of 7 m. The largest male was caught with a bottom trawl in open water, at a depth of c. 10 m. Since individuals were only caught with a bottom trawl and not with surface trawls, they apparently are benthic rather than pelagic. However, it was observed that individuals kept in tanks always stayed at a certain distance from the bottom.

— Food (fig. 61, table 12). To get an impression of the food of *H. tanaos*, the stomachs and guts of 41 specimens, with a SL range of 22-72 mm, were examined. The examined specimens were collected in different periods throughout the year. Seasonal differences in the food were not observed.

In juveniles as well as in adults the food mainly consisted of cladocerans (47.3 and 66.6 %, respectively), but insects are also an important food source (12.7 and 23.4 %).

Juveniles were found to differ from adults in having a large amount of chironomid larvae (1st an 2nd instars that live in the water column) in the intestines (38.7 % vs 0.5%). This difference apparently is not due to the fact that juveniles occur mainly

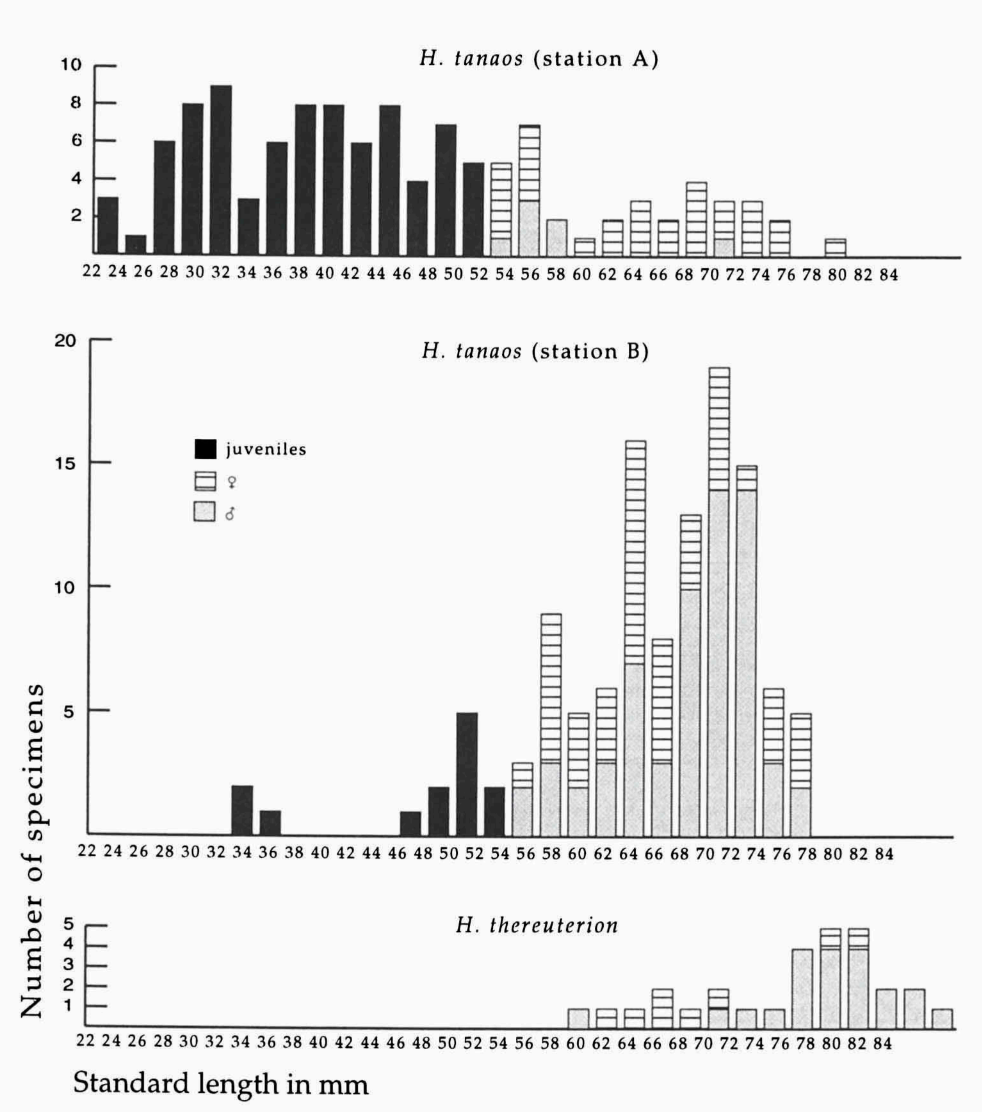


Fig. 33. Size distribution of specimens of *Haplochromis tanaos* spec. nov. in trawl catches over sand in the Butimba Bay (depth sta A, 2-4 m, sta B, 4-6 m) and size distribution of all specimens of *Haplochromis thereuterion* spec. nov.

at the shallower station A (see fig. 33). The diet of adults at station A and B reveals that although chironomids are of little importance (less than 1%), they are more frequently eaten by adult specimens at station B. Detritus was found only in small quantities (in adults only) which may indicate that the food is generally not collected from the substrate.

The food of *H. tanaos* differs in several aspects from that of other zooplanktivores from the Mwanza Gulf in the pre-*Lates* condition. In most other haplochromine zooplanktivores the zooplankton component consists mainly of copepods (Goldschmidt et al., 1990). Only in the intestines of *Haplochromis piceatus* Greenwood & Gee, 1969, besides copepods, a considerable amount of cladocerans is found (Galis, 1990; Witte, pers. obs.). In contrast, the zooplankton component of *H. tanaos* comprises almost exclusively cladocerans. It is not clear whether this is due to selective feeding or to the habitat where *H. tanaos* used to live. Juveniles of at least three piscivorous haplochromine species occurring in the same habitat also feed mainly on cladocerans (van Oijen, in prep.). Another difference with other zooplanktivores is the relatively low incidence of *Chaoborus* larvae in the food of *H. tanaos*. In the other zooplanktivores *Chaoborus* larvae were the main food item at night, when both fish and larvae migrated to the surface (Witte, 1984a; Goldschmidt et al., 1990). Although individuals of *H. tanaos* were not caught over a 24 hr period, it is to be expected that fishes caught in the morning would have some *Chaoborus* remains in the caudal part of the intestine as is the case in other zooplanktivores (e.g. Witte, 1987: chapter III). The relatively small contribution of *Chaoborus* to the diet thus indicates that *H. tanaos*, unlike the other zooplanktivores, does not follow the nocturnal migration of *Chaoborus* .

— Breeding and growth. Specimens of *H. tanaos* mature at approximately 55-60 mm SL. The largest specimen was a female of 81 mm SL. Generally however, the largest females are in the range 70-73 mm SL, while males usually remain smaller than 70 mm SL. *H. tanaos* is a maternal mouthbrooder. Mouthbrooding females were caught with eggs and larvae in various stages of development (figs 34 & 35). The right ovary grows to a larger size than than the left one. Eggs were counted in ovaries of three females. In a ripe female of 61.5 mm SL, the right ovary contained 24 eggs (length c. 2.9 mm, width c. 2 mm). The left ovary contained only a single egg. A ripe female of 70.2 mm SL had 19 eggs in the right ovary and 6 eggs in the left ovary (egg length 2.8-3 mm, width 1.8-2 mm). An almost ripe female, SL 70 mm, in the right ovary had 16 eggs (length 2.2 mm), and 7 eggs in the left ovary.

Brooding females with eggs and larvae of various ontogenetic stages were collected from both beach seine and bottom trawl catches. It seems that the number of juveniles that can be carried in the mouth of females of *H. tanaos* is very small. The largest number of juveniles, found in a female of 81 mm SL, was 17. Smaller females were found to carry even less juveniles. Twelve juveniles were found in a female of 72 mm, 11 and 9 juveniles in females of 70 mm, 10 juveniles in a female of 62 mm and 9 in a female of 65 mm.

It was observed that the brood of the female with 12 juveniles contained four specimens which differed in body shape from the other eight. It is not certain whether the four morphologically divergent specimens were just aberrant specimens (among the other eight was also an individual which lacked eyes), or that this could be an example of mixed species broods (Ribbink, 1977; Lewis, 1980) amongst Lake Victoria cichlids. Nearly ripe and ripe females were caught in March, May, August, September, November and December 1979, and in May and April 1980. Brooding females were collected in January, May, June, September, October and November 1979, and in January, April and August 1980. Sexually active males were found in catches in March, May, June, September, November and December 1979, and January, April, March, June and July 1980. From these data and the size composition in the monthly trawl catches in Butimba Bay (small juveniles were always present) it can be deduced that *H. tanaos* breeds throughout the year. The catch data are not sufficient to draw conclusions about the possible exsistence of breeding peaks.

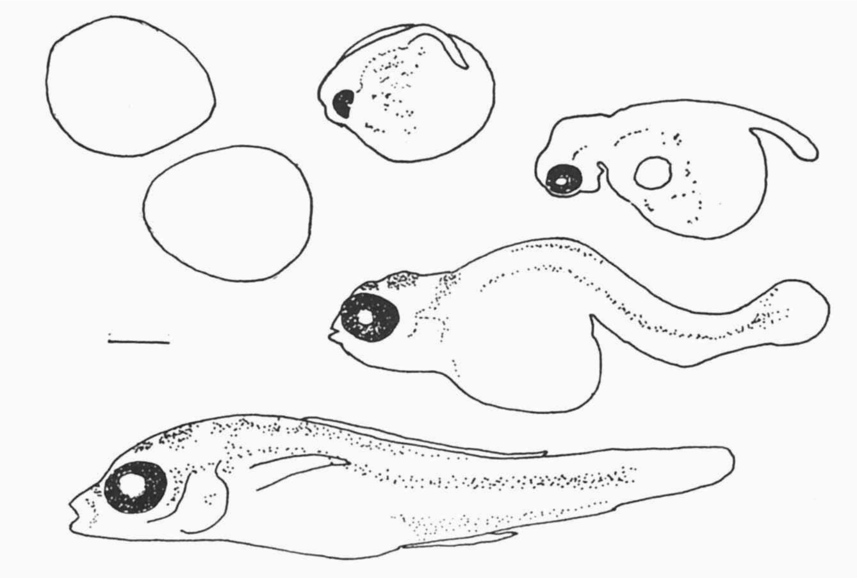


Fig. 34. *Haplochromis tanaos* spec. nov. Eggs and larval stages, with and without yolk sac, removed from the mouths of brooding females. Scale equals 1 mm.

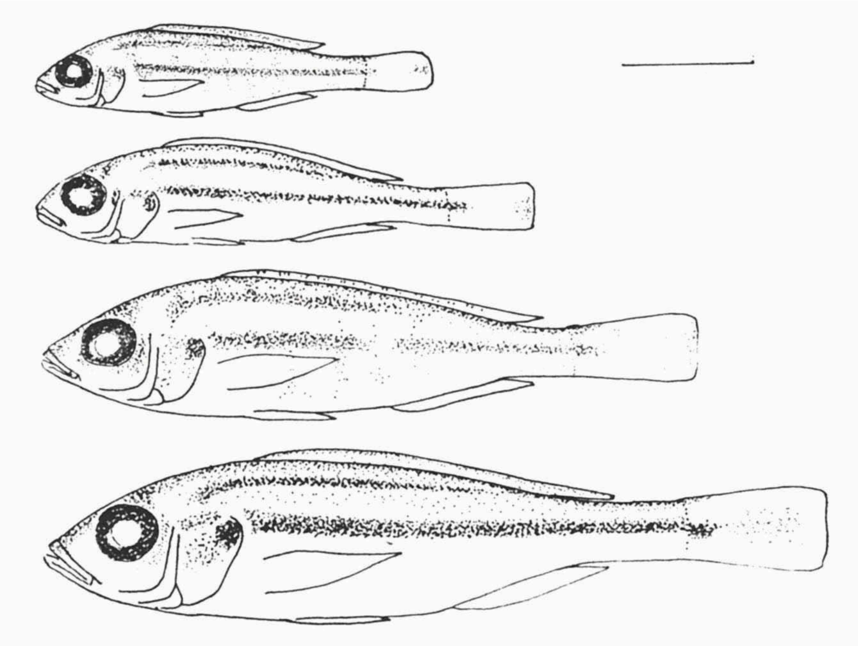


Fig. 35. *Haplochromis tanaos* spec. nov. Ontogenetic stages, juveniles 22-50 mm SL. Scale equals 1 mm.

A beach seine catch made in Butimba Bay in November 1978 contained 45 females (62-76 mm) and 24 males (60-74 mm) of *H. tanaos*. Out of the 45 females four were ripening and 13 were brooding (1 brooding eggs, 12 brooding larvae). None of the brooding females had food in the gut. Among the 24 males none was sexually active, all had food in the gut and flat and thin testis. This catch composition indicates that there are separate spawning and brooding areas for *H. tanaos*. The distribution of males and females in the trawl catches in Butimba Bay also indicates a different occurrence for the sexes (fig. 46). Of the 19 adult specimens (> 55 mm SL) caught over a sand bottom with a depth of 2-4 m (station A), 3 (16%) are male. Of the 68 adult specimens caught over sand bottoms with a depth of 4-6 m (station B), 47 (69%) were male. From this we conclude that males occur in deeper water. Five brooding females were caught over sand, at 2-4 m, and seven over sand, at 4-6 m.

Resembling species.— Because specimens of *H. tanaos* are much smaller than the holotype of *H. diplotaenia* it is difficult to compare the morphometric data of the two species. The largest specimens of *H. tanaos* differ from *H. diplotaenia* by having a relatively smaller SnL, BD, CPL, ChD, LJL and UJL, and a relatively larger PFL and HL. *Haplochromis diplotaenia* also differs in having a less compressed body, slightly thickened lips and a slightly expanded premaxilla, and a slightly higher number of oral teeth (POT 55 vs 48; LOT 45 vs 40). The differences in tooth shape are also distinct (compare figs 3 and 4 with 8 and 9).

Compared to other zooplanktivores, e.g. *H. megalops* "Mwanza", *H. laparogramma* "Mwanza" and *H. piceatus* "Mwanza" (Witte & Witte-Maas, 1987: figs 5, 6, 11), the teeth of *H. tanaos* are relatively stout. Nearly all other zooplanktivorous *Haplochromis* species from Lake Victoria (viz.: *H. heusinkveldi* Witte & Witte-Maas, 1987; *H. laparogramma* Greenwood & Gee, 1969; *H. megalops* Greenwood & Gee, 1969; *H. piceatus* Greenwood & Gee, 1969; *H. pyrrhocephalus* Witte & Witte-Maas, 1987) have a body depth mostly larger than that of *H. tanaos* (27-35 % SL vs 23.4-27.1 % SL). Only *H. fusiformis* Greenwood & Gee, 1969 is a more slender fish (BD 23.2-25.5 (M= 24.6) % SL). In this species however, lateral bands are missing. The combination of a very slender body and the two continuous longitudinal bands distinguishes *H. tanaos* from all these zooplanktivores. For differences of *H. tanaos* with *H. thereuterion*, see below.

