Just below the surface, the pelagic haplochromine cichlids from the Lake Edward system

Peer-reviewed author version

Vranken, Nathan; VAN STEENBERGE, Maarten; Mbalassa, Mulongaibalu & Snoeks, Jos (2023) Just below the surface, the pelagic haplochromine cichlids from the Lake Edward system. In: Hydrobiologia, 850 (14) , p. 3173-3195.

DOI: 10.1007/s10750-023-05246-y
Handle: http://hdl.handle.net/1942/40279

Just below the surface, the pelagic haplochromine cichlids from the Lake Edward system

Nathan Vranken[1,2,*], Maarten Van Steenberge[3,4], Mulongaibalu Mbalassa[5,6] & Jos Snoeks[1,2]

1. KU Leuven, Department of Biology, Fish diversity and Conservation, Charles Deberiotstraat 32, 3000 Leuven, Belgium
2. Royal Museum for Central Africa, Biology department, Section Vertebrates, Leuvensesteenweg 13, 3080 Tervuren, Belgium
3. Royal Belgian Institute of Natural Sciences, Operational Directorate Taxonomy and Phylogeny, Vautierstraat 29, 1000 Brussels, Belgium
4. Hasselt University, Research Group Zoology, Biodiversity and Toxicology, Centre for Environmental Sciences, Agoralaan Gebouw D, 3590 Diepenbeek, Belgium
5. Makerere University College of Agricultural and Environmental Sciences, Department of Environmental Management, Kampala, Uganda
6. Université Officielle de Bukavu, Faculté des Sciences et Sciences Appliquées, Département de Biologie, Section, Hydrobiologie, Bukavu, D. R. Congo

*Corresponding author: nathan.vranken@kuleuven.be

ORCID Nathan Vranken: 0000-0003-0728-4715
ORCID Maarten Van Steenberge: 0000-0002-6964-9014

Abstract

The East African Great Lakes are inhabited by impressive radiations of cichlids that display a large variation in morphology, diet, colour pattern, and behaviour and have adapted to a large array of niches. While most of these cichlids are bottom dwellers, a number of species have adapted to a pelagic environment and inhabit open waters. From the Lake Edward system, one pelagic species had been previously described, the zooplanktivorous *Haplochromis pappenheimi*. Our sampling revealed the Lake Edward system to be inhabited by two more pelagic species that were unknown to science and are formally described here, the zooplanktivorous *Haplochromis pelagicus* sp. nov. and the insectivorous *H. aureus* sp. nov. All three species seem mostly restricted to deepwater regions where the depth exceeds six meters in Lake Edward, except for *H. pelagicus* sp. nov., which also occurs in shallower regions of Lakes Edward and George and of the Kazinga Channel. Sexual dimorphism, mainly in head shape, was discovered in *H. pappenheimi* and *H. pelagicus* sp. nov. These differences suggest that females of these species have larger buccal cavities than males, which is most likely linked to female mouth brooding behaviour.

Keywords

Cichlidae, *Haplochromis*, new species, pelagic fishes, sexual dimorphism, *Yssichromis*

Statements and declarations

Competing interests

The authors declare that they have no competing interests.

Introduction

Cichlids are well known for their adaptive radiations in the East African Great Lakes. After the formation of these lakes, cichlids rapidly adapted to the various available habitats, resulting in large communities that comprise numerous species (Fryer & Iles, 1972; Malinsky et al., 2018; McGee et al., 2020; Ronco et al., 2021). Cichlids are especially abundant and diverse in near-shore and benthic habitats, where they dominate most available niches (Konings, 2016). In comparison, the open waters of the East African Great Lakes are relatively species-poor in cichlids. These habitats are mostly dominated by so called small pelagic fishes (*sensu* Kolding *et al.*, 2019) and their pelagic predators. In the rift lakes, the former group consists of clupeids (Tanganyika, introduced in Kivu), cyprinids (Albert, Malawi), alestids (Albert), and cichlids (Malawi) (Kolding *et al.*, 2019; Konings, 2016). Many of these small pelagic fishes are predated upon by latids (Albert, Tanganyika) and piscivorous cichlids (Malawi) in addition to them being targeted by pelagic fisheries for their value as food fishes. For Lake Victoria, the community composition of the open waters drastically changed over the past century largely due to increased fishing pressure, eutrophication, and the introduction of *Lates niloticus* (Linnaeus 1758). Previously dominated by a diverse community of small pelagic cichlids and some cichlid predators, the open waters are now dominated by the cyprinid *Rastrineobola argentea* (Pellegrin 1904) and *Lates niloticus* (Witte *et al.* 1992; Goudswaard *et al.*, 2008; Everson *et al.*, 2013). The community composition of the open waters of Lake Edward remains poorly known, but large pelagic predators such as latids and alestids are absent (Decru *et al.*, 2020, 2022). Limited scientific sampling led to the discovery and descriptions of the pelagic poeciliid *Laciris pelagicus* (Worthington 1932) and the pelagic zooplanktivorous cichlid *Haplochromis pappenheimi* (Boulenger 1914). Recent investigations indicate Lake Edward to be inhabited by more pelagic cichlid species, including the recently described piscivorous *H. latifrons* Vranken *et al.* 2022 (Vranken *et al.*, 2022).

The Lake Victoria region, which comprises the basins of Lakes Albert, Edward, Kivu, Kyoga, and Victoria is inhabited by about 700 species of *Haplochromis*. Nearly all of these cichlid species are very closely related and belong to the Lake Victoria Region Superflock (LVRS), an adaptive radiation that evolved rapidly 100–200 ka ago and forms a model system in evolutionary biology (Verheyen *et al.*, 2003; Meier *et al.*, 2017). The LVRS shows a large diversity in trophic morphology, diet and habitat preferences, behaviour, and colour patterns, and nearly all species are endemic to the basin of a single lake (Greenwood, 1974; Snoeks, 1994; Seehausen, 1996). The evolutionary relationships between species remain partly unknown and resolving them is severely complicated by a high degree of incomplete lineage sorting and admixture (Meier *et al.*, 2017; McGee *et al.*, 2020). Although a generic classification has been suggested for LVRS haplochromines (Greenwood, 1980), many species cannot be unambiguously allocated to a genus (van Oijen, 1996) and most genera were not supported by phylogenomic analyses (Meier *et al.*, 2017). Hence, we place all species of the LVRS in *Haplochromis* and refer to Greenwood's genera in single quotation marks (*e.g.*, *'Yssichromis'* Greenwood 1980) (Vranken *et al.*, 2019, 2022). Species of *Haplochromis* are often grouped in eco-morphological groups, *e.g.*, insectivores, piscivores, molluscivores, algae scrapers, phytoplanktivores, and zooplanktivores (Witte & van Oijen, 1990). As these mostly correspond to the genera *sensu* Greenwood (1979, 1980), this classification remains a valuable framework.

