Seven new species of detritivorous and phytoplanktivorous haplochromines from Lake Victoria

M.P. de Zeeuw, M. Mietes, P. Niemantsverdriet, S. ter Huurne & F. Witte

Zeeuw, M.P. de, M. Mietes, P. Niemantsverdriet, S. ter Huurne & F. Witte. Seven new species of detritivorous and phytoplanktivorous haplochromines from Lake Victoria.
Zool. Med. Leiden 84 (9), 15.x.2010: 201-250, figs 1-23, tables 1-7.— ISSN 0024-0672.

M.P. de Zeeuw, Netherlands Centre for Biodiversity, Naturalis, PO Box 9517, 2300 RA Leiden, The Netherlands (mpdezeeuw@kabelfoon.net).
M. Mietes, Institute of Biology Leiden, PO Box 9505, 2300 RA Leiden, The Netherlands.
P. Niemantsverdriet, Institute of Biology Leiden, PO Box 9505, 2300 RA Leiden, The Netherlands / Rotterdam Zoo, PO Box 532, 3000 AM Rotterdam, The Netherlands (P.Niemantsverdriet@rotterdamzoo.nl).
S. ter Huurne, Institute of Biology Leiden, PO Box 9505, 2300 RA Leiden, The Netherlands.
F. Witte, Netherlands Centre for Biodiversity, Naturalis, PO Box 9517, 2300 RA Leiden, The Netherlands / Institute of Biology Leiden, PO Box 9505, 2300 RA Leiden, The Netherlands (F.Witte@biology.leidenuniv.nl). Correspondence to last author.

Key words: Cichlidae; detritivores; East Africa; *Haplochromis*; phytoplanktivores.

Seven new species of haplochromine cichlids from Lake Victoria are described. They comprise four detritivorous and three phytoplanktivorous species. Their affinities to other Lake Victoria haplochromines are discussed.

Introduction

The haplochromine cichlids of Lake Victoria can be classified into several trophic groups according to their diet (Greenwood, 1974; Witte & van Oijen, 1990). Two common groups are the detritivores, mainly feeding on bottom debris, often mixed with phytoplankton, and the phytoplanktivores for which phytoplankton is the major food source (Greenwood, 1974; Witte, 1981; Goldschmidt et al., 1993).

In the 1980s the ecosystem of Lake Victoria changed dramatically due to the upsurge of the introduced predator the Nile perch (*Lates niloticus* Linnaeus, 1758) and eutrophication (*e.g.* Ogutu-Ohwayo, 1990; Kaufman, 1992; Witte et al., 1992a, b, 2005; Hecky et al., 1994; Seehausen et al., 1997a; Wanink et al., 2001; Goudswaard et al., 2008). Concomitantly, the haplochromine cichlids in the sub-littoral waters of Lake Victoria almost vanished (Ogutu Ohwayo, 1990; Witte et al., 1992b). Until the decline of the haplochromines, the detritivores and phytoplanktivores were both in number and biomass the most abundant fishes in sub-littoral areas of the Mwanza Gulf. A trawl shot of one hour contained on average 1250 kg of haplochromines (Goudswaard et al., 2008), of which 55% consisted of detritivores and phytoplanktivores (Witte, 1981; Goldschmidt et al., 1993), amounting to more than 200,000 individuals. Due to their importance for the trawl fishery, detritivorous and phytoplanktivorous species featured in several of the ecological studies that have been carried out in the Mwanza Gulf during the past three decades (*e.g.* Witte, 1981, 1984b; Goldschmidt et al., 1993; Kishe-Machumu et al., 2008). Apart from a few detritivorous and phytoplanktivorous species that were described by Greenwood and Gee (1969) from the northern part of the lake, most of the species encountered in the Mwanza Gulf were new. Pending formal taxonomic descriptions, these new species were given nicknames in the ongoing ecological studies.

This unsatisfactory situation lasted for many years, partly because the urge to describe these species declined after the disappearance of the haplochromines from the sub-littoral and offshore waters in the1980s (Ogutu Ohwayo, 1990; Witte et al., 1992b). From 1987 to 1992 haplochromines were extremely rare in trawl catches in the Mwanza Gulf, however, with the subsequent decline of Nile perch due to heavy fishing, a slow recovery of some zooplanktivorous species and, to a lesser degree, of detritivorous species, was noticed (Seehausen et al., 1997b; Witte et al., 2000, 2007a,b). This resurgence is still continuing and currently the detritivorous haplochromines that used to be the dominant trophic group are second in importance after the zooplanktivores (Witte et al., 2007a; M. Kishe-Machumu, pers. comm.).

Recent investigations revealed several ecological changes, including shifts in diet in the recovering zooplanktivores and detritivores. In both groups the macroinvertebrates became the dominant food source (Katunzi et al., 2003; Kishe-Machumu et al., 2008). Moreover, all the recovering species show remarkable morphological changes (*e.g.* van Oijen & Witte, 1996; Seehausen et al., 1997b; Kishe-Machumu et al., 2008; Witte et al., 2008). These changes may have been caused by adaptive responses to the changed environment, based on phenotypic plasticity and microevolution or by hybridization (Seehausen et al., 1997b; Witte et al., 2008). The contemporary ecological and morphological changes provide interesting opportunities to increase our understanding of basic ecological and evolutionary processes. It will be obvious that these changes can only be studied reliably if a proper description of the species is involved. For that purpose we describe in this paper four detritivorous and three phytoplanktivorous species that used to be common before the ecological changes in the mid 1980s and of which five species are probably still present.

Material and methods

The majority of the specimens were collected in the northern part of the Mwanza Gulf (between Nyamatala Island and Hippo Island, depth range about 6-16 m; Fig. 1) with bottom trawls and gill nets. Phytoplanktivores were collected also with surface trawls, beach seines and by angling (van Oijen et al., 1981; Witte, 1981; Goudswaard et al., 1995). The specimens that were collected in other areas than the Mwanza Gulf generally came from bottom trawls. All specimens were collected between 1975 and 1986, before the collapse of the haplochromines due to the Nile perch upsurge and the other ecological changes in the Mwanza Gulf (*e.g.* Witte et al., 1992a, b, 2005; Seehausen et al., 1997a; Wanink et al., 2001). The live colours of some individuals were photographed in a small perspex tank filled with water (see Barel et al., 1977). After their capture, the fish were stored on ice. In the laboratory they were preserved in formalin 10% neutralized with borax. Transport to the Netherlands took place after several months to several years, where the fish were rinsed with tap water and stepwise transferred to alcohol 70%. Terminology and measurements follow Barel et al. (1977), Hoogerhoud & Witte (1981) and Witte & Witte-Maas (1981). Measurements were taken to the nearest 0.1 mm using digital callipers with needles glued to the ends.

Of *Haplochromis vanoijeni* spec. nov., the oral and pharyngeal jaws of one specimen were dissected; of the other species these elements were dissected from three to four specimens. The description of oral and pharyngeal jaws and their dentition was based on the dissected elements. For the oral dentition additional specimens were investigated as well. Vertebrae counts were based on X-ray photographs from part of the type material. Apart from the measured specimens, we included additional specimens in

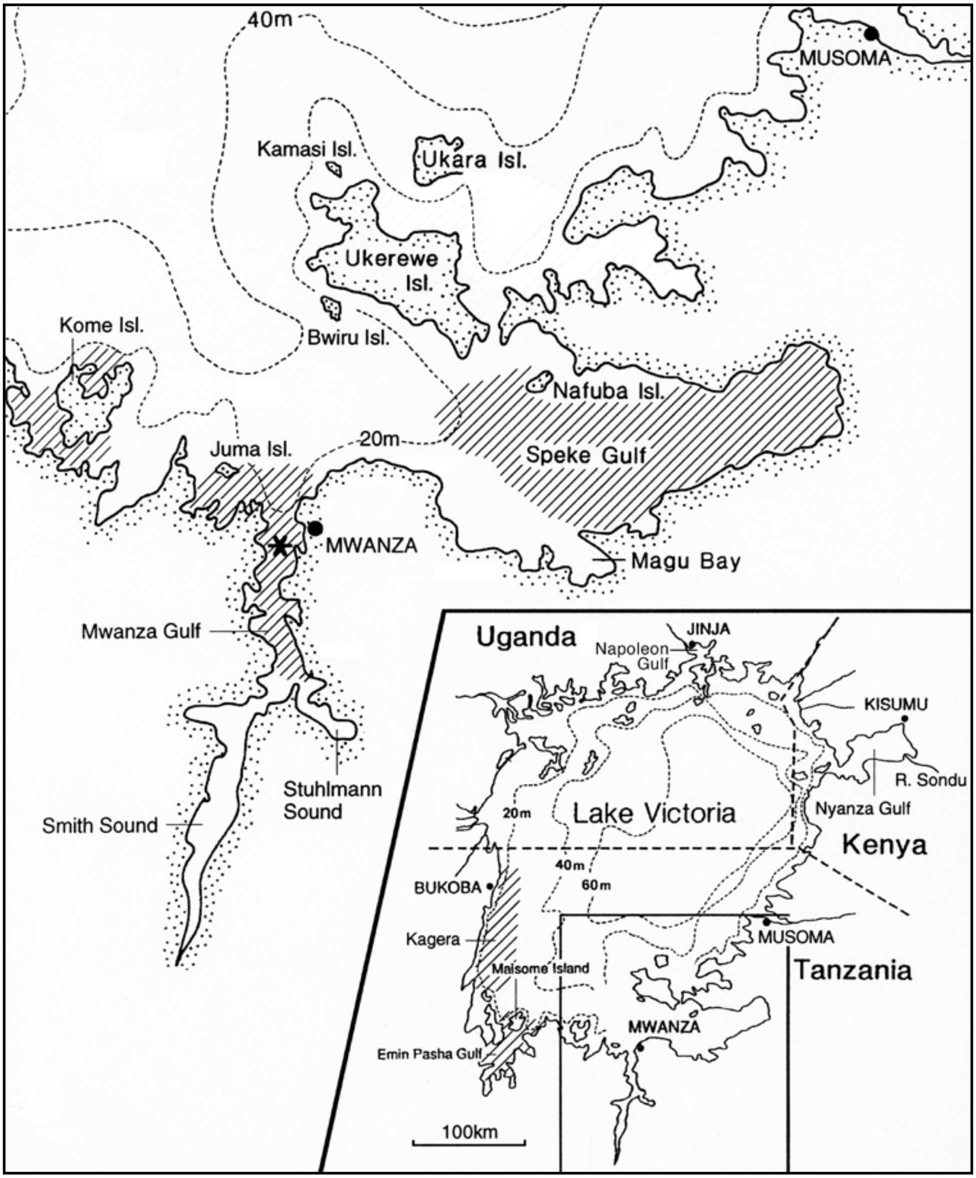

Fig. 1. Catch localities (hatched) in Lake Victoria of species described in this paper. Asterix indicates main sampling area.

the type material. Unless stated otherwise, qualitative characters described as being relatively small or large refer to the size of that character in *Haplochromis (Astatotilapia) elegans* Trewavas, 1933. Morphologically, this insectivore from Lake George is a modal haplochromine cichlid. Its skeletal elements are described in Barel et al. (1976). For abbreviations used in the text one is referred to the tables.

Systematic part

Description of four detritivorous species

Haplochromis antleter Mietes & Witte spec. nov.

(figs 2-4, table 1)

Haplochromis 'dusky wine-red fin'; Goldschmidt, 1989a: 98-100, 103, 107, 118, 119, 149, 167; Goldschmidt & de Visser, 1990: 131; Goldschmidt, 1991: 182, 185, 187; Witte et al., 1992b: 17, 25; Seehausen & Witte, 1994b: 52; Seehausen & Witte, 1995b: 28; Witte & Seehausen, 1995: 140; Seehausen et al., 1997b: 895, 897, 903.

Haplochromis 'dusky wine red fins'; Seehausen & Witte, 1995a: 101.

Haplochromis (Enterochromis) 'dusky wine red fin'; Witte et al., 2000: 234; Kishe-Machumu et al., 2008: 405, 408, 411.

Material examined (references to fish size concern standard length).— Holotype, ♂, 51.4 mm, RMNH 83944[3], Mwanza Gulf, Tanzania, Lake Victoria, 21.vi.1982, HEST; Paratypes: all males and collected by HEST in the Mwanza Gulf, Tanzania, Lake Victoria: ♂, 57.1 mm, RMNH 73283[2-4], 3.vi.1985; ♂, 50.1 mm, RMNH 73284[2-4], 4.vi.1985; ♂, 61.7 mm, RMNH 73285[2, 3], 7.ix.1977; ♂, 59.9 mm, RMNH 73286[2, 3], 13.ix.1977; ♂, 47.5 mm, RMNH 73287[2, 3], 28.iv.1978; ♂, 45.7 mm, RMNH 73288[2, 3], 12.viii.1981; ♂, 61.2 mm, RMNH 73289[2, 3], 3.xi.1978; ♂, 69.9 mm, RMNH 73290[2-4], 3.xi.1978; ♂, 66.9 mm, RMNH 73738[1, 3], 10.x.1977; ♂, 62.8 mm, RMNH 73739[1, 3], 7.ix.1977; ♂, 58.8 mm, RMNH 73740[1, 3], 3.xi.1978; ♂, 61.8 mm, RMNH 77777, 30.xii.1977; ♂, 55.5 mm, RMNH 77780[4], 4.vi.1985; ♂, 64.0 mm, RMNH 77781[4], 3.xi.1978; ♂, 57.0 mm, RMNH 77786[2, 3], 3.xi.1978; ♂, 53.3 mm, RMNH 80840[2-4], 3.vi.1985; ♂, 50.8 mm, RMNH 83914[2, 3], 13.ix.1977; ♂, 49.9 mm, RMNH 83915[2, 3], 13.ix.1977; ♂, 46.2 mm, RMNH 83916[2, 3], 12.viii.1981; ♂, 57.7 mm, RMNH 83917[2, 3], 3.xi.1978; ♂, 61.7 mm, RMNH 83918[2, 3], 3.xi.1978; ♂, 64.4 mm, RMNH 83926, 10.x.1977; ♂, 56.4 mm, RMNH 83927[2, 3], 7.ix.1977; ♂, 68.1 mm, RMNH 83928[2, 3], 7.ix.1977; ♂, 57.7 mm, NSMT-P 98078, 30.xii.1977; ♂, 55.8 mm, RMNH 83930, 30.xii.1977; ♂, 53.3 mm, RMNH 83932, 28.iv.1978; ♂, 62.5 mm, RMNH 83933, 3.xi.1978; ♂, 64.1 mm, RMNH 83934, 7.ix.1977; ♂, 48.7 mm, RMNH 83935, 9.iv.1982; ♂, 59.4 mm, BMNH 2010.3.23.1, 6.i.1978; ♂, 55.6 mm, RMNH 83937, 6.i.1978; ♂, 59.8 mm, AMNH 250803, 6.i.1978; ♂, 47.6 mm, RMNH 83939, 25.iii.1982; ♂, 52.7 mm, RMNH 83940, 25.iii.1982; ♂, 48.8 mm, RMNH 83941, 25.iii.1982; ♂, 47.4 mm, RMNH 83942, 21.vi.1982; ♂, 51.8 mm, RMNH 83943, 21.vi.1982; ♂, 48.5 mm, RMNH 83945, 15.xii.1981; ♂, 48.2 mm, RMNH 83946, 15.xii.1981; ♂, 59.8 mm, RMNH 83947, 25.iii.1982; ♂, 62.6 mm, RMNH 83948, 25.iii.1982.

Description.— Based on 43 male specimens (including the holotype) 45.7-69.9 mm SL.

Diagnosis.— *Haplochromis antleter* spec. nov. belongs to an assemblage of small sized (< 9 cm SL), relatively deep-bodied (BD > 35% SL) micrognathic (LJL < 45% HL) species with a moderately curved to straight dorsal head profile. The fish in this group

---

[1] Type specimen that has been dissected to describe gill apparatus, oral jaws and pharyngeal jaws; [2] type specimen of which an X-ray photograph is available; [3] type specimen of which morphometric measurements have been taken (Table 1); [4] type specimen of which a colour picture is available.

have relatively small, mainly bicuspid, teeth in the oral jaws. *H. antleter* spec. nov. can be distinguished from *Haplochromis cinctus* Greenwood & Gee, 1969, *Haplochromis paropius* Greenwood & Gee, 1969 and *Haplochromis katunzii* spec. nov., the other described species in this assemblage, by live colouration of sexually active males. *H. antleter* spec. nov. is dusky coloured with no or faint vertical bars and is the only species of the assemblage that has no or a faint lachrymal stripe. *H. paropius* has a red dorsum and a greenish flank with faint vertical bars. In contrast to the other three species *H. paropius* often has a mid-lateral band. *H. cinctus* has a red dorsum, an orange to yellowish flank and dark vertical bars (Greenwood & Gee, 1969). *H. katunzii* spec. nov. is sandy-brown and has, compared to *H. antleter* spec. nov., more distinctive vertical bars. *H. antleter* spec. nov. has a shallower cheek depth (16.1-21.1% of HL) than *H. katunzii* spec. nov. and *H. paropius* (18.6-24.6% and 18.1-24.2% of HL respectively; Tables 1, 2 and Greenwood & Gee, 1969). Further, the interorbital width is smaller (19.1-24.9% of HL), than in the type specimens of *H. cinctus* (24.3-27.2% of HL; Greenwood & Gee, 1969), but it should be noted that the type specimens of *H. antleter* spec. nov. are smaller than those of *H. cinctus* (Table 1; Greenwood & Gee, 1969). Compared to *H. katunzii* spec. nov., *H. antleter* spec. nov. has a less pronounced mental prominence on the lower jaw. For a comparison with *Haplochromis coprologus* spec. nov., see description of *H. coprologus* spec. nov.

Habitus (fig. 2).— Body relatively deep. Dorsal head profile moderately curved, rarely straight. Premaxillary pedicel not interrupting the profile. Mouth slightly oblique. Lips not thickened. Medial part of the premaxilla not expanded. Caudal part of the maxilla not bullate. The vertical through the caudal tip of the maxilla runs through the ligamentous ring around the eye, sometimes it runs through the iris. Lateral snout outline isognathous and obtuse. Jaws equal anteriorly. Mental prominence not pronounced. Retro-articular processes of right and left mandible generally not touching each other,

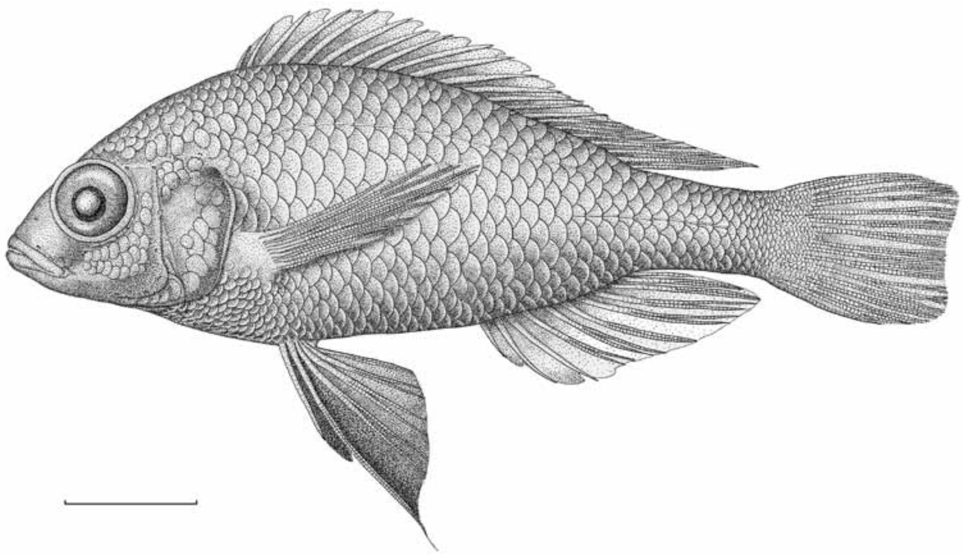

Fig. 2. *Haplochromis antleter* spec. nov., paratype, RMNH 77786, ♂. Scale equals 10 mm. Drawn by S. ter Huurne.

not interrupting the ventral body outline. Eye approximately circular. A small aphakic aperture may be present. Cephalic lateral line pores generally not enlarged.

Scales.— Cheek, gill cover, dorsal head surface, chest, greater part of dorsum and caudal fin base covered with cycloid scales, the remaining part of the body with ctenoid scales. A gradual size transition between scales of chest and flank. Four and a half to 6.5 (mode 6) scales between the upper lateral line and the dorsal fin origin, 4.5 to seven (mode 5) between the pectoral and the pelvic fin bases.

Fins.— Pelvic fins reach the rostral-most point of the anal fin origin, in some specimens extending further. First soft rays of pelvic fins produced and filamentous in some specimens. Anal fin just reaching caudal fin origin. Caudal fin outline truncate to emarginate.

Gill apparatus.— The description of the gill apparatus is based on the lateral gill rakers and the lateral hemibranch of the first gill arch. The number of gill rakers on the lower part of the gill arch is 10. The lower one to three rakers are reduced. The next four to five rakers are short to normal in size; tip blunt to acutely pointed. The remaining rakers are blunt and diamond-shaped or (weakly) bifid. The rakers are generally not touching each other. The number of gill filaments ranges from 85 to 89.

Viscera.— Ratio between intestine length and SL: 2.4-4.0, mean 2.9 ± 0.4, n = 11 (F. Witte, E. Witte-Maas & M. Kishe-Machumu, unpublished data).

Oral jaws.— Premaxillary dentigerous arm about as long as ascending arm (asc/

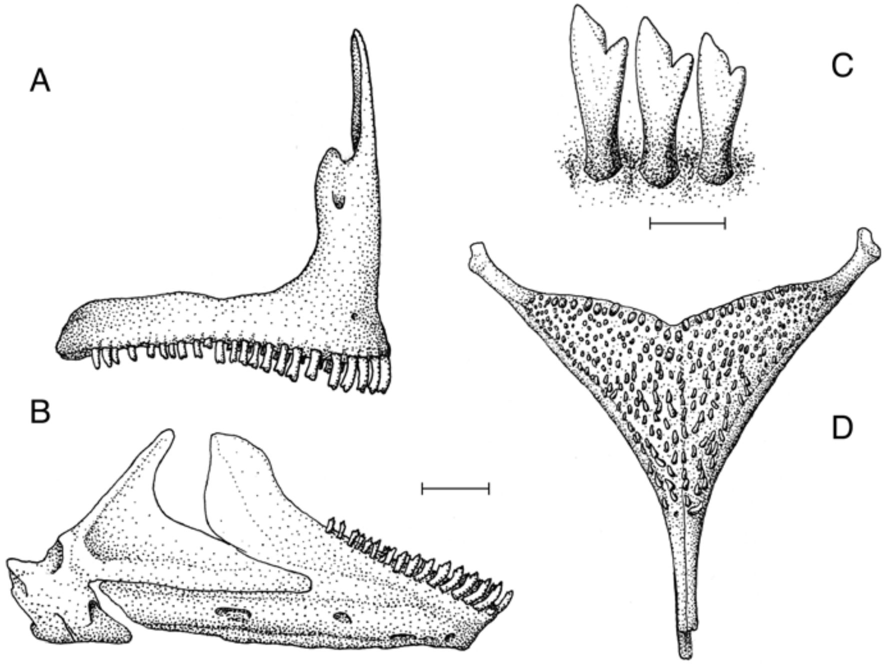

Fig. 3. *Haplochromis antleter* spec. nov. A, Premaxilla, lateral view; B, Lower jaw, lateral view; C, Premaxillary teeth; D, Lower pharyngeal element, dorsal view. Bony elements drawn from RMNH 73740, ♂, scale of bony elements = 10 mm. Teeth drawn from RMNH 73739, ♂, scale of teeth 0.25 mm. Drawn by S. ter Huurne.

dent arm ratio 1.0). The angle between the two arms is 86° to 91°. In one of the three dissected specimens a small symphyseal articulation facet is present (cf. Witte, 1984a). Lower jaw slightly elongated (length/height ratio 1.9 to 2.1). The upper half of the dentary has a moderate to distinct outwardly directed flare. Mental prominence slightly pronounced, which is not visible in intact specimens (see under Habitus).