Haplochromis thereuterion spec. nov.

(figs 8, 33, 36-51, 55, 57-60, 64, tables 7-10, 12, 14, 15)

"Haplochromis" "double stripe"; Kaufman, 1992: 849.

Material.— All.material collected by angling by HEST. Holotype, ♂. 76.0 mm, RMNH 32625. Anchor Island, Mwanza Gulf, Lake Victoria, Tanzania., 13.v.1978. Paratypes (22 ♂♂ + 5 ♀♀); Anchor Island: 1 ♂, 74.5 mm + 1 ♀, 67 mm, RMNH 32622-23, 18.ii.1978; 3 ♂♂, 74.5-80.2 mm, RMNH 32624, 32626-27, 13.v.1978; 2 ♂♂, 77-77.2 mm, RMNH 32628-29, 16.1.1979; 2 ♂♂, 74.6-78.5 mm, RMNH 32630-31, 24.viii.1979; 2 ♀♀, 73.2-76.3 mm, RMNH 32632-33, iv.1980; 2 ♂♂, 76.1-80.2 mm, RMNH 32634-35, 16.iv.80. Nyegezi Rocks, entrance Nyegezi Bay: 1 ♂, 66.2 mm + 1 ♀, 60 mm, RMNH 32636-37, 15.vii.1978; 2 ♂♂, 62.9-72.5 mm, RMNH 32638-39, 18.vii.1978; 1 ♂, 72.3 mm, RMNH 32640, 20.vii.1978. Mushroom Island, Nyegezi Bay: 2 ♂♂, 68-71 mm, RMNH 32641-42, 17.xii.1978; 1 ♂, 72.3 mm + 1♀♀, 63.2 mm, RMNH 32643-44, 5.ix.1979. Rocks at eastern shore Nyegezi Bay: 2 ♀♀, 63.1-64 mm RMNH 32645-46, 27.x.1978. Rocks near Mushroom Island: 1 ♂, 82 mm, RMNH 32647, 7.i.1979. Mwanza Gulf Rocks: 2 ♂♂, 55.5-75.7 mm, RMNH 32648-49, 29.vii.1978. Other material.— Hippo Island: 1 ♂, 70.5 mm, RMNH 32621, 24.ix.1979.

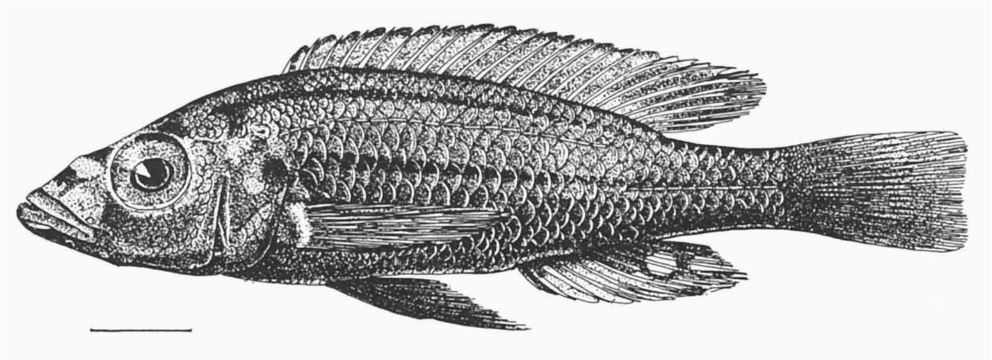


Fig. 36. *Haplochromis thereuterion* spec. nov., ♂ paratype. RMNH 32631. Scale equals 10 mm.

Etymology.— The name is derived from the diminutive of the Greek ϑηρευτηριων (hunter), referring to the predatory habits of this small species.

Diagnosis.— A small, slender, laterally compressed micrognathic species with a nearly straight dorsal head profile, distinctly interrupted by the premaxillary pedicel. The species has an acute snout, slightly thickened lips and the premaxilla slightly medially expanded. It has two continuous longitudinal bands on the body. In sexually active males, which may become pitch black, these bands may be difficult to distinguish.

Description.— Based on 28 specimens with a standard length of 55.5-82.0 mm. Morphometric measurements were taken from all specimens. Because males and females were found to differ in dentition and premaxilla shape it was believed they might also differ in certain other head proportions. Therefore, ranges, means and standard deviations of measurements of males and females were calculated separately.

Habitus (fig. 36).— A small and slender, laterally compressed haplochromine species with a rather acutely pointed snout (both in lateral and dorsal view) and a terminal mouth. Dorsal head profile slightly curved in the nape region, nearly straight from nape to snout tip. The premaxillary pedicel distinctly interrupting the profile in most specimens. Premaxilla in most specimens slightly expanded medially. Upper lip not produced above the dorsal head profile. Exposed part of maxilla small, the posterior tip reaching a vertical just posterior to the anterior eye border. Ventral outline of the head with a gentle bend at the articular process of the lower jaw. In adducted specimens the left and right articular process are touching each other. Sides of lower jaw sligthly oblique. Lower jaw ventral outline almost straight. The slightly receding rostral outline of lower jaw straight or slightly convex with a smoothly rounded mental area, no mental prominence. Jaws slightly prognathous in most specimens. Lips slightly thickened. Position of dorsal eye margin in lateral view almost touching or touching the dorsal head profile. Eye moderately large, circular. The pupil has an ovoid shape. Small aphakic apertures rostral and caudal to the lens. Preopercular horizontal limb horizontal, the vertical limb slightly reclining. The rostral part of the interoperculum is almost completely hidden under the preopercular horizontal limb. Lateral line canals and openings slightly enlarged in some specimens.

Scales (figs 8 & 55).— All scales on the head are cycloid. Operculum fully scaled except for a small area which partly covers the opercular blotch. Suboperculum scaled except for a thin ventral rim. Interoperculum scaled only on its caudal half (3-4 scales). In a few specimens these scales are almost completely covered by skin. Preoperculum scaleless. Cheek fully scaled in most specimens. A few specimens have the scales at the rostro-ventral corner rather deeply embedded under the skin. In a number of specimens this area (the rostral embayement of Lippitsch, 1993) is scaleless. The scaleless area may be extended caudad to include the entire ventral rim of the cheek. Postorbital column variable: most specimens have two scale rows, but specimens with one row are also found. Lachrymal scaleless. Occiput scaled, no distinct pattern recognizable on occiput or area in front of the dorsal fin. Scales on rostral part of dorsum cycloid or very weakly ctenoid, caudal part of dorsum with ctenoid scales. Scales on flank and caudal peduncle ctenoid. Ventral chest scales small and cycloid, lateral chest scales moderately small, weakly ctenoid. Size transition from chest scales to flank and belly scales gradual. In some specimens the chest scales are deeply embedded in the skin. The scale between the pelvic fins slightly enlarged. No scales or scale sheaths on dorsal or anal fins. The caudal fin has cycloid scales on its proximal half. The distal scales arranged in single rows between the rays.

Fins.— Pectorals just reaching the anus. Pelvics in females just not reaching a vertical through this point. In sexually active males the produced first pelvic ray reaches the anal spines. Dorsal fin rays slightly longer than those of the anal, nearly reaching the caudal fin base in some specimens. Caudal fin outline (sub)truncate, its caudal margin slightly biconvex or emarginate.

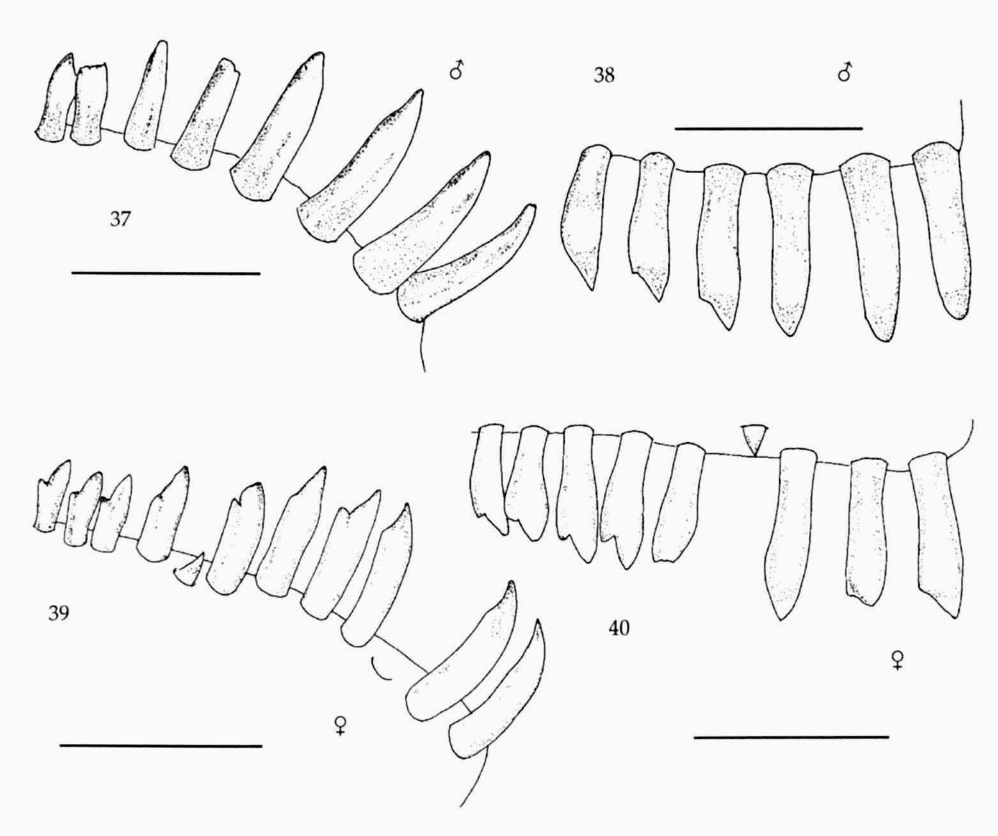
Gill apparatus.— Eight to ten gill-rakers on the lower part of the first gill-arch; the lowermost two reduced, the others mostly conical except for the dorsalmost two which are usually somewhat compressed and broadly ending. The number of gill filaments on the lateral hemibranch of the first gill-arch is about 94-100 (n= 3).

Viscera.— In specimens with food in the gut the intestine length varies from 0.78-1.25 times the standard length (n= 13). In two females with empty guts the intestine lengths were 0.5 and 0.68 times SL. Following the definitions of Zihler (1982) the arrangement of the digestive tract of adult *H. thereuterion* is of type E.

Oral teeth (figs 37-40).— Shape. There is a remarkable difference in tooth shape between adult males and females. Compared to males of a similar size, females have a much smaller number of unicuspid teeth in the outer row of both jaws (table 10). The largest males have only unicuspids in the outer rows of both jaws.

Females have in both jaws, usually one or two unicuspids rostrally, bicuspids laterally, and a mixture of bicuspids and tricuspids caudo-laterally. The unequal bicupids and tricuspids have compressed crowns. The major cusp of the bicuspid teeth sometimes has a small flange. The middle cusp of the tricuspid teeth is rather short. All teeth are slightly to moderately curved. The unicuspids are circular in cross section and acutely pointed. The rostral six to eight teeth are noticeable larger than the following ones. Tooth size decreases from rostral to caudal, but in the caudal part of the jaws the size difference between the teeth is very small. In males, even in specimens with bicuspids laterally, one to four caudal teeth often are unicuspids of a slightly larger size than the preceding ones. In females such unicuspid caudal teeth are only rarely found.

Inner rows: some rostrally situated inner teeth may be unicuspid, but the majority is tricuspid. Tricuspid teeth in the rostral part of the jaws have the middle cusp



Figs 37-40. *Haplochromis thereuterion* spec. nov., oral jaw teeth. Figs 37 & 39. Lower jaw teeth, lateral view. Figs 38 & 40. Premaxilla teeth, rostro-lateral view. Figs 37 & 38. ♂ Paratype, RMNH 32640, ♂, SL 72.3 mm. Figs 39 & 40. ♀ Paratype, RMNH 32632, SL 73.2 mm. Scale equals 1 mm.

more elongated than the lateral teeth. All inner teeth are moderately curved.

— Dental arcade and toothband. Dental arcade slightly acute in both jaws. Two inner rows in both jaws. Distance between outer row and first inner row larger than the distance between the inner rows.

— Counts and setting. Specimens of 55.5-82.0 mm SL have 36-44 teeth in the outer row of the upper jaw and 28-38 in the lower jaw. The outer row teeth are regularly set at a distance equal to or slightly less than the diameter of the toothbase. The outer row occupies 4/5 of the premaxilla and on the dentary just reaches the coronoid wing. In one dissected lower jaw the most caudal tooth is separated by a distinct gap from the other teeth and set relatively high on the coronoid process (fig. 45). The inner rows occupy 7/10 of the outer row length on the premaxilla and 3/5 of the outer row length on the mandible.

— Implantation. In the upper jaw, the outer row teeth are erect (medial teeth) to slightly recumbent (caudal teeth). In the lower jaw, the outer row teeth are slightly to moderately procumbent (medially) to erect (laterally and caudally). All teeth are slightly suspensoriad inclined. Implantation of inner row teeth in upper jaw strongly recumbent, in lower jaw erect.

Pharyngeal teeth.— Counts. Twenty-four teeth in the caudal row and 8-11 teeth in the two medial rows.

— Shape. Most pharyngeal teeth are of the bevelled type, relatively fine and acutely pointed; some medial teeth of the caudalmost row and some caudal teeth of the medial rows are slightly enlarged and hooked, with a blunt rostro-dorsad directed major cusp. Tooth size increasing from rostral to caudal and from lateral to medial.

Osteology.— The osteological descriptions are based on skeletal elements of three dissected specimens, SL 72.3-81.0 mm.

— Neurocranium. Because the number of specimens is limited, a skeletal preparation of a neurocranium was not made. Judging from radiographs of 15 specimens, the outline of the neurocranium is very similar to that of *H. tanaos*.