In the relatively shallow Lake Victoria (~80 m), Greenwood (1974) and Witte *et al.* (1992) divided habitats in three depth regions: littoral (< 6 m deep), sublittoral (6–20 m deep), and deepwater (> 20 m deep). In these habitats, fishes can have a benthic, *i.e.*, in association with the substrate, or a pelagic lifestyle. In Lake Victoria, different habitats and lifestyles were dominated by different trophic groups: benthic algae scrapers and oral mollusc shellers were most abundant in littoral regions, some benthic insectivores and piscivores inhabited deepwater regions, while other piscivores and some zooplanktivores occupied the open waters in deepwater regions (Witte & van Oijen, 1990). Based on this division, we here define deepwater pelagic species of *Haplochromis* as those species that are most abundant in the open waters of sublittoral and deepwater regions (> 6 m deep).

The Lake Edward system consists of the basins of Lakes Edward and George. Lake Edward is a relatively deep (~120 m) and relatively turbid lake. It is connected through the Kazinga Channel to the very shallow (< 4 m) and very turbid Lake George (Levring & Fish, 1956). The Lake Edward system is inhabited by about 80 endemic species of *Haplochromis*, 44 of which have been formally described (Vranken *et al.*, 2022), including one presumed deepwater pelagic species, the zooplanktivorous *H. pappenheimi*. Based on recent gill-net sampling in the Lake Edward system, we delineate and formally describe the deepwater pelagic species of *Haplochromis* from the Lake Edward system and discuss their distribution, relative abundance, eco-morphology, and sexual dimorphism.

Material and methods

Within the framework of the HIPE project (Human impacts on Lake Edward), four expeditions to the Ugandan part of the Lake Edward system (HIPE 1–4; 2016–2019) were undertaken. A large collection of haplochromine cichlids was made from various catches using gill nets of various mesh sizes (8–40 mm) with a net height of 1.5 m (Decru *et al.*, 2020). Pelagic and benthic catches were defined as being done with surface (floating) and bottom (sinking) gill nets, respectively. A total of 42 catches from the Lake Edward system were investigated (Table S1), including four pelagic catches of sublittoral and deepwater regions. The specimens from the pelagic catches were investigated, in which three species were recognised (see below). The relative abundance of these three species was estimated in all pelagic and non-pelagic catches. Catches were non-standardised as timing (day or night catches), duration (between ~1–10 h), and used material (sinking or floating gill nets with various mesh sizes) differed. For each catch, species-specific estimates of relative abundances were calculated as proportions of the total number of specimens in the catch. For all three species, gut contents were observed under a binocular stereo microscope (6.5–50x). The digestive tracts were removed, dissected, and their contents identified.

A taxonomic revision of the deepwater pelagic species of *Haplochromis* from the Lake Edward system was performed. For this, 425 specimens (see Taxonomic account below for detailed lists) were investigated for qualitative traits and for the descriptions, including 69 specimens from which measurements and counts were taken. These consist of 233 specimens from the Royal Museum for Central Africa, Tervuren (RMCA), 164 from the Royal Belgian institute of Natural Sciences, Brussels (IRSNB), 26 from the Natural History Museum, London (NHMUK), and 15 from the Museum für Naturkunde, Berlin (ZMB), including the lectotype and fifteen paralectotypes of *H. pappenheimi*. To exclude conspecific status with other pelagic species, these specimens from the Lake Edward system were also compared to (re)descriptions of species from Lake Victoria (Greenwood & Gee, 1969; Witte & Witte-Maas, 1987; van Oijen & Witte, 1996; de Zeeuw *et al.*, 2012) and of *H. kamiranzovu* Snoeks *et al.* 1984 from Lake Kivu (Snoeks, 1994).

All taxonomic techniques and terminology used follow Barel *et al.* (1977) and Vranken *et al.* (2022). A total of 54 morphometrics were taken under a binocular stereo microscope (6.5–50x) by a single person (NV) following Vranken *et al.* (2022). These consisted of 28 linear measurements (taken with a pair of callipers, ± 0.1 mm), 24 counts (Table 1), and two angular measurements. Vertebrae counts were taken from X-ray scans made by the VisiX X-ray system (Medex Loncin SA) with a DeReO WA detector and a GemX-160 generator. The angular measurements, gape and snout inclinations, were taken following Barel (1983), with the parasphenoid used as a reference line from X-rays in ImageJ (Rasband, 2018).

Qualitative characteristics follow Barel *et al.* (1977) and Vranken *et al.* (2022) and were described in reference to the generalised *Haplochromis* morphology *sensu* Barel *et al.* (1976), which was based on *H. elegans* Trewavas 1933, an insectivorous species from the Lake Edward system. Described qualitative characteristics include: body shape, dorsal outlines of head and snout, lateral outline of snout, maxillary posterior extension (using a line perpendicular to body axis), caudal- and pelvic-fin outlines, gill-raker shape, and shape and dentition of oral and pharyngeal jaws. The colour patterns in live specimens (from photographs of freshly caught specimens) and in specimens fixed in formalin and preserved in alcohol were described. A distinction was made between terms that describe the relative size of structures in the dorso-ventral axis, *i.e.*, shallow and deep, in the antero-posterior axis, *i.e.*, short and long, and in the medial-lateral axis, *i.e.*, narrow and broad. Characteristics that correspond to the generalised *Haplochromis* morphology *sensu* Barel *et al.* (1976) were described as 'average'. Specimens were sexed by investigation of the genital papillae.

Measurements and counts were analysed separately using principal component analyses (PCA). These were performed on the 21 log-transformed measurements and on 21 scaled raw counts. To allow for comparison, all measurements, except for SL, were expressed as percentages of a reference measurement (mostly SL and HL). Pairwise inter-group comparisons of the proportional measurements and of the raw counts were performed with Mann-Whitney *U* (MW*U*) tests. To avoid size effects, all MW*U* tests were performed on subsets of specimens of a similar standard-length class [MW*U*(SL): $P > 0.5$]. For each comparison between two groups of specimens, the *P*-values resulting from the sets of measurements and counts were corrected with a sequential Bonferroni correction (Rice, 1989). Measurements with fin tips as reference points (VL and PL) and measurements and counts taken on a subset of specimens (LPL, LPW, DAL, DAW, LPTp, LPTm, and snout and gape inclinations) were excluded from all analyses. All analyses were performed in R stats and graphics packages (Murrell, 2005).