Oral teeth.— *Shape.* Teeth in the rostral ⅔ of the dentigerous area of both jaws generally unequally bicuspid, occasionally with a few tricuspids or weakly bicuspids among them. Caudally tricuspids, weakly bicuspids or blunt unicuspids can be found. The caudal-most two to three teeth of the premaxilla are stout, generally blunt unicuspids or weakly bicuspids, sometimes tricuspids.

In bicuspid teeth, the major cusp is subequilateral, often slightly protracted. A small but distinct flange is present, which is less clearly visible in caudally positioned teeth. The cusp gap is wide, the minor cusp is distinct. In labial view, the neck is moderately slender to stout, the crown slightly expanded. In lateral view, the crown is compressed. The premaxillary outer row teeth are recurved, those of the lower jaw slightly recurved. The inner row teeth in both premaxilla and lower jaw are tricuspid.

Size. Teeth are relatively small and slender.

Dental arcade and tooth band. Dental arcade rounded and U-shaped. Premaxilla generally two, occasionally three inner rows anteriorly, none posteriorly. Lower jaw two inner rows anteriorly, none posteriorly.

Counts and setting. There are 45 to 57 teeth in the outer row of the upper jaw (l+r premaxilla). Premaxillary teeth closely to widely and regularly set, lower jaw teeth closely set.

Implantation. Outer row teeth of premaxilla erect, inner row teeth recumbent. Lower

Table 1. Measurements of *Haplochromis antleter* spec. nov. Means and standard deviations have been calculated over all measured type specimens (including the holotype).

		Holotype	Paratypes (n = 20)	Mean ± st. dev (n = 21)
standard length (mm)		51.4	45.7-69.9	56.9 ± 6.9
body depth (BD)	%SL	40.5	35.0-39.4	37.7 ± 1.3
pectoral fin length (PFL)	%SL	31.9	30.2-33.9	32.4 ± 1.1
caudal peduncle length (CPL)	%SL	16.9	15.4-18.4	17.1 ± 0.8
caudal peduncle depth (CPD)	%SL	12.3	10.4-12.8	11.2 ± 0.6
caudal fin length (CFL)	%SL	27.8	24.8-30.1	26.8 ± 1.4
head length (HL)	%SL	35.2	31.9-35.7	33.4 ± 1.1
snout length (SnL)	%HL	28.2	23.5-30.8	26.8 ± 1.7
snout width (SnW)	%HL	29.8	28.9-34.6	31.3 ± 1.6
head width (HW)	%HL	47.5	44.1-51.2	47.2 ± 1.8
interorbital width (IOW)	%HL	21.5	19.1-24.9	22.4 ± 1.4
preorbital width (POW)	%HL	26.5	22.9-29.1	26.4 ± 1.4
lachrymal width (LaW)	%HL	24.9	19.0-31.2	24.8 ± 2.3
preorbital depth (POD)	%HL	14.4	12.9-16.5	14.4 ± 0.9
eye length (EyL)	%HL	34.3	31.2-38.4	34.7 ± 1.5
eye depth EyD)	%HL	30.9	29.5-35.2	32.5 ± 1.3
cheek depth (ChD)	%HL	16.6	16.1-21.1	18.3 ± 1.5
lower jaw length (LJL)	%HL	35.9	34.6-38.8	36.7 ± 1.1
lower jaw width (LJW)	%HL	22.7	17.2-24.1	20.7 ± 2.0
EyD/EyL		0.9	0.8-1.0	0.9 ± 0.0
LJL/LJW		1.6	1.6-2.1	1.8 ± 0.2

jaw outer row teeth slightly procumbent, inner row teeth erect.

Lower pharyngeal element.— As long as it is broad, or slightly longer than broad (length/width ratio 1.0 to 1.1). The dentigerous area is distinctly broader than long (length/width ratio 0.7 to 0.8). The suture is straight.

Pharyngeal teeth.— *Counts.* There are 34 to 39 teeth in the caudal-most transverse row, 11 to 12 teeth in medial length rows.

Shape. Teeth in caudal-most transverse row hooked, major cusp only slightly incurved and blunt. Other teeth pronounced or bevelled. All teeth are relatively fine and slender, medial teeth not coarser than other teeth. One specimen has a few teeth in the rostral part of the lower pharyngeal element, which look somewhat like unicuspid oral teeth; they have no distinct minor cusp or cusp protuberance.

Vertebrae.— The total number of vertebrae in 17 X-rayed specimens is 28 (1), 29 (13) or 30 (3), comprising 12-13 abdominal and 16-17 caudal vertebrae.

Live colouration.— Colours are only known from males, they have the snout, dorsal head surface, interoperculum, cheek and gill cover dusky with a bluish sheen. The eye has a dark grey outer ring and a light yellowish inner ring. Lips are greyish with an iridescent turquoise flush. Lower jaw grey to dusky. Rostral part of the dorsum and flank dusky, with a caudad increasing blue-turquoise to greenish (in some specimens yellowish) iridescent sheen. Belly, chest, and ventral side slightly lighter than dorsum and flank. The iridescent sheen on the body varies in intensity. Nostril-, lachrymal-, supra orbital stripe and nape band if present, faint. Opercular blotch present. Three to five faint vertical bars may be present on the flank. Pectoral fins hyaline with dusky rays, pelvic fins black. Anal fin with a black base, rostro-ventral part wine-red, dorso-caudal part hyaline with two yolk-yellow egg dummies surrounded by a dusky ring. Caudal fin with a dusky base, the remaining part wine-red. Dorsal fin dusky, with wine-red maculae on the caudal part. Lappets rostral dusky, caudally some red ones.

Preserved colouration of males. Entire body dark brown, ventral side slightly lighter. Pectoral fins brownish-hyaline, pelvic fins black. Anal fin brownish with a dusky base and a more hyaline distal part. Caudal fin brownish with a dark base and a dark me-

Fig. 4. *Haplochromis antleter* spec. nov., paratype, RMNH 77781, sexually active ♂, 64.0 mm SL.

dial part. Dorsal fin and lappets dusky. No, or very faint vertical bars visible.

Distribution.— *Haplochromis antleter* spec. nov. is only known from Lake Victoria.

Habitat.— *Haplochromis antleter* spec. nov. is a benthic species and was caught in sub-littoral areas of the Mwanza Gulf mainly over mud bottoms. The depth range is 2-11 m (Witte et al., 1992b) which is shallower than that of *H. cinctus* (13-60 m; Greenwood & Gee, 1969; Van Oijen et al., 1981; Witte et al., 1992b).

Food.— Before the ecological changes in Lake Victoria, *H. antleter* spec. nov. fed mainly on detritus, but also included phytoplankton (mainly *Aulacoseira*) and occasionally insect larvae and zooplankton in its diet. *H. antleter* spec. nov. fed mostly during the day (T. Goldschmidt, pers. comm.).

Breeding.— Based on the egg dummies on the anal fin of males and the egg size in ripe females (3.1 mm; Goldschmidt & Goudswaard, 1989), *H. antleter* spec. nov. is a female mouth brooder.

Etymology.— The name antleter comes from the Greek word for scooper, dredger; ‘ἀντλητήϱ’, from the stem of the verb ‘ἀντλεῖν’ (‘to scoop’, ‘to dredge’) and the ending -τήϱ that indicates the acting person. The name refers to the dredging of mud bottoms, the ‘core business’ of this species.

Haplochromis katunzii ter Huurne & Witte spec. nov.
(figs 5-7, table 2)

Haplochromis ‘75’; van Oijen et al., 1981: 157; Hoogerhoud et al. 1983: 298; Hoogerhoud, 1984: 558; Witte, 1984a: 603; Witte, 1984b: 159; Witte, 1987, chapter 1: 603; Witte, 1987, chapter 3: 8; Goldschmidt, 1989a: 149; Goldschmidt, 1991: 182, 185, 187; Witte et al., 1992b: 25; Witte & van Oijen, 1990: 13; Goldschmidt et al., 1993: 688, 690; Seehausen & Witte, 1994b: 52; Witte & Seehausen, 1995: 140; Seehausen & Witte, 1995a: 101; Seehausen & Witte, 1995b: 28; Seehausen et al., 1997b: 865, 897, 901, 903.

Enterochromis ‘75’; Hoogerhoud, 1984: 564; Seehausen et al., 2003: 281.

Haplochromis (Enterochromis) ‘75’; Witte et al., 2000; 234; Sibbing & Witte, 2005: 120, 122; Kishe-Machumu et al., 2008: 405, 411; Witte et al., 2009: 658.

Material examined (references to fish size concern standard length).— Holotype, ♂, 65.3 mm, RMNH 73255[2], Mwanza Gulf, Tanzania, Lake Victoria, 20.iv.1979, HEST; Paratypes: all males and collected by HEST in the Mwanza Gulf, Tanzania, Lake Victoria: ♂, 67.4 mm, RMNH 72832[3], 4.vi.1980; ♂, 73.8 mm, RMNH 73249[2], 9.vi.1978; ♂, 65.4 mm, RMNH 73250[2], 9.vi.1978; ♂, 79.5 mm, RMNH 73251[2], 21.iv.1978; ♂, 68.6 mm, RMNH 73252[2], 23.xii.1977; ♂, 75.7 mm, RMNH 73253[2], 5.v.1978; ♂, 59.1 mm, RMNH 73254[2, 3], 3.vi.1985; ♂, 65.4 mm, RMNH 73256[2], 8.iii.1979; ♂, 66.6 mm, RMNH 73257[2], 20.iv.1979; ♂, 63.7 mm, RMNH 73258[2], 20.iv.1979; ♂, 60.2 mm, RMNH 73259[2], 24.iv.1980; ♂, 68.0 mm, RMNH 73389, 14.x.1977; ♂, 66.7 mm, RMNH 73393, 7.ix.1977; ♂, 61.4 mm, RMNH 73395[1], 24.iv.1980; ♂, 63.6 mm, RMNH 73396[1], 9.iv.1979; ♂, 70.5 mm, RMNH 73418[1], 5.v.1978; ♂, 63.5 mm, RMNH 77788[2], 20.iv.1979; ♂, 64.1 mm, RMNH 77789[2], 9.vi.1978; ♂, 64.6 mm, RMNH 80896, 7.ix.1977; ♂, 66.2 mm, RMNH 80897[1], 5.v.1978; ♂, 66.5 mm, RMNH 80955[2], 9.vi.1978; ♂, 63.4 mm, RMNH 80956[2], 9.vi.1978; ♂, 69.8 mm, RMNH 81250[3], 9.vi.1975; ♂, 69.8 mm, RMNH 81275[3], 25.viii.1981; ♂, 66.3 mm, RMNH 81836[3], 7.vi.1975; ♂, 65.4 mm, RMNH 83730[4], 9.vi.1978; ♂, 66.2 mm, RMNH 83910[2], 20.iv.1979; ♂, 54.2 mm,

---

[1] Type specimen that has been dissected to describe gill apparatus, oral jaws and pharyngeal jaws; [2] type specimen of which an X-ray photograph is available and of which morphometric measurements have been taken (Table 2); [3] type specimen of which a colour picture is available; [4] type specimen that has been dissected, but was not used for description of the skeletal elements.

RMNH 83911[2], 24.iv.1980; ♂, 62.1 mm, RMNH 83931[2], 20.iv.1979; ♂, 66.5 mm, NSMT-P 98080, 5.ii.1979; ♂, 68.4 mm, AMNH 250805, 5.ii.1979; ♂, 68.9 mm, BMNH 2010.3.23.3, 5.ii.1979; ♂, 64.6 mm, RMNH 83973, 5.ii.1979; ♂, 54.6 mm, RMNH 83974, 4.vi.1979; ♂, 58.2 mm, RMNH 83975, 4.vi.1979; ♂, 58.0 mm, RMNH 83976, 4.vi.1979; ♂, 56.9 mm, RMNH 83977, 4.vi.1979; ♂, 53.6 mm, RMNH 83978, 4.vi.1979; ♂, 57.8 mm, RMNH 83979, 13.ix.1977; ♂, 52.1 mm, RMNH 83980, 13.vi.1979; ♂, 57.2 mm, RMNH 83981, 13.vi.1979; ♂, 62.1 mm, RMNH 83982, 13.vi.1979; ♂, 61.1 mm, RMNH 83983, 13.vi.1979; ♂, 52.6 mm, RMNH 83984, 13.vi.1979; ♂, 64.2 mm, RMNH 83985, 5.ii.1979; ♂, 61.7 mm, RMNH 83989, 9.vi.1978.

Description.— Description based on 47 male specimens 52.1-79.5 mm SL.

Diagnosis.— *Haplochromis katunzii* spec. nov. belongs to an assemblage of small sized (< 9 cm SL), relatively deep-bodied (BD > 35% SL) micrognathic (LJL< 45% HL) species with a moderately curved to straight dorsal head profile. The fish in this group have relatively small, mainly bicuspid, teeth in the oral jaws. *H. katunzii* spec. nov. can be distinguished from *Haplochromis paropius, H. cinctus* and *Haplochromis antleter* spec. nov., the three other described species in this assemblage, by live colouration of sexually active males. *H. katunzii* spec. nov. is sandy-brown, and has rather distinct vertical bars. *H. antleter* spec. nov. is dusky coloured, has faint vertical bars and no or a faint lachrymal stripe. *H. cinctus* has a red dorsum, an orange to yellowish flank and dark vertical bars (Greenwood & Gee, 1969). *H. paropius* has a red dorsum, a greenish flank and is the only species of the assemblage that often has a mid-lateral band (Greenwood & Gee, 1969). Further, *H. katunzii* spec. nov. has a larger cheek depth (18.6-24.6% of HL) than *H. antleter* spec. nov. (16.1-21.1% of HL), as well as a more pronounced mental prominence on the lower jaw. *H. katunzii* spec. nov. has a smaller interorbital width (19.2-24. 1% of HL) than *H. cinctus* (24.3-27.2% of HL; Greenwood & Gee, 1969).

Habitus (fig. 5).— Body relatively deep. Dorsal head profile straight to moderately curved. Premaxillary pedicel not or slightly interrupting the profile. Mouth slightly oblique. Lips not thickened. Medial part of the premaxilla not to slightly expanded. Caudal part of maxilla not bullate. The vertical through the caudal tip of the maxilla

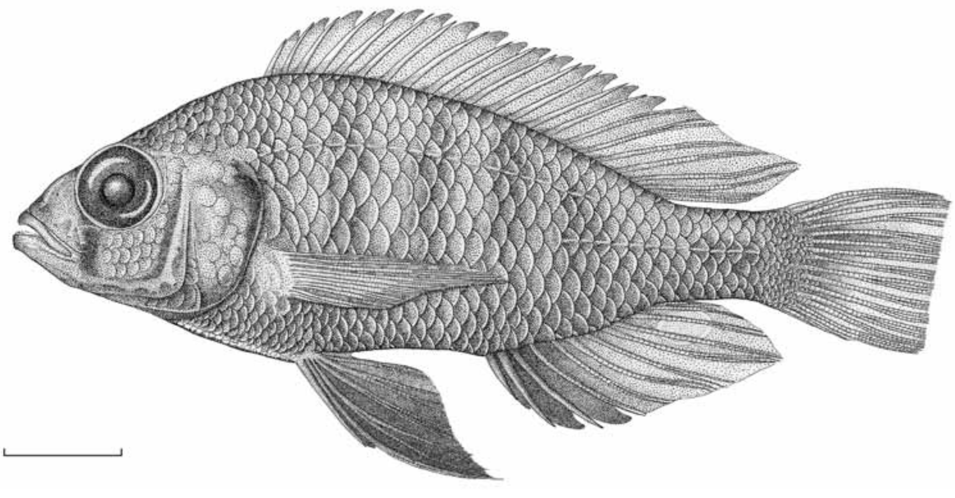

Fig. 5. *Haplochromis katunzii* spec. nov., paratype, RMNH 77788, ♂. Scale equals 10 mm. Drawn by S. ter Huurne.

runs through the iris. Lateral snout outline isognathous and obtuse. Jaws equal anteriorly. Mental prominence not or slightly pronounced. Retro-articular processes of right and left mandible may just touch each other, not interrupting the ventral body outline. Eye approximately circular. A small aphakic aperture may be present. Cephalic lateral line pores generally not enlarged.

Scales.— Cheek, gill cover, dorsal head surface, greater part of dorsum and caudal fin base covered with cycloid scales. Chest mainly with cycloid scales and some weakly ctenoid scales. Remaining part of the body with ctenoid scales. A gradual size transition between scales of chest and flank. Four to 6.5 (mode 6) scales between the upper lateral line and the dorsal fin origin, four to six (mode 5) between the pectoral and the pelvic fin bases.

Fins.— Pelvic fins reaching the anal fin origin, in some specimens extending further. First soft rays of pelvic fins often produced and filamentous. Anal fin reaching caudal fin origin. Caudal fin outline truncate to emarginate.

Gill apparatus.— The description of the gill apparatus is based on the lateral gill rakers and the lateral hemibranch of the first gill arch. The number of gill rakers on the lower part of the first gill arch is eight to nine. The first raker is reduced, the next one to three rakers are short or normal. The shape of the remaining rakers may be blunt, (weakly) bifid or trifid. The rakers on the first gill arch may or may not touch each

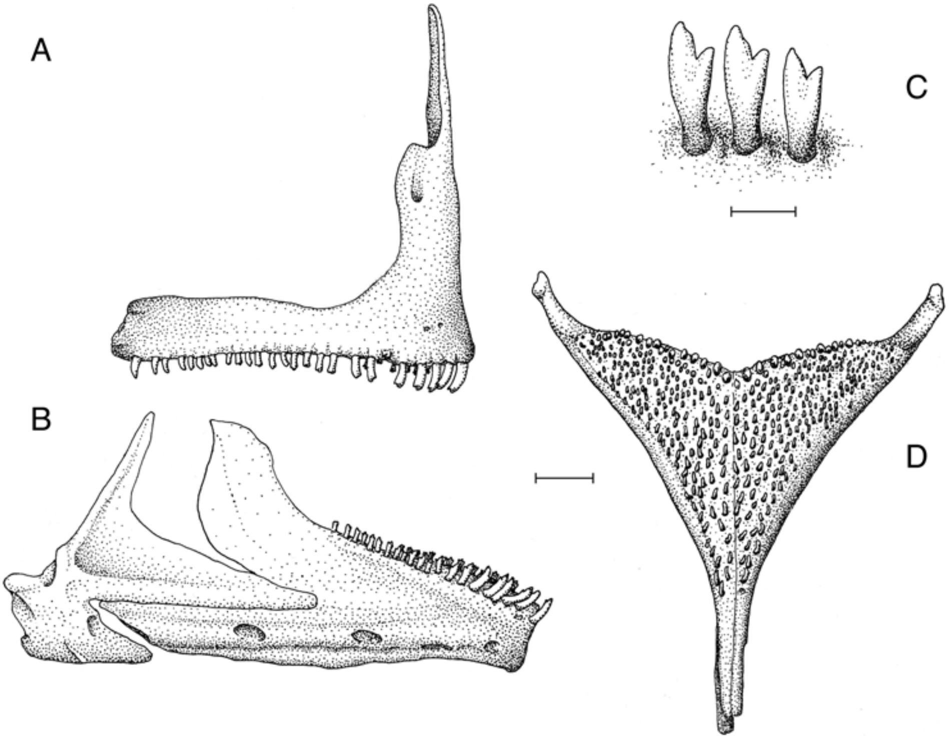

Fig. 6. *Haplochromis katunzii* spec. nov. A, Premaxilla, lateral view; B, Lower jaw, lateral view; C, Lower jaw teeth; D, Lower pharyngeal element, dorsal view. Bony elements drawn from RMNH 80897, ♂, scale of bony elements = 10 mm. Teeth drawn from RMNH 73396, ♂, scale of teeth 0.25 mm. Drawn by S. ter Huurne.

other. The number of gill filaments on the lateral hemibranch of the first gill arch ranges from 89 to 96.

Viscera.— Ratio between intestine length and SL: 1.5-3.3, mean 2.4 ± 0.4, n = 25 (F. Witte, E. Witte-Maas & M. Kishe-Machumu, unpublished data)

Oral jaws.— Premaxillary dentigerous arm about as long as, or slightly longer than ascending arm (asc/dent arm ratio 0.9 to 1.0). The angle between the two arms is 83° to 89°. In two specimens a small symphysead articulation facet is present (cf. Witte, 1984a). Lower jaw slightly elongated (length/height ratio 1.8 to 1.9; one specimen 2.2). The upper half of the dentary has a moderate to distinct outwardly directed flare. A small mental prominence is present.

Oral teeth.— *Shape.* Generally the teeth in the rostral part (ca. ⅔ of dentigerous area) of both premaxilla and lower jaw are unequally bicuspid. Sometimes, however, a few unicuspids or tricuspids can be found among them. In the caudal part of the premaxilla, blunt unicuspids, weakly bicuspids or tricuspids can be found. The caudal-most two to three teeth are stout unicuspids or (weakly) bicuspids. The teeth in the caudal part of the lower jaw are generally tricuspid or subequally bicuspid, sometimes weakly bicuspid or unicuspid.

In bicuspid teeth, the shape of the major cusp is isoscelene to subequilateral. A small flange is present, which is moderately distinct in rostral teeth, but hardly visible in more caudally placed teeth. The cusp gap is wide, the minor cusp distinct. Tricuspid teeth sometimes may have a slightly protracted middle cusp. In labial view, the neck is moderately slender to stout, the crown slightly expanded. In lateral view, the crown is compressed. The premaxilla outer row teeth are recurved, those of the lower jaw slight-

Table 2. Measurements of *Haplochromis katunzii* spec. nov. Means and standard deviations have been calculated over all measured type specimens (including the holotype).

		holotype	paratypes (n = 17)	mean ± st. dev (n = 18)
standard length (mm)		65.3	54.2-79.5	65.7 ± 5.8
body depth (BD)	%SL	39.8	36.9-42.1	39.1 ± 1.5
pectoral fin length (PFL)	%SL	33.5	30.7-37.5	33.2 ± 1.6
caudal peduncle length (CPL)	%SL	18.2	13.7-18.4	16.7 ± 1.1
caudal peduncle depth (CPD)	%SL	11.2	10.6-12.7	11.5 ± 0.6
caudal fin length (CFL)	%SL	27.9	26.1-29.3	27.8 ± 1.0
head length (HL)	%SL	33.8	32.8-36.0	34.4 ± 0.8
snout length (SnL)	%HL	27.1	24.4-29.2	27.1 ± 1.5
snout width (SnW)	%HL	33.0	27.1-34.1	31.3 ± 2.1
head width (HW)	%HL	49.8	40.2-48.8	45.2 ± 2.6
interorbital width (IOW)	%HL	20.4	19.2-24.1	21.6 ± 1.2
preorbital width (POW)	%HL	27.6	24.0-28.8	27.2 ± 1.2
lachrymal width (LaW)	%HL	27.6	22.0-29.9	26.0 ± 1.8
preorbital depth (POD)	%HL	14.9	13.5-16.6	15.0 ± 0.8
eye length (EyL)	%HL	35.3	28.9-35.6	33.0 ± 1.7
eye depth EyD)	%HL	33.5	28.9-34.1	31.8 ± 1.5
cheek depth (ChD)	%HL	20.8	18.6-24.6	20.8 ± 1.3
lower jaw length (LJL)	%HL	40.7	35.7-42.9	38.5 ± 1.6
lower jaw width (LJW)	%HL	23.1	16.7-23.3	20.7 ± 2.0
EyD/EyL		0.9	0.9-1.1	1.0 ± 0.0
LJL/LJW		1.8	1.5-2.4	1.9 ± 0.2

ly recurved. The inner row teeth of both premaxilla and lower jaw are tricuspid.
Size. Teeth are relatively small and slender.
Dental arcade and tooth band. Dental arcade rounded to U-shaped. Premaxilla with two to three inner rows anteriorly, none posteriorly. The lower jaw has one to three inner rows anteriorly, none posteriorly
Counts and setting. There are 52 to 67 teeth in the outer row of the upper jaw (l+r premaxilla). Premaxillary teeth are closely to widely and regularly set. Lower jaw teeth generally closely set, but in a few specimens they are widely and regularly set in the rostral part.
Implantation. Outer row teeth of premaxilla erect, inner row teeth recumbent. Lower jaw outer row teeth slightly procumbent, inner row teeth erect.