— Oral jaws (figs 41-46). Premaxilla; ascending arm longer than dentigerous arm, angle between the arms 73-78°(n= 3) Ventral outline of dentigerous arm slightly concave. Ventral part of the ascending arm very slightly expanded. Mandible relatively stout, with a rather steep coronoid process and a relatively large suspensoriad articulation facet. The tooth bearing part is slightly less than half the jaw length. Especially rostrally, the toothbearing part of the jaw is flaring outwards.

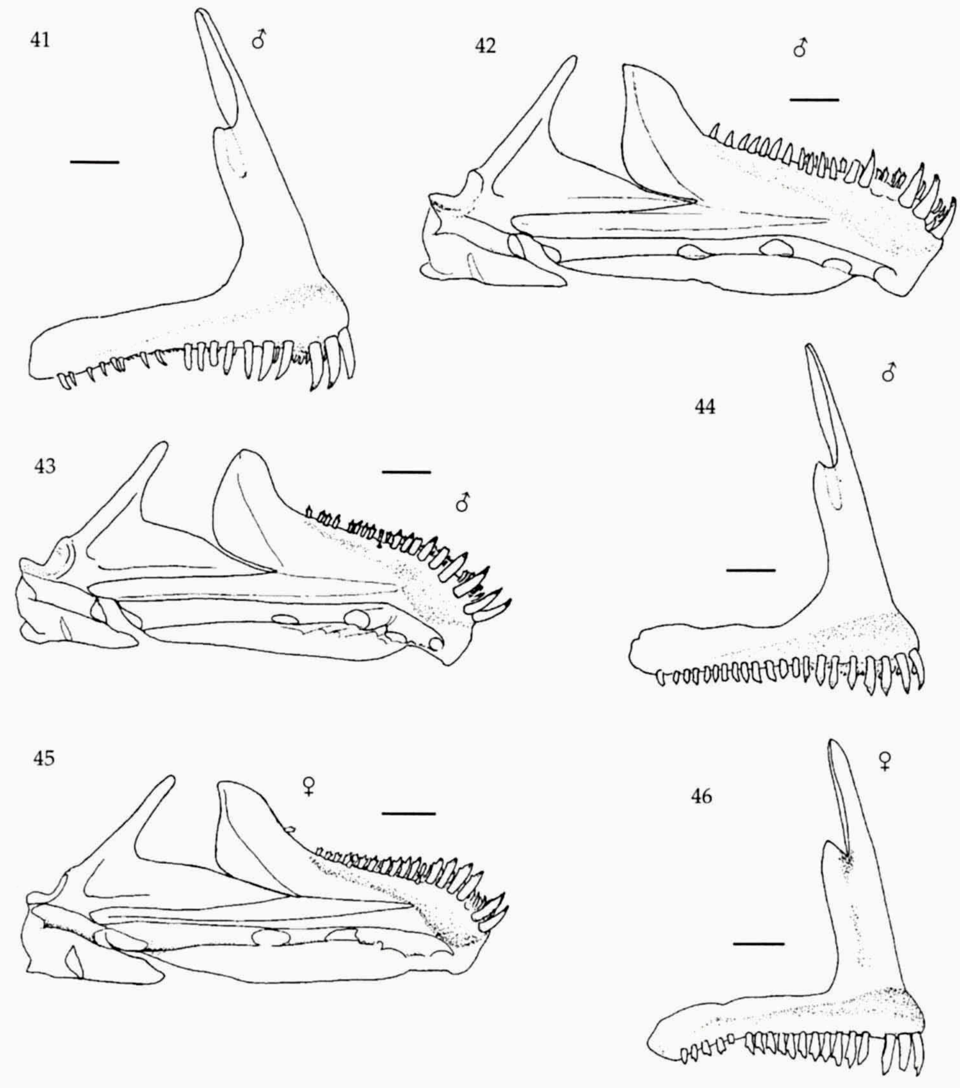
— Lower pharyngeal element (fig. 25). Lower pharyngeal element rather shallow, slightly longer than broad (length/width = 1.09-1.14). Dentigerous area about as broad as long (length/width = 0.94-1.08).

— Vertebrae. The total number of vertebrae in 15 radiographed specimens was 29 (1), 30 (3), 31 (11), or 32 (1), comprising 12-14 abdominal and 16-18 caudal vertebrae.

Coloration.— Live quiescent males have a coloration like that of quiescent males of *H. tanaos* (see p. 16). Sexually active males have a pitch black head and body. Dorsal fin black on the proximal half dark, grey distally. Lappets black. Proximal third of caudal black, the remaining third greyish and the fin corners and caudal margin red. Anal fin black between the spines, basally and along the caudal margin. Remaining part of fin membrane dark red. Egg dummies, when present, orange yellow. Pectorals hyaline, pelvics black.

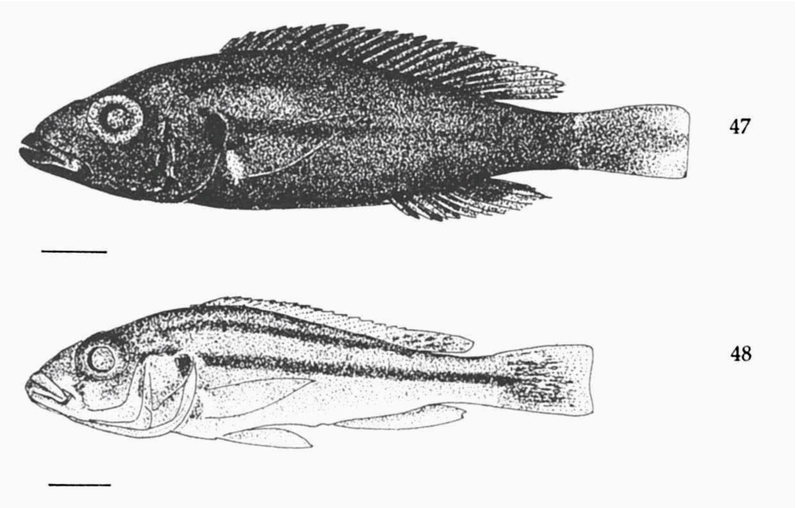
— Females of *H. thereuterion* are coloured like females of *H. tanaos.*, but have the cheek slightly more greyish.

Preserved coloration of males (fig. 47).— There is a large variation in the overall darkness and the distinctness of the head markings of the preserved specimens. All specimens have a continuous mid lateral band, a dorsal lateral band, and a dorsal medial band which may be interrupted. Relatively broad lachrymal, nasal, interorbital, and supraorbital stripes are present in most specimens. In some specimens the starting point of the dorsal lateral line is an indistinct nape band. The lachrymal stripe often merges into an equally dark cheek. An opercular blotch is always present. Many males are very dark grey to nearly black below the mid lateral line. These specimens often have the lips a shade lighter and the snout area very light, strongly contrasting with the dark cheek and the nasal and orbital stripes. The dorsal parts of body and head are greyish. In males which have the entire body and head dark brown to black, the head and body markings are almost indistinguishable. The membranes of the dorsal and caudal fin of these males are dark grey. The caudal margin of the caudal fin may be ivory in some specimens. Lappets of dorsal fin black. Pectoral fin hyaline, pelvic black. In lighter males the membranes of the dorsal and cau-



Figs 41-46. *Haplochromis thereuterion* spec. nov. Oral jaws. Figs 41, 44, 46. Right premaxilla, lateral view. Figs 42, 43, 45. Right lower jaw, lateral view. Figs 41 & 42. ♂ Paratype, RMNH 32624, ♂, SL 80.2 mm. Figs 43 & 44. ♂ Paratype, RMNH 32640, ♂, SL 72.3 mm. Figs 45 & 46. ♀ Paratype, RMNH 32632, SL 73.2 mm. Scale equals 1 mm.

dal fins are light grey, lappets of dorsal fin black. Anal dark grey to black basally and along the caudal margin, remainder of fin membrane light grey. There are usually one or two egg dummies placed just rostral to the dark caudal margin. In a number of specimens no egg dummies could be discerned (figs 49-51). All males have a light area at the base of the pectoral fin. This area is more strongly contrasting in the darker males.



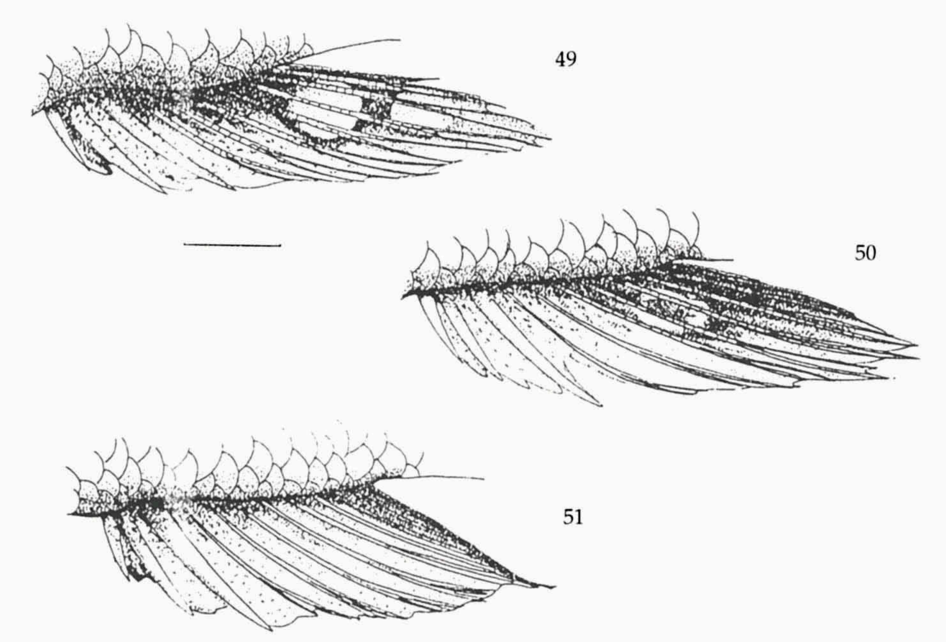
Figs 47 & 48. *Haplochromis thereuterion* spec. nov. Patterns of markings in adult specimens. Fig. 47. Sexually active ♂. Fig. 48. Quiescent ♀. Scale equals 10 mm.

Preserved coloration of females (fig. 48).— Head darker grey brown dorsally, whitish laterally. Dorsal part of cheek and gill cover sooty greyish. Body above dorsal lateral band dark greyish brown, between the mid lateral and dorsal lateral band greyish, and below the mid lateral band ivory white.

Sexual dimorphism.— Although the number of females as compared to males is low (6 vs 22), and no females in the length class 80-90 mm were caught, the following significant differences between the ratios of morphometric measurements of the sexes were found in the two remaining length classes and the total range (table 14): Compared to females of a similar size males have a higher ratio for Body Depth/SL. In the length class 60-69 mm, females have a higher Caudal Peducle Length/Depth ratio. In the length class 70-79 mm males have a higher ratio for Interorbital Width/HL. Over the total range of 60-82 mm, males have a higher ratio for Pectoral Fin Length/SL.

In males, a significant negative correlation was found between the Standard Length and the Caudal Peduncle Depth/SL ratio. For females a significant positive correlation between Standard Length and the Snout Length/HL ratio was found (table 15).

— Intraspecific variation. Specimens caught near different islands (even as close as Anchor Island and Mushroom Island) seem to exhibit small differences in habitus and dentition, difficult to quantify in proportional measurements. The only specimen of the *H.* "double stripe" complex caught from the rocks of Hippo Island, although resembling *H. thereuterion* in dentition and thickened lips, diverges in proportional measurements and its very light preserved coloration. As was shown by Witte (1984a), the islands in the Mwanze Gulf are often surrounded by a relatively deep trough, which may form a considerable barrier to the dispersal of the species occurring at their margins (Dorit, 1990). Bouton investigated the isolation of rock-frequenting haplochromines on islands in the Mwanza Gulf and the Speke Gulf. Working with much larger sample sizes he was able to show differences in morphometric



Figs 49-51. Variation in anal fin markings of adult males of *Haplochromis thereuterion* spec. nov. Fig. 49. RMNH 32631. Fig. 50. RMNH 32625. Fig. 51. RMNH 32622. Scale equals 5 mm.

measurements in many algae grazing species occurring at different islands (Bouton, pers. com.). Therefore, it is not unlikely that populations of *H. thereuterion* from different islands would exhibit morphological differences.

Distribution.— *H. thereuterion* is known only from Lake Victoria. Specimens were caught only at rocky margins of the Butimba Bay and Nyegezi Bay and near rocky islands in the northern part of the Mwanza Gulf (fig. 52).

Ecology.— Occurrence. Amongst the species living at the periphery of rocks *H . thereuterion* was a relatively rare species. Since the explosive increase of the Nile perch population in the Mwanza Gulf area it has disappeared from the catches (Witte et al., 1992b; Seehausen, 1991, 1995).

— Habitat. *H. thereuterion* was only caught at the periphery of the rocks, never between rock crevices. All specimens were caught between 50 and 100 cm below the surface in water with a depth between 2-4 m. This indicates that *H. thereuterion* occurs in the upper layers of the water column.

— Food (fig. 61, table 12). Of the 18 examined specimens two were completely empty (both large females), one had mainly copepods in the gut, and the remaining fifteen all fed on insects and insect larvae. Among the insects were many ants and Diptera, which probably were taken from the water surface. Among the insect larvae chironomids predominated. In the guts of two specimens collected from a site where rocks are bordering a sandy beach, Trichoptera larvae were found. One specimen had remains of a small *Haplochromis* in its gut. It seems that *H. thereuterion* is a pelagic insectivorous species which collects part of its food from the water surface.

— Breeding and growth. All investigated specimens of *H. thereuterion* are mature, so the species matures at less than 55 mm SL. Judging from the available specimens, males grow to a larger size than females. As this species probably is a maternal mouthbrooder and all specimens were collected by angling, it is not surprising that no brooding females were caught.

Resembling species.— *H. thereuterion* is very similar to *H. tanaos*, though in the morphometric measurements of the two species small differences are found (tables 3, 4, 7, 8). Significant differences between *H. tanaos* and *H. thereuterion* were found for the following measurements and size classes: Body Depth/SL ratio higher in 60-80 mm males of *H. thereuterion*; Preorbital Depth/HL ratio higher in males of *H. thereuterion*; Eye Length/HL ratio lower in 70-80 mm males of *H. thereuterion*; Eye Depth/HL ratio lower in males and in females of *H. thereuterion*; Cheek Depth/HL ratio higher in 60-70 mm males of *H. thereuterion*; Snout length/HL ratio higher in 60-70 mm females of *H. thereuterion*.