Results

The deepwater pelagic species of *Haplochromis*

Four pelagic catches from the upper water layers of sublittoral and deepwater regions (> 6 m deep) within the Lake Edward system were made using floating gill nets (Fig. 1b-d: catches 7, 8, 10 & 12). These contained a total of 302 fish specimens (Table S1). Except for a single specimen of *H. mentatus* Regan 1925 in catch 7, all could be assigned to three deepwater pelagic species of *Haplochromis*: *H. pappenheimi*, *H. pelagicus* sp. nov., and *H. aureus* sp. nov. (Fig. 1a) (for species confirmation, see Taxonomic revision below). *Haplochromis aureus* sp. nov. was easily distinguishable from the other two species by its larger size, deeper cheeks, and longer jaws set with larger and sharper oral teeth. The remaining two species closely resembled each other in overall habitus but were first recognised by the colour pattern of their anal fin and subtle differences in their oral tooth morphology. Specimens of *H. pappenheimi* had a dusky to blackish anal fin and small outer oral teeth that were mostly bicuspids and some tricuspids, all with small to large minor cusps and acutely pointed major cusps. Specimens of *H. pelagicus* sp. nov. had a hyaline to rarely faint dusky anal fin, and small outer oral teeth that were mostly bicuspid with large minor cusps and bluntly pointed major cusps.

Species distribution, abundance, and diet

A total of 42 catches from the Lake Edward system were investigated (Table S1). Of these, 12 catches contained more than 2% deepwater pelagic species, including the four aforementioned pelagic catches (Fig. 1). The three species, *H. pappenheimi*, *H. pelagicus* sp. nov., and *H. aureus* sp. nov., that made up all but one of the caught specimens in these pelagic catches (Fig. 1b-d: catches 7, 8, 10 & 12), were absent from benthic catches at the same locations (catches 9, 11 & 13). All three species were encountered in some benthic (catches 1–5, 14 & 15) and pelagic (catch 6) catches from littoral regions. However, *H. pappenheimi* and *H. aureus* sp. nov. were absent from Lake George and the Kazinga Channel, and very rare around the Channel's mouth (catches 3–6). *Haplochromis pelagicus* sp. nov. was rare in Lake George (Table S1) and most specimens caught there were small (< 71 mm SL).

Gut contents in *H. pappenheimi* (n=5; GL 130–219 (172) % SL; from catches 7, 10 & 14 in Fig. 1b-d & Table S1) contained copepods, cladocerans, and few midge larvae, pupae, and emerging adults. Guts of *H. pelagicus* sp. nov. (n=5; GL 157–201 (171) % SL; from catches 8 & 10) contained midge larvae, pupae, and emerging adults, some copepods, and a few cladocerans, and those of *H. aureus* sp. nov. (n=5; GL 150–169 (161) % SL; from catches 10 & 12) contained emerging midges and winged ants.

Taxonomic revision

We performed a taxonomic revision to support the validity of the deepwater pelagic species of *Haplochromis* from the Lake Edward system. Amongst the 425 specimens that were investigated, we identified 315 specimens as *H. pappenheimi*, 73 as *H. pelagicus* sp. nov., and 37 as *H. aureus* sp. nov. (Fig. 2). For detailed lists of specimens, see Taxonomic account below.

Haplochromis aureus sp. nov. was easily distinguishable from both *H. pappenheimi* and *H. pelagicus* sp. nov. by its generally larger size (maximum 116.5 vs. 87.5–101.6 mm SL), deeper body [BD 30.7–33.5 (32.1) vs. 25.4–31.0 (27.7–29.3) % SL], deeper cheeks [ChD 19.5–25.8 (22.5) vs. 15.4–21.4 (18.3–18.8) % HL], and longer upper jaw [UJL 29.3–35.6 (32.9) vs. 26.5–29.4 (27.7–28.3) % HL] set with a larger number of more acutely pointed teeth [UOT 53–62 (median 59) vs. 33–57 (41–46)], in addition to a strongly divergent dominant male colouration, especially with its yellow cheeks instead of dark grey or silver cheeks in the other two species (Fig. 1a). This was further corroborated by PCAs and MWU tests on measurements and counts (Fig. S1; Tables S2 & S3). No further patterns that would suggest additional species diversity, was observed in PCAs restricted to themorphometrics of *H. aureus* sp. nov. (not shown).

Haplochromis pappenheimi and *H. pelagicus* sp. nov. are morphologically very similar. In a PCA on the log-transformed measurements of both species (Table S4), PC 1 (86.6% of variance) had large positive values of a similar magnitude for all variables and was interpreted as a variable describing size (Zelditch *et al.*, 2004). Principal component 2 (3.1%) was mainly determined by lower jaw width and eye depth in the positive direction, followed by lacrimal depth in the negative direction; PC 3 (2.8%) by cheek depth in the positive direction and eye depth in the negative direction. In a plot of PC 2 against PC 3 (Fig. 3a), specimens of *H. pelagicus* sp. nov. were almost completely separated from those of *H. pappenheimi* by their mostly lower values for PCs 2 and 3. Within each species, a partial separation was observed between the sexes with male specimens having mostly higher values for PC 2 and slightly lower values for PC 3 than female specimens. Other PC axes were also investigated, but no additional patterns were observed.

In a PCA on the counts of *H. pappenheimi* and *H. pelagicus* sp. nov. (Table S5), PC 1 (15.9% of variance) was mainly determined by the numbers of caudal vertebrae, upper lateral line scales, and longitudinal line scales, all in the negative direction; PC 2 (12.2%) by the numbers of postorbital cheek scales and caudal peduncle scales in the positive direction and upper outer teeth in the negative direction. In a plot of PC 1 against PC 2 (Fig. 3b), values for specimens of both species strongly overlapped, which was also the case within each species for specimens of both sexes. No additional patterns were observed in other axes or in all axes plotted against standard length.

In qualitative traits, *H. pappenheimi* and *H. pelagicus* sp. nov. were first recognised to differ in the colour patterns of their anal fins and in the shapes of their oral outer teeth (see above). Additional qualitative differences were found in morphology and dominant male colouration, in addition to differences in habitat preferences (Fig. 1). Males of *H. pappenheimi* had slightly longer pelvic fins than those of *H. pelagicus* sp. nov. [VL 25.2–33.5 (28.6) vs. 23.3–27.0 (25.4) % SL]. Dominant males of *H. pappenheimi* had a body that was dark-grey ventrally with crimson distal parts of the anal and caudal fins, while those of *H. pelagicus* sp. nov. had a body that was silver ventrally with a specked black chest and hyaline to rarely faint dusky anal and caudal fins.

For the deepwater pelagic species of *Haplochromis* from the Lake Edward system, inter-species pairwise comparisons of the proportional measurements and of the raw counts were performed with MW*U* tests (Tables S6 & S7). A comparison between *H. aureus* sp. nov. and *H. pappenheimi* revealed significant differences ($P < 0.05$) in body depth, head width, and upper jaw length; between *H. aureus* sp. nov. and *H. pelagicus* sp. nov. in body depth, upper jaw length, lower jaw width, and caudal peduncle length and depth. A comparison between *H. pappenheimi* and *H. pelagicus* sp. nov. revealed significant differences in lower jaw width, head width, body depth, eye depth, and upper jaw length. Given the partial morphological separation between males and females of *H. pappenheimi* and *H. pelagicus* sp. nov. in a PCA (Fig. 3a), pairwise intraspecific comparisons with MW*U* tests were also performed between specimens of the same sex (Tables S8 & S9). In these comparisons, females of both species differed significantly in dorsal fin base length and males in lower jaw width. Many of the differences that were significant in the MW*U* tests on all specimens were probably not significant in these analyses due to reduced sample sizes.