Lower pharyngeal element.— Relatively slender when compared to that of *H. elegans*. As long as it is broad or slightly longer than broad (length/width ratio 1.0 to 1.1). The dentigerous area is broader than long (length/width ratio 0.8 to 0.9). The suture is straight.

Pharyngeal teeth.— *Counts.* There are 38 to 42 teeth in the caudal-most transverse row, 14 to15 teeth in the medial rows.
Shape. Teeth in caudal-most transverse row hooked, major cusp only slightly incurved and blunt. Other teeth pronounced or bevelled. In general, the teeth are fine and slender, but the medial teeth are sometimes coarser than the other teeth.

Vertebrae.— The total number of vertebrae in 18 X-rayed specimens is 28 (3), 29 (11), 30 (3) or 31 (1), comprising 12-14 abdominal and 16-17 caudal vertebrae.

Live colouration.— Males have the snout, dorsal head surface, lips, lower jaw and cheek sandy-brown. Gill cover, chest and belly varying from light sandy-brown to black with a turquoise sheen. The eye has a dark grey outer ring and a yellowish inner ring. The lachrymal- and supraorbital stripes extend over the iris. Dorsum, flank and caudal peduncle sandy-brown, the latter two with a turquoise sheen. Rostral part of the ventral side silvery to black, the caudal part sandy-brown to black with a turquoise

Fig. 7. *Haplochromis katunzii* spec. nov., paratype, RMNH 81250, sexually active ♂, 69.8 mm SL.

sheen. Nostril-, interorbital- and preopercular vertical stripes, nape band and opercular blotch present. There are four to six vertical bars on the flank. Pectoral fins hyaline, pelvic fins black. The rostral part of the anal fin is black, caudal part orange-red gradually changing into hyaline. Anal fin with two yolk-yellow to orange, egg dummies surrounded by a dusky ring, in the caudal-most egg dummy the ring is partly hyaline. The caudal fin is orange-red, with a black base. Dorsal fin dusky, with (sometimes faint) red maculae. Lappets on the rostral half of the dorsal fin are sooty; those on the caudal half are orange-red. *Preserved colouration of males*. Entire body yellow-brown. Flank, belly, and ventral side dusky. Chest yellow-brown to dusky. Nostril-, interorbital-, lachrymal-, supraorbital- and preopercular vertical stripes are present; the supraorbital stripe extends into the iris. The nape band is interrupted medially. An opercular blotch is present and ventrally extended. Four to six vertical bars on the flank. Pectoral fins hyaline, pelvic fins black. Generally the rostral part of the anal fin is dusky, caudally only the base of the fin is dusky and the remainder hyaline. Egg dummies with a dusky or hyaline ring may be visible. The dorso-rostral part of the caudal fin is often dusky. The dorsal fin is somewhat sooty; the lappets in the rostral part are dusky. In some specimens the base is dusky.

Distribution.— *Haplochromis katunzii* spec. nov. is only known from Lake Victoria.

Ecology.— Information on the ecology of *H. katunzii* spec. nov. is given by, among others, Goldschmidt et al. (1993). However, in this paper *H. katunzii* spec. nov. was treated jointly with *H. cinctus* as the detritivorous 'curved head' group because the females of these species and some other detritivorous species were hard to distinguish.

Habitat.— *Haplochromis katunzii* spec. nov. was caught in sub-littoral areas of the Mwanza Gulf, mainly over mud bottoms. The depth range is 2-15 m, which is shallower than that of *H. cinctus* (13-60 m; Greenwood & Gee, 1969; Van Oijen et al., 1981). *H. katunzii* spec. nov. is a benthic species. At night they occurred slightly higher in the water column (Goldschmidt et al., 1993; F.W., unpublished data).

Food.— Before the ecological changes in Lake Victoria, *H. katunzii* spec. nov. fed mainly on detritus, but also included phytoplankton, insect larvae and copepods in its diet. *H. katunzii* spec. nov. fed mostly during the day (Goldschmidt et al., 1993; F.Witte, unpublished data).

Breeding.— Based on the egg dummies on the anal fin, *H. katunzii* spec. nov. is supposed to be a female mouth brooder.

Etymology.— This species is named in honour of Mr Egid F.B. Katunzi (MSc), the current Director of the Mwanza Centre of the Tanzania Fisheries Research Institute (TAFIRI). Mr Katunzi has collaborated with the Haplochromis Ecology Survey Team (HEST) of Leiden University since 1979, when he did his MSc study on food preferences of four haplochromine species from the Mwanza Gulf. Mr Katunzi published several papers on Lake Victoria haplochromines. During the past thirty years he has continuously supported the fieldwork of HEST.

Haplochromis coprologus Niemantsverdriet & Witte spec. nov.
(figs 8-10, table 3)

Haplochromis 'nigrofasciatus'; van Oijen et al., 1981: 164; Witte, 1981: 187, 189, 192; Witte, 1984b: 162; Witte & Goudswaard, 1985a: 82; Witte & Goudswaard, 1985b: 299, 301, 302; Goldschmidt, 1986: 45-48, 50; Witte, 1987, chapter 3: 22; Witte, 1987, chapter 4: 4, 6, 14; Goldschmidt, 1989a: 31, 98-101, 103, 107, 108, 118, 119, 149; Goldschmidt, 1989b: 125, 130; Goldschmidt et al., 1990: 347; Goldschmidt, 1991: 182, 185, 187; Witte et al., 1992b: 17, 25; Witte & van Oijen, 1990: 13; Goldschmidt et al., 1993: 690-695, 697; de Visser & Barel, 1996: 4; Seehausen et al., 1997b: 895, 897, 899, 901, 903; de Visser, 2000: 18.

Enterochromis 'nigrofasciatus'; Huber et al., 1997: 170; Rinkes, 1999: 29.

Haplochromis (Enterochromis) 'nigrofasciatus'; Witte et al., 2000: 234; Kishe-Machumu et al., 2008: 405, 408, 411.

Material examined (references to fish size concern standard length).— Holotype, ♂, 67.5 mm, RMNH 73270[2, 3], Mwanza Gulf, Tanzania, Lake Victoria, 23.iv.1980, HEST; Paratypes: all collected by HEST in the Mwanza Gulf, Tanzania, Lake Victoria, except where noted otherwise: ♀, 63.8 mm, RMNH 73269[2, 3], 18.viii.1981; ♂, 61.5 mm, RMNH 73271[3], 5.v.1978; ♀, 63.4 mm, RMNH 73272[2, 3], 2.vi.1978; ♂, 57.3 mm, RMNH 73273[2-4], 25.iv.1980; ♂, 61.6 mm, RMNH 73274[2-4], 14.iv.1981; ♂, 51.2 mm, RMNH 73275[2-4], 3.vi.1985; ♂, 57.2 mm, RMNH 73467[1, 3], 23.iv.1980; ♀, 52.3 mm, RMNH 73468[1, 3], 8.viii.1981; ♂, 48.2 mm, RMNH 73469[1, 3], 17.viii.1981; ♂, 75.1 mm, RMNH 73476[4], 14.iv.1981; ♂, 45.4 mm, RMNH 77772[4], 4.vi.1985; ♂, 66.2 mm, RMNH 77787[2, 3], 25.iv.1980; ♂, 62.2 mm, RMNH 77790[2, 3], 5.v.1978; ♂, 41.9 mm, RMNH 80847[4], 4.vi.1985; ♂, 62.5 mm, RMNH 80957[2, 3], 5.v.1978; ♀, 54.6 mm, RMNH 80958[2, 3], 2.vi.1978; ♂, 54.0 mm, RMNH 80959[2, 3], 2.vi.1978; ♀, 57.7 mm, RMNH 80960[2, 3], 2.vi.1978; ♂, 71.1 mm, RMNH 80967[4], 14.iv.1981; ♂, 56.9 mm, RMNH 81128[4], 25.iv.1980; ♀, 59.8 mm, RMNH 81555, 2.vi.1978; ♂, 65.9 mm, RMNH 81782[4], 2.vi.1975; ♀, 55.1 mm, RMNH 83919[2, 3], 18.viii.1981; ♂, 64.2 mm, RMNH 83920[2, 3], 23.iv.1980; ♂, 55.9 mm, RMNH 83921[2, 3], 23.iv.1980; ♂, 62.5 mm, RMNH 83922[2, 3], 23.iv.1980; ♂, 69.0 mm, RMNH 83949[1, 3], 23.iv.1980; ♂, 58.3 mm, NSMT-P 98079, 25.viii.1981; ♂, 67.8 mm, RMNH 83951, 25.viii.1981; ♂, 59.1 mm, BMNH 2010.3.23.2, 25.viii.1981; ♂, 62.9 mm, RMNH 83953, 25.viii.1981; ♀, 64.9 mm, RMNH 83954, 13.vi.1979; ♀, 65.5 mm, RMNH 83955, 13.vi.1979; ♂, 48.8 mm, RMNH 83956, 13.vi.1979; ♂, 53.6 mm, RMNH 83957, 13.vi.1979; ♂, 64.5 mm, RMNH 83958, 13.vi.1979; ♂, 54.0 mm, RMNH 83959, 13.vi.1979; ♂, 52.4 mm, RMNH 83960, 13.vi.1979; ♂, 52.4 mm, RMNH 83961, 13.vi.1979; ♂, 52.8 mm, RMNH 83962, 31.viii.1981; ♀, 50.1 mm, RMNH 83963, 19.vi.1982; ♂, 45.3 mm, RMNH 83964, 19.vi.1982; ♂, 55.6 mm, RMNH 83965, 19.vi.1982; ♂, 44.1 mm, RMNH 83966, 19.vi.1982; ♂, 49.5 mm, RMNH 83967, 6.iv.1982; ♂, 58.2 mm, AMNH 250804, 6.iv.1982; ♂, 62.8 mm, RMNH 83969, 6.iv.1982.

Description.— Based on 48 specimens (including the holotype) 41.9-75.1 mm SL.

Diagnosis.— A small sized (< 8 cm SL), micrognathic (LJL < 45% HL) species with a diamond-shaped body outline, dorsal head profile straight to incurved above the eye. Mouth oblique with relatively small, mainly bicuspid teeth. *H. coprologus* spec. nov. differs from *Haplochromis erythrocephalus* Greenwood & Gee, 1969, the only other described small species with similar body outline, in live colouration of sexually active males. *H. coprologus* spec. nov. is almost completely black, whereas *H. erythrocephalus* has a bright red head. The remainder of the body colouration of *H. erythrocephalus* is yellowish. Further, differences are present in interorbital width, snout length, eye length, lower jaw length and the lower jaw length/width ratio. *H. coprologus* spec. nov. differs from the similarly coloured *Haplochromis piceatus* Greenwood & Gee, 1969 mainly in body depth, which is higher in *H. coprologus* spec. nov. (mean 36.1 ± 1.3% of SL) than in the sympatric population of *H. piceatus* from the Mwanza Gulf (mean 31.8 ± 1.0% of SL; Witte & Witte-Maas, 1987). Further, *H. coprologus* spec. nov. has a larger eye length than *H. piceatus* (mean 35.1 ± 1.4% of HL vs. mean 32.8 ± 0.9% of HL in *H. piceatus* from the Mwanza Gulf). The reddish parts in the caudal and anal fin of *H. coprologus* spec. nov. are generally

---

[1] Type specimen that has been dissected to describe gill apparatus, oral jaws and pharyngeal jaws; [2] type specimen of which an X-ray photograph is available; [3] type specimen of which morphometric measurements have been taken (Table 3); [4] type specimen of which a colour picture is available.

smaller than in *H. piceatus*. Moreover, in *H. coprologus* spec. nov. these parts are generally dark red and in *H. piceatus* orange to orange-red. *H. coprologus* spec. nov. differs from *H. antleter* spec. nov., which has a similar male colouration, in its dorsal head profile which is straight to incurved above the eye in *H. coprologus* spec. nov. and moderately curved in *H. antleter* spec. nov. The lower jaw in *H. coprologus* spec. nov. is longer, narrower and more oblique than in *H. antleter* spec. nov. (tables 1 and 3). The number of gill rakers on the lower part of the first gill arch is higher in *H. coprologus* spec. nov. (11-12) than in *H. antleter* spec. nov. (10).

Habitus (fig. 8).— Body outline diamond shaped. Dorsal head profile straight to incurved above the eye. Premaxillary pedicel often slightly interrupting the profile. Mouth oblique. Lips not thickened. Medial part of the premaxilla slightly expanded. Caudal part of the maxilla not bullate. The vertical through the caudal tip of the maxilla runs through the iris, sometimes through the pupil. Lateral snout outline isognathous to slightly prognathous, obtuse. If isognathous, lower jaw not or slightly protruding. Mental prominence slightly pronounced. Retro-articular processes of right and left mandible generally touching each other, slightly interrupting the ventral body outline. Eye approximately circular. Aphakic aperture generally present. Cephalic lateral line pores slightly enlarged.

Scales.— Cheek, gill cover, dorsal head surface, greater part of dorsum and caudal fin base covered with cycloid scales, the remaining part of the body with ctenoid scales. A gradual size transition between scales of chest and flank. Four and a half to six (mode 5) scales between the upper lateral line and the dorsal fin origin, four to six (mode 5) between the pectoral and the pelvic fin bases.

Fins.— In females the pelvic fins just reach the anal fin origin; in males the pelvic fins reach the anal fin origin, sometimes extending further. First soft rays of pelvic fins may be produced and filamentous in males. Anal fin just reaching caudal fin origin. Caudal fin outline truncate to emarginate.

Gill apparatus.— The description of the gill apparatus is based on the lateral gill rakers and the lateral hemibranch of the first gill arch. The number of gill rakers on the

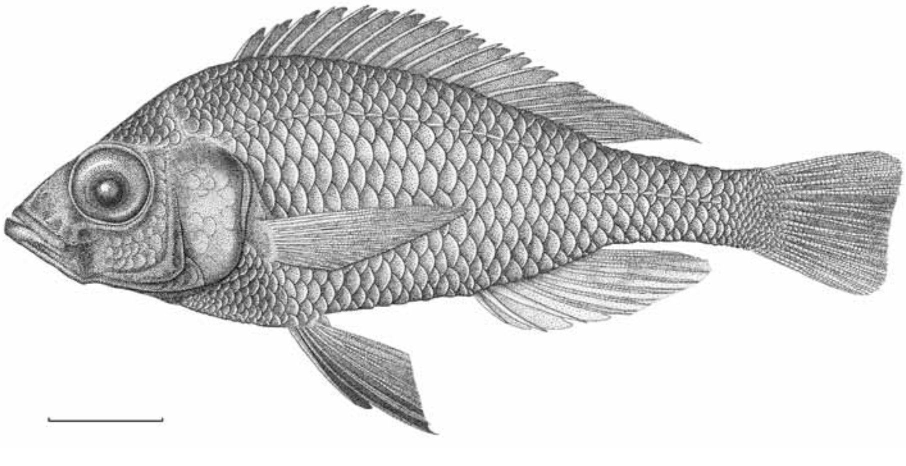

Fig. 8. *Haplochromis coprologus* spec. nov., paratype, RMNH 77790, ♂. Scale equals 10 mm. Drawn by S. ter Huurne.

lower part of the first gill arch is 11 to 12. The lower one to two rakers are reduced. The next two to three rakers are short and blunt to pointed in shape. These are followed by two to seven long and slender rakers, their shape is pointed to acutely pointed. The remaining rakers are acutely pointed to blunt or bifid. The rakers on the first gill arch are touching each other. The number of gill filaments on the lateral hemibranch of the first gill arch ranges from 84 to 104.

Viscera.— Ratio between intestine length and SL: 1.2-2.8, mean 1.9 ± 0.4, n = 19 (F. Witte, E. Witte-Maas & M. Kishe-Machumu, unpublished data).

Oral jaws.— Premaxillary dentigerous arm as long as or slightly shorter than ascending arm (asc/dent arm ratio 1.0 to 1.2). The angle between the two arms is 82° to 86°. Symphysead articulation facet not present. Lower jaw is relatively elongated (length/height ratio 2.1 to 2.2. The upper half of the dentary has a distinct outwardly directed flare. A small mental prominence is present on the chin.

Oral teeth.— *Shape.* Teeth in the rostral part (ca. ⅔ of dentigerous area) of premaxilla and lower jaw generally unequally bicuspid, often with a few tricuspids among them. Teeth in caudal part of premaxilla are small, (weakly) tricuspids or blunt unicuspids; teeth in caudal part of lower jaw are small subequally bicuspids, weakly bicuspids or tricuspids.

In bicuspid teeth, the shape of the major cusp is isoscelene to subequilateral. A small, not very distinct flange is present on rostrally positioned teeth, in caudally

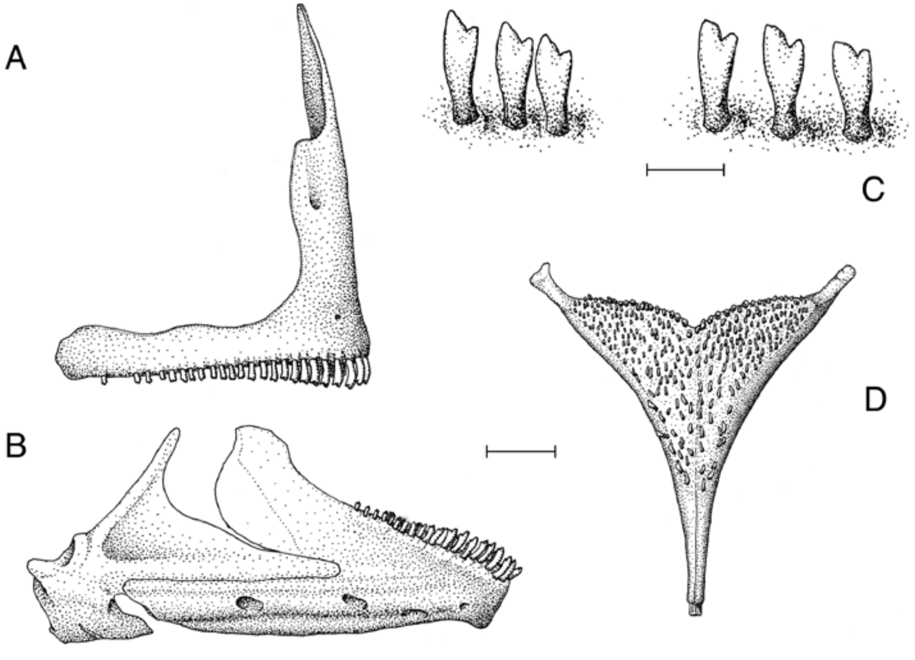

Fig. 9. *Haplochromis coprologus* spec. nov. A, Premaxilla, lateral view; B, Lower jaw, lateral view; C, Premaxillary teeth; D, Lower pharyngeal element, dorsal view. Bony elements drawn from RMNH 73469, ♂, scale of bony elements = 10 mm. Three left-most teeth drawn from RMNH 73469, other from RMNH 73468, ♀, scale of teeth 0.25 mm Drawn by S. ter Huurne.

positioned teeth it is hardly visible or absent. The cusp gap is wide, the minor cusp is distinct. In labial view the neck is moderately slender, the crown not to slightly expanded. In lateral view, the crown is compressed. The premaxilla outer row teeth are slightly to strongly recurved; those of the lower jaw are slightly recurved. The inner row teeth of both premaxilla and lower jaw are tricuspid.

Size. Teeth relatively small and slender. Caudal teeth of premaxilla very small, deeply embedded in tooth gum.

Dental arcade and tooth band. Dental arcade rounded and U-shaped. Premaxilla generally has two, rarely three inner rows anteriorly, none posteriorly. Lower jaw with one to two inner rows anteriorly, none posteriorly. In the dissectioned female the caudalmost quarter of the dentigerous arm is edentulous, in males the edentulous part is much smaller.

Counts and setting. There are 51 to 63 teeth in the outer row of the upper jaw (l+r premaxilla). The setting varies in both premaxilla and lower jaw from closely to widely and regularly set. Caudally, teeth may be more widely set than rostrally.

Implantation. Outer row teeth of premaxilla erect, inner row teeth recumbent. Lower jaw outer row teeth slightly procumbent, inner row teeth erect.

Lower pharyngeal element.— Lower pharyngeal element relatively long and slender. Longer than broad (length/width ratio 1.1 to 1.2). The dentigerous area is broader than long (length/width ratio 0.8 to 0.9). The suture is straight.

Pharyngeal teeth.— *Counts.* There are 37 to 40 teeth in caudal-most transverse row, 10 to12 teeth in the medial length rows.

Table 3. Measurements of *Haplochromis coprologus* spec. nov. Means and standard deviations have been calculated over all measured type specimens (including the holotype).

		holotype	paratypes (n = 20)	mean ± st. dev(n = 21)
standard length (mm)		67.5	48.2-69.0	59.4 ± 5.5
body depth (BD)	%SL	35.7	34.4-39.4	36.1 ± 1.3
pectoral fin length (PFL)	%SL	29.2	29.3-35.8	32.2 ± 2.0
caudal peduncle length (CPL)	%SL	17.2	15.1-20.6	18.0 ± 1.3
caudal peduncle depth (CPD)	%SL	10.5	10.1-12.2	11.0 ± 0.5
caudal fin length (CFL)	%SL	25.6	24.4-30.2	26.9 ± 1.3
head length (HL)	%SL	34.1	32.5-35.6	34.5 ± 0.8
snout length (SnL)	%HL	27.8	24.1-28.3	25.8 ± 1.1
snout width (SnW)	%HL	29.1	24.0-31.4	27.8 ± 1.6
head width (HW)	%HL	44.8	39.4-45.5	42.4 ± 1.6
interorbital width (IOW)	%HL	21.3	19.9-23.8	22.0 ± 1.1
preorbital width (POW)	%HL	25.7	23.0-28.5	25.6 ± 1.2
lachrymal width (LaW)	%HL	26.1	21.1-26.7	23.7 ± 1.5
preorbital depth (POD)	%HL	13.9	12.8-16.1	14.3 ± 0.8
eye length (EyL)	%HL	34.8	32.6-38.7	35.1 ± 1.4
eye depth EyD)	%HL	32.6	29.5-33.5	31.5 ± 1.0
cheek depth (ChD)	%HL	17.4	15.7-20.2	18.2 ± 1.2
lower jaw length (LJL)	%HL	41.3	38.2-42.5	40.8 ± 1.1
lower jaw width (LJW)	%HL	19.1	13.4-19.9	16.0 ± 1.9
EyD/EyL		0.9	0.8-1.0	0.9 ± 0.0
LJL/LJW		2.2	2.0-3.1	2.6 ± 0.3

Shape. Teeth in caudal-most transverse row hooked, major cusp only slightly incurved and blunt. Other teeth pronounced or bevelled. All teeth relatively fine and slender, medial teeth not coarser than other teeth.

Vertebrae.— The total number of vertebrae in 17 X-rayed specimens is 28 (2), 29 (10) or 30 (5) comprising 12-13 abdominal and 16-17 caudal vertebrae.

Live colouration.— Males have the snout, dorsal head surface, lips, lower jaw, interoperculum, cheek, gill cover, belly and ventral side black. Dorsum, flank and chest are black with a silvery sheen. The eye has a very dark grey outer ring and an orange-yellow inner ring. An opercular blotch may be visible. Pectoral fins hyaline, pelvic fins black. Anal fin dusky, with variable amount of red and two to three yolk-yellow egg dummies with a dusky ring. Caudal fin dusky, with a variable amount of dark-red in the caudo-ventral part. Dorsal fin dusky with a black base, lappets black.

Females. Live females have the entire body silvery to light brownish.

Preserved colouration of males. Body grey-brown to dark brown. Operculum sometimes partly silver. Snout, lower jaw and branchiostegal membrane sometimes darker than remainder of the head. An opercular blotch is present. Pectoral fins brownish-hyaline, pelvic fins black. Anal fin greyish-hyaline, sometimes with a dusky base. Dusky rings around the egg dummies are occasionally present. Caudal fin brownish with a dark base and a dark medial part, dorsal fin brownish, lappets black.

Preserved colouration of females. Body sandy-grey to sandy-brown. Snout, cheek, gill cover, dorsal head surface and dorsum darker than flank. Belly, chest and ventral side lighter than flank, more yellow-brownish. Opercular blotch present. Pectoral fins brownish-hyaline. Pelvic and anal fins hyaline. Caudal fin hyaline with a brown base. Dorsal fin brownish-hyaline, lappets brown.