H. thereuterion also differs by having the premaxilla slightly expanded and by its slightly thickened lips. In *H. thereuterion* the outer teeth are relatively larger, less acutely pointed and more procumbently implanted. Moreover, the size difference between the rostralmost outer teeth and the lateral teeth seems larger. Most important however, is the difference in the live coloration of sexually active males, which is black in *H. thereuterion* and darker blue in *H. tanaos*. Another difference is found in the relative size of the sexes in the two species: in *H. thereuterion* the males reach a larger size than the females (as in other rockfrequenting species: Witte & Witte-Maas, 1987), whereas in *H. tanaos* the females grow larger. *H. tanaos* occurs near the substrate, whereas *H. thereuterion* occurs higher in the water column. Although *H. tanaos* and *H. thereuterion* are very similar, both in external morphology and dentition, the two species show very little overlap in diet. The body shape indicates that both species are capable of quick darts at a prey. In the case of *H. thereuterion* the prey are mainly insects, while for *H. tanaos* the main prey are cladocerans.

It is remarkable that all adult males of *H. tanaos*, except one, were caught close to the bottom at some distance from the shore over a depth of 4-6 m, whereas all adult specimens (both male and females) of *H. thereuterion* were caught close to the rocks 50-100 cm under the water surface. This is another indication that two species are concerned.

When the morphometric measurements of the largest specimens of *H. thereuterion* are compared to those of the holotype of *H. diplotaenia*, the same differences are found as between *H. diplotaenia* and *H. tanaos*, except for the Head Length. The HL/SL ratio of *H. diplotaenia* (SL 89.9 mm) lies in the range of specimens of 80-82 mm of *H. thereuterion*. *H. thereuterion* resembles *H. diplotaenia* in having slightly thickened lips and a slightly expanded premaxilla, but the tooth shape of the two species is quite different. The differences between *H. thereuterion* and the haplochromine zooplanktivorous species from Lake Victoria are similar to those of *H. tanaos* (see p. 24).

Compared to specialized rock-frequenting insect eaters like *H. chilotes* Boulenger, 1911, and *H. chromogynos* Greenwood, 1959 (see Greenwood, 1974: fig. 33), the teeth of *H. thereuterion* are relatively small. Even compared to *H. nyererei* Witte-Maas & Witte, 1985, a rock-frequenting species that eats both zooplankton and chironomid larvae, the lower jaw and the oral teeth of *H. thereuterion* are relatively slender.

Selbrink (1985) published some interesting notes on breeding habits of a rock-frequenting species he named "*H.* sp. aff. *longirostris*", which, judging from colour photographs of both male and female specimens, show a great similarity in body shape and coloration with the species of the *H.* "double stripe" complex. Selbrink observed in aquaria that the males have large territories and that females after having completed the mating occupy a small area in this territory where they seem to be actively protected by the male. One male may have several females carrying eggs in his territory. Selbrink noted that immediately after spawning the female adopts "egg carrying colors", which change after she has released her fry. When the female loses her brooding colours she is chased from the male's territory. After a few weeks when the female is ready to breed again she again changes colour. Unfortunately no descriptions of the three colour patterns are given. Selbrink (1985: 69) noted that few eggs are laid "20 is a good number for a large female". It must be stressed that only examination of the teeth can reveal the identity of the specimens.

Generic placement of *H. diplotaenia* and the species of the *H.* "double stripe" complex

In part II of his revision of the *Haplochromis* generic concept, Greenwood (1980) made a genus for very slender haplochromine cichlids aptly named *Yssichromis*. This genus was defined on two apomorphic characters concerning the Body Depth and the dentition of the premaxilla, respectively. In his diagnosis of *Yssichromis* Greenwood (1980: 23) writes: "Shallow bodied, elongate haplochromines (body depth 23-30% SL, modal range 27-29%, caudal peduncle 17-25% SL, (modal range 19-22%), its depth contained 1.7-2.1 times (modally 1.8-2.0) in its length, reaching a small adult size (85-110 mm SL)." Thus, on the basis of their Body Depth the holotype of *H. diplotaenia* as well as the new species *H. tanaos* and *H. thereuterion* would fit in *Yssichromis*. However, the second character considered apomorphic for the genus is that "the premaxilla is edentulous over the posterior 1/4-1/3 of its dentigerous arm." In the three species described above the dentigerous area occupies at least 4/5 of the dentigerous arm of the premaxilla. Therefore, they cannot be placed in the genus *Yssichromis* as it is defined at present. Witte & Witte Maas (1987) encountered similar problems with the definition of *Yssichromis* in the generic placing of new zooplanktivorous species. After an analysis of Greenwood's data these authors concluded that there was no clear distinction between the genera *Yssichromis* and *Astatotilapia*. Therefore, they decided to place their new species in the genus *Haplochromis* as it was used prior to the revision of Greenwoood.

Greenwood (1980: 13) on the basis of its neurocranial architecture as seen on a radiograph provisionally placed *Haplochromis diplotaenia* near *Harpagochromis* Greenwood, 1980. However, our tracing of a radiograph of the holotype of *Haplochromis diplotaenia* revealed that this specimen (like *H. laparogramma*) has a rather low, wedge shaped occipital crest comparable to that of some species placed by Greenwood (1980) in his new genus *Prognathochromis*. As the distinction between *Prognathochromis* and *Harpagochromis* based on neurocranial characters is considered artificial (van Oijen, 1991) and as we consider there are many other problems with the haplochromine genera defined by Greenwood in 1980 (van Oijen, 1996) we prefer to place both species in the genus *Haplochromis*.

Disappearance and return of fishes of the *H.* " double stripe"complex in the research transect of the Mwanza Gulf

In the period of November 1977-November 1981, *H. tanaos* was a common species over sand bottoms in the Butimba Bay (100% occurrence in bottom trawl catches). After 1981 the monthly sampling program at the transect was changed. From 1982-1987 sampling was mainly done at stations E and G (fig. 2). In the period 1987-1993 all stations were fished occasionally with bottom trawls again, while gill net and floating trawl catches were made more frequently. In none of the catches until October 1993 *H. tanaos* was present. However, between October and December 1993 fishes of the *H.* "double stripe" complex were caught regularly at stations J and K over mud in Kissenda Bay (figs 2, 52). In total 17 fishes (22-65.2 mm SL) were collected at these stations (table 11; Seehausen et al., submitted). In a trawlshot with R.V. Kiboko around the papyrus island in the Kissenda Bay on 22.x.1993 another 7 individuals were caught. It is surprising that the specimens were not caught in their former habitat at the sheltered sand stations in the Butimba Bay (fig. 1, sta. A & B), but at relatively more exposed shallow stations with a mud bottom at the opposite side of the Mwanza Gulf.

Material.— 1 ♂, 65.2 mm + 3 ♀♀, 51.7- 62.2 mm, RMNH 32655-58, 19.x.1993, Mwanza Gulf, sta. J; 7 juv, 23-50 mm, RMNH 32659-65 , 19.x.1993, Mwanza Gulf sta. K. All specimens collected by HEST with a bottom trawl.

Description (figs 53-61).— In body shape and markings these specimens are very similar to equally sized specimens of *H. tanaos*. In head shape they are nearer the "angular" than the "smooth" type (compare figs 53, 54, 56). Morphometric measurements were taken from all specimens above 50 mm SL (viz., four specimens: 51.7; 55.1; 62.2 and 65.2 mm SL). Comparison of the measurements of these specimens with those of similarly sized specimens of *H. tanaos* made clear that they fall in the known ranges.

The upper jaw and lower jaw from the right side of the largest specimen, proba-

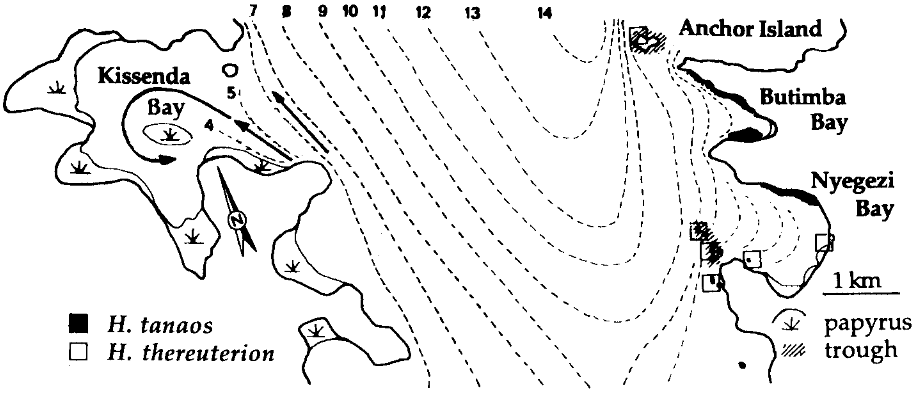
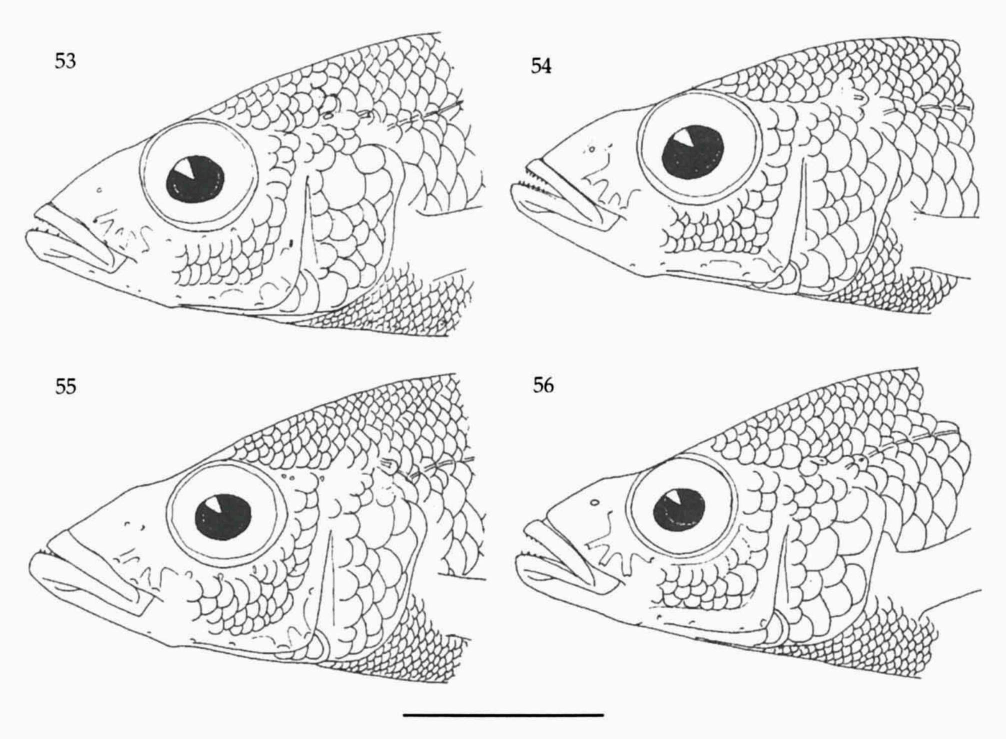


Fig. 52. Map of the research transect in the Mwanza Gulf with catch localities of specimens of the *Haplochromis* "double stripe" complex. Arrows indicate trawl tows from which the specimens in 1993 were collected.

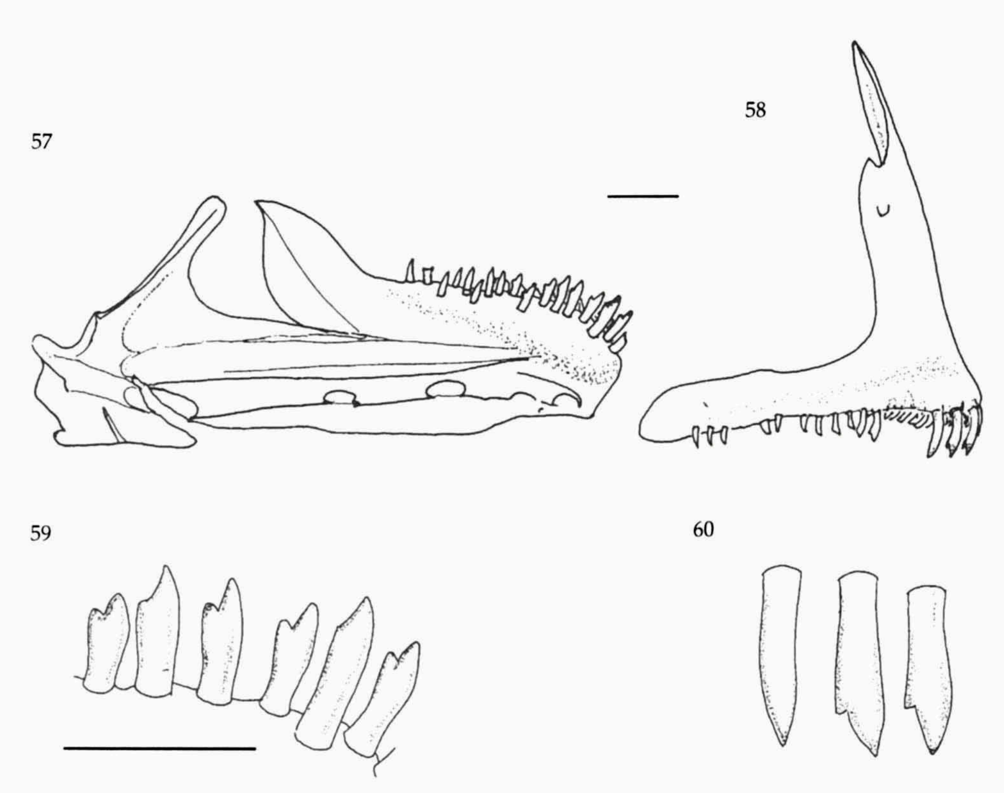


Figs 53-56. Variation in head shape in the *Haplochromis* "double stripe" complex. Fig. 53. *Haplochromis tanaos* spec. nov. "smooth" form, RMNH 32600, SL 66.9 mm. Fig. 54. *H. tanaos* spec. nov. "angular" form, RMNH 32529, SL 70.5 mm. Fig. 55. *Haplochromis thereuterion* spec. nov., RMNH 32631, SL 74.6 mm. Fig. 56. ♂ specimen caught in 1993, RMNH 32655, SL 65.2 mm. Scale equals 10 mm.

bly a ripening male, were dissected and figured (figs 57-60). Compared to the lower jaw of *H. tanaos*, it is slightly more stout and the teeth in the outer row are less acutely tapering. The premaxilla is very similar to that of *H. tanaos*. In both jaws the number of unicuspid teeth is relatively small.