Sexual dimorphism

To test for intraspecific sexual differences, morphometrics of the sexes of each pelagic species were compared with MW*U* tests (Tables S10 & S11). For *H. pappenheimi*, this comparison revealed a significant ($P < 0.05$) difference in cheek depth (♂<♀), lacrimal depth (♂<♀), and eye depth (♂>♀) and without sequential Bonferroni correction, low raw *P* values ($P_{\text{raw}} < 0.05$) were observed for pre-anal distance (♂>♀), caudal peduncle length (♂<♀), dorsal fin base length (♂<♀), and lower jaw length (♂>♀). A comparison between males and females of *H. pelagicus* sp. nov. revealed a significant difference in cheek depth (♂<♀) and low raw *P* values for dorsal fin base length (♂>♀), caudal peduncle length (♂<♀) and depth (♂>♀), and the number of scales between the pelvic and pectoral fins (♂>♀). For *H. aureus* sp. nov., no significant differences were found, but a low raw *P* value for caudal peduncle depth (♂<♀) was found.

Taxonomic account

A taxonomic revision of three deepwater pelagic species of *Haplochromis* from the Lake Edward system revealed consistent differences between all species in PCAs and MW*U* tests of measurements and counts, qualitative traits, and habitat preferences. We confirm that all represent valid species, of which two were, so far, unknown to science. Below, we present a redescription of *H. pappenheimi* and formal descriptions of *H. pelagicus* sp. nov. and *H. aureus* sp. nov. Proportional measurements and raw counts for all species are summarised in Table 2 and for both sexes of all species separately in Table S12.

Haplochromis pappenheimi (Boulenger 1914)

(Figs. 1, 2 & 4; Tables 2, S1, & S12)

Tilapia pappenheimi: Boulenger, 1914 (part), 1915 (part; redescription)

Haplochromis pappenheimi: Regan, 1921 (redescription); Trewavas, 1933 (redescription); Greenwood, 1973 (part; designation lectotype; redescription in which none of the type specimens of *H. pappenheimi* were included, but that included only specimens from Lake George here reidentified as *H. pelagicus* sp. nov.)

Yssichromis pappenheimi: Greenwood, 1980 (part)

For each lot, the number of specimens from which measurements and counts were taken is indicated between brackets.

Lectotype: ZMB 19110; Lake Albert-Edward (*i.e.*, former name of Lake Edward); H. Schubotz; 1907–1908 [n=1 (1); 71.3 mm SL].

Paralectotypes: NHMUK 1914.4.8.9–12; Lake Albert-Edward; H. Schubotz; 1907–1908 [n=4 (3); 49.3–70.5 mm SL]. ZMB 19111; same as previous [n=1 (1); 69.6 mm SL]. ZMB 22689; same as previous [n=8 (2); 42.9–69.3 mm SL]. ZMB 22696; same as previous [n=1 (0); 52.0 mm SL]. ZMB 38016; same as previous [n=1 (0); 50.8 mm SL].

The remaining 16 paralectotypes are not conspecific with the lectotype, see also Systematic comments below: NHMUK 1914.4.8.13; Lake Albert-Edward; H. Schubotz; 1907–1908 [n=1; 61.7 mm SL; holotype of *H. eduardii* Regan 1921]. NHMUK 1914.4.8.14; same as previous [n=1; 63.5 mm SL; holotype of *H. nigripinnis* Regan 1921]. ZMB 22690; same as previous [n=1; 77.5 mm SL; paratype of *H. pelagicus* sp. nov.]. ZMB 22691; same as previous [n=1; 61.5 mm SL; reidentified as *H angustifrons* Boulenger 1914]. ZMB 22692; same as previous [n=1; 66.4 mm SL; reidentified as *H. vicarius* Trewavas 1933]. ZMB 22693; same as previous [n=6; 49.7–69.1 mm SL; reidentified as *H. oregosoma* Greenwood 1973]. ZMB 22694; same as previous [n=1; 50.6 mm SL; reidentified as *H. vicarius*]. ZMB 22695; same as previous [n=1; 64.7 mm SL; reidentified as *H. oregosoma*]. ZMB 22697; same as previous [n=1; 72.7 mm SL; paratype of *H. pelagicus* sp. nov.]. ZMB 22698; same as previous [n=1; 62.6 mm SL; reidentified as *H. oregosoma*]. ZMB 38011; same as previous [n=1; 90.8 mm SL; paratype of *H. pelagicus* sp. nov.].

Other material examined: IRSNB 12811; Lac Edouard, au large de la rivière Talia; Exp. KEA; 23/04/1953 [n=131 (2); 28.6–96.7 mm SL]. IRSNB 12812; Lac Edouard, au large de la rivière Talia; Exp. KEA; 23/04/1953 [n=18 (1); 55.7–75.4 mm SL]. RMCA 2016.035.P.0361; Katoko breeding ground, soft substrate offshore of Katwe, Lake Edward: 0°09’43.2”S 29°53’16.8”E; Exp. HIPE1; 20/10/2016 [n=1 (1); 77.1 mm SL]. RMCA 2016.035.P.0362–435; Lake Edward, pelagic catch, open water ± 10 m deep: 0°12’07.2”S 29°49’51.6”E; Exp. HIPE1; 21/10/2016 [n=74 (1); 61.3–73.8 mm SL]. RMCA 2017.006.P.0474-520; Rwenshama, rocky shore, Lake Edward: 0°24’05.7”S 29°46’35.1”E; Exp. HIPE2; 25/03/2017 [n=47 (4); 63.0–78.4 mm SL]. RMCA 2017.006.P.0521-530; same as previous [n=10 (1); 66.7–77.8 mm SL]. RMCA 2018.008.P.0507; Islands near Katwe, Lake Edward: 0°10’04.9”S 29°52’27.4”E; Exp. HIPE3; 19/01/2018 [n=1 (1); 75.8 mm SL]. RMCA 2018.008.P.0508; Kayanja, offshore, Lake Edward: 0°05’31.2”S 29°45’30.3”E; Exp. HIPE3; 21/01/2018 [n=1 (1); 68.3 mm SL]. RMCA 2018.008.P.0509–513; Lake Edward, pelagic catch, open water ± 20 m deep: 0°08’47.4”S 29°43’31.1”E; Exp. HIPE3; 29/01/2018 [n=5 (3); 74.7–76.2 mm SL]. RMCA 2018.008.P.0514–515; same as previous [n=2 (1); 66.9, 77.2 mm SL]. RMCA 2018.008.P.0516–519; Lake Edward, pelagic catch, open water ± 30 m deep: 0°21’34.8”S 29°43’17.7”E; Exp. HIPE3; 01/02/2018 [n=4 (1); 65.5–73.0 mm SL]. RMCA 2018.008.P0520–521; same as previous [n=2 (1); 71.0, 72.1 mm SL]. RMCA 2019.002.P.0149–151; Lake Edward, pelagic catch, open water near border: 0°16’34.5”S 29°42’44.0”E; Exp. HIPE4; 31/03/2019 [n=3 (2); 69.5–76.4 mm SL].