Distribution.— *Haplochromis coprologus* spec. nov. is only known from Lake Victoria.

Habitat.— Before the ecological changes, *H. coprologus* spec. nov. occurred in the sublittoral areas of the Mwanza Gulf, mainly over mud bottoms (Witte et al., 1992b; Goldschmidt et al., 1993). *H. coprologus* spec. nov. dwelled slightly higher in the water column than *H. antleter* spec. nov. and *H. katunzii* spec. nov. (Goldschmidt et al., 1993). Juveniles of *H. coprologus* spec. nov. occurred in sheltered bays (Goldschmidt et al., 1993).

Food.—Before the ecological changes in Lake Victoria, *H. coprologus* spec. nov. fed mainly on detritus during daytime. Other important food items comprised the diatom *Aulacoseira* and copepods. By night, when they fed less than during the day, *Aulacoseira* made up a larger portion of the diet (Goldschmidt et al., 1993).

Breeding.— *Haplochromis coprologus* spec. nov. is a female mouth brooder. Like most other detritivorous species, it is a seasonal spawner. Sexually active males were abundant from March till October (Witte, 1981), brooding females were abundant from March till September (Goldschmidt et al., 1993). Length frequency analysis indicated cohorts of juveniles that could be followed over a period of one year (Witte, 1981; 1984; 1987; Goldschmidt et al., 1993).

Etymology.— The name coprologus comes from the Greek word for dustman; ‘κοπϱολόγος’, the name refers to the detritivorous feeding habits of this species, collecting detritus from mud bottoms.

Haplochromis vanoijeni de Zeeuw & Witte spec. nov.
(figs 11-14, table 4)

Haplochromis 'red tridens'; Zihler, 1982: 568; Witte, 1984b: 162; Witte, 1987, chapter 2: 15; Witte, 1987, chapter 3: 17; Goldschmidt, 1989a: 98-100, 103, 107, 118, 119, 129, 149, 167; Goldschmidt 1989b: 130; Goldschmidt & de Visser, 1990: 131; Goldschmidt, 1991: 182, 185, 187; Witte et al., 1992b: 25; Seehausen & Witte, 1995a: 101; Seehausen et al., 1997b: 895, 897; Witte et al., 2003: 111.

Material examined (references to fish size concern standard length).— Holotype, ♂, 68.6 mm, RMNH 81522[1, 2], Tanzania, Lake Victoria, 7.x.1977, HEST; Paratypes: all collected by HEST in the Mwanza Gulf, Tanzania, Lake Victoria, except where noted otherwise: ♂, 64.5 mm, RMNH 67826[2], 4.x.1984, Napoleon Gulf, Uganda; ♂, 69.9 mm, RMNH 69732[3], 28.vii.1978; ♀, 72.9 mm, RMNH 69735, 28.iv.1978; ♂, 75.0 mm, RMNH 69739, 18.i.1980; ♂, 88.6 mm, RMNH 69741, 7.xi.1978; ♂, 65.0 mm, RMNH 77874[2], 7.vi.1985; ♂, 59.8 mm, RMNH 77901[2], 3.vi.1985; ♂, 85.2 mm, RMNH 77938[2], 7.vi.1985; ♂, 69.4 mm, RMNH 77991[2], 12.vi.1985, Kome Channel; ♂, 80.0 mm, RMNH 78055[2], 18.vi.1985, Maisome Channel; ♂, 80.4 mm, RMNH 80517, 28.iv.1978; ♂, 69.1 mm, RMNH 80531, 18.vi.1985, Maisome Channel; ♂, 73.7 mm, RMNH 80533, 18.vi.1985, Maisome Channel; ♂, 69.2 mm, RMNH 80549, 18.vi.1985, Maisome Channel; ♂, 74.1 mm, RMNH 80557, 18.vi.1985, Maisome Channel; ♀, 64.8 mm, RMNH 80660[2], 3.vi.1985; ♂, 78.7 mm, RMNH 80705[2], 18.vi.1985, Maisome Channel; ♂, 70.1 mm, RMNH 80706[2], 18.vi.1985, Maisome Channel; ♂, 69.2 mm, RMNH 81167, 26.i.1981; ♂, 88.8 mm, RMNH 81290[2], 24.ix.1981; ♀, 77.5 mm, RMNH 81523[1, 2], 7.x.1977; ♂, 66.3 mm, RMNH 82694[1], 30.ix.1977; ♂, 69.1 mm, RMNH 82695[1], 30.ix.1977; ♀, 74.0 mm, RMNH 82696[1], 30.ix.1977; ♀, 69.8 mm, RMNH 82697[1], 14.x.1977; ♀, 73.3 mm, RMNH 82698[1], 14.x.1977; ♂, 64.0 mm, RMNH 82699[1], 14.x.1977; ♂, 64.2 mm, RMNH 82700[1], 30.ix.1977; ♀, 69.6 mm, RMNH 82701[1], 30.ix.1977; ♂, 68.3 mm, BMNH 2010.3.23.4, 10.x.1977; ♂, 53.0 mm, RMNH 84053, 10.x.1977; ♀, 70.9 mm, RMNH 84054, 7.x.1977; ♂, 74.1 mm, RMNH 84055, 17.i.1983, Speke Gulf; ♂, 71.9 mm, RMNH 84056, 17.i.1983, Speke Gulf; ♂, 64.9 mm, RMNH 84057, 9.ix.1977; ♂, 67.5 mm, AMNH 250806, 9.ix.1977; ♂, 80.8 mm, RMNH 84059, 17.iii.1978; ♂, 68.9 mm, NSMT-P 98081, 17.iii.1978; ♂, 72.2 mm, RMNH 84061, 2.viii.1978, Speke Gulf; ♂, 68.8 mm, RMNH 84062, 2.viii.1978, Speke Gulf.

---

[1] Type specimen of which morphometric measurements have been taken (Table 4); [2] type specimen of which a colour picture is available; [3] type specimen that has been dissected.

Fig. 10. *Haplochromis coprologus* spec. nov., paratype, RMNH 80967, sexually active ♂, 71.1 mm SL.

Description.— Based on 41 specimens (including the holotype) 53.0-88.8 mm SL.

Diagnosis.— A small sized (< 9 cm SL), micrognathic (LJL < 45% HL) species with generalized body profile, but with a relatively long and acute snout. Because of the latter, and its relatively small interorbital width (see below), the species bears some resemblance with species of the 'tridens' group (Greenwood & Gee, 1969). Indeed, *H. vanoijeni* spec. nov. frequently has some tricuspid teeth rostrally in the outer row of the oral jaws.

Haplochromis vanoijeni spec. nov. differs from eight of the nine described species in the tridens group in the colouration of sexually active males. Dorsum and flanks in sexually active males of *H. vanoijeni* spec. nov. are bright red. Both males and females have conspicuously silverish-white cheeks, contrasting with the remaining head colours, which is a unique character among Lake Victoria haplochromines. From *Haplochromis tridens* Regan & Trewavas, 1928, of which the colouration of live, sexually active males is unknown *H. vanoijeni* spec. nov. differs in the following characters: The lower jaw of *H. vanoijeni* spec. nov. is shorter than that of *H. tridens* (LJL 40.9-44.7% of HL, mean 43.8% vs. 43.3-51.8%, mean 47.5%). Further, *H. vanoijeni* spec. nov. has a larger interorbital width (IOW 17.6-20.5% of HL, mean 19.0) than *H. tridens* (IOW 15.0-19.5% of HL, mean 16.7%). In contrast to *H. vanoijeni* spec. nov., *H. tridens* has a dorsal head profile that is interrupted by a prominent premaxillary pedicel, and a cephalic line system with prominent pores (Greenwood, 1967).

Besides by its specific coloration pattern, *H. vanoijeni* spec. nov. can be distinguished from all described species in the 'tridens group' by its larger body depth. In *H. vanoijeni* spec. nov. the mean body depth is 34.9% (range 33.1-36.2% of SL) in the 'tridens group' the means range from 30.6-33.6% (Greenwood, 1967; Greenwood & Gee, 1969; Greenwood & Barel, 1978). The lower jaw of *H. vanoijeni* spec. nov. is shorter (LJL 40.9-44.7% of HL, mean 43.8%) than that of most described species in the 'tridens group' (means ca 47.0% of HL) except for that of *H. cryptogramma* Greenwood & Gee, 1969 (LJL 40.0-48.5% of HL, mean 44.8%) and that of *H. plutonius* Greenwood & Barel, 1978 (LJL 41.0-46.0% of HL, mean 44.0%).

Habitus (fig. 11).— Generalized body profile. Dorsal head profile straight to slightly curved, sometimes with a slight incurvation above the eye. Premaxillary pedicel not or slightly interrupting the dorsal head profile. Mouth moderately oblique. Lips not thickened. Premaxilla not or only slightly expanded medially. Caudal part of the maxilla not bullate. The vertical through the caudal tip of the maxilla is passing through the eye. Lateral snout outline prognathous and acute. Lower jaw slightly to moderately protruding. Mental prominence moderately to strongly pronounced. Retro-articular processes of right and left mandible are touching each other, and interrupting the ventral body outline. Eye circular to slightly elliptic, with rostrally an aphakic aperture. Cephalic lateral line pores normal to slightly enlarged.

Scales.— Dorsal head surface, cheek and operculum covered with cycloid scales, gradually changing into ctenoid scales on the dorsum and flank. Caudal fin base with cycloid scales. Ctenoid scales on the remainder of the body.

Fins.— Pelvic fins reaching or surpassing the anal fin origin. First soft rays of pelvic fins not produced or slightly produced and filamentous. Male anal fin generally reaching or surpassing the caudal fin origin. Female anal fin not reaching the caudal fin origin. Caudal fin outline subtruncate.

Gill apparatus (based on one male and one female).— The description of the gill

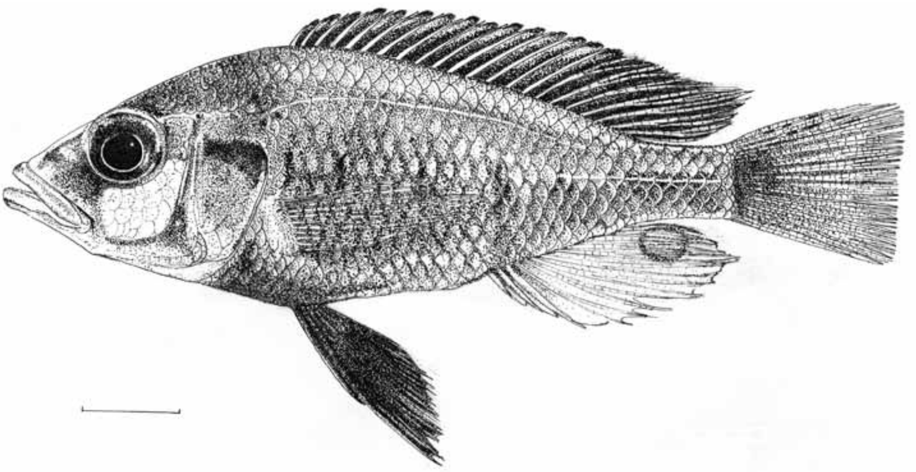

Fig. 11. *Haplochromis vanoijeni* spec. nov., holotype, RMNH 81522, ♂. Scale equals 10 mm. Drawn by M.J.P. van Oijen.

apparatus is based on the lateral gill rakers and the lateral hemibranch of the first gill arch. The number of gill rakers on the lower part of the first gill arch are eight and 10. The gill rakers are long, slender and flattened with some bifids and trifids. The two rostral-most rakers are reduced or small. The rakers on the first gill arch are generally touching each other.

Viscera.— Ratio between intestine length and SL: 0.7-2.7, mean 1.7 ± 0.6, n = 15 (T. Goldschmidt and F. Witte unpublished data).

Oral jaws.— Premaxillary dentigerous arm slightly longer than ascending arm (asc/dent arm ratio 0.94). The angle between the two arms is 79°. Lower jaw slightly elongated (length/height ratio 2.1). A small mental prominence is present.

Oral teeth.— *Shape.* Generally the teeth of both premaxilla and lower jaw are unequally bicuspid, frequently interspersed with distinct tricuspids. In the caudal part of the premaxilla small tricuspids and weakly tricuspids can be found. In bicuspid teeth, the shape of the major cusp is isoscelene to subequilateral protracted. A small flange can be present. The cusp gap is wide, the minor cusp is distinct. Tricuspid teeth may sometimes have a protracted middle cusp. In labial view, the neck is moderate, the crown is slightly expanded. In lateral view, the crown is slightly compressed. The premaxilla outer row teeth are straight to slightly recurved, those of the lower jaw slightly recurved. The inner row teeth of both premaxilla and lower jaw are tricuspid.
Size. Teeth are relatively small and slender.
Dental arcade and tooth band. Dental arcade U shaped. Premaxilla and lower jaw have two to three inner rows anteriorly (occasionally four).
Counts and setting. There are 52-70 teeth in the outer row of the upper jaw (l+r premaxilla); teeth in both jaws regularly set. The crown distance varies from 1/3 to 1 times the crown width, laterally somewhat closer set than rostrally.
Implantation. Outer row teeth of premaxilla erect. Lower jaw outer row teeth erect to slightly procumbent. Inner row teeth of lower jaw recumbent to strongly recumbent,

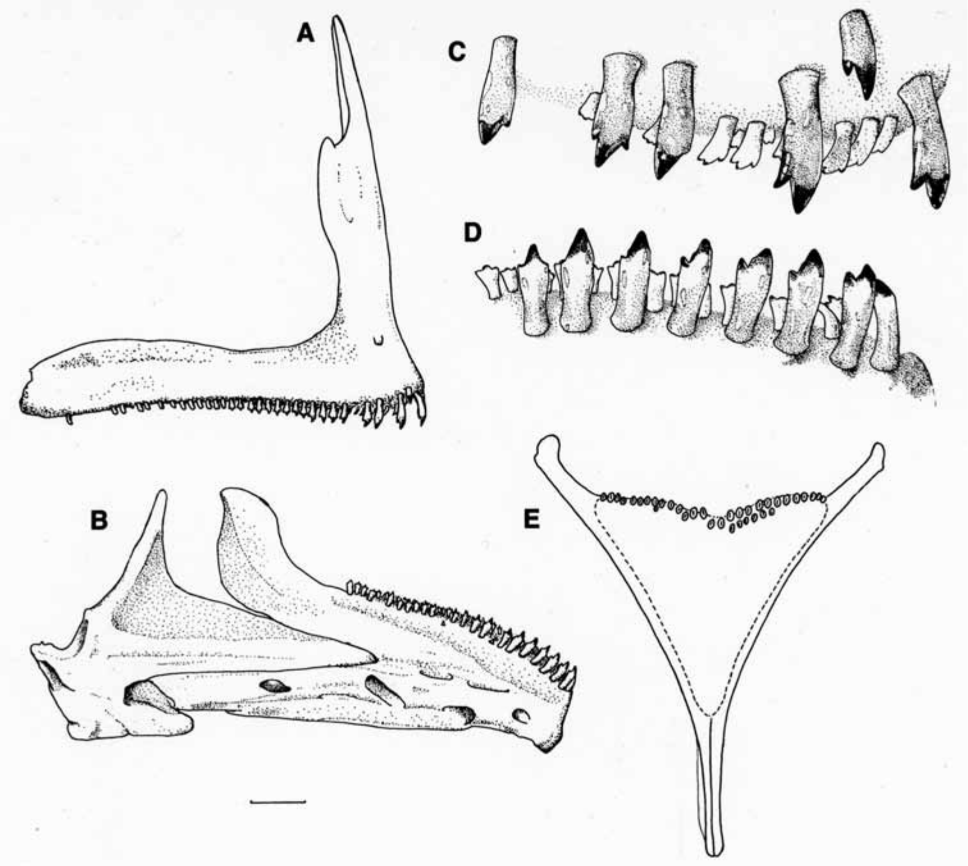

Fig. 12. *Haplochromis vanoijeni* spec. nov., RMNH 69732, ♂. A, Premaxilla, lateral view; B, Lower jaw, lateral view; C, Rostral premaxillary teeth, lateral view; D, Rostral lower jaw teeth, lateral view; E, Outline of lower pharyngeal element, with caudal most teeth, dorsal view. Dentigerous area indicated by dashed line. Scale of bony elements = 10 mm, scale of teeth 0.25 mm. Drawn by M.J.P. van Oijen.

inner row teeth of premaxilla recumbent. In both jaws, a slight to distinct gap between outer row and inner rows is present.

Lower pharyngeal element.— Relatively slender when compared to that of *H. elegans*. As long as it is broad or slightly longer than broad (length/width ratio 1.1). The dentigerous area is broader than long (length/width ratio 0.9). The suture is straight.

Live colouration.— Males have the dorsal head surface, gill cover and major part of dorsum and flank bright red, caudally changing into brownish-yellow. Snout, lips and lower jaw yellowish to brownish, in a few specimens some bluish-grey present. The eye has a dark outer ring and a golden inner ring. Caudal peduncle brownish-yellow. Cheek silverish-white, sometimes with a red flush. Chest silverish-white with a blackish, yellowish or a reddish flush. Belly brownish-yellow with a reddish or blackish flush. Ventral side silverish to yellowish-brown. Lachrymal stripe generally present, sometimes faintly, in some specimens extending over the eye. Nostril stripe

Table 4. Measurements of *Haplochromis vanoijeni* spec. nov. Means and standard deviations have been calculated over all measured type specimens (including the holotype).

		holotype	paratypes (n = 9)	mean ± st. dev (n = 10)
standard length (mm)		68.6	64.0-77.5	69.6 ± 4.1
body depth (BD)	%SL	34.3	33.1-36.2	34.9 ± 1.0
pectoral fin length (PFL)	%SL	30.2	30.5-33.3	31.9 ± 0.9
caudal peduncle length (CPL)	%SL	16.8	17.0-18.9	17.7 ± 0.7
caudal peduncle depth (CPD)	%SL	10.5	10.3-11.7	11.1 ± 0.5
caudal fin length (CFL)	%SL	-	-	-
head length (HL)	%SL	34.0	33.9-36.2	34.9 ± 0.9
snout length (SnL)	%HL	30.5	27.3-31.7	30.0 ± 1.2
snout width (SnW)	%HL	31.3	25.8-31.0	29.0 ± 1.7
head width (HW)	%HL	42.8	40.4-44.1	42.1 ± 1.1
interorbital width (IOW)	%HL	18.0	17.6-20.5	19.0 ± 0.9
preorbital width (POW)	%HL	25.8	23.8-27.8	25.5 ± 1.4
lachrymal width (LaW)	%HL	27.2	22.5-24.5	24.2 ± 1.2
preorbital depth (POD)	%HL	18.0	15.9-18.4	17.1 ± 0.9
eye length (EyL)	%HL	33.0	29.8-33.8	31.4 ± 1.3
eye depth EyD)	%HL	30.9	27.5-31.6	29.6 ± 1.4
cheek depth (ChD)	%HL	22.3	19.8-22.7	21.7 ± 0.8
lower jaw length (LJL)	%HL	45.1	40.9-44.7	43.8 ± 1.1
lower jaw width (LJW)	%HL	19.7	17.1-22.0	18.6 ± 1.4
EyD/EyL		0.9	0.9-1.0	0.9 ± 0.0
LJL/LJW		2.3	2.0-2.6	2.4 ± 0.2

present, sometimes faint. Supraorbital stripe occasionally present. The opercular blotch generally faintly present. Occasionally faint traces of vertical bars are present; in some specimens more distinct. Pectoral fins hyaline, pelvic fins black. Dorsal fin rostrally red, caudally brownish-yellow with red streaks, lappets on rostral part dusky. Anal fin greyish-white with one to two large yolk-yellow egg dummies surrounded by a dusky ring. Caudal-most part of caudal fin dusky, the remainder brownish-yellow with a red

Fig. 13. *Haplochromis vanoijeni* spec. nov., holotype, RMNH 81522, sexually active ♂, 68.6 mm SL.

flush. Note: Goldschmidt (1989b) described the egg dummies as whitish, which does not agree with our observations.

Females (based on two specimens). General impression: golden-yellow over a whitish ground colour. Snout, lips and lower jaw yellowish to brownish. Dorsal head surface and caudal peduncle yellow to brownish-yellow. Dorsum and flank, a red flush may be present. Cheek, gill cover, chest, belly and ventral side silverish-white. The eye has a dark iris with a golden inner ring. Lachrymal stripe faintly present. Opercular blotch as well as faint traces of vertical bars may be present. Pectoral fins hyaline, pelvic fins dusky or hyaline. Dorsal fin yellow, dusky streaks may be present at the base with red streaks above them. Lappets dusky. Anal fin greyish-white at base, remainder hyaline-yellow (yolk-yellow ocelli may be present). Caudal-most part of caudal fin hyaline, remainder hyaline-yellow, fin may have dusky streaks.

Preserved colouration of males. Grey-brown to brown. Chest and belly somewhat dusky. Lachrymal stripe and opercular blotch present. Nostril stripe generally present, sometimes faint. Supraorbital stripe occasionally present. Faint vertical bars may be present, in some specimens more distinct. Pectoral fin hyaline-grey-brown, pelvic fins black. Dorsal and anal fin hyaline-grey-brown; caudal fin slightly darker. Lappets in rostral part of dorsal fin may be dusky.

Preserved colouration of females. Grey-brown to brown. Opercular blotch present. Lachrymal stripe if present, faint. Faint vertical bars may be present. Pelvic fins dusky to blackish. Pectoral, dorsal and anal fins hyaline-grey-brown; caudal fin slightly darker. Lappets in rostral part of dorsal fin may be dusky.

Distribution.— *Haplochromis vanoijeni* spec. nov. is only known from Lake Victoria.

Habitat.— *Haplochromis vanoijeni* spec. nov. is a benthic species that was caught with bottom trawls mainly in the deeper parts (> 10 m) of the Mwanza Gulf, over mud bottoms. Occasionally it was caught over mud in shallower areas more southward in the

Fig. 14. *Haplochromis vanoijeni* spec. nov., paratype, RMNH 77991, sexually active ♂. Specimen from Kome Channel. Scale equals 3 mm. Drawn by I. van Noortwijk.

gulf. On the research transect across the Mwanza Gulf the species was most common at station H (Witte et al., 1992b; unpublished data). In Tanzania *H. vanoijeni* spec. nov. was also present in bottom trawls in the Speke Gulf (one at a sand bottom of 28 m deep) and in Maisome Channel (Emin Pasha Gulf); furthermore, a specimen was collected with a bottom trawl in the Napoleon Gulf (Uganda). The specimen depicted in Fig. 14, was caught in Kome Channel (Tanzania); it has a slightly shorter and broader lower jaw than average, also its snout is somewhat broader.

Food.— Before the ecological changes in Lake Victoria, *H. vanoijeni* spec. nov. fed mainly on detritus. Occasionally remains were found in the gut that could belong to shrimps and insects.

Breeding.— *Haplochromis vanoijeni* spec. nov. is a female mouth brooder. Two brooding females were collected at station H (13-14 m deep) on 13 June 1979.

Etymology.— This species is named in honour of Dr Martien J.P. van Oijen, ichthyologist of the Netherlands Centre of Biodiversity, Naturalis, in appreciation for his work on taxonomy and ecology of the haplochromine cichlids of Lake Victoria. Dr van Oijen was one of the pioneers of the Haplochromis Ecology Survey Team (HEST) of Leiden University that started its fieldwork on Lake Victoria in 1977.

Description of three phytoplanktivorous species

Haplochromis sphex ter Huurne & Witte spec. nov.
(figs 15-17, table 5)

Haplochromis 'citrus'; Goldschmidt, 1989a: 148; Goldschmidt, 1991: 182, 185, 187; Witte et al., 1992b: 25, 27, 28; Seehausen & Witte, 1994a: 588; Seehausen, 1996: 51, 255.