The preserved coloration of the female and juvenile specimens is like that of *H. tanaos*. However, the preserved coloration of the male is much lighter than that of male *H. tanaos*. Fortunately, a photograph of this male was taken by O. Seehausen immediately after capture. The live colours of the male as recorded on this photograph are as follows.

Markings.— Medially on the snout, short nasal and interorbital stripes are present. Rostro-ventrally to the eye a lachrymal stripe, which is as broad as it is long, reaches the middle of the lachrymal. Above the eye the supraorbital stripe seems to reach the median. The opercular blotch is more or less connected to the caudal margin of the eye by a broad horizontal band. The ventro-rostral triangular part of the operculum is dark grey. On the body a distinct mid lateral band runs uninterrupted from slightly behind the gill cover to the caudal fin base. It continues on the basal part of the fin. Parallel to the mid lateral band a slightly thinner dorsal lateral band runs from a point under the dorsal fin origin to the end of the dorsal fin base where



Figs 57-60. Oral jaws and oral jaw teeth of a 65.2 mm, ♂ specimen of the *Haplochromis* "double stripe" complex caught in 1993. RMNH 32655. Fig. 57. Right lower jaw, lateral view. Fig. 58. Right premaxilla, lateral view. Fig. 59. Rostral lower jaw teeth, lateral view. Fig. 60. Rostral premaxilla teeth, rostrolateral view. Scale equals 1 mm.

it continues as a medial dorsal band on the caudal peduncle. On the rostral half of the body five relatively broad but faint vertical bars are visible. Body and head dorsal to the mid lateral band light brownish grey, except for a yellowish-silvery area caudal to the eye and dorsal to the gill cover. Snout and upper lip light brownish grey. Suboperculum, vertical preopercular limb, cheek and ventral part of head light yellowish silver. Horizontal preopercular limb, lower jaw laterally and lower lip iridiscent green. Body ventral to the mid lateral band light yellowish. Ventral part of chest and belly sooty. Dorsal fin membrane hyaline between the spines, on the membrane between the rays long black streaks are present. Lappets black. Caudal fin membrane brownish grey, rays lighter. The dorsal and ventral corners of the fin have a light red sheen. The anal fin is black between the spines, and has a red fan shaped area with the tip at the fin base behind the third spine. Distally to this red fan the membrane is hyaline with a red flush, caudally the membrane is hyaline with a grey flush. Two relatively large orange-red egg dummies with a thin yellow rim are present. One lies close to the red area, the other in the grey-hyaline area. Pelvic fins hyaline, pectorals black.

Although these colours match those of *H. tanaos* in most respects it lacks the characteristic overall bluish coloration of that species.

Food (fig. 61).— The intestines of all specimens were examined for food remains. The intestines of all specimens contained remains of insects or insect larvae. Trichoptera were found in five specimens, chironomid larvae in four specimens. Six specimens contained zooplanktonic crustaceans. Cladocera were found in five, Copepoda in six, and Ostracoda in three specimens. In two specimens remains of the cyprinid *Rastrineobola argentea* Pellegrin, 1904, were found. One, a specimen of 62.5 mm SL, had eaten a *Rastrineobola* of c. 12 mm, and a specimen of 51 mm SL had swallowed two fishes of c. 18 mm. The densities of *Rastrineobola* have increased considerably since the Nile perch upsurge (Wanink, 1991; Witte et al., 1992a). *Rastrineobola* currently is a major component in the bottom trawl catches of the small trawler at stations J and K (O. Seehausen, pers comm.). Judging from the volume percentage of the food, the specimens taken together, can be considered predominantly insectivorous.

In conclusion it can be said that in their feeding habits the recently caught specimens resemble *H. thereuterion* more than they resemble *H. tanaos*, while morphologically and in male coloration they are nearer to *H. tanaos*. However, the resemblance in coloration with the male caught in deeper water off Ukerewe (see p. 20) is much greater. The Mwanza Gulf 1993 specimen differs from the latter specimen only in having a yellow flush on its body. As the information on male coloration is based on

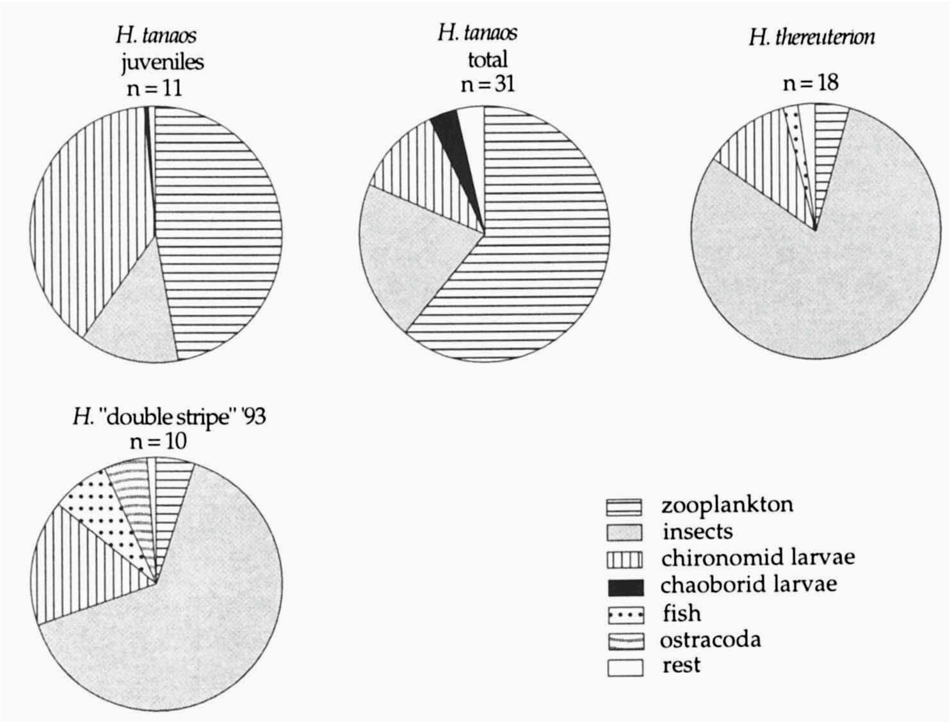


Fig. 61. Food composition (mean volume percentage) of species of the *Haplochromis* "double stripe" complex. Empty guts were discarded.

only a single specimen, a decision on the taxonomic status of the specimens must be postponed until more material becomes available.

Discussion

Sexual dimorphism

Sexual dimorphism in morphometric measurements in haplochromines has been described by Witte & Witte-Maas (1987) and Snoeks (1994). Witte & Witte-Maas, examining five zooplanktivorous species, found differences in lower jaw length (in 2 species), in cheek depth (2), in eye depth (2), in eye length (1), in premaxillary pedicel inclination (3) and in lower jaw obliqueness (3). These authors suggest that the differences could be instrumental in increasing the size of the buccal cavity. An increased size of the buccal cavity would make it possible to brood a larger number of eggs, which could be of great importance in small species.

In a study on the 15 species of Lake Kivu haplochromines, Snoeks (1994) found sexual dimorphism in morphometric measurements for all twelve species of which males and females were available. Most difference was found in Head Length, which was relatively larger in females of five species. In three species males had a relatively larger Head Width and Lower Pharyngeal Width. Males of one of these three and of two other species had relatively longer premaxillary pedicels. Sexual dimorphism was also found in eight other characters. But in each of these only one or two species were involved. Snoeks (1994) moreover, found many differences in lengths of dorsal and anal fin bases, and in the distance of snout to fin origins. Snoeks (1994: 178) regarded the presence of differences outside the head region as a contrast between the Lake Kivu species and the zooplanktivores of Lake Victoria in which Witte & Witte-Maas (1987) found the sexual differences concentrated in the head region, but Witte & Witte-Maas included relatively few measurements outside this region. The absence of differences in measurements of Cheek Depth and Eye Diameter in Lake Kivu haplochromines may be explained in two ways. One, because both Cheek Depth and Eye Diameter are measurements which show considerable allometric growth, differences in these measurements may only become clear when specimens of similar, small size ranges of adult specimens are compared. Two, sexual differences in these characters may only be developed in a few species.

The differences in morphometric characters between males and females of *H. tanaos* seem to support the suggestion of Witte & Witte-Maas (1987): summing all the differences in the females, the relatively larger head with smaller eyes, a deeper cheek, a longer snout and longer lower jaws could all contribute to a larger buccal cavity. Only the fact that the head, rostrally, is relatively more compressed (SnW ♂>♀, LJW ♂>♀) would seem contradictory.

Sexual dimorphism in oral jaw teeth of haplochromines has been described by Spataru & Gophen (1985), Witte & Witte-Maas (1987) and Snoeks (1994). These authors describe species in which males have (more) unicuspids, whereas females of a similar size have mainly bicuspid teeth in the outer rows of the oral jaws. The differentiation apparently starts at maturity. In the species described by these authors there are many interspecific differences in tooth shape and size, both in the bicuspids as well as in the unicuspids which makes it difficult to find a functional explanation which holds for all species. The sexual dimorphy in tooth shape could be related either with the different roles of the sexes in reproductive activities (e. g. nest building in males) or with differences in food or feeding techniques (e.g. Spataru & Gophen, 1985). In the gut contents of males and females of *H. tanaos* no differences have been observed.

As far as sexual dimorphism in size is concerned, *H. tanaos* and *H. thereuterion* confirm the observations of Goldschmidt & Witte (1990) that in rock frequenting species the males are larger while in zooplanktivores females are larger. This may be related to the strong territoriality of rock frequenting species in contrast to the mainly pelagically living zooplanktivores.

Habitat changes and speciation

It is clear from the research of HEST, summarized in Witte et al. (1992a, b), that in the period from 1980-1990, concurrent with the Nile perch (*Lates* spec.) upsurge, the sublittoral area of the Mwanza Gulf had become almost devoid of haplochromine cichlids.

Seehausen & Witte (1994b) in an article about what they called "the second wave of extinction in Lake Victoria", summarized changes in the aquatic ecosystem which have occurred after the 1980's. Among others they mentioned an increase of turbidity, an enormous expansion of the Water hyacinth (*Eichhornia crassipes*), and the increased use of fish poison in shallow water fishery. In 1992, nearly half of Butimba Bay was covered with plants of the Water hyacinth, resulting in reduced light intensities in the water column, reduced wave action and water turbulence, reduced oxygen concentrations, and accumulation of detritus. More recently there were indications that fish poison has been used in Butimba Bay to catch *Oreochromis* species which have a relatively high tolerance for low oxygen concentrations. The added effects of Water hyacinth and fish poison may have made Butimba Bay uninhabitable for haplochromine species.

On the other hand, a slight increase, mainly of zooplanktivores and detritivorous haplochromine species has been observed since 1991 at stations of the transect outside Butimba Bay (Seehausen & Witte, 1995; Witte et al., 1995). This increase may be due to a decrease in *Lates* densities. Apart from species that were already known from the transect, some species apparently had immigrated from other habitats (e.g. deep water). Beside these, there were species which, at first glance, resembled species which were already known from the transect and others which were completely unknown. Obviously, the specimens of the "double stripe" complex caught in 1993 belong to the third category. It is the first case which has been taxonomically analyzed in some detail.

Seehausen & Witte (1995) and Witte et al. (1995) presented a number of hypotheses for the appearance of species of the last two categories: migration from areas until now uninvestigated; phenotypic plasticity; hybridization; and genetic changes. A combination of these factors may also have played a role.

If genetic changes are involved it could represent an example of the speciation model of Paterson (1985, 1992). The explosive increase of the *Lates* population, the concomitant increase of the predation on the haplochromine cichlids and the other changes in the ecosystem could well have created those circumstances which, according to Paterson (1985, 1992), are essential for speciation (see also Ribbink, 1994). Paterson (1985: 26, 27) stated that the characters for the fertilization system as well as other adaptive characters are maintained (i.e. buffered from directional change) when members of a species occupy their normal habitat. For speciation to occur, the buffering of adaptive characters must be overcome, so that a new constellation of adaptive characters can evolve. This is most likely to happen if a small population of conspecific individuals becomes displaced into, and restricted to a new habitat. Because of the changes in the aquatic environment, specimens of the *H.* "double stripe" complex and other surviving haplochromine species at the moment may be in a situation which is denoted by Paterson as "allopatric isolation induced by extrinsic circumstances". According to Paterson, any adaptive characters, including those of the fertilization system, which are now less well adapted will become subject to directional selection. Eventually, when the character states of the population members have shifted under selection to become appropriate and effective under the new conditions, they will return once more to the control of stabilizing selection. Only at this point we say that the individual organisms of the population are adapted to their new habitat. Speciation will have occurred if the new fertilization system has become sufficiently different from that of the members of the parent population, for then the new fertilization system will delimit a new field for gene recombination.

If specimens of the *H.* "double stripe" complex have moved from either a rocky habitat or a sand substrate to a mud bottom (fig. 52), adaptation to different light conditions could involve changes in male coloration, an important character of the Specific Mate Recognition System (Marsh et al., 1981; Ribbink, 1986; Ribbink et al., 1983; Hoogerhoudt et al., 1983). The different substrate type and food will most probably influence reproductive strategies, since species living over mud bottoms usually have restricted breeding periods or breeding peaks different from those of species occurring over sand and rocks (Witte, 1981; Goldschmidt & Witte, 1990). Judging from the size of the smallest specimen (22 mm SL), the 1993 specimens of the *H.* "double stripe" complex are already breeding in their new habitat. However, future catches will have to show if they can permanently establish themselves in this new habitat.

We can only speak of cladogenesis when the parent species can still be found. It could be argued that what we witness here is "only" anagenesis, the adaptation to a changing habitat.

Paterson (1985: 27) refers to the cichlids of Lake Nabugabo (Greenwood, 1965) as an example of a relative short period (i.e. c. 4000 years) that would be needed for his speciation model. However, recent data from Lake Malawi (Owen et al., 1990) indicate that speciation in lacustrine cichlids can take place in a much shorter period. As for possibly very rapid evolution in Lake Victoria, we have to keep in mind that the situation in the lake is still far from stable. However, we are certainly witnessing unique events which deserve detailed attention of scientists working on systematics and evolution. For this reason, regular monitoring of the changes in Lake Victoria is highly recommended.