Comparative material: Type specimens of *H. oregosoma*: NHMUK 1972.6.2.141; Lake George, north end of Kankuranga Island; Greenwood P.H. & Dunn I.G.; 01/05/1971 [n=1 (1); 65.7 mm SL]. NHMUK 1972.6.2.147; Lake George, Kankuranga Island northern tip; Greenwood P.H. & Dunn I.G.; 01/05/1971 [n=1 (1); 70.0 mm SL]. NHMUK 1972.6.2.148-152; Lake George, Kankuranga Island northern tip; Greenwood P.H. & Dunn I.G.; 01/04/1971 [n=5 (1); 65.6 mm SL].

Differential diagnosis: Species with a shallow body [BD 27.2–31.0 (mean 29.3) % SL]; long and shallow caudal peduncle [CPL 17.4–19.6 (18.4) % SL, CPD 55.0–69.1 (61.6) % CPL]; short upper jaw compared to lower jaw [UJL 64.2–73.2 (69.0) % LJL]; posterior ~1/4–1/5 of premaxillary dentigerous arm sometimes edentulous; many gill rakers [GR (GRc+1+Gre) 13–17].

It differs from *H. aureus* sp. nov. by a shallower body [BD 27.2–31.0 (29.3) vs. 30.7–33.5 (32.9) % SL]; shorter upper jaw [UJL 26.8–29.4 (28.3) vs. 29.3–35.6 (32.9)% HL]; more gill rakers [GR (GRc+1+Gre) 13–17 vs. 12–14]; dominant males with dark grey vs. yellow snout and cheeks.

Similar to *H. oregosoma* in body shape and dominant male colour pattern, differs by deeper lacrimals [LaD 16.1–18.1 (17.0) vs. 10.5–15.2 (13.3) % HL] and a broader interorbital area [IOW 54.0–63.5 (59.9) vs. 45.9–48.8 (46.9) % HW].

Very similar to *H. pelagicus* sp. nov., differs by anal fin dark-dusky vs. hyaline to rarely faintly dusky; major cusps of outer oral teeth acutely vs. bluntly pointed, and with no to a small flange (rarely a large flange) vs. with a small to large flange; anterior outer oral teeth including often several vs. rarely some tricuspid teeth. Dominant males differ further from those of *H. pelagicus* sp. nov. by anal and caudal fins crimson vs. hyaline; belly and chest dark-coloured vs. light-coloured belly and speckled-black chest; cheek dark-coloured with a well-defined lacrimal stripe vs. light-coloured with a very well-defined lacrimal stripe; pelvic fins slightly longer [VL ♂ 25.2–33.5 (28.6) vs. 23.3–27.0 (25.4) % SL].

Etymology: specific name in honour of Paul Pappenheim (1878-1945), at that time curator of fishes at the Museum für Naturkunde in Berlin, who co-authored the book in which the description appeared.

Description: based on 315 specimens (28.6–96.7 mm SL); body oval to pyriform and shallow; caudal peduncle long and shallow. Head short and average in width with a straight to gently convex dorsal outline; snout short, rather acute in lateral view with an inclination of 35–43°, and rather acute in dorsal view. Interorbital area broad and oral jaws very narrow, which give head an obovoid (*i.e.*, inverted egg-shaped) to triangular outline in anterior view. Eye large; lacrimal average in depth; cheek very shallow. Lower jaw average in length; upper jaw short, especially in comparison to lower jaw [UJL 64.2–73.2 (69.0) % LJL]; both jaws very narrow, slim, and with a moderate gape inclination of 25–35°; maxilla extends to between vertical through anterior margin of orbit and just anterior to this point; lips thin.

Outer oral teeth average in number, small, and weakly embedded in oral mucosa. Necks slender, laterally compressed, and weakly recurved; crowns straight, bicuspid with often some tricuspid teeth in most specimens; in large males (> 70 mm SL), anteriorly with some unicuspid teeth. Major cusp equilateral, mostly acutely pointed, and with a small to no flange, rarely a large flange; minor cusps small to large and rounded. Dental arcades rounded; outer teeth closely and regularly set with neck-distances of < 1/2 neck-width. Posterior ~1/4–1/5 of premaxillary dentigerous arm sometimes edentulous, often set with very small teeth; posteriormost premaxillary outer teeth very small and uni- or tricuspid. Inner teeth small, recurved, tricuspid, and bluntly pointed. Tooth bands very slender crescent-shaped with 1–2 rows of inner teeth, narrowing posteriorly until only outer row remains past 2/3 length of tooth band. Inner rows very closely and regularly set on 1 neck-width from outer row in both jaws, implantation erect; size uniform throughout tooth band.

Lower pharyngeal bone short, narrow, very slim, and very shallow over entire length (Fig. S1). Pharyngeal teeth small, very slender, and recurved; major cusps acutely pointed; minor cusp gap concave; minor cusp and cusp protuberance small. Teeth in two median longitudinal rows almost equal in size and form to lateral teeth, 9–10 in each row. Posterior transverse row with 29–30 teeth, implanted erectly; major cusp bluntly pointed, and laterally compressed; minor cusp gap concave; minor cusp small.

Chest scales generalised; transition to flank scales gradual. Minute scales on proximal half of caudal fin.

Caudal fin emarginate to truncate; dorsal and anal fins reach to vertical through 1–4 scales anterior to caudal-fin base. Pectoral fin reaches to between anal opening and first anal fin spine; pelvic fin reaches to between genital opening and first anal fin spine, in dominant males to third anal fin spine; first branched pelvic-fin ray slightly elongated in juveniles and females and elongated in dominant males.

Ceratobranchial gill rakers in outer row of first gill arch relatively long, slender, and simple; anteriormost 1–3 rakers often reduced; posteriormost rakers simple to bifid. Epibranchial gill rakers slender and simple.