Material examined (references to fish size concern standard length).— Holotype, ♂, 76.3 mm, RMNH 77784[2, 3], Mwanza Gulf, Tanzania, Lake Victoria, 12.vii.1979, HEST; Paratypes: all collected by HEST in the Mwanza Gulf, Tanzania, Lake Victoria, except where noted otherwise : ♂, 64.9 mm, RMNH 64215, 26.iv.1984; ♂, 72.7 mm, RMNH 72839[4], 12.vi.1980; ♂, 74.1 mm, RMNH 73261[2, 3], 15.vii.1978; ♂, 75.5 mm, RMNH 73262[2, 3], 12.vii.1979; ♀, 76.9 mm, RMNH 73263[2, 3], 20.iii.1979; ♂, 77.0 mm, RMNH 73264[2, 3], 10.iii.1978; ♂, 63.8 mm, RMNH 73265[2, 3], 24.xi.1978; ♂, 75.8 mm, RMNH 73266[3, 4], 7.x.1977; ♂, 80.2 mm, RMNH 73267[3, 4], 24.vi.1975; ♂, 68.8 mm, RMNH 73268[3, 4], 14.iv.1981; ♂, 68.6 mm, RMNH 73438[3, 4], Emin Pasha Gulf, 21.vi.1985; ♂, 71.1 mm, RMNH 73620[1, 3], 21.xi.1978; ♂, 67.8 mm, RMNH 73621[1, 3], 12.vii.1979; ♂, 73.7 mm, RMNH 73622[1, 3], 8.xii.1978; ♂, 82.1 mm, NSMT-P 98082, 23.xii.1977; ♂, 75.2 mm, BMNH 2010.3.23.5, 15.vii.1978; ♂, 16.4 mm HL, RMNH 79197[5], Speke Gulf, 19.viii.1986; ♂, 67.5 mm, RMNH 79198[5], Speke Gulf, 19.viii.1986; ♂, 61.7 mm, RMNH 79199[5], Speke Gulf, 19.viii.1986; ♂, 72.2 mm, RMNH 79764[4], 9.ix.1986; ♂, 70.8 mm, RMNH 79765[4], 9.ix.1986; ♂, 72.7 mm, RMNH 79766[4], 9.ix.1986; ♂, 66.8 mm, RMNH 79767[4], 19.ix.1986; ♂, 65.4 mm, RMNH 79768[4], 23.ix.1986; ♀, 71.0 mm, RMNH 79769[4], 23.ix.1986; ♂, 66.1 mm, RMNH 79770[4], 23.ix.1986; ♀, 67.3 mm, RMNH 79771[4], 23.ix.1986; ♀, 67.5 mm, RMNH 79772[4], 23.ix.1986; ♀, 69.5 mm, RMNH 79773[4], 23.ix.1986; ♂, 76.5 mm, RMNH 79774[4], 23.ix.1986; ♂, 72.4 mm, RMNH 79775[4], 25.ix.1986; ♂, 69.8 mm, RMNH 79776[4], 25.ix.1986; ♂, 62.4 mm, RMNH 79777[4], 25.ix.1986; ♀, 73.3 mm, RMNH 84007, 5.v.1984; ♀, 49.6 mm, RMNH 84008, 5.v.1984; ♂, 70.1 mm, AMNH 250807, 5.v.1978; ♂, 55.8 mm,

---

[1] Type specimen that has been dissected to describe gill apparatus, oral jaws and pharyngeal jaws; [2] type specimen of which an X-ray photograph is available; [3] type specimen of which morphometric measurements have been taken (Table 5); [4] type specimen of which a colour picture is available; [5] type specimen of which E. Verheijen has taken a tissue sample for DNA analysis.

RMNH 84010, 21.xi.1978; ♂, 75.5 mm, RMNH 84011[2, 3], 12.vii.1979; ♂, 73.3 mm, RMNH 84012[2, 3], 12.vii.1979; ♀, 71.6 mm, RMNH 84013[2, 3], 12.vii.1979; ♂, 60.8 mm, RMNH 84014[2, 3], 12.vii.1979; ♂, 68.5 mm, RMNH 84015[3], 12.vii.1979; ♂, 72.2 mm, RMNH 84016[2, 3], 12.vii.1979; ♂, 67.4 mm, RMNH 84017[2, 3], 12.vii.1979; ♂, 67.1 mm, RMNH 84018[2, 3], 12.vii.1979; ♀, 74.4 mm, RMNH 84019[2, 3], 20.iii.1979; ♂, 74.4 mm, RMNH 84020[2, 3], 20.iii.1979; ♀, 73.7 mm, RMNH 84021[2, 3], 20.iii.1979; ♂, 77.8 mm, RMNH 84022[2, 3], 24.xi.1978; ♂, 67.2 mm, RMNH 84023[2, 3], 24.xi.1978; ♂, 70.2 mm, RMNH 84024[2, 3], 12.vii.1979.

Description.— Based on 52 specimens 49.6-82.1 mm SL.

Diagnosis.— A small sized (< 9 cm SL), slender (BD < 32% SL) micrognathic (LJL < 45% HL) species, with mainly bicuspid teeth in the oral jaws. Dorsal head profile straight to moderately curved. The colouration of sexually active males is yellow with blackish longitudinal, interrupted bands and vertical bars, producing a so-called 'chess board pattern'. This pattern also occurs in several oral shelling molluscivores, insectivores and algae scrapers, but these species generally are larger, have a deeper body (> 33%), have a strongly curved dorsal head profile and a lower jaw length/width ratio of less than 1.5, whereas in *Haplochromis sphex* spec. nov. it ranges from 1.5 to 2.7. *H. sphex* spec. nov. differs from other small species with a 'chess board pattern', *H. bwathondii* spec. nov. and *H. sauvagei* (Pfeffer, 1896), sensu Seegers (2008), by its shallower body. Sexually active males of *H. sauvagei* generally have a more distinct 'chess board pattern' than *H. sphex* spec. nov. In contrast to *H. sphex* spec. nov., sexually active males of both *H. bwathondii* spec. nov. and *H. sauvagei* develop a red chest and belly. The colouration of females and quiescent males of *H. sauvagei* is rather similar to that of sexually active males of *H. sphex* spec. nov.

Habitus (fig. 15).— Body slender. Dorsal head profile straight to moderately curved. Premaxillary pedicel not prominent. Mouth slightly oblique. Lips normal. Medial part of the premaxilla not expanded. Caudal part of the maxilla not bullate. The vertical through the caudal tip of the maxilla runs through the iris. Lateral snout outline isognathous to slightly prognathous and obtuse. Jaws equal anteriorly or lower jaw slightly protruding. Mental prominence not pronounced. Retro-articular processes of right and left mandibles generally just not touching each other, slightly interrupting the ventral

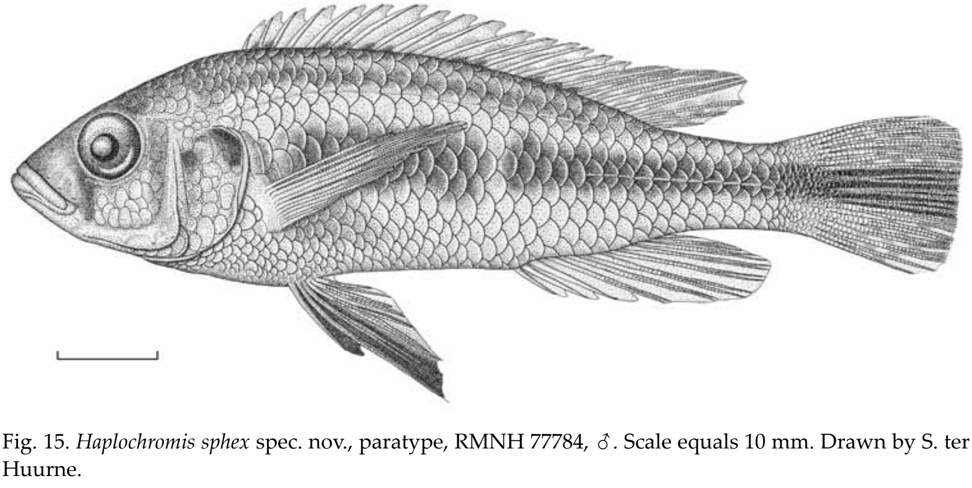

Fig. 15. *Haplochromis sphex* spec. nov., paratype, RMNH 77784, ♂. Scale equals 10 mm. Drawn by S. ter Huurne.

outline. Eye approximately circular. A small aphakic aperture may be present. Cephalic lateral line pores generally not enlarged.

Scales.— Cheek, gill cover, dorsal head surface, greater part of dorsum and caudal fin base covered with cycloid scales, the remaining part of the body with ctenoid scales. A gradual size transition between scales of chest and flank. Four to six (mode 5) scales between the upper lateral line and the dorsal fin origin, five to seven (mode 5) between the pectoral and the pelvic fin bases.

Fins.— Pelvic fins just reaching the anal fin origin. First soft rays of pelvic fins slightly produced, occasionally filamentous. Anal fin just not reaching caudal fin origin. Caudal fin outline truncate to slightly emarginate.

Gill apparatus.— The description of the gill apparatus is based on the lateral gill rakers and the lateral hemibranch of the first gill arch. The number of gill rakers on the lower part of the first gill arch is 12 to 13. The lower two to three rakers are reduced. Next one to three rakers are short. These are followed by two to four long, acutely pointed rakers. The remaining rakers are long, their shape is acutely pointed to bifid or quadrifid. The rakers on the first gill arch are touching each other. The number of gill filaments on the lateral hemibranch of the first gill arch ranges from 97 to 100.

Viscera.— Ratio between intestine length and SL: 1.5-2.2, mean 1.9 ± 0.2, n = 11 (T. Goldschmidt, unpublished data).

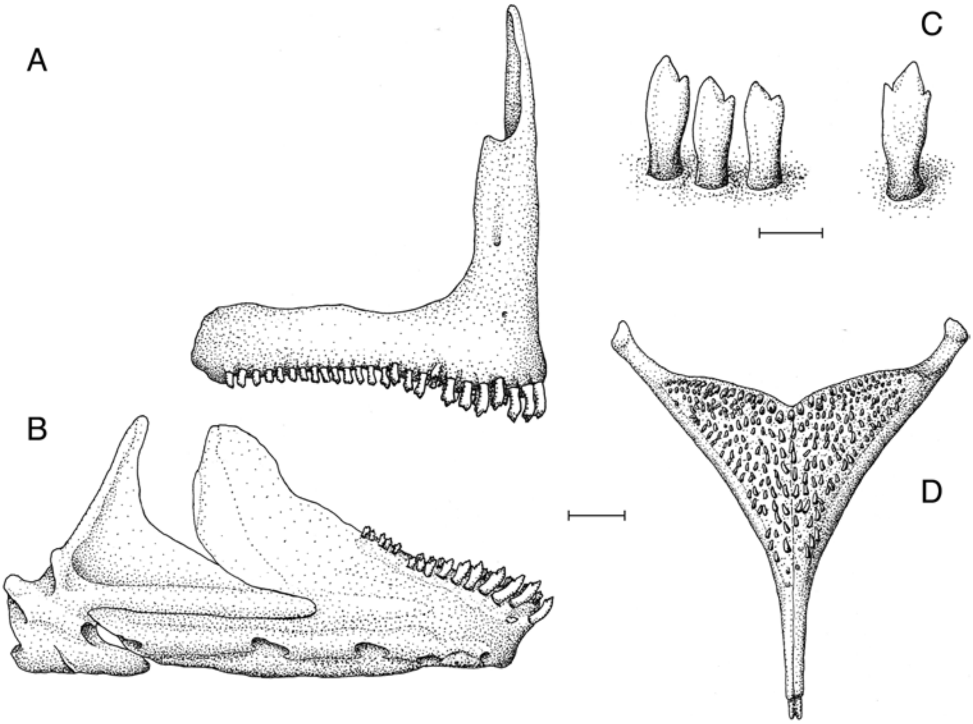

Fig. 16. *Haplochromis sphex* spec. nov. A, Premaxilla, lateral view; B, Lower jaw, lateral view; C, Lower jaw teeth; D, Lower pharyngeal element, dorsal view. Bony elements drawn from RMNH 73622, ♂, scale of bony elements equals 10 mm. Right-most tooth drawn from RMNH 73622, other from RMNH 73621, ♂, scale of teeth 0.25 mm. Drawn by S. ter Huurne.

Oral jaws.— Premaxillary dentigerous arm slightly shorter than, or as long as ascending arm (asc/dent arm ratio 1.0 to 1.1). The angle between the two arms is 83° to 84°. Symphyseal articulation facet not present. Lower jaw slightly elongated (length/height ratio 1.9 to 2.0). The upper half of the dentary has an outwardly directed flare, which is slightly to moderately distinct. Mental prominence not pronounced.

Oral teeth.— *Shape.* Teeth in the rostral part (ca. ⅔ of dentigerous area) of both premaxilla and lower jaw generally unequally bicuspid, often with a few tricuspids among them. In the caudal part of the premaxilla, tricuspids, weakly bicuspids and unicuspids can be found. In males the caudal-most teeth are slightly enlarged to enlarged weakly bicuspids or unicuspids, in females the caudal-most teeth are not enlarged and tricuspid. The teeth in the caudal part of the lower jaw may be either tricuspid, weakly bicuspid or bluntly unicuspid.

The shape of the major cusp in bicuspid teeth is isoscelene to subequilateral. A very small to small flange is present on rostrally positioned teeth; in caudally positioned teeth the flange can be absent. The tip of the major cusp is elevated above the flange. The cusp gap is wide to moderately wide, the minor cusp is small but distinct. In labial view, the neck is stout, the crown not expanded to slightly expanded. In lateral view, the crown is slightly compressed. Premaxillary outer row teeth slightly to strongly recurved, lower jaw outer row teeth slightly recurved. The inner row teeth of both premaxilla and lower jaw are tricuspid.

Size. Teeth are relatively small and slender.

Dental arcade and tooth band. Dental arcade rounded and U-shaped. Premaxilla two to three or four inner rows anteriorly, none posteriorly. Lower jaw, one (rarely) to three inner rows anteriorly, none posteriorly.

Counts and setting. There are 42 to 56 teeth in the outer row of the upper jaw (l+r premaxilla). The outer row teeth in both premaxilla and lower jaw are normal to closely set, caudal-most positioned teeth may be somewhat more widely set.

Implantation. Outer row teeth of premaxilla erect, inner row teeth recumbent. Lower jaw outer row teeth erect to slightly procumbent, inner row teeth erect.

Lower pharyngeal element.— Relatively slender, as broad as it is long or slightly longer than broad (length/width ratio 1.0 to 1.1). The dentigerous area is broader than long (length/ width ratio 0.8 to 0.9). The suture is straight.

Fig. 17. *Haplochromis sphex* spec. nov., paratype, RMNH 73268, sexually active ♂, 68.8 mm SL.

Pharyngeal teeth.— *Counts.* There are 31 to 34 teeth in the caudal-most transverse row, 9 to 11 teeth in the medial rows.
Shape. Caudal-most one to two transverse rows hooked, major cusp only slightly incurved and blunt. Other teeth pronounced or bevelled. All teeth relatively fine and slender, medial teeth not coarser than other teeth.

Vertebrae.— The total number of vertebrae in 23 X-rayed specimens is 29 (3), 30 (19) or 31 (1), comprising 13-14 abdominal and 15-17 caudal vertebrae.

Live colouration.— Males have the snout and dorsal head surface yellow. Eye with a dusky outer ring and a yellow inner ring. Lips yellow to sooty. Lower jaw yellow to ivory. Interoperculum and gill cover yellow. Cheek, chest, dorsum, flank and belly yellow, with sometimes a silverish ground colour shining through. Ventral side yellow to ivory, sometimes a bit sooty. Nostril-, interorbital-, lachrymal-, supraorbital-, preopercular vertical stripes and nape band present. There are four to six, rarely seven vertical bars on the flank. An interrupted mid-lateral- and dorsal lateral band are present, as well as traces of a dorsal medial band. The mid-lateral band is anteriorly extended until the eye and posteriorly over the entire caudal fin. The markings are dusky to black. In cases where vertical bars are present and the horizontal bands are uninterrupted a so-called 'chess board pattern' emerges. Pectoral fins hyaline with a sometimes brown-red or dusky base, pelvic fins laterally black, medially yellowish-hyaline. The anal fin is hyaline-grey, caudally becoming more hyaline, generally with three yellow to yolk-yellow egg dummies surrounded by a hyaline ring. Caudal fin hyaline with faint brown-reddish streaks and spots, a dusky base and the extension of the mid-lateral

Table 5. Measurements of *Haplochromis sphex* spec. nov. Means and standard deviations have been calculated over all measured type specimens (including the holotype).

		holotype	paratypes (n = 26)	mean ± st. dev (n = 27)
standard length (mm)		77.6	60.8-79.4	71.9 ± 4.5
body depth (BD)	%SL	30.3	28.3-31.6	29.8 ± 0.9
pectoral fin length (PFL)	%SL	29.4	25.0-31.0	27.7 ± 1.4
caudal peduncle length (CPL)	%SL	17.7	15.7-21.7	18.2 ± 1.4
caudal peduncle depth (CPD)	%SL	11.0	9.6-11.9	10.8 ± 0.5
caudal fin length (CFL)	%SL	24.5	22.9-26.8	24.6 ± 1.0
head length (HL)	%SL	30.0	29.6-32.3	30.8 ± 0.7
snout length (SnL)	%HL	30.5	24.3-30.8	28.4 ± 1.5
snout width (SnW)	%HL	34.8	28.6-33.5	31.1 ± 1.5
head width (HW)	%HL	46.4	42.0-46.8	44.5 ± 1.3
interorbital width (IOW)	%HL	25.3	22.5-27.3	25.0 ± 1.2
preorbital width (POW)	%HL	30.0	25.4-29.4	27.9 ± 1.1
lachrymal width (LaW)	%HL	27.0	22.1-27.7	25.2 ± 1.6
preorbital depth (POD)	%HL	17.2	14.1-16.8	15.7 ± 0.8
eye length (EyL)	%HL	31.8	28.2-34.2	31.0 ± 1.5
eye depth EyD)	%HL	29.2	25.7-31.1	28.6 ± 1.3
cheek depth (ChD)	%HL	20.2	15.5-22.3	19.3 ± 1.3
lower jaw length (LJL)	%HL	38.6	35.4-42.2	39.0 ± 1.8
lower jaw width (LJW)	%HL	18.5	14.6-27.0	18.3 ± 2.5
EyD/EyL		0.9	0.9-1.0	0.9 ± 0.0
LJL/LJW		2.1	1.5-2.7	2.2 ± 0.3

band. Dorsal fin sooty-yellow, caudally becoming hyaline, with faint red-brown streaks and spots. Dorsal fin base partly black, lappets dusky.

Females are coloured like males but the yellow parts generally are olive-green, though a faint yellow flush is present at the ventral side of the flank. In the centre of the flank, some traces of blue may be present. Chest, belly and ventral side silverish. Branchiostegal membrane yellowish. Faint traces of lachrymal-, supraorbital- and preopercular vertical stripes and nape band may be present. There are four to six vertical bars on the flank, which are less distinct than in males. Black opercular blotch present, as are an interrupted mid-lateral-, dorsal lateral- and dorsal medial band. Mid-lateral band extending to one third of the caudal fin. Pectoral fins hyaline, pelvic fins yellow. Anal fin hyaline-yellow with yolk-yellow spots. Dorsal and caudal fin hyaline-grey with brownish streaks and spots.

Preserved colouration of males. Males have the entire body grey-brown to yellow-brown, generally ventrally lighter than dorsally. Markings as in live, sexually active males. Pectoral fins brownish-hyaline. Pelvic fins laterally black, medially brownish-hyaline to dusky. Dorsal fin brownish-hyaline, occasionally with darker streaks and spots, lappets sometimes dusky.

Preserved colouration of females. The females are coloured like males, except for the nostril-, interorbital-, lachrymal-, supraorbital- and preopercular vertical stripes, which are absent.

Distribution.— *Haplochromis sphex* spec. nov. is only known from Lake Victoria

Habitat.— *Haplochromis sphex* spec. nov. was found in waters up to a depth of 10 m both over sand and mud. During the night *H. sphex* spec. nov. was caught with a surface trawl at the entrance of Butimba Bay (station E) (Witte et al., 1992b) and at station G, further off shore (T. Goldschmidt, pers. comm.). An exceptional large catch was made with a beach seine at the north-west corner of Butimba Bay in July 1979 (F.Witte, pers. obs.). Occasionally specimens were caught by angling at rocky shores (Witte et al., 1992b; Seehausen, 1996).

Food.— *Haplochromis sphex* spec. nov. fed mainly on phytoplankton (Cyanophyta and *Aulacoseira*) and occasionally on copepods (T. Goldschmidt, unpublished data).

Breeding.— *Haplochromis sphex* spec. nov. is a female mouth brooder, the catch of July 1979 contained one brooding female.

Etymology.— From the Greek σφήξ (wasp), referring to the colouration of males. Like the wasp, males of *H. sphex* spec. nov. are typically yellow with black stripes.

Haplochromis bwathondii Niemantsverdriet & Witte spec. nov.

(figs 18-20, table 6)

Haplochromis 'kribensis'; Goldschmidt, 1986: 45-50; Goldschmidt, 1989a: 97-104, 107, 118, 119, 148; Goldschmidt, 1989b: 130; Goldschmidt, 1991: 182, 185, 187; Kaufman, 1992: 849; Witte et al., 1992b: 13, 17, 25, 27, 28; Goldschmidt et al., 1993: 690-692, 694; Kaufman & Ochumba, 1993: 724; Seehausen & Witte, 1994b: 51, 52; Witte & Seehausen, 1995: 138; Seehausen & Witte, 1995a: 100, 101; Seehausen & Witte, 1995b: 27, 28; Seehausen, 1996: 250, 254-256, 278; Huber et al., 1997: 170; Seehausen et al., 1997b: 895, 899; Witte et al., 1997: 586; Sibbing & Witte, 2005: 127; Witte et al., 2009: 658.