Acknowledgements

We are indebted to Dr C.D.N. Barel for his constant interest in our research and encouragement. We are grateful to Mr Ole Seehausen for collecting specimens of the *H.*"double stripe" complex in 1993, and providing the photograph of the male specimen. Aloys, Mhoja and Ruben are thanked for assistence during the fishing activities. We thank Mr Schelte Zeilstra for making radiographs, Mr Adri 't Hooft for processing the photographs, Drs L.P. van Ofwegen for the lay-out of the figures, and Dr F.T. van Straten for suggesting suitable latinized Greek names. We thank Dr C.D.N. Barel, Prof. Dr E. Gittenberger, Dr G.G. Teugels and Mr G.J. Howes for critically reviewing the manuscript. We are also indebted to Mr Howes and Dr R.A. Travers for comments on the English text. The Tanzanian Fisheries Research Institute (TAFIRI) and the Freshwater Fisheries Training Institute at Nyegezi are acknowledged for their hospitality and technical support. The fieldwork of HEST was financially supported by the Organisation for the Advancement of Tropical Research (WOTRO), grants W87-129, W87- 161, W87-189, W84-282. The project was also supported by the section for Research and Technology of the Netherlands Ministery of Development Cooperation.

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Received: 1.xi.1995
Accepted: 8.xi.1995
Edited: C. van Achterberg

Table 1. Linear measurements of the holotype of *H. diplotaenia* Regan & Trewavas, 1928

Standard Length (in mm)		89.9
Body Depth	%SL	27.8
Pectoral Fin Length	%SL	22.2
Caudal Peduncle Length	%SL	20.1
Caudal Peduncle Depth	%SL	10.2
CPL/CPD		1.96
Caudal fin Length	%SL	21.3
Head length	%SL	32.9
Snout Length	%HL	30.0
Snout Width	%HL	28.0
SnL/SnW		1.07
Head Width	%HL	40.8
Interorbital Width	%HL	19.9
Preorbital Width	%HL	27.0
Lachrymal Width	%HL	24.6
PoW/LaW		1.09
Preorbital Depth	%HL	18.9
Eye Length	%HL	28.0
Eye Depth	%HL	27.3
EyL/EyD		1.02
Cheek Depth	%HL	16.8
Lower Jaw Length	%HL	44.2
Lower Jaw Width	%HL	-
LJL/LJW		-
Upper Jaw Length	%HL	31.0
Prem. Pedicel Length	%HL	29.7

Table 2. Scale- and Fin Ray counts of the holotype of *H. diplotaenia* Regan & Trewavas, 1928

Lateral Line Scales	33
Lateral Line- Dorsal Fin (Scale rows)	6
Pectoral- Pelvic Fin Bases (Scale rows)	8
Cheek scales in a vertical row	4
Dorsal Fin Spines/Rays	XV10
Anal Fin Spines/Rays	III8

Table 3. Ranges of linear measurements of *Haplochromis tanaos* spec. nov.

SL in mm		50.3-59.0	50.9-59.0	61.0-69.2	60.0-69.5	70.0-73.0	70.0-73.0
n		10	9	14	15	5	9
Sex		♂	♀	♂	♀	♂	♀
Body Depth	%SL	25.1-27.1	24.7-26.4	24.4-27.1	23.4-26.7	22.1-25.3	23.4-25.4
Pectoral Fin Length	%SL	17.6-24.7	21.2-23.9	21.5-25.3	21.7-30.1	22.6-24.2	23.1-25.4
Caudal Peduncle Length	%SL	19.3-23.1	19.5-22.0	17.6-21.3	17.9-22.8	17.6-19.4	17.5-19.5
Caudal Peduncle Depth	%SL	9.3-10.7	8.9-11.4	9.3-10.9	9.5-10.4	9.1-10.0	9.0-10.4
CPL/CPD		1.8- 2.3	1.7- 2.2	1.7- 2.0	1.8- 2.2	1.8- 2.1	1.7- 2.1
Caudal fin Length	%SL	21.7-24.7	22.5-24.5	20.2-24.0	21.4-24.2	22.5-24.2	20.5-23.9
Head length	%SL	31.6-36.1	31.6-33.5	31.6-35.2	31.6-35.2	32.3-33.7	32.9-34.5
Snout Length	%HL	25.5-31.0	24.7-30.4	27.1-30.7	27.1-31.8	29.2-33.7	29.9-34.5
Snout Width	%HL	23.2-25.2	25.2-27.9	25.2-28.5	22.4-26.6	25.0-26.0	21.7-24.8
SnL/SnW		1.0- 1.2	1.0- 1.2	0.9- 1.2	1.1- 1.4	1.1- 1.3	1.2- 1.4
Head Width	%HL	38.0-41.8	37.8-42.2	38.3-41.2	36.9-40.4	38.1-40.2	37.9-40.0
Interorbital Width	%HL	18.7-22.0	18.3-21.7	17.3-20.3	17.2-21.1	18.2-20.9	17.1-20.9
Preorbital Width	%HL	23.9-27.2	24.2-27.9	24.1-26.7	24.1-27.3	25.4-26.3	25.2-27.8
Lachrymal Width	%HL	19.2-23.0	20.7-24.2	19.9-23.0	17.6-22.1	20.5-21.7	16.0-19.5
PoW/LaW		1.1- 1.4	1.1- 1.2	1.1- 1.3	1.1- 1.4	1.2- 1.2	1.2- 1.4
Preorbital Depth	%HL	16.2-17.8	16.4-18.0	15.6-18.0	16.2-19.2	16.5-17.9	16.0-19.5
Eye Length	%HL	27.8-31.0	27.5-31.4	27.2-31.4	26.2-30.9	30.4-31.7	28.5-31.2
Eye Depth	%HL	27.9-29.7	27.8-30.4	26.5-32.2	26.7-30.5	29.4-31.3	28.0-30.0
EyL/EyD		1.0-1.08	0.98-1.07	0.95-1.02	0.96-1.09	1.00-1.04	1.03-1.11
Cheek Depth	%HL	14.0-16.6	13.6-16.6	12.0-14.8	11.7-14.3	13.5-15.2	13.0-16.3
Lower Jaw Length	%HL	38.3-41.8	36.6-42.2	37.7-42.7	37.8-44.9	40.0-42.7	42.4-44.0
Lower Jaw Width	%HL	11.8-13.9	10.6-14.4	13.5-15.8	11.4-14.7	13.5-17.0	12.6-15.2
LJL/LJW		2.5- 3.3	2.8- 3.4	2.8- 3.4	2.8- 3.4	2.5- 3.0	2.8- 3.5
Upper Jaw Length	%HL	26.1-27.5	24.8-27.7	26.6-29.8	25.7-30.0	29.1-29.9	28.1-30.3
Premaxillary Pedicel Length	%HL	27.3-30.5	27.2-30.9	26.5-29.7	26.0-30.4	27.9-29.0	28.1-32.4
Angular measurements							
Dorsal Head Inclination		25°-32°	27°-33°	19°-30°	21°-36°	21°-30°	23°-33°
Premaxillary Pedicel Inclination		33°-40°	29°-39°	31°-42°	31°-40°	32°-38°	34°-40°
Snout Acuteness		57°-73°	53°-68°	59°-69°	59°-68°	58°-68°	61°-68°
Gape inclination		29°-40°	29°-38°	26°-38°	28°-40°	33°-38°	32°-42°

Table 4. Means and standard deviations of linear measurements of *H. tanaos* spec. nov.

SL in mm		50.3-59.0	50.9-59.0	61.0-69.2	60.0-69.5	70.0-73.0	70.0-73.0
n		10	10	14	15	5	9
Sex		♂	♀	♂	♀	♂	♀
Standard Length		54.7±2.9	55.1±3.0	64.9±2.5	64.1±3.4	71.3±1.2	71.6±0.9
Body Depth	%SL	26.0±2.6	25.5±0.7	25.9±0.7	25.4±0.8	23.9±1.1	24.5±0.6
Pectoral Fin Length	%SL	22.4±2.1	22.5±0.9	23.8±1.1	24.3±1.9	23.7±1.0	24.1±0.7
Caudal Peduncle Length	%SL	21.4±1.2	20.5±0.5	19.3±1.1	19.9±1.3	18.0±0.8	18.7±0.6
Caudal Peduncle Depth	%SL	10.0±0.4	10.4±0.7	10.2±0.3	9.9±0.3	9.6±0.3	9.6±0.5
CPL/CPD		2.09±0.12	1.93±0.17	1.86±0.11	2.0±0.1	1.9±0.1	1.9±0.1
Caudal fin Length	%SL	23.5±0.9	23.4±0.5	22.9±1.0	23.1±0.9	23.3±0.6	22.5±1.1
Head length	%SL	32.9±1.2	32.6±0.6	33.1±0.9	33.3±1.0	32.9±0.5	34.2±0.6
Snout Length	%HL	28.7±1.4	28.6±0.8	28.9±0.9	29.4±1.4	30.5±1.8	30.8±0.7
Snout Width	%HL	24.1±0.7	26.2±0.9	26.9±1.2	24.6±1.2	25.5±0.4	23.7±0.9
SnL/SnW		1.12±0.07	1.07±0.06	1.09±0.09	1.2±0.1	1.2±0.1	1.3±0.1
Head Width	%HL	39.8±1.2	39.8±1.4	39.4±0.6	39.0±1.1	39.1±0.8	38.8±0.7
Interorbital Width	%HL	20.4±1.2	20.0±1.2	18.9±0.9	19.3±1.1	19.2±1.1	19.1±1.1
Preorbital Width	%HL	25.7±1.2	25.2±1.0	25.4±0.8	25.3±0.8	25.8±0.3	25.8±1.1
Lachrymal Width	%HL	20.9±1.3	21.9±1.1	21.3±1.0	20.1±1.3	21.1±0.6	19.5±0.8
PoW/LaW		1.22±0.08	1.16±0.05	1.20±0.07	1.2±0.1	1.2±0.1	1.3±0.1
Preorbital Depth	%HL	17.0±0.6	16.8±0.7	16.9±0.7	17.4±0.9	17.1±0.6	17.8±1.1
Eye Length	%HL	29.2±0.9	28.9±0.9	29.1±1.1	28.9±1.5	30.8±0.6	29.7±0.9
Eye Depth	%HL	28.4±0.8	28.4±0.8	29.3±1.4	28.6±1.1	30.6±0.8	28.8±0.7
EyL/EyD		1.02±0.03	1.01±0.02	1.00±0.02	1.02±0.01	1.02±0.01	1.03±0.03
Cheek Depth	%HL	14.9±1.1	15.3±1.0	13.4±0.9	13.9±1.5	14.0±0.7	14.9±1.6
Lower Jaw Length	%HL	40.0±1.1	39.4±1.6	40.5±1.5	41.3±1.7	41.6±0.9	43.0±1.3
Lower Jaw Width	%HL	12.9±0.7	13.2±1.7	14.1±0.9	13.1±1.2	15.5±1.7	13.6±1.0
LJL/LJW		2.96±0.27	3.07±0.22	2.83±0.22	3.0±0.2	2.7±0.2	3.1±0.2
Upper Jaw Length	%HL	26.9±0.4	26.5±0.9	28.1±0.9	28.1±1.3	29.4±0.3	28.4±0.7
Premaxillary Pedicel Length	%HL	28.1±1.1	28.3±1.5	28.1±0.9	28.0±1.3	28.6±0.7	29.1±1.3
Angular measurements							
Dorsal Head Inclination		29.4°±2.1°	29.3°±1.7°	28.0°±2.1°	28.2°±3.9°	27.0°±3.4°	28.4°±4.3°
Premaxillary Pedicel Inclination		36.2°±3.1°	36.0°±3.4°	36.8°±2.8°	35.9°±2.6°	35.1°±1.9°	36.0°±2.1°
Snout acuteness		62.3°±4.8°	60.8°±5.0°	63.5°±3.2°	62.2°±2.7°	63.0°±4.2°	65.0°±2.3°
Gape Inclination		34.2°±3.6°	34.8°±3.2°	34.0°±2.5°	34.6°±3.2°	35.8°±2.1°	36.1°±3.7°

Table 5. Qualitative measurements and counts of *Haplochromis tanaos* spec. nov.

Dorsal Head Profile (curvature)	0						
Premaxillary Pedicel Prominence	+/+(+)						
Lower Jaw nterior Extension	±/+						
Lateral Snout Outline	+						
Mental Prominence	0						
Lip Thickening	0						
Premaxilla Beaked	0						
Premaxilla Expanded	0						
Maxilla Posterior Extension	-/0						
Cephalic Lateral Line Pores: Width	0						
Lateral Line Scales	32 (f=4)	33 (f=19)	34 (f=31)	35 (f=18)	36 (f=1)		
Lateral Line- Dorsal Fin (Scale rows)	6 (f=38)	7 (f=27)	8 (f=2)				
Pectoral- Pelvic Fin Bases (Scale rows)	5 (f=4)	6 (f= 31)	7 (f=30)	8 (f=4)			
Cheek scales in a vertical row)	3 (f=62)	4 (f= 7)					
Dorsal Fin Spines/Rays	XIV8 (f=1)	XIV10 (f= 1)	XV9 (f=18)	XV10 (f=7)	XVI8 (f=7)	XVI9 (f=32)	XVI 10 (f=4)
Anal Fin Spines/Rays	III7 (f=3)	III8 (f=45)	III9 (f=15)	III10 (f=1)			

Table 6. Numbers of (unicuspid) outer teeth in left upper and lower jaw of *Haplochromis tanaosus* spec. nov.

SL	50.3-59.0		50.9-59.0		61.0-69.2		60.0-69.5		70.2-73.0		70.0-73.0	
n	10		9		14		15		5		9	
Sex	♂		♀		♂		♀		♂		♀	
	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD
POT	16-20	18.6±1.5	17-20	18.5±1.1	17-22	19.5±1.3	18-24	19.8±1.9	19-25	21.6±2.4	19-24	21.7±1.5
POTU	0-4	1.3±0.1	0		6-21	11.6±6.0	0-3	0.5±0.9	9-21	12.8±4.8	0-5	2±2.2
LOT	13-16	14.4±0.8	14-17	15.1±0.9	14-19	15.4±1.6	15-18	16.0±1.2	15-18	16.2±1.3	15-20	16.8±1.7
LOTU	0-3	0.3±0.1	0		4-14	8±2.8	0-2	0.2±0.7	7-10	8±1.2	0-4	0.6±0.1

POT=Premaxillary Outer Teeth; POTU=Unicuspid Premaxillary Outer Teeth; LOT= Lower Jaw Outer Teeth; LOTU= Unicuspid Lower Jaw Outer Teeth.