Live colouration of dominant males (Fig. 4c): dorsal halves of body and head, snout, and lips dark green; ventral halves of body and operculum, and cheek dark grey; transitions mostly gradual; chest and branchiostegal rays black; flank, cheek, and lower jaw with a blue sheen. Flank with a faint mid-lateral band. Nostril, lacrimal, supraorbital, and vertical preopercular stripes and nape band faint; eye brownish with a golden inner ring. Pectoral fin hyaline; pelvic fin black; dorsal and caudal fins dusky to blackish, dorsal fin with black lappets, caudal fin with a crimson posteroventral part; anal fin dusky to blackish and with black base, crimson spines and distal part, and 1–2 very large (three times distance between two fin rays) yellow egg spots with dusky borders. Subdominant males: same as dominant males except for uniformly dusky caudal and anal fins and flanks without longitudinal band but sometimes with 6–8 faint vertical stripes.

Live colouration of females and juveniles (Fig. 4d): dorsum, flank, dorsal part of head, snout, and lips yellowish to dark green; belly, chest, ventral half of operculum, and cheek whitish; transitions mostly gradual. Nostril, supraorbital, and lacrimal stripes very faint; 6–8 very faint vertical stripes sometimes present; eye brownish with a golden inner ring. Pectoral fin hyaline to dusky; pelvic fin hyaline; dorsal and caudal fins dusky to blackish, dorsal fin with black lappets; anal fin blackish to yellow and with 1–2 spots resembling egg spots. Soon after death, dorsum, flank, and dorsal part of head light yellowish and flank often with a faint mid-lateral band.

Preserved colouration (Fig. 4a): in dominant males; body and head uniformly dark brown; preopercular stripe and lacrimal stripe well-defined; pelvic fin black; anal fin dusky to blackish and with 1–2 very large egg-spots. In juveniles and females; dorsum and dorsal part of head brown; flank and dorsal part of operculum light brown; ventral parts of body and operculum, cheek, and lower jaw white to yellow; transitions mostly gradual; vertical preopercular stripe faint and lacrimal stripe present; pelvic fin hyaline; anal fin dusky to blackish. In all specimens, flank often with a mid-lateral band from opercular blotch to caudal-fin base and rarely 4–5 very faint vertical stripes; lacrimal, snout and lips dusky; nostril and interorbital stripes faint. Dorsal fin dusky and with black lappets; caudal fin uniformly dusky.

Distribution and ecology: only known from Lake Edward, abundant in and near sublittoral regions, present in deepwater regions (Figs. 1b–d & 2). Five guts (GL 130–219 (172) % SL) were examined and contained copepods, cladocerans, and few midge larvae, pupae, and emerging adults. Zooplankton and midges were generally found in separate parts of the gut, suggesting a diel rhythm in diet.

Systematic comments: Boulenger (1914) assigned 32 type specimens, all from Lake Edward, from which Greenwood (1973) selected the lectotype. Both Regan (1921) and Greenwood (1973) recognised that the type series of *H. pappenheimi* is polyspecific. Besides the lectotype, we consider an additional 15 type specimens as *H. pappenheimi* (see Paralectotypes above). The remaining 16 specimens consist of the holotypes of *H. eduardii* and *H. nigripinnis*, three paratypes of *H. pelagicus* sp. nov., and a specimen that we reidentified as *H. angustifrons*, eight as *H. oregosoma*, and two as *H. vicarius*. A skeleton that is probably *H. pappenheimi* (NHMUK 1914.4.8.37) is currently registered as a paralectotype of this species, probably by mistake as both Boulenger (1914) and Greenwood (1973) listed only 32 type specimens without mention of a skeleton. Boulenger (1915) did mention a skeleton, possibly this specimen. While he did not refer to it as a type, his mention of it may have resulted in it being mistaken as one.

The redescription of *Haplochromis pappenheimi* by Greenwood (1973) was based solely on specimens from Lake George, here all reidentified as *H. pelagicus* sp. nov. Although he assigned the lectotype of *H. pappenheimi*, none of the types of this species were included in his redescription. Many subsequent authors also mentioned *H. pappenheimi* from Lake George and the Kazinga Channel (Buris *et al.*, 1973; Moriarty *et al.*, 1973; Dunn, 1975; Greenwood, 1980). We examined all specimens from Lake George and the Kazinga Channel registered as *H. pappenheimi* at the RMCA, RBINS, and NHMUK and reidentified all specimens as *H. pelagicus* sp. nov. Therefore, all published information about *H. pappenheimi* from Lake George and the Kazinga Channel most likely refers to *H. pelagicus* sp. nov.

Several lots of specimens of the IRSNB caught in the Congolese part of Lake Edward in 1953, at least two from Kiavinionge (IRSNB 12815, n=24; IRSNB 12819, n=205) and one from an unspecified location (IRSNB 15646, n=6), contained specimens that strongly resembled *H. pappenheimi*. Morphometrics were taken of six of these specimens 66.2–88.1 mm SL) and they had a longer upper jaw [UJL 29.7–30.5 (29.9) vs. 26.8–29.4 (28.2) % HL] and a deeper body [BD 30.2–33.9 (32.1) vs. 27.2–30.4 (29.1) % SL] than the examined specimens of *H. pappenheimi*, but no other clear differences were found, and the live colour pattern of dominant males remains unknown. Therefore, these specimens were not included in the present redescription. Currently, we did not find any specimens from nearby Kiavinionge that correspond to our redescription of *H. pappenheimi*. As the status of the specimens from Kiavinionge remains unclear, we will refer to them as *H.* cf. *pappenheimi*.

Haplochromis pelagicus sp. nov.

(Figs. 1, 2 & 5; Tables 2, S1, & S12)

Tilapia pappenheimi: Boulenger, 1914 (part), 1915 (part; redescription)

Haplochromis pappenheimi: Greenwood, 1973 (part; redescription based solely on specimens here reidentified as *H. pelagicus* sp. nov.)

Yssichromis pappenheimi: Greenwood, 1980 (part)

For each lot, the number of specimens from which measurements and counts were taken is indicated between brackets.

Holotype: RMCA 2019.002.P.0138; Lake Edward, pelagic catch, open water near border: 0°16’34.5”S 29°42’44.0”E; Exp. HIPE4; 31/03/2019 [n=1 (1); 76.0 mm SL].