Material examined (references to fish size concern standard length).— Holotype, ♂, 70.7 mm, RMNH 73244[2, 3], Mwanza Gulf, Tanzania, Lake Victoria, 26.i.1981, HEST; Paratypes: all collected by HEST in the Mwanza Gulf, Tanzania, Lake Victoria, except where noted otherwise: ♂, 74.3 mm, RMNH 66834, 18.vi.1982; ♂, 71.1 mm, RMNH 73240[2, 3], 17.viii.1981; ♂, 73.8 mm, RMNH 73241[2, 3], 21.iii.1980; ♂, 69.9 mm, RMNH 73242[2, 3], 24.xi.1978; ♀, 69.2 mm, RMNH 73243[2, 3], 17.viii.1981; ♂, 68.2 mm, RMNH 73245[2-4], 7.x.1977; ♂, 65.0 mm, RMNH 73246[2, 3], 30.ix.1977; ♂, 74.3 mm, RMNH 73247[2, 3], 2.ix.1977; ♂, 58.7 mm, RMNH 73248[2, 3], 13.ix.1977; ♂, 70.0 mm, RMNH 73431[1, 3], 9.ii.1979; ♂, 69.9 mm, RMNH 73432[1, 3], 24.viii.1979; ♂, 64.1 mm, RMNH 73433[1, 3], 6.i.1978; ♀, 65.2 mm, RMNH 73434[1, 3], 3.ii.1981; ♀, 81.7 mm, RMNH 73482, 23.xii.1977; ♀, 69.6 mm, RMNH 73745[4], 3.vi.1985; ♂, 58.5 mm, RMNH 73746[4], Emin Pasha Gulf, 19.vi.1985; ♂, 50.9 mm, RMNH 73747[4], Emin Pasha Gulf, 22.vi.1985; ♂, 65.1 mm, RMNH 77783[3], 26.i.1981; ♂, 64.7 mm, RMNH 77881[4], Kome Channel, 11.vi.1985; ♂, 62.9 mm, RMNH 79221[5], 15.viii.1986; ♂, 64.3 mm, RMNH 79222[5], 15.viii.1986; ♂, 59.7 mm, RMNH 79223[2], 15.viii.1986; ♂, 63.9 mm, RMNH 79224[5], 15.viii.1986; ♂, 61.9 mm, RMNH 79225[5], 15.viii.1986; ♂, 62.4 mm, RMNH 79226[5], 15.viii.1986; ♂, 55.3 mm, RMNH 79227[5], 15.viii.1986; ♂, 68.9 mm, RMNH 79228[5], 15.viii.1986; ♂, 59.3 mm, RMNH 79229[5], 15.viii.1986; ♂, 64.8 mm, RMNH 79230[5], 15.viii.1986; ♂, 60.4 mm, RMNH 79231[5], 15.viii.1986; ♂, 62.6 mm, RMNH 79232[5], 15.viii.1986; ♂, 62.8 mm, RMNH 79233[5], 15.viii.1986; ♂, 67.5 mm, RMNH 79234[5], 15.viii.1986; ♂, 69.7 mm, RMNH 79235[5], 15.viii.1986; ♂, 64.0 mm, RMNH 79237[5], Kome Channel, 25.viii.1986; ♂, 65.8 mm, RMNH 79238[5], Kome Channel, 25.viii.1986; ♂, 66.2 mm, RMNH 79239[5], Kome Channel, 25.viii.1986; ♂, 64.7 mm, RMNH 79240[5], Kome Channel, 25.viii.1986; ♂, 77.3 mm, RMNH 79241[5], Kome Channel, 25.viii.1986; ♂, 56.3 mm, RMNH 79864[4], 12.viii.1986; ♂, 58.7 mm, RMNH 79865[4], Emin Pasha Gulf, 31.viii.1986; ♂, 69.2 mm, RMNH 79866[4], Emin Pasha Gulf, 2.ix.1986; ♂, 71.8 mm, RMNH 79867[4], 23.ix.1986; ♂, 61.3 mm, RMNH 80470[4], Emin Pasha Gulf, 22.vi.1985; ♂, 59.0 mm, RMNH 80471[4], Emin Pasha Gulf, 22.vi.1985; ♂, 59.3 mm, RMNH 80841[4], Emin Pasha Gulf, 19.vi.1985; ♂, 67.5 mm, RMNH 80950[3, 4], 7.x.1977; ♂, 62.0 mm, RMNH 80951[3], 30.ix.1977; ♂, 60.9 mm, RMNH 80952[3], 2.ix.1977; ♂, 73.4 mm, RMNH 80953[3], 2.ix.1977; ♂, 75.3 mm, RMNH 80954[3], 2.ix.1977; ♂, 66.7 mm, RMNH 81562[4], 7.x.1977; ♂, 72.3 mm, RMNH 84025, 18.vi.1982; ♂, 65.9 mm, NSMT-P 98083, 18.vi.1982; ♀, 52.5 mm, RMNH 84027, 18.vi.1982; ♂, 67.8 mm, RMNH 84028, 22.iii.1982; ♀, 68.2 mm, RMNH 84029, 22.iii.1982; ♀, 58.6 mm, RMNH 84030, 22.iii.1982; ♂, 68.5 mm, RMNH 84031, 3.vi.1982; ♀, 64.8 mm, RMNH 84032, 3.vi.1982; ♀, 69.5 mm, RMNH 84033, 3.vi.1982; ♀, 70.9 mm, RMNH 84034, 3.vi.1982; ♂, 62.0 mm, RMNH 84035, 21.iv.1978; ♂, 66.0 mm, RMNH 84036, 10.xii.1981; ♂, 68.7 mm, BMNH 2010.3.23.6, 10.xii.1981; ♂, 72.7 mm, AMNH 250808, 10.xii.1981; ♀, 69.6 mm, RMNH 84039, 10.xii.1981; ♀, 78.1 mm, RMNH 84040, 10.xii.1981; ♀, 67.3 mm, RMNH 84041, 10.xii.1981; ♀, 68.0 mm, RMNH 84042, 10.xii.1981; ♀, 69.1 mm, RMNH 84043, 10.xii.1981; ♀, 59.3 mm, RMNH 84044, 10.xii.1981.

Description.— Based on 73 specimens (including the holotype) 50.9-81.7 mm SL.

Diagnosis.— A small sized (< 9 cm SL), micrognathic species (LJL < 45% HL) with a normal to relatively slender body outline (BD 29.7-35.7% of SL, mean 33.4%). *H. bwathondii* spec. nov. has bicuspid and tricuspid teeth in the oral jaws and a moderately curved dorsal head profile. *H. bwathondii* spec. nov. has a melanin pattern of dusky, interrupted, longitudinal bands and vertical bars, producing a so-called 'chess board pattern'. This pattern also occurs in several oral shelling molluscivores, insectivores and algae scrapers, but these species generally are larger, have a strongly curved dorsal head profile and a lower jaw length/width ratio of less than 1.5, whereas in *H. bwathondii* spec. nov. it ranges from 2.0 to 2.8.

Haplochromis bwathondii spec. nov. differs from other small species with a 'chess board pattern' and a lower jaw length/width ratio of more than 1.5, viz. *Haplochromis sphex* spec. nov. and *H. sauvagei*, (sensu Seegers, 2008, which is called H. 'rockkribensis' in Seehausen, 1996), in live colouration of sexually active males, by having red in the

---

[1] Type specimen that has been dissected to describe gill apparatus, oral jaws and pharyngeal jaws;[2] type specimen of which an X-ray photograph is available;[3] type specimen of which morphometric measurements have been taken (Table 6);[4] type specimen of which a colour picture is available; [5] type specimen of which E. Verheijen has taken a tissue sample for DNA analysis.

rostral part of the body. Further, it differs from *H. sphex* spec. nov. by having a deeper body and a larger eye (Tables 5, 6). As already noticed by Seehausen (1996), on first impression the colours of sexually active males of *H. bwathondii* spec. nov. and *Haplochromis sauvagei* look alike. However, males of *H. bwathondii* spec. nov. have a less distinct 'chess board pattern', are 'less yellow and have a silvery iridescent area on each scale, giving them a silvery ('pelagic') appearance'. Furthermore, *H. bwathondii* spec. nov. has a larger eye, thinner lips, a narrower lower jaw and less stout teeth with a relatively larger flange than *H. sauvagei* (pers. obs.).

Habitus (fig. 18).— Body relatively slender to normal. Dorsal head profile straight to moderately curved. Premaxillary pedicel not prominent. Mouth oblique. Lips not thickened. Medial part of premaxilla not expanded. Caudal part of the maxilla not bullate. The vertical through the caudal tip of the maxilla runs through the iris. Lower jaw isognathous and obtuse. Jaws equal anteriorly, lower jaw slightly protruding in a few specimens. Mental prominence not pronounced. Retro-articular processes of right and left mandible halves occasionally touching, slightly interrupting the ventral outline. Eye approximately circular. A small aphakic aperture may be present. Cephalic lateral line pores not or slightly enlarged.

Scales.— Cheek, gill cover, dorsal head surface, greater part of dorsum and caudal fin base covered with cycloid scales, the remaining part of the body with ctenoid scales. A gradual size transition between scales of chest and flank. Four to six (mode 5) scales between the upper lateral line and the dorsal fin origin, four to six (mode 5) between the pectoral and the pelvic fin bases.

Fins.— Pelvic fins reaching the anal fin origin. First soft rays of pelvic fins slightly produced, occasionally filamentous. Anal fin just or just not reaching the caudal fin origin. Caudal fin outline truncate to slightly emarginate.

Gill apparatus.— The description of the gill apparatus is based on the lateral gill rakers and the lateral hemibranch of the first gill arch. The number of gill rakers on the lower part of the first gill arch is 10 to 11. The lower two to four rakers are reduced. Next

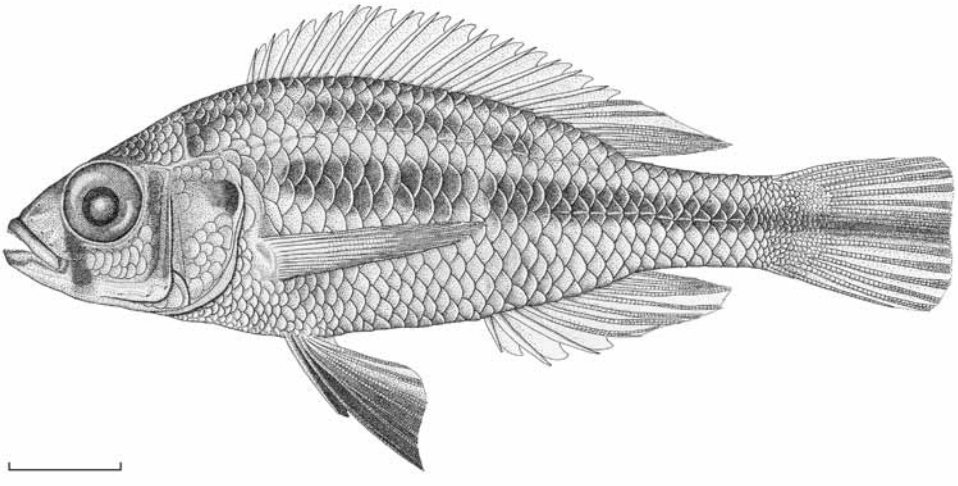

Fig. 18. *Haplochromis bwathondii* spec. nov., paratype, RMNH 77783, ♂. Scale equals 10 mm. Drawn by S. ter Huurne.

one to two rakers are short. These are followed by three to five long rakers, their shape is pointed to acutely pointed. The remaining upper two to four rakers are long, their shape is acutely pointed to bluntly pointed or bifid. The rakers on the first gill arch generally are touching each other. The number of gill filaments on the lateral hemibranch of the first gill arch ranges from 88 to 97.

Viscera.— Ratio between intestine length and SL: 1.5-3.0, mean 2.3 ± 0.4, n = 33 (T. Goldschmidt & F. Witte, unpublished data).

Oral jaws.— Premaxillary dentigerous arm as long as ascending arm (asc/dent arm ratio 1.0) in males, slightly shorter in female (asc/dent arm ratio 1.1). The angle between the two arms is 87° to 91°. The ascending arm is slightly broader than the dentigerous arm. One male showed traces of a symphyseal articulation facet (cf. Witte, 1984a) . Lower jaw relatively elongated (length/height ratio 2.1 to 2.2). The upper half of the dentary has a distinct outwardly directed flare. Mental prominence not pronounced.

Oral teeth.— *Shape.* Both premaxilla and lower jaw generally show an admixture of unequally bicuspid and tricuspid teeth in the rostral part (ca. ⅔ of dentigerous area), caudally mostly tricuspid teeth are found. The caudal-most teeth in the premaxilla are not

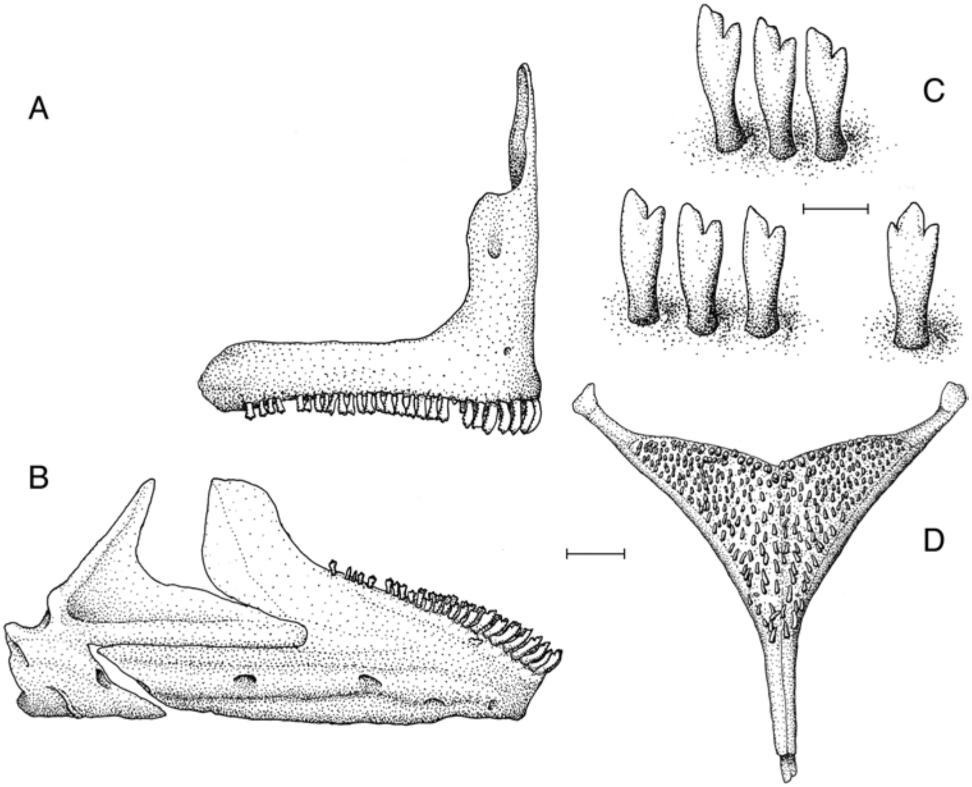

Fig. 19. *Haplochromis bwathondii* spec. nov. A, Premaxilla, lateral view; B, Lower jaw, lateral view; C, Lower jaw teeth; D, Lower pharyngeal element, dorsal view. Bony elements drawn from RMNH 73432, ♂, scale of bony elements equals 10 mm. Upper three teeth drawn from RMNH 73434, ♀, right-most tooth drawn from RMNH 73431, ♂, other teeth from RMNH 73432, scale of teeth 0.25 mm. Drawn by S. ter Huurne.

enlarged, tricuspid, occasionally bicuspid. The number of tricuspids in the premaxilla may vary from just a few to all teeth; in the lower jaw relatively less teeth are tricuspid.

In bicuspid teeth, the shape of the major cusp is isoscelene to subequilateral, sometimes obliquely truncated, especially in females. A flange is present, which may be very large in rostrally positioned teeth. The tip of the major cusp is generally not elevated above the flange. The cusp gap is wide, occasionally the minor cusp is only slightly smaller than the major cusp. In labial view, the neck is moderately slender, the crown slightly (in bicuspids) to moderately (in tricuspids) expanded. In lateral view, the crown is compressed. The outer row teeth of both premaxilla and lower jaw are slightly to strongly recurved. The inner row teeth are tricuspid.

Size. Teeth are relatively small and slender.

Dental arcade and tooth band. Dental arcade rounded and u-shaped. Premaxilla has two (rarely) to four inner rows anteriorly, none posteriorly. Lower jaw two to three inner rows anteriorly, none posteriorly.

Counts and setting. There are 46 to 57 teeth in the outer row of the upper jaw (l+r premaxilla). Teeth of premaxilla and lower jaw closely set, the most caudally positioned teeth may be somewhat more widely set.

Implantation. Outer row teeth of premaxilla erect, inner row teeth recumbent. Lower jaw outer row teeth slightly procumbent, inner row teeth erect.

Lower pharyngeal element.— Relatively slender. As broad as long, or slightly longer than broad (length/width ratio 1.0 to 1.1). The dentigerous area is broader than long (length/width ratio 0.8 to 0.9). The suture is straight.

Table 6. Measurements of *Haplochromis bwathondii* spec. nov. Means and standard deviations have been calculated over all measured type specimens (including the holotype).

		holotype	paratypes (n = 18)	mean ± st. dev (n = 19)
standard length (mm)		70.7	58.7-75.3	68.1 ± 4.6
body depth (BD)	%SL	34.2	29.7-35.7	33.4 ± 1.4
pectoral fin length (PFL)	%SL	31.7	28.1-33.8	31.0 ± 1.7
caudal peduncle length (CPL)	%SL	17.4	16.5-19.9	18.4 ± 1.1
caudal peduncle depth (CPD)	%SL	12.9	10.3-13.9	11.9 ± 0.8
caudal fin length (CFL)	%SL	26.6	24.3-30.3	26.5 ± 1.5
head length (HL)	%SL	32.1	30.8-34.1	32.3 ± 1.0
snout length (SnL)	%HL	26.0	23.6-29.6	26.1 ± 1.4
snout width (SnW)	%HL	30.0	25.1-33.7	29.8 ± 1.9
head width (HW)	%HL	47.6	42.9-47.3	45.5 ± 1.2
interorbital width (IOW)	%HL	27.8	25.8-29.7	27.7 ± 0.9
preorbital width (POW)	%HL	29.1	26.4-32.0	28.9 ± 1.4
lachrymal width (LaW)	%HL	23.8	21.8-26.6	24.3 ± 1.3
preorbital depth (POD)	%HL	14.5	13.3-16.4	14.8 ± 0.9
eye length (EyL)	%HL	33.0	32.3-37.9	35.3 ± 1.8
eye depth EyD)	%HL	30.0	30.1-34.7	32.4 ± 1.4
cheek depth (ChD)	%HL	17.6	14.2-19.0	17.2 ± 1.2
lower jaw length (LJL)	%HL	37.0	35.0-40.7	37.9 ± 1.7
lower jaw width (LJW)	%HL	17.6	14.3-19.0	16.9 ± 1.5
EyD/EyL		0.9	0.9-1.0	0.9 ± 0.0
LJL/LJW		2.1	2.0-2.8	2.3 ± 0.2

Pharyngeal teeth.— *Counts.* There are 29 to 37 teeth in caudal-most transverse row, 10 to 11 teeth in medial rows.

Shape. Caudal-most transverse row hooked, major cusp only slightly incurved and blunt. Other teeth pronounced or bevelled. All teeth are relatively fine and slender, medial teeth are not coarser than other teeth.

Vertebrae.— The total number of vertebrae in eight X-rayed specimens is 28 (2), 29 (5) or 30 (1), comprising 13-14 abdominal and 15-16 caudal vertebrae.

Live colouration.— Males have the snout, dorsal head surface and dorsum dark grey to light gold-brown, a bluish sheen is generally present. Lips light grey to grey, often with a bluish sheen. Lower jaw ivory to light grey. The eye has a dark grey outer ring and a golden-yellow inner ring. The cheek is light brownish to grey with a red flush. Interoperculum and gill cover red. The rostral part of the flank is grey with a red flush, the caudal part and the caudal peduncle grey with a green-yellow flush. Belly, chest and rostral part of ventral side ivory with red, remainder of ventral side ivory with a green-yellow flush. Nostril-, interorbital-, lachrymal-, and preopercular vertical stripes and nape band present; the supraorbital stripe may be interrupted. The lachrymal- and supraorbital stripes are prominent. Opercular blotch present; an additional blotch often present dorsal to the pectoral fin base. There are five to six dark grey to black vertical bars on the flank. An interrupted mid-lateral- and dorsal lateral band are present, as well as traces of a dorsal medial band, all dark grey to black. Due to the crossing of horizontal bands and vertical bars the so-called 'chess board pattern' may emerge, although not distinct. Pectoral fins hyaline, pelvic fins with a black lateral side; medial side dusky with a reddish flush. Anal fin hyaline-grey with two yolk-yellow egg dummies surrounded by a hyaline ring. Caudal fin base often coloured as caudal peduncle, with an extension of the mid-lateral band in the medial part. On the distal part of the caudal fin reddish to dusky maculae may be present. Dorsal fin faint hyaline to light greyish, with reddish to dusky streaks and spots. Rostral lappets dusky.

Females have the snout dark grey, dorsal head surface, dorsum and flank olive-green, the colour gradually becoming less intense caudally and ventrally. Dorsum and flank with a bluish sheen. Lips olive-green. Lower jaw, chest, belly and ventral side

Fig. 20. *Haplochromis bwathondii* spec. nov., paratype, RMNH 77881, sexually active ♂, 64.7 mm SL.

ivory to silver. An opercular blotch and a preopercular vertical stripe are present. The remainder of the stripe pattern is faint, three to five vertical bars, and an interrupted mid-lateral band may be visible. Pectoral fins hyaline, pelvic fins hyaline-yellow. Caudal fin hyaline-grey, anal fin olive-green to hyaline, generally with one faint yellow spot. Dorsal fin hyaline-grey with an olive-green base, lappets dusky.

Preserved colouration of males. Males have the dorsal parts darker brown, ventrally khaki-brown. Markings are the same as in sexually active, live males. Pectoral fins hyaline, pelvic fins black laterally, medially hyaline-brown to dusky. Anal fin brownish-hyaline occasionally with dusky spots. Caudal fin brownish-hyaline with an extension of the mid-lateral band over a part of the fin. Dorsal fin brownish-hyaline, lappets on the rostral part dusky.

Preserved colouration of females. Females are coloured like preserved males, but the markings are less distinct and the pelvic fins are hyaline.

Distribution.— *Haplochromis bwathondii* spec. nov. is only known from Lake Victoria.

Habitat.— *Haplochromis bwathondii* spec. nov. was caught mainly in the sub-littoral areas of the Mwanza Gulf (Witte et al., 1992b; Goldschmidt et al., 1993), over mud bottoms. The occurrence and distribution in deep water is unknown. *H. bwathondii* spec. nov. is a mainly pelagic species. Juveniles of *H. bwathondii* spec. nov. occurred in shallow southern part of the Mwanza Gulf (< 5 m deep; Goldschmidt et al., 1993). Occasionally specimens were caught by angling at rocky shores (Witte et al., 1992b). Seehausen (1996) describes a remnant population of *H. bwathondii* spec. nov. (then *H.* 'kribensis') at a rocky island in the northern Speke Gulf, where it occurred in mixed schools with *Haplochromis* 'macula' in the upper 1 m of the rocky littoral.

Food.— Before the ecological changes in Lake Victoria, *H. bwathondii* spec. nov. fed mainly on Cyanophyta, both during day and night. During the daytime, *Aulacoseira* (formerly *Melosira*) and occasionally other small diatoms such as *Nitzschia,* were also consumed. By night *H. bwathondii* spec. nov. fed also on adult insects and insect pupae from the water surface (Goldschmidt et al., 1993).

Breeding.— *Haplochromis bwathondii* spec. nov. is a female mouth brooder that spawns the whole year (Goldschmidt et al., 1993). For general fecundity characteristics concerning phytoplanktivorous species, see Goldschmidt et al. (1993).

Etymology.— This species is named in honour of Prof. Dr Philip O.J. Bwathondi, Director General of the Tanzania Fisheries Research Institute (TAFIRI) from August 1983 until the end of 2006. During this period Professor Bwathondi supported the research of the Haplochromis Ecology Survey Team (HEST) in many ways.

Haplochromis pancitrinus Mietes & Witte spec. nov.

(figs 21-23, table 7)

Haplochromis 'yellow'; Goldschmidt, 1989a: 148; Goldschmidt, 1991: 182, 185, 187; Witte et al., 1992b: 25, 27.

Material examined (references to fish size concern standard length).— Holotype, ♂, 69.1 mm, RMNH 83923[2], Mwanza Gulf, Tanzania, Lake Victoria, 7.ix.1981, HEST; Paratypes: all collected by HEST in the Mwanza Gulf, Tanzania, Lake Victoria, except where noted otherwise : ♂, 74.6 mm, RMNH 73276[2], 16.vi.1978; ♂, 78.1 mm, RMNH 73277[2], 2.iv.1981; ♂, 71.8 mm, RMNH 73278[2], 7.ix.1981; ♂, 62.6 mm, RMNH 73279[2], 26.i.1981; ♂, 51.3 mm, RMNH 73280[2, 3], 3.vi.1985; ♂, 60.6 mm, RMNH 73281[2], 5.v.1978; ♂, 77.0 mm, RMNH 73282[2], 21.iv.1978; ♂, 61.3 mm, RMNH 73458, 21.iv.1978; ♂, 72.2 mm, RMNH 73464[1], 1.vi.1981; ♂, 82.2 mm, RMNH 73465[1], 4.viii.1978; ♂, 65.1 mm, RMNH 73466[1], 9.vi.1978; ♂, 72.0 mm, RMNH 77785[2], 26.i.1981; ♂, 63.6 mm, RMNH 79137[5], 15.viii.1986; ♂, 60.9 mm, RMNH 80839[2, 3], 3.vi.1985; ♂, 70.0 mm, RMNH 80961[2], 5.v.1978; ♂, 65.4 mm, RMNH 80962[2], 5.v.1978; ♂, 73.0 mm, RMNH 80963[2], 23.xii.1977; ♂, 73.3 mm, RMNH 80964[2], 21.iv.1978; ♂, 63.3 mm, RMNH 80965[2], 21.iv.1978; ♂, 63.2 mm, RMNH 80966[2], 21.iv.1978; ♂, 66.1 mm, RMNH 81265[3], 9.vi.1975; ♂, 71.5 mm, RMNH 81781[3], 2.vi.1975; ♂, 85.9 mm, RMNH 81789[3], 7.vi.1975; ♂, 80.0 mm, RMNH 82496, 5.v.1978; ♂, 61.1 mm, RMNH 83924[2], 7.ix.1981; ♂, 74.5 mm, RMNH 83925[2], 26.i.1981; ♂, 72.5 mm, NSMT-P 98084, 4.viii.1978; ♂, 73.6 mm, RMNH 83994, 6.v.1982; ♂, 74.8 mm, RMNH 83995, 6.v.1982; ♂, 56.8 mm, RMNH 83996, 6.v.1982; ♂, 57.9 mm, RMNH 83997, 19.vi.1982; ♂, 72.1 mm, RMNH 83998, 19.vi.1982; ♂, 61.3 mm, RMNH 83999, 19.vi.1982; ♂, 60.7 mm, RMNH 84000, 21.iv.1978; ♂, 74.4 mm, BMNH 2010.3.23.7, 21.iv.1978; ♂, 65.0 mm, RMNH 84002, 21.iv.1978; ♀, 72.9 mm, RMNH 84003, 5.v.1984; ♂, 62.2 mm, RMNH 84004, 5.v.1984; ♂, 68.4 mm, AMNH 250809, 7.ix.1981; ♂, 67.5 mm, RMNH 84006, 7.ix.1981.