Table 7. Ranges of linear measurements of *Haplochromis thereuterion* spec. nov.

Sl in mm		62.9-68.0	60.0-67.0	71.0-78.5	73.2-76.2	80.2-82.0
n		3	4	13	2	3
Sex		♂	♀	♂	♀	♂
Body Depth	%SL	27.0-27.6	25.0-26.5	25.2-27.2	24.4-25.5	25.0-27.5
Pectoral Fin Length	%SL	22.9-25.2	20.9-23.3	22.8-26.1	22.9-23.9	23.9-25.0
Caudal Peduncle Length	%SL	19.1-19.7	18.9-22.3	17.8-21.7	16.9-19.1	17.1-18.0
Caudal Peduncle Depth	%SL	10.2-11.1	10.1-10.8	9.0-10.7	9.1- 9.5	9.5-10.2
CPL/CPD		1.7- 1.8	1.9- 2.1	1.7- 2.2	1.8- 2.0	1.7- 1.8
Caudal fin Length	%SL	23.5-24.1	20.4-24.6	21.5-25.0	21.1-22.3	21.0-24.1
Head length	%SL	33.0-33.5	32.8-33.1	32.3-34.6	33.4-36.9	32.7-35.1
Snout Length	%HL	28.8-31.3	28.1-31.9	29.6-32.3	33.4-36.9	30.0-33.3
Snout Width	%HL	-	27.0 (1)	22.0-27.6	24.1-24.8	23.5-26.5
SnL/SnW		-	-	1.1- 1.2	1.3- 1.3	1.2- 1.3
Head Width	%HL	39.4-40.7	36.9-40.2	38.3-41.6	37.5-38.9	38.3-41.8
Interorbital Width	%HL	19.7-21.8	18.0-20.6	17.8-21.7	17.6-18.3	18.5-19.8
Preorbital Width	%HL	25.0-26.5	25.4-26.6	24.0-26.3	25.6-26.1	25.1-26.6
Lachrymal Width	%HL	22.5 (1)	22.5 (1)	19.7-22.8	20.5-20.8	21.8-23.7
PoW/LaW		-	-	1.1- 1.2	1.2- 1.2	1.1- 1.2
Preorbital Depth	%HL	16.8-18.4	17.5-19.2	16.1-19.0	17.6-19.5	17.1-18.1
Eye Length	%HL	27.6-28.8	27.4-30.1	26.3-29.0	28.5-28.5	26.9-29.2
Eye Depth	%HL	26.4-27.7	27.4-30.1	25.9-30.4	25.9-27.3	25.1-29.2
EyL/EyD		1.0- 1.1	1.0- 1.0	0.9- 1.1	1.0- 1.1	0.9- 1.0
Cheek Depth	%HL	14.5-15.3	13.0-14.9	14.3-16.5	16.3-16.6	13.4-15.5
Lower Jaw Length	%HL	41.6-43.2	36.9-41.2	39.1-43.3	40.4-40.8	41.8-42.1
Lower Jaw Width	%HL	-	12.6 (1)	13.5-17.8	14.6 (1)	14.8-17.3
LJL/LJW		-	2.9 (1)	2.3- 2.9	2.7 (1)	2.4- 2.8
Upper Jaw Length	%HL	-	29.3-30.6	27.9-31.1	25.9-27.7	29.4-30.3
Premaxillary Pedicel Length	%HL	27.1-28.8	27.6-30.6	26.3-30.7	28.1-28.8	27.0-28.0
Angular measurements						
Dorsal Head Inclination		28° (1)	28° (1)	21°-35°	28°-30°	30°-30°
Premaxillary Pedicel Inclination		31° (1)	33° (1)	29°-42°	37°-38°	33°-36°
Snout acuteness		63° (1)	60° (1)	59°-68°	60°-62°	60°-68°
Gape inclination		37° (1)	36° (1)	28°-40°	30°-35°	36°-38°

Table 8. Means and standard deviations of linear measurements of *Haplochromis thereuterion* spec. nov.

Sl in mm		62.9-68.0	60.0-67.0	71.0-78.5	73.2-76.2	80.2-82.0
n		3	4	13	2	3
Sex		♂	♀	♂	♀	♂
Standard Length		65.7±2.5	63.5±2.8	75.0±2.1	74.7±2.1	80.8±1.0
Body Depth	%SL	27.2±0.3	25.8±0.7	26.4±0.5	24.9±1.5	26.2±1.2
Pectoral Fin Length	%SL	23.9±1.1	22.0±1.0	24.4±1.0	23.4±0.7	24.4±0.5
Caudal Peduncle Length	%SL	19.3±0.3	20.2±1.4	19.4±1.0	18.0±1.5	17.5±0.4
Caudal Peduncle Depth	%SL	10.7±0.4	10.3±0.3	9.8±0.5	9.3±0.2	9.9±0.4
CPL/CPD		1.7±0.1	1.9±0.1	1.8±0.1	1.9±1.4	1.7±0.05
Caudal fin Length	%SL	23.7±0.3	23.0±1.8	23.3±1.0	21.7±0.8	23.0±1.7
Head Length	%SL	33.2±0.3	32.9±0.1	33.5±0.6	35.1±0.4	33.5±1.3
Snout Length	%HL	30.0±1.7	30.0±2.6	30.9±0.7	32.5±0.4	31.8±1.6
Snout Width	%HL	-	-	25.4±1.6	24.4±0.4	25.1±1.5
SnL/SnW		-	-	1.2±0.1	1.3	1.3±0.1
Head Width	%HL	40.0±0.6	39.3±1.7	39.8±1.1	39.2±0.4	39.9±1.64
Interorbital Width	%HL	20.5±1.1	19.4±1.0	19.4±1.0	17.9±0.4	19.1±0.6
Preorbital Width	%HL	25.9±0.7	26.2±0.5	25.3±0.8	25.8±0.3	26.1±0.8
Lachrymal Width	%HL	-	-	21.2±0.9	20.6±2.1	22.7±0.9
PoW/LaW		-	-	1.2±0.03	1.2±0.05	1.2±0.05
Preorbital Depth	%HL	17.6±0.8	18.2±0.7	17.9±0.8	18.5±1.3	17.7±0.5
Eye Length	%HL	28.0±0.6	28.3±1.2	27.8±0.9	28.5	27.7±2.0
Eye Depth	%HL	27.0±0.6	26.4±0.9	27.9±1.2	26.5±0.9	28.0±1.1
EyL/EyD		1.0±0.1	1.0±0	1.0±0.04	1.06±0.03	0.97±0.03
Cheek Depth	%HL	14.9±0.4	13.9±0.8	15.3±0.6	16.4±0.2	14.5±1.0
Lower Jaw Length	%HL	42.2±0.8	40.6±2.6	40.8±1.2	40.6±0.2	41.9±0.1
Lower Jaw Width	%HL	-	-	15.1±1.2	14.6	16.0±1.7
LJL/LJW		-	-	2.6±0.2	2.7	2.6±0.03
Upper Jaw Length	%HL	-	29.9±0.9	29.7±1.0	26.8±1.2	29.7±0.4
Premaxillary Pedicel Length	%HL	27.8±0.8	29.2±1.2	28.9±1.2	28.4±0.4	28.5±1.5
Angular measurements						
Dorsal Head Inclination		-	-	27.6°±4.6°	29.0°±1.4°	30.0°
Premaxillary Pedicel Inclination		-	-	35.2°±4.2°	37.5°±0.7°	34.6°±1.5°
Snout acuteness		-	-	63.1°±3.3°	61.0°±1.4°	61.3°±4.1°
Gape inclination		-	-	34.0°±4.1°	32.5°±3.5°	37.0°±1.0°

Table 9. Qualitative measurements and counts of *Haplochromis thereuterion* spec. nov.

Dorsal Head Profile (curvature)	0				
Premaxillary Pedicel Prominence	(+)/+				
Lower Jaw nterior Extension	±/+				
Lateral Snout Outline	+				
Mental Prominence	0				
Lip Thickening	(+)				
Premaxilla Beaked	0				
Premaxilla Expanded	(+)/+				
Maxilla Posterior Extension	0/+				
Cephalic Lateral Line Pores: Width	0				
Lateral Line Scales	32 (n=3)	33 (n=10)	34 (n=8)	35 (n=3)	
Lateral Line- Dorsal Fin (Scale rows)	5 (n=1)	6 (n=12)	7 (n=12)	8 (n=1)	
Pectoral- Pelvic Fin Bases (Scale rows)	6 (n=7)	7 (n=14)	8 (n=5)		
Cheek (Vertical Scale rows)	3 (n=22)	4 (n=4)			
Dorsal Fin Spines/Rays	XV8 (n=2)	XV9 (n=5)	XV10 (n=2)	XVI8 (n=2)	XVI9 (n=13)
Anal Fin Spines/Rays	III7 (n=2)	III8 (n=9)	III9 (n=13)	III10 (n=1)	

Table 10. Numbers of (unicuspid) outer teeth in left upper and lower jaw of *Haplochromis thereuterion* spec. nov.

SL	62.9-68.0		60.0-67.0		71.0-78.5		73.2-76.2		80.2-82.0	
n	3		4		13		2		3	
Sex	♂		♀		♂		♀		♂	
	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD
POT	18-19	18.5±0.7	17-20	18.7±1.2	17-25	20.3±2.1	21-23	22±1	20-22	21±1
POTU	4-11	7.5±4.9	1-2	1.5±0.5	4-22	12.4±5.9	3-4	3.5±0.5	20-22	21±1
LOT	16-19	17.5±2.1	15-15	15±0	15-19	16.8±1.6	17-18	18±1	14-17	15.6±1.5
LOTU	5-11	8±4.2	0-2	1±1.4	6-19	9.5±4.2	0-7	3.5±3.5	14-16	15.3±1.1

POT=Premaxillary Outer Teeth; POTU=Unicuspid Premaxillary Outer Teeth; LOT= Lower Jaw Outer Teeth; LOTU= Unicuspid Lower Jaw Outer Teeth.

Table 11. Mean number and standard deviation of specimens of *Haplochromis tanaos* in trawl catches of ten minutes duration at stations on a transect across the Mwanza Gulf.

	Sand		I	Mud								
	I———Butimba Bay———I										I Kissenda Bay I	
Stations	A	B	I	C	D	E	F	G	H	I	J	K
Depth (in meters)	2-4	4-6	I	2-4	4-6	7-8	10-11	13-14	13-24	10-11	7-8	4
March 1979 - July 1980	5.7±5.2	7.1±%5.3	I	+	+	+	0	0	0	0	0	0
Number of catches	16	16	I	16	16	18	18	18	10	9	10	7
October - December 1993	0	0	I	0	0	0	0	0	0	0	1.0±1.4	1.8±2.5
Number of catches	6	6	I	6	6	6	6	6	6	6	6	6

+ indicates values less than 0.1.

Tabel 12. Diet composition of species of the *Haplochromis* "double stripe" complex.

Habitat	Period	SLrange in mm	SL mean in mm	Number of fish	Cladocera %	Copepoda %	Ostracoda %	Chir. lar. %	Chaob. lar. %	Insects %	Trichoptera %	Fish %	Detritus %	Rest %
Haplochromis tanaos spec. nov.														
Sand	'77-'81	52-72	65.7	31	66.6	0.2	0.0	0.5	4.7	23.4	0.0	0.1	2.1	2.4
Sand	'79-'81	22-49	37.3	11	47.3	0.0	0.0	38.7	0.7	12.7	0.0	0.0	0.0	0.7
Haplochromis thereuterion spec nov.														
Rocks	'78-'80	57-81	72.2	18	0.2	4.4	0.0	11.2	0.0	71.2	9.0	1.9	0.0	2.2
Haplochromis "double stripe" complex														
Mud	'93	34-65	49.9	10	3.0	2.1	5.4	16.0	0.0	51.4	51.9	7.5	0.7	0.4

Table 13. *H. tanaos* spec. nov., sexual dimorphism in taxonomic measurements (Wilcoxon unpaired test). Only those measurements are considered for which a significant difference is found in at least one length class. Significant differences underlined.

SL in mm	50-59	60-69	70-73	Total range 50-73
CPL/SL	11♂, 9♀ ♂<♀ (p=0.237)	16♂, 14♀ ♂<♀ (p=0.026)	6♂, 9♀ ♂=♀ (p=1)	
HL/SL	11♂, 9♀ ♂>♀ (p=0.909)	16♂, 14♀ ♂<♀ (p=0.632)	6♂, 9♀ ♂<♀ (p=0.008)	
SnW/HL	10♂, 8♀ ♂<♀ (p=0.156)	16♂, 14♀ ♂>♀ (p=0.001)	6♂, 9♀ ♂>♀ (p=0.002)	
SnL/SnW	11♂, 9♀ ♂>♀ (p=0.392)	16♂, 14♀ ♂<♀ (p=0.005)	6♂, 9♀ ♂<♀ (p=0.059)	
LaW/HL	10♂, 9♀ ♂<♀ (p=0.111)	16♂, 13♀ ♂>♀ (p=0.012)	4♂, 9♀ ♂>♀ (p=0.010)	
PoW/LaW	10♂, 9♀ ♂>♀ (p=0.296)	15♂, 13♀ ♂<♀ (p=0.083)	4♂, 9♀ ♂<♀ (p=0.003)	
EyD/HL	11♂, 9♀ ♂>♀ (p=0.159)	16♂, 14♀ ♂>♀ (p=0.298)	6♂, 9♀ ♂>♀ (p=0.175)	33♂, 32♀ ♂>♀ (p=0.046)
LJL/HL	11♂, 9♀ ♂>♀ (p=0.543)	16♂, 14♀ ♂<♀ (p=0.884)	6♂, 9♀ ♂<♀ (p=0.008)	
LJW/HL	10♂, 7♀ ♂>♀ (p=0.591)	13♂, 10♀ ♂<♀ (p=0.054)	5♂, 7♀ ♂>♀ (p=0.087)	
LJL/LJW	11♂, 7♀ ♂<♀ (p=0.293)	13♂, 10♀ ♂<♀ (p=0.051)	5♂, 7♀ ♂<♀ (p=0.018)	

Table 14. *H. thereuterion* spec. nov., sexual dimorphism in taxonomic characters (Wilcoxon unpaired test). Only those measurements are considered for which a significant difference is found in at least one length class. Significant differences underlined.