Paratypes:

IRSNB 12811; Lac Edouard, au large de la rivière Talia; Exp. KEA; 23/04/1953 [n=9 (1); 31.6–85.6 mm SL]. IRSNB 12812; same as previous [n=2 (1); 59.6, 72.2 mm SL]. NHMUK 1972.6.2.333–336; Small island north of Kankurunga Island, Lake George; P. Greenwood & I. Dunn; 1967 [n=4 (1); 40.9–60.7 mm SL]. NHMUK 1972.6.2.349–350; IBP (International Biological Programme) Jetty, Lake George; P. Greenwood & I. Dunn; 1967 [n=2 (1); 58.8–60.3 mm SL]. NHMUK 1987.2.25.125–139; At the junction of Kazinga Channel and grid reg. 212 774 over sandy-muddy substrate, Lake Edward; I. Dunn; 2/12/1967 [n=15 (1); 88.9–101.6 mm SL]. RMCA 2016.035.P.0353; Katoko breeding ground, soft substrate offshore of Katwe, Lake Edward : 0°09'43.2"S 29°53'16.8"E; Exp. HIPE1; 20/10/2016 [n=1 (1); 82.3 mm SL]. RMCA 2016.035.P.0354–356; Lake Edward, pelagic catch, open water ± 10 m deep: 0°12'07.2"S 29°49'51.6"E; Exp. HIPE1; 21/10/2016 [n=3 (1); 70.0–72.7 mm SL]. RMCA 2016.035.P0357–360; Kazinga Channel, near Queen Elisabeth Bush Lodge: 0°08'09.6"S 30°02'27.6"E; Exp. HIPE1; 04/11/2016 [n=4 (2); 73.0–82.7 mm SL]. RMCA 2017.006.P.0472–473; Rwenshama, rocky shore, Lake Edward: 0°24'05.7"S 29°46'35.1"E; Exp. HIPE2; 25/03/2017 [n=2 (2); 76.0, 77.7 mm SL]. RMCA 2018.008.P.0490–491; Islands near Katwe, Lake Edward: 0°10'04.9"S 29°52'27.4"E; Exp. HIPE3; 19/01/2018 [n=2 (1); 69.8, 77.3 mm SL]. RMCA 2018.008.P.0492; Kayanja, offshore, Lake Edward: 0°05'31.2"S 29°45'30.3"E; Exp. HIPE3; 21/01/2018 [n=1 (1); 72.9 mm SL]. RMCA 2018.008.P.0493; Lake Edward, pelagic catch, open water ± 20 m deep: 0°08'47.4"S 29°43'31.1"E; Exp. HIPE3; 29/01/2018 [n=1 (1); 83.3 mm SL]. RMCA 2018.008.P.0494–499; same as previous [n=6 (3); 68.9–78.6 mm SL]. RMCA 2018.008.P.500–503; Lake Edward, pelagic catch, open water ± 30 m deep: 0°21'34.8"S 29°43'17.7"E; Exp. HIPE3; 01/02/2018 [n=4 (2); 68.8–74.9 mm SL]. RMCA 2018.008.P.0504; Kashaka bay, south of inlet, Lake George: 0°05'04.6"S 30°10'45.6"E; Exp. HIPE3; 02/02/2018 [n=1 (1); 64.4 mm SL]. RMCA 2018.008.P.0505–506; same as previous [n=2 (1); 62.0, 70.8 mm SL]. RMCA 2019.002.P.0139–148; Lake Edward, pelagic catch, open water near border: 0°16'34.5"S 29°42'44.0"E; Exp. HIPE4; 31/03/2019 [n=10 (1); 70.5–82.8 mm SL]. ZMB 22690; Lake Albert-Edward; H. Schubotz; 1907–1908 [n=1 (1); 77.5 mm SL]. ZMB 22697; same as previous [n=1 (0); 72.7 mm SL]. ZMB 38011; same as previous [n=1 (1); 90.8 mm SL].

Differential diagnosis: Species with a very shallow body [BD 25.4–30.7 (mean 27.7) % SL]; long and very shallow caudal peduncle [CPL 17.2–20.1 (18.6) % SL, CPD 49.4–66.3 (58.3) % CPL]; short upper jaw compared to lower jaw [UJL 63.4–71.5 (67.9) % LJL]; mostly inverted-triangular shaped head in anterior view with a very narrow lower jaw [LJW 31.1–36.5 (33.9) % LJL]; posterior ~1/4–1/5 of premaxillary dentigerous arm often edentulous; many gill rakers [GR (GRc+1+Gre) 14–18].

It differs from *H. aureus* sp. nov. by a shallower body [BD 25.4–30.7 (27.7) vs. 30.7–33.5 (32.9) % SL]; shorter upper jaw [UJL 26.5–29.0 (27.7) vs. 29.3–35.6 (32.9)% HL]; more gill rakers [GR (GRc+1+Gre) 14–18 vs. 12–14]; dominant males with iridescent silver vs. yellow snout and cheeks, and hyaline vs. dusky and crimson anal fin.

Very similar to *H. pappenheimi*, differs by anal fin hyaline to rarely faint dusky vs. dark-dusky; major cusps of outer oral teeth bluntly vs. acutely pointed, and with a small to large flange vs. with no to a small flange (rarely a large flange); anterior outer oral teeth including rarely some vs. often several tricuspid teeth. Dominant males differ further from those of *H. pappenheimi* by anal and caudal fins hyaline vs. crimson; belly and chest light-coloured vs. belly dark-coloured and chest speckled-black; cheek light-coloured with a very well-defined lacrimal stripe vs. dark-coloured with a well-defined lacrimal stripe; pelvic fin slightly shorter [VL ♂ 23.3–27.0 (25.4) vs. 25.2–33.5 (28.6) % SL].

Etymology: specific name from Latin '*pelagicus*', pelagic; referring to its occurrence in open waters of Lakes Edward and George and the Kazinga Channel.

Description: based on 73 specimens (31.6–101.6 mm SL); body oval to pyriform and very shallow; caudal peduncle long and very shallow. Head short and narrow with a gently convex to very gently concave dorsal outline; snout short, acute in lateral view with an inclination of 35–42°, and rather acute in dorsal view. Interorbital area flattened and broad and oral jaws very narrow, which give head a characteristic triangular to obovoid (*i.e.*, inverted egg-shaped) outline in anterior view. Eye average in size; lacrimal average in depth; cheek very shallow. Lower jaw average in length; upper jaw short, especially in comparison to lower jaw [UJL 63.4–71.5 (67.9) % LJL]; both jaws very narrow, slim, and with a moderate gape inclination of 25–35°; maxilla extends to just anterior of vertical through anterior margin of orbit; lips very thin.

Outer oral teeth average in number, small, and not embedded in oral mucosa. Necks slender, constricted, laterally compressed, and weakly recurved; crowns weakly recurved, bicuspid in small specimens (< 75 mm SL), bicuspid to a mixture of bicuspid and unicuspid in large specimens (> 75 mm SL), rarely some tricuspid teeth in specimens of all sizes. Bicuspid teeth bluntly pointed and with a subequilateral major cusp with a small to large flange, and a large and rounded minor cusp. Unicuspid teeth with a subequilateral cusp with a large flange, giving teeth dorsally flattened appearance. Dental arcades rounded; outer teeth closely and regularly set with neck-distances of 1/2 neck-width. Posterior ~1/4–1/5 of premaxillary dentigerous arm often edentulous; posteriormost premaxillary outer teeth very small and uni-, bi-, or tricuspid. Inner teeth small, recurved, tricuspid, and bluntly pointed. Tooth bands very slender crescent-shaped with 1–2 rows of inner teeth, narrowing posteriorly until only outer row remains past 2/3 length of tooth band. Inner rows very closely and regularly set on 1 neck-width from outer row in both jaws, implantation erect; size uniform throughout tooth band.