Description.— Based on 41 specimens 51.3-85.9 mm.

Diagnosis.— A small sized (SL < 9 cm), relatively slender (BD 29.0-33.5% of SL), mean 31.2%) micrognathic (LJL < 44%) species. *H. pancitrinus* spec. nov. has mainly bicuspid teeth in the oral jaws. Although there are many species that resemble *H. pancitrinus* spec. nov. in habitus, no other species are known with the typical golden-yellow colouration of sexually active males, without any distinct markings.

Habitus (fig. 21).— Body relatively slender. Dorsal head profile gently curved over the whole dorsal outline. Premaxillary pedicel slightly interrupting the dorsal head profile. Mouth oblique. Lips normal. Medial part of the premaxilla not expanded. Caudal part of the maxilla not bullate. The vertical through the caudal tip of the maxilla runs through the anterior part of the iris. Lateral snout outline isognathous, in a few specimens prognathous. Lower jaw often slightly protruding. Mental prominence not or slightly pronounced. Retro-articular processes of right and left mandible halves generally touching each other, not or slightly interrupting the ventral body outline. Eye approximately circular, a small aphakic aperture may be present. Cephalic lateral line pores not or slightly enlarged.

Scales.— Cheek, gill cover, dorsal head surface, greater part of dorsum and caudal fin base covered with cycloid scales. Chest covered with a few cycloid scales and a majority of weakly ctenoid scales. Remaining part of the body with ctenoid scales. A gradual size transition between scales of chest and flank. Four to six (mode 5) scales between the upper lateral line and the dorsal fin origin, four to six (mode 5) between the pectoral and the pelvic fin bases.

Fins.— Pelvic fins just reaching the anal fin origin. First soft rays of pelvic fins slightly produced, occasionally filamentous. Anal fin not reaching caudal fin origin. Caudal fin outline truncate to emarginate; in most specimens emarginate.

Gill apparatus.— The description of the gill apparatus is based on the lateral gill rakers and the lateral hemibranch of the first gill arch. The number of gill rakers on the lower part of the first gill arch is 10. The first raker is reduced, the following two to three

---

[1] Type specimen that has been dissected to describe gill apparatus, oral jaws and pharyngeal jaws and of which morphometric measurements have been taken (Table 7); [2] type specimen of which an X-ray photograph is available and of which morphometric measurements have been taken (Table 7); [3] type specimen of which a colour picture is available; [4] type specimen of which E. Verheijen has taken a tissue sample for DNA analysis.

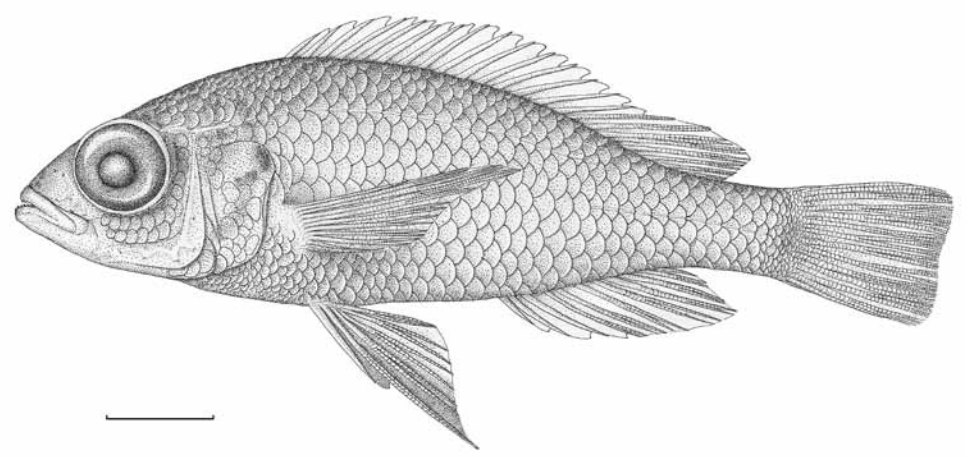

Fig. 21. *Haplochromis pancitrinus* spec. nov., paratype, RMNH 77785, ♂. Scale equals 10 mm. Drawn by S. ter Huurne.

short. The next three to six are long and slender, their shape is acutely pointed. The upper one to three rakers are long and blunt to acutely pointed in shape. The rakers on the first gill arch may touch each other. The number of gill filaments on the lateral hemibranch of the first gill arch ranges from 90 to 101.

Viscera.— Ratio between intestine length and SL: 1.5-2.7, mean 2.1 ± 0.4, n = 14 (T. Goldschmidt & F. Witte, unpublished data).

Oral jaws.— Premaxillary dentigerous arm slightly shorter than, or as long as, ascending arm (asc/dent arm ratio 1.0 to 1.1). The angle between the two arms is 83° to 85°. Symphyseal articulation facet not present. Lower jaw slightly elongated (length/height ratio 1.9 to 2.0). The upper half of the dentary has an outwardly directed flare, which is slightly distinct to distinct. Mental prominence not or slightly pronounced.

Oral teeth.— *Shape.* Teeth in rostral part (ca. ⅔ of dentigerous area) of premaxilla and lower jaw unequally bicuspid, often with a few tricuspids among them. Occasionally an admixture of bicuspids and tricuspids is found. In the caudal part of premaxilla and lower jaw mostly tricuspids are found, sometimes also subequally bicuspids. The caudal-most teeth in the premaxilla are not enlarged.

In bicuspid teeth, the major cusp is isoscelene to subequilateral. A small to distinct flange is present in the more rostrally placed teeth. The tip of the major cusp may or may not be elevated above the flange. The cusp gap is wide to moderately wide, the minor cusp is relatively large compared to the major cusp. In labial view, the neck is moderately stout to stout, the crown slightly expanded (bicuspids) to expanded (tricuspids). In lateral view, the crown is slightly compressed. Both premaxilla and lower jaw teeth are slightly recurved to recurved. The inner row teeth of both premaxilla and lower jaw consist of tricuspid teeth.

Size. Teeth are relatively small and slender, caudal teeth very small.

Dental arcade and tooth band. Dental arcade rounded and U-shaped. The premaxilla has one to three inner rows anteriorly, none posteriorly. Caudal-most part of dentigerous

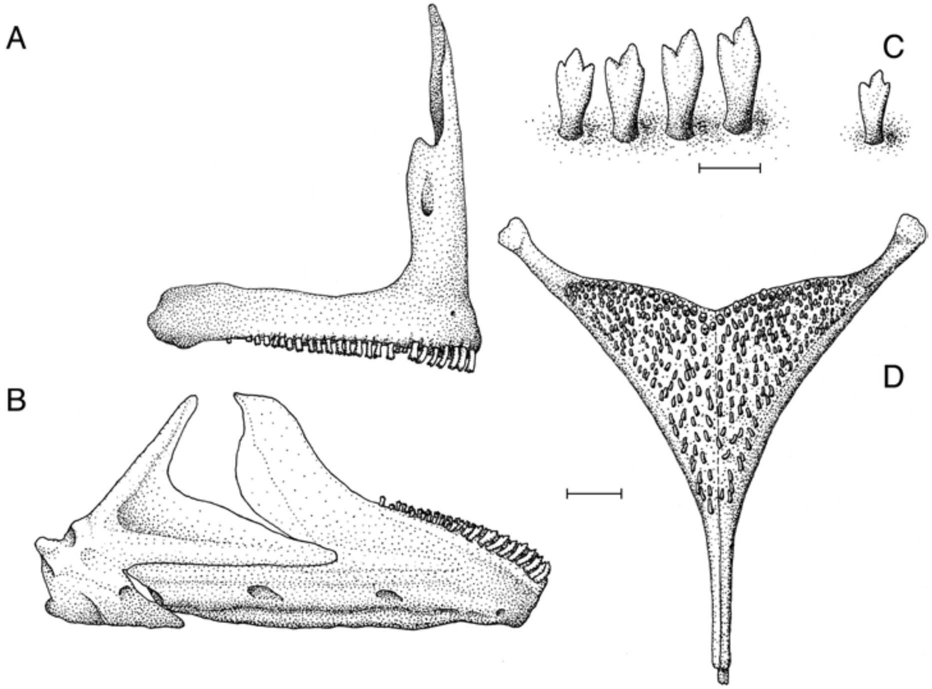

Fig. 22. *Haplochromis pancitrinus* spec. nov. A, Premaxilla, lateral view; B, Lower jaw, lateral view; C, Lower jaw teeth; D, Lower pharyngeal element, dorsal view. Bony elements of RMNH 73464, ♂, scale of bony elements = 10 mm. Right most tooth drawn from RMNH 73464, other from RMNH 73466, ♂, scale of teeth 0.25 mm. Drawn by S. ter Huurne.

arm edentulous. Lower jaw has one or two inner rows anteriorly, none posteriorly.

Counts and setting. There are 37 to 56 teeth in the outer row of the upper jaw (l+r premaxilla). Teeth in both premaxilla and lower jaw normal to closely set, caudal-most teeth of premaxilla may be more widely set.

Implantation. Outer row teeth of premaxilla erect, inner row teeth recumbent. Lower jaw outer row teeth slightly procumbent, inner row teeth erect.

Lower pharyngeal element.— Relatively long and slender. Longer than broad (length/width ratio 1.1 to 1.2). The dentigerous area is broader than long (length/width ratio 0.8 to 0.9). The suture is straight.

Pharyngeal teeth.— *Counts.* 35 to 39 teeth in caudal-most transverse row, 10 to 12 teeth in medial rows.

Shape. Caudal-most transverse row hooked, major cusp only slightly incurved and blunt. Other teeth bevelled; minor cusp in some of these teeth strongly pronounced. All teeth relatively small and slender. Medial teeth not coarser than other teeth.

Vertebrae.— The total number of vertebrae in 18 X-rayed specimens is 29 (1), 30 (13), 31 (3), or 32 (1) comprising 13-14 abdominal and 16-18 caudal vertebrae.

Live colouration.— Sexually active males have the snout, dorsal head surface, lips, lower jaw, cheek, interoperculum and gill cover golden-yellow. Eye with a grey outer

Table 7. Measurements of *Haplochromis pancitrinus* spec. nov. Means and standard deviations have been calculated over all measured type specimens (including the holotype).

		holotype	paratypes (n = 20)	mean ± st. dev (n = 21)
standard length (mm)		69.1	51.3-82.2	68.6 ± 7.2
body depth (BD)	%SL	32.1	29.0-33.5	31.2 ± 1.2
pectoral fin length (PFL)	%SL	28.2	24.7-31.8	28.6 ± 1.4
caudal peduncle length (CPL)	%SL	18.1	17.1-22.3	19.6 ± 1.4
caudal peduncle depth (CPD)	%SL	10.6	10.3-12.2	11.2 ± 0.5
caudal fin length (CFL)	%SL	25.2	23.2-27.5	25.3 ± 1.2
head length (HL)	%SL	32.9	30.4-33.8	32.2 ± 0.9
snout length (SnL)	%HL	25.6	22.8-29.3	25.8 ± 1.6
snout width (SnW)	%HL	26.9	25.8-31.0	28.2 ± 1.6
head width (HW)	%HL	44.9	41.6-47.0	44.9 ± 1.3
interorbital width (IOW)	%HL	25.6	21.7-27.6	25.3 ± 1.3
preorbital width (POW)	%HL	26.0	25.1-28.5	27.0 ± 1.1
lachrymal width (LaW)	%HL	21.6	20.4-24.4	22.6 ± 1.2
preorbital depth (POD)	%HL	14.5	13.3-15.6	14.4 ± 0.6
eye length (EyL)	%HL	36.6	31.7-37.9	35.4 ± 1.9
eye depth EyD)	%HL	32.6	30.7-35.4	32.7 ± 1.3
cheek depth (ChD)	%HL	16.3	14.8-17.6	16.2 ± 0.9
lower jaw length (LJL)	%HL	41.0	37.1-44.1	39.2 ± 1.4
lower jaw width (LJW)	%HL	16.3	12.8-18.7	15.7 ± 1.7
EyD/EyL		0.9	0.9-1.0	0.9 ± 0.0
LJL/LJW		2.5	2.1-3.0	2.5 ± 0.3

ring and a golden inner ring. Flank golden-yellow with a faint blue-grey ground colour, which is slightly darker in the dorsum. Belly, chest and ventral side ivory with a yellow flush. An opercular blotch is present, the nostril- and interorbital stripe are faint. Pectoral fins hyaline, pelvic fins blackish and blue on lateral side and hyaline-yellowish medially. Anal fin dorso-rostrally light blue or yellow, ventro-caudally hyaline-yellowish. One or two yolk-yellow egg dummies, surrounded by a hyaline ring, are present. Caudal fin yellow, caudally becoming more hyaline. Dorsal fin base yellow, distally greyish-hyaline. Lappets hyaline to yellow.

Live colouration of adult females unknown.

Preserved colouration of males. Males have the entire body light grey-brown; ventral side slightly lighter. An opercular blotch is present, interorbital and nostril stripe sometimes faintly present. Occasionally very faint traces of vertical bars a dorsal-lateral band and a mid-lateral band are present. Pectoral fins hyaline, lateral side of the pelvic fins black, remainder hyaline to dusky. Anal and dorsal fin hyaline. Caudal fin hyaline, sometimes with a few dark brown streaks.

Preserved colouration of females (based on 1 specimen). The female is coloured like preserved males, but the interorbital and nostril stripe are absent and the pelvic fins are hyaline.

Distribution.— *Haplochromis pancitrinus* spec. nov. is only known from Lake Victoria.

Habitat.— *Haplochromis pancitrinus* spec. nov. was caught with bottom trawls in sub-littoral waters of the northern part of the Mwanza Gulf over mud bottoms and also in surface trawls in the same area (stations E and G; Witte et al., 1992b; T. Goldschmidt, pers. comm.). Occasionally it was caught over mud bottoms, in shallower areas more

Fig. 23. *Haplochromis pancitrinus* spec. nov., paratype, RMNH 73280, sexually active ♂, 51.3 mm SL.

southward in the Gulf.

Food.— Before the ecological changes in Lake Victoria, *H. pancitrinus* spec. nov. fed on phytoplankton, mainly Cyanophyta. The diet further included *Chaoborus* larvae, copepods and occasionally detritus (T. Goldschmidt, pers. comm.).

Breeding.— Based on the egg dummies on the anal fin and the egg size in ripe females (3.1 mm; Goldschmidt 1991), *H. pancitrinus* spec. nov. is a female mouth brooder.

Etymology.— The name pancitrinus (παγκίτϱινος) is composed of the Greek words for complete, whole; ‘πᾶν’ and ‘κίτϱινος’ which means yellow. It refers to the live colouration of males.

Discussion

Identification of females

In the present paper, females of *H. antleter* spec, nov. and *H. katunzii* spec. nov. are not described since it was difficult to distinguish the females of these two species from each other (and from other related species) in the field. Because these species have a curved to straight dorsal head profile, the females were collectively referred to as the ‘curved head’ females (*e.g.* Goldschmidt et al. 1993). Occasionally females were found during our ecological surveys that (based on coloration) could be allocated to one of the species, unfortunately, we could not trace these among the museum material.

Generic classification

Greenwood (1979, 1980) revised the Lake Victoria haplochromines, splitting them into more than 20 genera and subgenera. During the past decades there have been extensive debates on the validity of the genera defined by Greenwood (Hoogerhoud, 1984; Meyer et al., 1990; Lippitsch, 1993; Snoeks, 1994; Seehausen, 1996; van Oijen, 1996; Seehausen et al., 1998). Because of the disagreements, and as a considerable number of the haplochromine species from Lake Victoria cannot be assigned to the 'new' genera, we prefer to keep the species in the genus *Haplochromis* and, where possible, add the new generic names in parenthesis, i.e. use them as subgenera. In the sections below we will compare the newly described species with the genera described by Greenwood (1980).

Detritivores

Three of the detritivores described in this paper resemble species that were placed in the genus *Enterochromis* by Greenwood (1980). Both *H. katunzii* spec. nov. and *H. antleter* spec. nov. are morphologically similar to *H. (Enterochromis) cinctus*, whereas *H. coprologus* spec. nov. resembles *H. (E.) erythrocephalus*, the type species of *Enterochromis*. The main diagnostic characters of this genus are 'a long, much coiled intestine that is at least 3 or 4 times longer than the standard length' and having the anterior opening to the nasal lateral line canal as large as, or larger than the nostril. The latter sets it apart from other haplochromines with long intestines, which comprise Greenwood's genera *Xystichromis*, *Neochromis* and the redefined genus *Haplochromis* (Greenwood, 1980).

The average ratios between intestine- and standard lengths (IL/SL), measured in *H. katunzii* spec. nov., *H. antleter* spec. nov., and *H. coprologus* spec. nov. are 2.4, 2.9 and 1.9 respectively. These ratios are considerably lower than those given by Greenwood (1980) for species belonging to the genus *Enterochromis*. However, the same holds for the IL/SL ratio of *H. cinctus* from the Mwanza Gulf (2.5 ± 0.5, n = 17; T. Goldschmidt & F. Witte, unpublished data) and for *Haplochromis* 'paropius-like', which probably is conspecific to *Haplochromis paropius* Greenwood & Gee, 1969 (1.8 ± 0.2, n = 14; Kishe-Machumu et al., 2008). Witte & van Oijen (1990) report an IL/SL ratio of 1.4-3.3 (mostly 1.7-2.8) for 51 specimens of 12 detritivorous species. Unfortunately, neither Greenwood & Gee (1969), who described *H. cinctus*, *H. paropius* and *H. erythrocephalus*, nor Greenwood (1980) present IL/SL ratios of individual species. However, for *H. nigripinnis* from Lake George, which was also included in *Enterochromis* by Greenwood (1980), an IL/SL ratio of ca. 2-2.5 was given (Greenwood, 1973). This is similar to the values found for the three species described in this paper and lower than the range given by Greenwood (1980). It suggests that the IL/SL ratio for *Enterochromis* of 'at least 3 or 4' should be scaled down. Further, the differences in IL/SL ratios between the above mentioned detritivorous species and the *Enterochromis* species of Greenwood (1980) could be due to differences in the way of measuring (*e.g.* the degree in which intestines were stretched) or to differences in the populations from the north and south of the lake. With respect to the latter, it is remarkable that the IL/SL ratio of the detritivores in the Mwanza Gulf decreased by about 30% during the past 30 years (see below). Concerning the anterior opening to the nasal lateral line canal, it should be noticed that in *H. katunzii* spec. nov., *H. antleter* spec. nov. and *H. coprologus* spec. nov. it ranges from *smaller* than, to as large as, the nostril. However, even in cases where the nasal lateral line opening was smaller than the nostril, the opening was much larger than the nasal lateral line opening in *Haplochromis obliquidens* Hilgendorf, 1888, which is the type species of Greenwood's (1980) redefined genus *Haplochromis*. Though the measures of intestine length and of the nasal lateral line opening of *H. katunzii* spec. nov., *H. antleter* spec. nov. and *H. coprologus* spec. nov. do not completely match Greenwood's diagnostic characters of the genus *Enterochromis*, we have indications that the three species are closer related to *Enterochromis* than to other genera proposed by Greenwood. Consequently we will use

Enterochromis as a subgenus for these species where appropriate.

In earlier papers (*e.g.* Goldschmidt et al., 1993) *H. coprologus* spec. nov. (nicknamed *H.* 'nigrofasciatus') was differentiated from *H. katunzii* spec. nov., *H. antleter* spec. nov. and *H. cinctus* by dorsal head profile shape. *H. coprologus* spec. nov. has a dorsal head profile that is incurved above the eye, whereas the others have a head profile that is curved to straight. In head shape *H. coprologus* spec. nov. resembles *H. erythrocephalus*, the type species of *Enterochromis*. According to Greenwood (1980), this species differs from the other three that he allocated to *Enterochromis* by its shallow preorbital skull depth, a feature that we did not measure. However, there are other features that are similar between *H. erythrocephalus* and *H. coprologus* spec. nov. and separate them from the other species. One of these is the relatively high number of gill rakers in *H. erythrocephalus* (mode 12, Greenwood & Gee, 1969) and *H. coprologus* spec. nov. (11-12) compared to those in the curved head species (*H. paropius* mode 9, *H. cinctus* 9 (Greenwood & Gee, 1969); *H. katunzii* spec. nov. 8-9, *H. antleter* spec. nov. 10).

Haplochromis coprologus spec. nov. shares a number of morphological features with the zooplanktivorous *Haplochromis piceatus* Greenwood & Gee, 1969. Apart from body colouration (see Fig. 10) these features comprise the incurved dorsal head profile and the longer edentulous caudal part of the premaxilla in females; in *H. piceatus* males 'the outer tooth row often extends further caudad than in females' (Witte & Witte-Maas, 1987). In fact, *H. coprologus* spec. nov. might be described as a deep bodied *H. piceatus* with a relatively long intestine length (mean IL/SL *H. coprologus* spec. nov. 1.9 ± 0.4, range 1.2-2.8, n = 19; mean IL/SL *H. piceatus* 1.5 ± 0.2, range 1.1-2.0, n = 32; F. Witte, unpublished data). Ecologically the species differ in diet, *H. piceatus* feeds on zooplankton and insect larvae (Witte, 1987 and unpublished data; Galis, 1990) and *H. coprologus* spec. nov. feeds on detritus and phytoplankton (Goldschmidt et al., 1993). As for their distribution, adult *H. coprologus* spec. nov. are common in deeper waters (from 6 to at least 20 m) than adult *H. piceatus* (mainly from 6 to 10 m) (Goldschmidt et al., 1990, 1993; Witte et al., 1992b; F. Witte, unpublished data). Furthermore, both species are seasonal spawners, with *H. piceatus* breeding shallower than *H. coprologus* spec. nov. (Witte, 1987; Goldschmidt et al., 1990, 1993). Both species have nurseries in shallow bays from where the young gradually migrate into deeper water (Witte, 1981, 1984, 1987; Goldschmidt et al., 1990, 1993). Based on the similarities and dissimilarities between the two species one could speculate that they represent sibling species that evolved by ecological speciation, similar to the benthic and limnetic species pairs of sticklebacks in Canadian lakes (McPhail, 1994). Interestingly, Greenwood (1980) allocated *H. piceatus* to *Astatotilapia* (a genus which he regarded to be polyphyletic), whereas Witte & Witte-Maas (1987) suggested that it might bridge the gap between *Astatotilapia* and *Yssichromis*, and Seehausen et al. (2002) considered it to belong to *Yssichromis*. Our present observations suggest that a close relation to *Enterochromis* is also possible.

Though *H. katunzii* spec. nov. is not blue, but sandy-brown with a turquoise sheen, *H. katunzii* spec. nov. and *H. cinctus* seem to represent an example of a morphologically similar 'blue-red' sibling species pair, just like *H. (Gaurochromis) iris* Hoogerhoud & Witte, 1981 and *H. (G.) hiatus* Hoogerhoud & Witte, 1981, and like *Haplochromis (Pundamilia) nyererei* Witte & Witte-Maas, 1985 and *H. (P.) pundamilia* Seehausen & Bouton, 1997. As in the foregoing species (Hoogerhoud et al., 1983; Seehausen et al., 2008), *H. cinctus*, the red one of the pair is the deeper dwelling of the two (van Oijen et al., 1981, Witte et al., 1992b). Research during the past decade has provided ample evidence that such morphologically similar 'blue-red' species pairs are probably the result of sympatric speciation. (*e.g.* Seehausen et al., 1997a, 2008; Maan et al., 2004; Verzijden & ten Cate 2007; van der Sluis et al., 2008).