SL in mm	60-69		70-79		Total range 60-82	
BD/SL	3♂, 4♀	♂>♀ (p=0.051)	13♂, 2♀	♂>♀ (p=0.051)	16♂, 6♀	♂>♀ (p=0.013)
PFL/SL	3♂, 4♀	♂>♀ (p=0.112)	13♂, 2♀	♂>♀ (p=0.202)	16♂, 6♀	♂>♀ (p=0.006)
CPL/CPD	3♂, 4♀	♂<♀ (p=0.042)	13♂, 2♀	♂>♀ (p=0.791)		
IOW/HL	3♂, 4♀	♂>♀ (p=0.258)	13♂, 2♀	♂>♀ (p=0.051)	16♂, 6♀	♂>♀ (p=0.284)

Table 15. Spearman rank correlations of ratios of morphometric measurements with Standard Length. Only those ratios are considered for which in at least one of the sexes a significant correlation was found. Significant correlations underlined.

Haplochromis tanaos spec. nov.				
Sex	♂		♀	
SL in mm	50.3-73.0		50.9-73.0	
	n		n	
BD/SL	33	-0.5105 (p=0.004)	33	-0.3564 (p=0.044)
CPL/SL	33	-0.6266 (p=0.000)	33	-0.5417 (p=0.002)
HL/SL	33	0.0822 (p=0.642)	33	0.6143 (p=0.001)
SnL/HL	33	0.4592 (p=0.011)	33	0.6081 (p=0.001)
SnL/SnW	32	0.6881 (p=0.001)	33	0.6685 (p=0.000)
IOW/HL	33	-0.4260 (p=0.016)	33	-0.0946 (p=0.593)
LaW/HL	30	0.1279 (p=0.491)	32	-0.6172 (p=0.001)
POD/HL	33	0.2987 (p=0.091)	33	0.4275 (p=0.016)
LJL/HL	33	0.4169 (p=0.018)	33	0.6972 (p=0.000)
LJW/HL	28	0.5846 (p=0.002)	24	-0.0100 (p=0.962)
UJL/HL	32	0.6881 (p=0.000)	33	0.5339 (p=0.003)
Haplochromis thereuterion spec. nov.				
Sex	♂		♀	
SL in mm	62.9-82.0		60.0-76.2	
	n		n	
CPD/SL	16	-0.5240 (p=0.042)	6	-0.8117 (p=0.069)
SnL/HL	15	0.0188 (p=0.944)	4	1.000 (p=0.000)

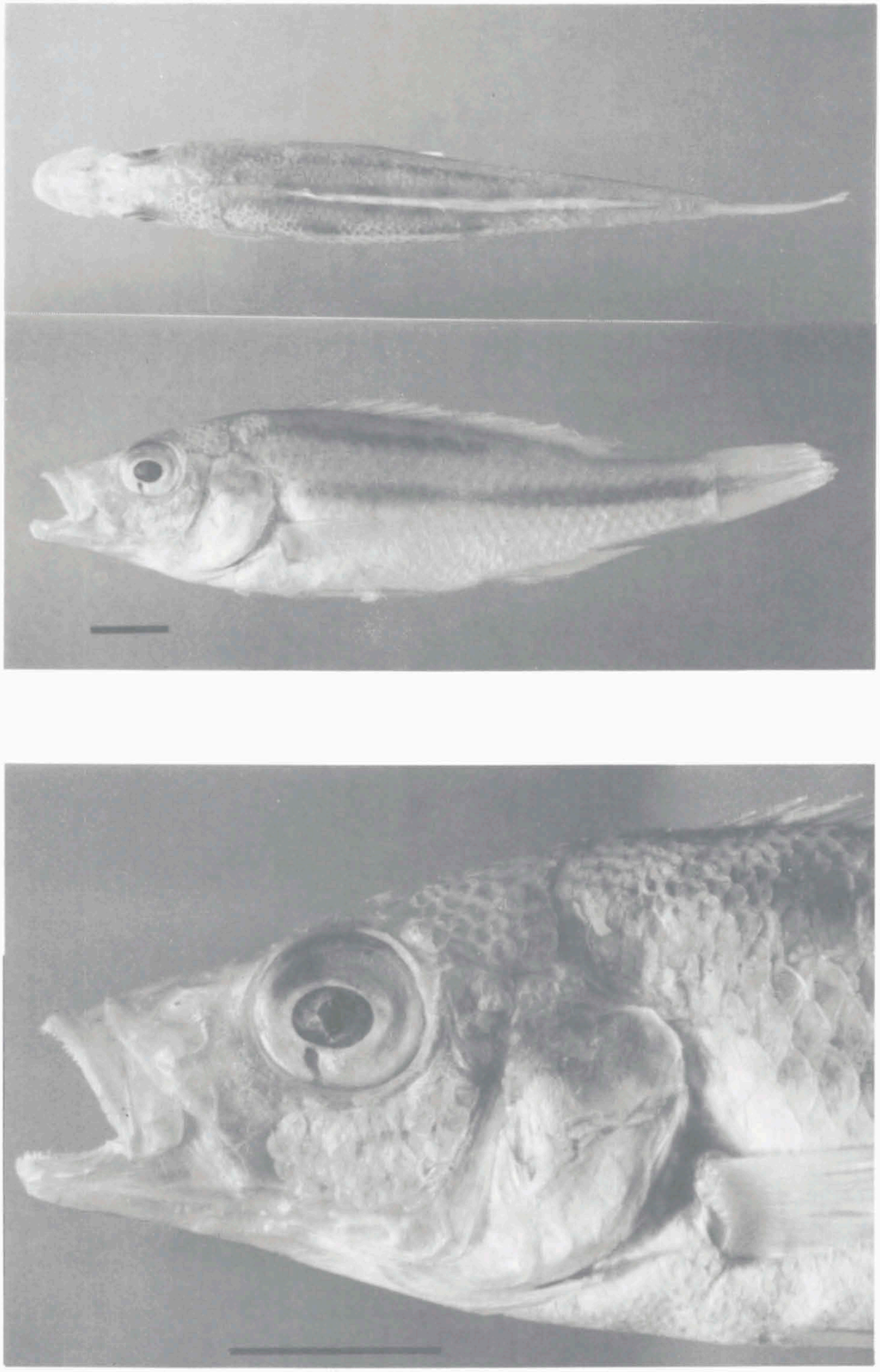

Fig. 62. *Haplochromis diplotaenia* Regan & Trewavas, 1928. Holotype, ♀, BMNH 1928.6.2.44. Left lateral and dorsal view of habitus and lateral view of head. Scale equals 1 mm.

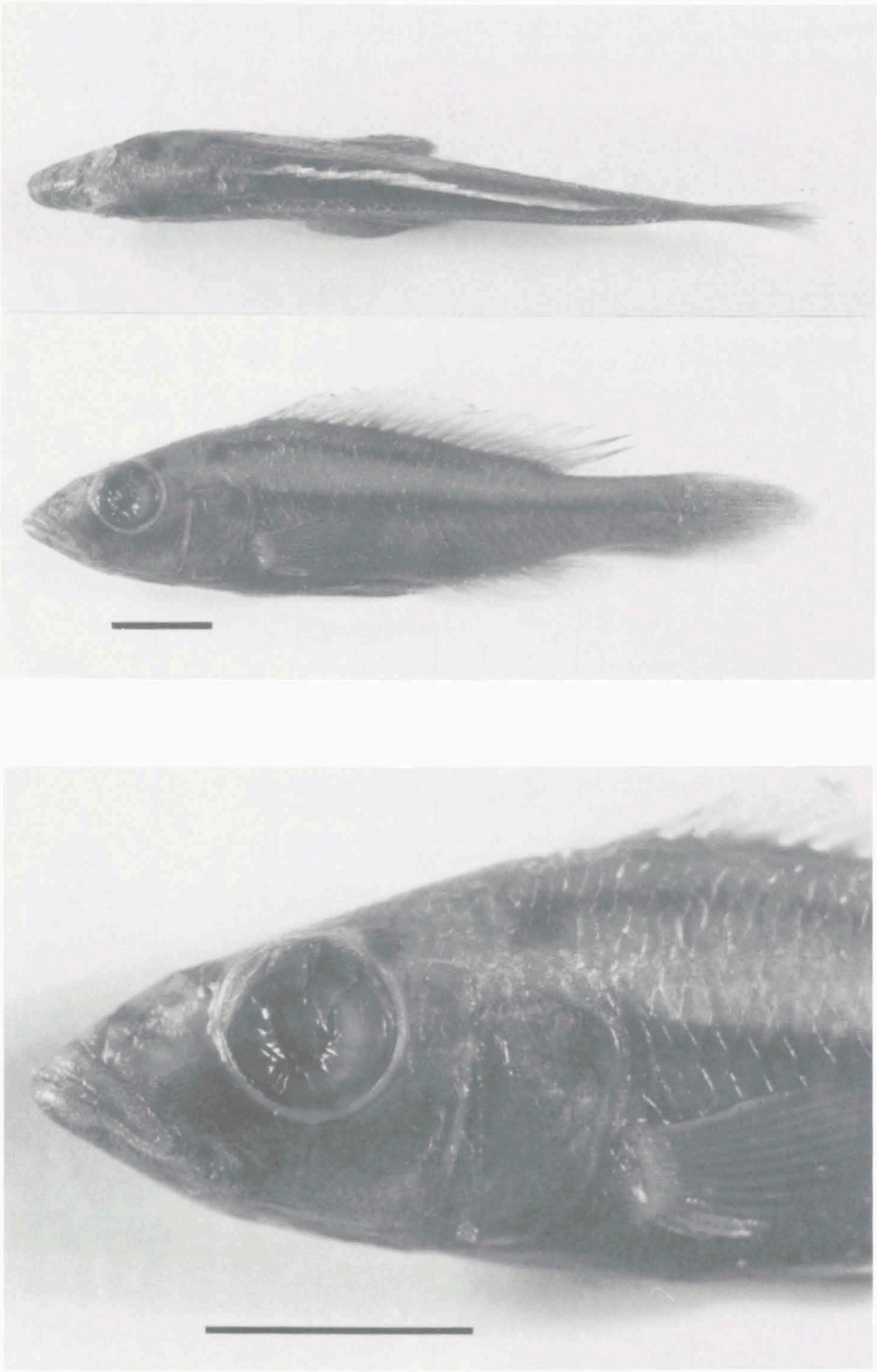

Fig. 63. *Haplochromis tanaos* spec. nov. Holotype, ♂, RMNH 32544. Left lateral and dorsal view of habitus and lateral view of head. Scale equals 1 mm.

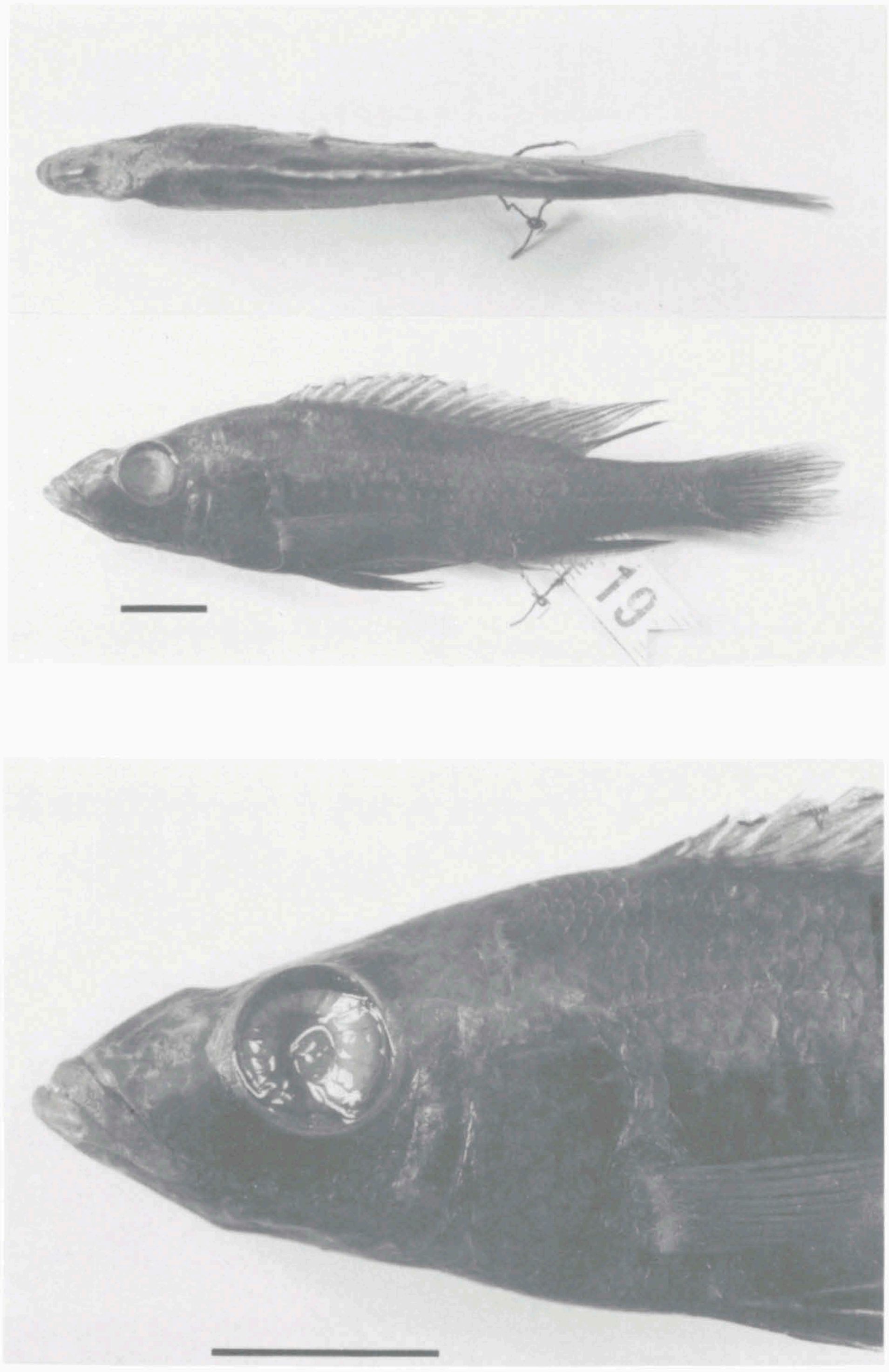

Fig. 64. *Haplochromis thereuterion* spec. nov. Holotype, ♂, RMNH 32625. Left lateral and dorsal view of habitus and lateral view of head. Scale equals 1 mm.