Haplochromis vanoijeni spec. nov. is a detritivorous species that in some features is morphologically intermediate between the prawn eating 'tridens' group (allocated by Greenwood to *Prognathochromis*, subgenus *Tridontochromis*) and *Enterochromis*. Compared to the latter group *H. vanoijeni* spec. nov. has more three-cuspid teeth in the outer rows of the oral jaw. The lower jaw is relatively long (mean 43.8%) compared to the detritivorous species described in this paper (means 36.7-41.2%, tables 1-3) and the detritivorous species described in Greenwood & Gee (1969), except for *H. erythrocephalus* (mean 43.6%). However, the lower jaw is relatively short compared to the species of the '*tridens*' group (modal range > 45%, Greenwood, 1980; Witte & van Oijen, 1990, except for *Haplochromis plutonius* Greenwood & Barel, 1978, mean 44.0% and *Haplochromis cryptogramma* Greenwood & Gee, 1969, mean 44.8%). Its intestine length/ standard length ratio (mean 1.7 ± 0.6) is also longer than in the tridens group (0.8-1.4, mostly 1.0-1.1, Witte & van Oijen, 1990), but shorter than in other detritivores (1.4-3.3, mostly 1.7-2.8, Witte & van Oijen, 1990).

Phytoplanktivores

The generic allocation of the three new phytoplanktivorous species is even more difficult than that of the above mentioned species. The teeth in the outer row of *H. bwathondii* spec. nov. show some resemblance to those of *Haplochromis lividus* Greenwood, 1956 in having a large flange and being sometimes obliquely truncated. *H. lividus* was placed in the genus *Haplochromis* by Greenwood (1979). *H. bwathondii* spec. nov. and *H. sphex* spec. nov. have a mixture of longitudinal stripes and vertical bars, which are generally also present in the monotypic genera *Platytaeniodus* and *Macropleurodus* and in *Ptyochromis* and *Paralabidochromis* species. According to Greenwood (1980), these groups belong to one of the primary divisions of the *Psammochromis-Macropleurodus* super-lineage. However, *H. bwathondii* spec. nov. and *H. sphex* spec. nov. lack the apomorphic features of the lower jaw and its dentition which are characteristic for this division.

Recovering species

As mentioned in the introduction, the detritivorous and phytoplanktivorous haplochromines virtually disappeared from the sub-littoral waters of Lake Victoria in the 1980s. On a research transect in the Mwanza Gulf, where we used to catch more than 1000 individuals per ten minutes with a small trawl (head rope 4.6 m) in the 1970s, on average less than 1 individual per haul was caught between 1987 and 1992 (Witte et al., 2007b). Since then a slow recovery has been observed and in February 2005 the average number had risen to about 160 per 10 min trawling (Witte et al., 2007a).

Though the resurging fish are clearly recognized as detritivorous haplochromines, species identification is difficult for most of them. Some individuals do resemble one of the four former common species *H. cinctus, H. katunzii* spec. nov., *H. antleter* spec. nov. or *H. coprologus* spec. nov., but the majority of the individuals cannot be allocated unequivocally to one of these species. A thorough study still has to be made, but they seem to represent a range of intermediate forms, both in colour and shape, and could well represent hybrids. Hybridization may have been caused by the strong decrease in abundance of the detritivores in the 1980s, reducing the chance to meet conspecific mates, and also by the deprived light conditions, hampering mate selection through male colouration by females (Seehausen et al., 1997a, 2008; Seehausen & van Alphen, 1998).

Additionally, morphological changes may have been caused by adaptive responses to the environmental changes, both through natural selection and phenotypic plasticity. Such adaptive changes have been found for the zooplanktivore *Haplochromis (Yssichromis) pyrrhocephalus* Witte and Witte-Maas, 1987 and several other fish species in Lake Victoria (Wanink & Witte, 2000; Witte et al., 2008; Chapman et al., 2008). The decrease in intestine length in the resurging detritivores may well represent an adaptive response to their more carnivorous diet (Kishe-Machumu et al., 2008). *Haplochromis vanoijeni* spec. nov. was rarely caught after the ecological changes in the lake (Seehausen et al., 1997b) and nothing is known about its current ecology and morphology.

Of the phytoplanktivorous species, only *H. bwathondii* spec. nov. has been occasionally caught during the past few years. We are not sure if *H. sphex* spec. nov. and *H. pancitrinus* spec. nov. still occur in the lake. The current specimens of *H. bwathondii* spec. nov. still have to be compared with those of the past, to check if any morphological changes occurred in this species. Obviously, the recovering detritivores and phytoplanktivores are of great interest for future research, and the species descriptions in this paper will provide the taxonomical baseline for these studies.

Acknowledgements

We thank our colleagues from the Haplochromis Ecology Survey Team (HEST), the Tanzania Fisheries Research Institute (TAFIRI) and the Freshwater Fisheries Training Institute at Nyegezi, for support and co-operation during the fieldwork. We wish to thank Mhoja Kayeba, the late Aloys Peter, and the other crew members of the trawlers for their skilful labour. Dr Tijs Goldschmidt is acknowledged for kindly providing some of his data on diets and intestine lenghts. We are indebted to Dr Jos Snoeks and Dr Martien van Oijen for comments on an earlier draft of the paper. Dr Folkert van Straaten is acknowledged for his help with finding proper Latinized names for the new species. We thank Inge van Noortwijk and Martien van Oijen for the drawings of *H. vanoijeni* spec. nov. The fieldwork, as a result of which the species described in this paper were collected, was financially supported by The Netherlands Foundation for the Advancement of Tropical Research (WOTRO; grants W87-129, W87-161, W87-189) and by the Section for Research and Technology of the Netherlands' Ministry of Development Co-operation.

References

Barel, C.D.N., M.J.P. van Oijen, F. Witte & E.L.M. Witte-Maas, 1977. An introduction to the taxonomy and morphology of the haplochromine Cichlidae from Lake Victoria.— Netherlands Journal of Zoology 27: 333-389.

Barel, C.D.N., F. Witte & M.J.P. van Oijen, 1976. The shape of the skeletal elements in the head of a generalized *Haplochromis* species: *H. elegans* Trewavas 1933 (Pisces, Cichlidae).— Netherlands Journal of Zoology 26: 163-265.

Chapman, L.J., C.A. Chapman, L. Kaufman, F. Witte & J. Balirwa, 2008. Biodiversity conservation in African inland waters: lessons of the Lake Victoria region.— Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 30: 16-34.

Galis, F., 1990. Ecological and morphological aspects of changes in food uptake through the ontogeny of *Haplochromis piceatus*. Pp. 281-302 in: R.N. Hughes (ed.), Behavioural mechanisms of food selection.— NATO ASI Series, Vol. G 20. Springer-Verlag, Berlin, Heidelberg.

Goldschmidt, T., 1986. Niche differentiation in planktivorous haplochromines in the Mwanza Gulf of Lake Victoria and a hypothesis on the speciation of haplochromines in general.— Annalen van het Koninklijk Museum voor Midden-Afrika, Zoologische Wetenschappen 251: 45-52.

Goldschmidt, T., 1989a. An ecological and morphological field study on the haplochromine cichlid fishes (Pisces, Cichlidae) of Lake Victoria.— PhD Thesis, Leiden University.

Goldschmidt, T., 1989b. Reproductive strategies, subtrophic niche differentiation and the role of competition for food in haplochromine cichlids (Pisces) from Lake Victoria, Tanzania.— Annalen van het Koninklijk Museum voor Midden-Afrika, Zoologische Wetenschappen 257: 119-132.

Goldschmidt, T., 1991. Egg mimics in haplochromine cichlids (Pisces, Perciformes) from Lake Victoria.— Ethology 88: 177-190.

Goldschmidt, T. & P.C. Goudswaard, 1989. Reproductive strategies in haplochromines (Pisces, Cichlidae) from Lake Victoria. Pp. 93-119 in: T. Goldschmidt, An ecological and morphological field study on the haplochromine cichlid fishes (Pisces, Cichlidae) of Lake Victoria.— PhD Thesis, Leiden University.

Goldschmidt, T. & J. de Visser, 1990. On the possible role of egg mimics in speciation.— Acta Biotheoretica 38: 125-134.

Goldschmidt, T., F. Witte & J. de Visser, 1990. Ecological segregation of zooplanktivorous haplochromine species (Pisces, Cichlidae) from Lake Victoria.— Oikos 58: 343-355.

Goldschmidt, T., F. Witte & J.H. Wanink, 1993. Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria.— Conservation Biology 7: 686-700.

Goudswaard, P.C., P.J. Mous, W. Ligtvoet & W.L.T. Densen, 1995. Gears and boats. Pp. 83-117 in: F. Witte & W.L.T. Densen (eds), Fish stocks and fisheries of Lake Victoria. A handbook for field observations.— Cardigan, Dyfed, U.K.

Goudswaard, K. (P.C.), F. Witte & E.F.B. Katunzi, 2008. The invasion of an introduced predator, Nile perch (*Lates niloticus*, L.) in Lake Victoria (East Africa): chronology and causes.— Environmental Biology of Fishes 81: 127-139.

Greenwood, P.H., 1967. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae), Part VI.— Bulletin British Museum of Natural History (Zoology) 15 (2): 29-119.

Greenwood, P.H., 1973. A revision of the *Haplochromis* and related species (Pisces, Cichlidae) from Lake George, Uganda.— Bulletin British Museum of Natural History (Zoology) 25 (5): 139-242.

Greenwood, P.H., 1974. Cichlid fishes of Lake Victoria, east Africa: the biology and evolution of a species flock.— Bulletin British Museum of Natural History (Zoology), Supplement 6: 1-134.

Greenwood, P.H., 1979. Towards a phyletic classification of the 'genus' *Haplochromis* and related taxa. Part I.— Bulletin British Museum of Natural History (Zoology) 35 (4): 265-322.

Greenwood, P.H., 1980. Towards a phyletic classification of the 'genus' *Haplochromis* and related taxa. Part II.— Bulletin British Museum of Natural History (Zoology) 39 (1): 1-101.

Greenwood, P.H. & C.D.N. Barel, 1978. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae) Part VIII.— Bulletin British Museum of Natural History (Zoology) 33 (2): 141-192.

Greenwood, P.H. & J.M. Gee, 1969. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae), Part VII.— Bulletin British Museum of Natural History (Zoology), 18 (1): 1-65.

Hecky, R.E., F.W.B. Bugenyi, P. Ochumba, J.F. Talling, R. Mugidde, M. Gophen & L. Kaufman, 1994. Deoxygenation of the deep water of Lake Victoria, East Africa.— Limnology and Oceanography 39: 1476-1481.

Hoogerhoud, R.J.C., 1984. A taxonomic reconsideration of the haplochromine genera *Gaurochromis* Greenwood, 1980 and *Labrochromis* Regan, 1920 (Pisces, Cichlidae).— Netherlands Journal of Zoology 34 (4): 539-565.

Hoogerhoud, R.J.C. & F. Witte, 1981. Revision of species from the '*Haplochromis*' *empodisma* group.— Netherlands Journal of Zoology 31: 232-273.

Hoogerhoud, R.J.C., F. Witte & C.D.N. Barel, 1983. The ecological differentiation of two closely resembling *Haplochromis* species from Lake Victoria *H. iris* and *H. hiatus*; (Pisces, Cichlidae).— Netherlands Journal of Zoology 33: 283-305.

Huber, R., M.J. van Staaden, L.S. Kaufman & K.F. Liem, 1997. Microhabitat use, trophic patterns, and the evolution of brain structure in African cichlids.— Brain, Behaviour and Evolution 50: 167-182.

Katunzi, E.F.B., J. Zoutendijk, T. Goldschmidt, J.H. Wanink & F. Witte, 2003. Lost zooplanktivorous cichlid from Lake Victoria reappears with a new trade.— Ecology of Freshwater Fish 12: 237-240.

Kaufman, L., 1992. Catastrophic change in species-rich freshwater ecosystems.— BioScience 42 (11): 846-858.

Kaufman, L. & P. Ochumba, 1993. Evolutionary and conservation biology of cichlid fishes as revealed by faunal remnants in northern Lake Victoria.— Conservation Biology 7: 719-730.

Kishe-Machumu, M., F. Witte & J.H. Wanink, 2008. Dietary shift in benthivorous cichlids after the ecological changes in Lake Victoria.— Animal Biology 58: 401-417.

Lippitsch, E., 1993. A phyletic study on lacustrine haplochromine fishes (Perciformes, Cichlidae) of East Africa, based on scale and squamation characters.— Journal of Fish Biology 42: 903-946.

Maan, E.M., O. Seehausen, L. Söderberg, L. Johnson, E.A.P. Ripmeester, H.D.J. Mrosso, M.I. Taylor, T.J.M. van Dooren & J.J.M.van Alphen, 2004. Intraspecific sexual selection on a speciation trait, male colouration, in the Lake Victoria cichlid *P. nyererei*.— Proceedings of the Royal Society London B 271: 2445-2452.

McPhail, J.D., 1994. Speciation and the evolution of reproductive isolation in the sticklebacks (*Gasterosteus*) of southwestern British Columbia. Pp. 399-437 in: A.M. Bell & S.A. Foster (eds), The evolutionary biology of the threespine stickleback. Oxford University Press, Oxford.

Meyer, A., T.D. Kocher, P. Basasibwaki & A.C. Wilson, 1990. Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences.— Nature 347: 550-553.

Ogutu-Ohwayo R., 1990. The decline of the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus* and the Nile tilapia, *Oreochromis niloticus*.— Environmental Biology of Fishes 27: 81-96.

Oijen, M.J.P. van, 1996. The generic classification of the haplochromine cichlids of Lake Victoria, East Africa.— Zoologische Verhandelingen Leiden 302: 57-110.

Oijen, M.J.P. van & F. Witte, 1996. Taxonomical and ecological description of a species complex of zooplanktivorous and insectivorous cichlids from Lake Victoria.— Zoologische Verhandelingen Leiden 302: 1-56.

Oijen, M.J.P. van, F. Witte & E.L.M. Witte-Maas, 1981. An introduction to ecological and taxonomic investigations on the haplochromine cichlids from the Mwanza Gulf of Lake Victoria.— Netherlands Journal of Zoology 31: 149-174.

Rinkes, M., 1999. Conflicts in cichlid head morphology due to optimization of functional demands on suction feeding.— PhD Thesis, Leiden University.

Seegers, L., 2008. The fishes collected by G.A. Fischer in East Africa in 1883 and 1885/86.— Zoosystematics and Evolution 84: 149-195.

Seehausen, O., 1996. Lake Victoria rock cichlids: taxonomy, ecology and distribution.— Verduijn Cichlids, Zevenhuizen.

Seehausen, O. & J.J.M. van Alphen, 1998. The effect of male colouration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex).— Behavioural Ecology and Sociobiology 42: 1-8.

Seehausen, O., J.J.M. van Alphen & F. Witte, 1997a. Cichlid fish diversity threatened by euthrofication that curbs sexual selection.— Science 277: 1808-1811.

Seehausen, O., J.J.M. van Alphen & F. Witte, 2003. Implications of eutrophication for fish vision, behavioral ecology, and species coexistence: a theoretical framework. Pp. 268-287 in: T.L. Crisman, L.J. Chapman, C.A. Chapman & L.S. Kaufman (eds), Conservation, Ecology, and Management of African Fresh Waters.— University Press of Florida, Florida.

Seehausen, O., E. Koetsier, M.V. Schneider, L.J. Chapman, M.E. Knight, G.F. Turner, J.J.M. van Alphen & R. Bills, 2002. Nuclear markers reveal unexpected genetic variation and a Congolese-Nilotic origin of the Lake Victoria cichlid species flock.— Proceedings of the Royal Society London B 270: 129-137.

Seehausen, O., E. Lippitsch, N. Bouton & H. Zwennes, 1998. Mbipi, the rock-dwelling cichlids of Lake Victoria: description of three new genera and fifteen new species (Teleostei).—Ichthyological Explorations of Freshwaters 9: 129-228.

Seehausen, O., Y. Terai, I.S. Magalhaes, K.L. Carleton, H.D.J. Mrosso, R. Myagi, I. van der Sluijs, M.V. Schneider, M.E. Maan, H. Tachida, H. Imai & N. Okada, 2008. Speciation through sensory drive in cichlid fish.— Nature 455: 620-625.

Seehausen, O. & F. Witte, 1994a. Eine zweite Austerbewelle im Victoriasee und die Notwendigkeit der Verknüpfung von Forschung und Naturschutz.— DATZ 47: 586-591.

Seehausen, O. & F. Witte, 1994b. Massenaussterben und Überleben.— Tetra Informationen (TI Magazin) 26 (4): 48-53.

Seehausen, O. & F. Witte, 1995a. Extinction of many and survival of some: the current situation of the endemic cichlids in southern Lake Victoria.— Tropical Fish Hobbyist 43 (7): 96-105.

Seehausen, O. & F. Witte, 1995b. Hromadné vymírání a přežití.— Tetra Magazín 2: 24-29.

Seehausen, O., F. Witte, E.F. Katunzi, J. Smits & N. Bouton, 1997b. Patterns of the remnant cichlid fauna in southern Lake Victoria.— Conservation Biology 11: 890-904.

Sibbing, F.A. & F. Witte, 2005. Adaptations to Feeding in Herbivorous Fish. Pp. 113-140 in: M.E. Azim, M.C.J. Verdegem, A.A. van Dam & M.C.M. Beveridge (eds), Periphyton: Ecology, Exploitation and Management.— CABI Publishing, Wallingford, UK.

Sluijs, I. van der, T.J.M. van Dooren, K.D. Hofker, J.J.M. van Alphen, R.B. Stelkens & O. Seehausen, 2008. Female mating preference functions predict sexual selection against hybrids between sibling species of cichlid fish.— Philosophical Transactions of the Royal Society B 363: 2871-2877.

Snoeks, J., 1994. The haplochromines (Teleostei, Cichlidae) of Lake Kivu (East Africa). A taxonomic revision with notes on their ecology.— Annalen van het Koninklijk Museum voor Midden-Afrika, Zoologische Wetenschappen 270: 1-221.

Verzijden, M.N. & C. ten Cate, 2006. Early learning influences species assortative mating preferences in Lake Victoria cichlid fish.— Biology letters 3: 134-136.

Visser, J. de, 2000. Tongue in Cheek. A study in biological engineering of fish.— PhD Thesis, Leiden University.

Visser, J. de & C.D.N. Barel, 1996. Architectonic constraints on the hyoid's optimal starting position for suction feeding of fish.— Journal of Morphology 228: 1-18.

Wanink, J.H., J.J. Kashindye, P.C. Goudswaard & F. Witte, 2001. Dwelling at the oxycline: does increased stratification provide a refugium for the Lake Victoria sardine *Rastrineobola argentea*?— Freshwater Biology 46: 75-85.

Wanink J.H. & F. Witte, 2000. Rapid morphological changes following niche shift in the zooplanktivorous cyprinid *Rastrineobola argentea* from Lake Victoria.— Netherlands Journal of Zoology 50: 365-372.

Witte, F., 1981. Initial results of the ecological survey of the haplochromine cichlid species from the Mwanza Gulf of Lake Victoria (Tanzania): breeding patterns, trophic and species distribution with recommendations for commercial trawl-fishery.— Netherlands Journal of Zoology 31: 175-202.

Witte, F., 1984a. Consistency and functional significance of morphological differences between wild-caught and domestic *H. squamipinnis* (Pisces Cichlidae).— Netherlands Journal of Zoology 34: 596-612.

Witte, F., 1984b. Ecological differentiation in Lake Victoria haplochromines: comparison of cichlid species flocks in African Lakes. Pp. 155-167 in: A.A. Echelle & I. Kornfield (eds), Evolution of fish species flocks.— Orono Press, University of Maine, Maine.

Witte, F., 1987. From form to fishery. An ecological and taxonomical contribution to morphology and fishery of Lake Victoria cichlids.— PhD Thesis, Leiden University.

Witte, F., C.D.N. Barel & M.J.P. van Oijen, 1997. Intraspecific variation of haplochromine cichlids from Lake Victoria and its taxonomic implications.— South African Journal of Science 93: 585-594.

Witte, F., T. Goldschmidt, P.C. Goudswaard, W. Ligtvoet, M.J.P. Van Oijen & J.H. Wanink, 1992a. Species extinction and concomitant ecological changes in Lake Victoria.— Netherlands Journal of Zoology 42: 214-232.

Witte, F., T. Goldschmidt, J. Wanink, M. van Oijen, K. Goudswaard, E. Witte-Maas & N. Bouton, 1992b. The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria.— Environmental Biology of Fishes 34: 1-28.

Witte, F. & P.C. Goudswaard, 1985a. Aspects of the haplochromine fishery in southern Lake Victoria.— FAO Fisheries Report 335: 81-88.

Witte, F. & P.C. Goudswaard, 1985b. Exploitatie van *Haplochromis* in het Victoriameer.— Visserij 38: 297-305.

Witte, F., H. van der Meer & K. Barel, 2003. Door cichlidenogen bezien: het belang van het gezichtsvermogen bij haplochromine cichlden voor het ontstaan en in stand houden van diversiteit.— Cichlidae 29 (4): 104-114.

Witte, F., B.S. Msuku, J.H. Wanink, O. Seehausen, E.F.B. Katunzi, P.C. Goudswaard & T. Goldschmidt, 2000. Recovery of cichlid species in Lake Victoria: an examination of factors leading to differential extinction.— Reviews in Fish Biology and Fisheries 10: 233-241.

Witte, F. & M.J.P. van Oijen, 1990. Taxonomy, ecology and fishery of Lake Victoria haplochromine trophic groups.— Zoologische Verhandelingen 262: 1-47.

Witte, F., M.J.P. van Oijen & F.A. Sibbing, 2009. Fish fauna of the Nile. Pp. 647-675 in: H.J. Dumont (ed.), The Nile: origin environments, limnology and human use— Springer Science + Business Media B.V.

Witte, F. & O. Seehausen, 1995. Massenaussterben, Überleben und Veränderung von Victoriasee-Cichliden. Pp.137-142 in: R. Stawikowski (ed.), Cichliden, Festschrift zum 25jährigen Jubiläum der DCG.— Deutsche Cichliden-Gesellschaft, Frankfurt am Main, Germany.

Witte, F., J.H. Wanink & M.A. Kishe, 2007a. Species distinction and the biodiversity crisis in Lake Victoria.—Transactions of the American Fisheries Society 136: 1146-1159.

Witte, F., J.H. Wanink, M.A. Kishe, O.C. Mkumbo, P.C. Goudswaard & O. Seehausen, 2007b. Differential decline and recovery of haplochromine trophic groups in the Mwanza Gulf of Lake Victoria.— Aquatic Ecosystem Health and Management 10: 416-433.

Witte, F., J.H. Wanink, H.A. Rutjes, H.J. van der Meer & G.E.E.J.M. van den Thillart, 2005. Eutrophication and the fish fauna of Lake Victoria. Pp. 301-338 in: V.M. Reddy (ed.), Restoration and management of tropical eutrophic lakes.— Science Publishers, Inc., Enfield (NH), USA.

Witte F., M. Welten, M. Heemskerk, I. van der Stap, L. Ham, C. Rutjes & J. Wanink, 2008. Major morphological changes in a Lake Victoria fish within two decades.— Biological Journal of the Linnean Society 94: 41-52.

Witte, F. & E.L.M. Witte-Maas, 1981. Haplochromine cleaner fishes: a taxonomic and eco-morphological description of two new species.— Netherlands Journal of Zoology 31: 203-231.

Witte, F. & E.L.M. Witte-Maas, 1987. Implications for taxonomy and functional morphology of intraspecific variation in haplochromine cichlids of Lake Victoria. Pp. 1-83 in: F. Witte, From form to fishery. An ecological and taxonomical contribution to morphology and fishery of Lake Victoria cichlids.— PhD Thesis, Leiden University.

Zihler, F., 1982. Gross morphology and configuration of the digestive tract of Cichlidae (Teleostei, Perciformes): phylogenetic and functional significance.— Netherlands Journal of Zoology 32: 544-571.

Received: 28 August 2009
Accepted: 23 March 2010
Edited: M.J.P. van Oijen