Lower pharyngeal bone very short, narrow, very slim, and very shallow over entire length. Pharyngeal teeth small, very slender, and recurved; major cusps acutely pointed; minor cusp gap concave; minor cusps small to large; cusp protuberances small. Teeth in two median longitudinal rows almost equal in size and form to lateral teeth, about 10 in each row. Posterior transverse row with 27–37 teeth, implanted erectly; major cusp bluntly pointed, and laterally compressed; minor cusp gap straight; minor cusp present.

Chest scales generalised; transition to flank scales gradual. Minute scales on proximal half of caudal fin.

Caudal fin emarginate to truncate; dorsal and anal fins reach to vertical through 2–5 scales anterior to caudal-fin base. Pectoral and pelvic fins reach to around anal opening; in dominant males, pelvic fin reaches to first anal fin spine; first branched pelvic-fin ray slightly elongated in all specimens.

Ceratobranchial gill rakers in outer row of first gill arch relatively long, slender, and simple; posteriormost rakers simple to bifid. Epibranchial gill rakers slender and simple.

Live colouration of dominant males (Fig. 5c): dorsal half of body iridescent blue to blue-green; ventral half of flank, operculum, and cheek iridescent silver; transition rather abrupt at horizontal through lower lateral line. Belly whitish; chest speckled black; branchiostegal membrane black; snout and lips dusky. Nostril and supraorbital stripes and nape band faint; lacrimal stripe well-defined; eye brownish with a golden to silver inner ring. Pectoral fin hyaline; pelvic fin black; dorsal and caudal fins dusky, dorsal fin with black lappets; anal fin hyaline to rarely faintly dusky and with 1–3 very large (three times distance between two fin rays) yellow egg spots with hyaline borders. Subdominant males: same as dominant males except for whitish chest and faint lacrimal stripe.

Live colouration of females and juveniles (Fig. 5d): dorsal half of body iridescent green to blue-green; ventral half of flank, operculum, and cheek iridescent silver; transition rather abrupt at horizontal through lower lateral line. Belly and chest whitish; snout and lips dusky. Nostril, supraorbital, and lacrimal stripes very faint; eye whitish to brownish with a silver to golden inner ring. Pectoral, pelvic, and anal fins hyaline, anal fin with 1–3 spots resembling egg spots; dorsal and caudal fins dusky to hyaline, dorsal fin with dusky lappets.

Preserved colouration (Fig. 5a): in all specimens; dorsal parts of body and head brown; ventral part of body, operculum, and cheek white to yellow; transition rather abrupt at horizontal through lower lateral line. Lacrimal, snout, and lips dusky. Flank often with a faint mid-lateral band from opercular blotch to caudal-fin base. Nostril and interorbital stripes faint; vertical preopercular stripe faint to absent. Pectoral fin hyaline; dorsal fin dusky and with black lappets; caudal fin faint dusky with a dusky distal margin. In dominant males, chest speckled black; branchiostegal membrane black; lower jaw dusky; lacrimal stripe well-defined; pelvic fin black; anal fin hyaline to faint dusky and with 1–3 very large egg spots. In juveniles and females; chest, branchiostegal membrane, and lower jaw white to yellow; lacrimal stripe present; pelvic and anal fins hyaline.

Distribution and ecology: endemic to the Lake Edward system; abundant in upper water layers of deepwater regions of Lake Edward, occasionally found in upper water layers of sublittoral areas of Lakes Edward and George and Kazinga Channel (Figs. 1b–d & 2). Five guts (GL 157–201 (171) % SL) from Lake Edward specimens and some, by Greenwood (1973), from Lake George specimens were examined and contained copepods, cladocerans, and midge larvae, pupae, and emerging adults. Zooplankton and midges were generally found in separate parts of the gut, suggesting a diel rhythm in diet.

Systematic comment: three paralectotypes of *H. pappenheimi* correspond to *H. pelagicus* sp. nov. (ZMB 22690, 22697, 38011) and are here included as paratypes.

Greenwood's (1973) redescription of *Haplochromis pappenheimi* was based solely on specimens from Lake George that were all reidentified as *H. pelagicus* sp. nov. Many subsequent authors also mentioned *H. pappenheimi* from Lake George and the Kazinga Channel (Buris *et al.*, 1973; Moriarty *et al.*, 1973; Dunn, 1975; Greenwood, 1980). We examined the specimens from Lake George and the Kazinga Channel registered as *H. pappenheimi* at the RMCA, RBINS, and NHMUK and reidentified all of them as *H. pelagicus* sp. nov. Therefore, all published information about *H. pappenheimi* from Lake George and the Kazinga Channel most likely refers to *H. pelagicus* sp. nov.

Haplochromis aureus sp. nov.

(Figs. 1, 2 & 6; Tables 2, S1 & S12)

For each lot, the number of specimens from which measurements and counts were taken is indicated between brackets.

Holotype:

RMCA 2019.002.P.0136; Lake Edward, pelagic catch, open water near border: 0°16'34.5"S 29°42'44.0"E; Exp. HIPE4; 31/03/2019 [n=1 (1); 90.0 mm SL].

Paratypes:

IRSNB 966–969; Lake Edward, pelagic catch, open water ± 20 m deep: 0°08'47.4"S 29°43'31.1"E; Exp. HIPE3; 29/01/2018 [n=4 (1); 61.6–89.5 mm SL]. NHMUK 1914.4.8.30; Lake Albert-Edward; H. Schubotz; 1907–1908 [n=1 (1); 104.9 mm SL]. RMCA 31096–31100; Lac Edouard, Rutshuru; Taramelli; 1930 [n=4 (4); 98.5–116.5 mm SL]. RMCA 2016.035.P.0351; Katoko breeding ground, soft substrate offshore of Katwe, Lake Edward : 0°09'43.2"S 29°53'16.8"E; Exp. HIPE1; 20/10/2016 [n=1 (1); 76.2 mm SL]. RMCA 2016.035.P.0352; Mouth of Kazinga Channel, Lake Edward: 0°12'32.4"S 29°53'06.0"E; Exp. HIPE1; 24/10/2016 [n=1 (1); 107.6 mm SL]. RMCA 2017.006.P.0457–466; Rwenshama, rocky shore, Lake Edward: 0°24'05.7"S 29°46'35.1"E; Exp. HIPE2; 25/03/2017 [n=10 (2); 49.8–94.9 mm SL]. RMCA 2017.006.P.0467–471; same as previous [n=5 (1); 61.2–110.4 mm SL]. RMCA 2018.008.P.0481; Islands near Katwe, Lake Edward: 0°10'04.9"S 29°52'27.4"E; Exp. HIPE3; 18/01/2018 [n=1 (1); 98.2mm SL]. RMCA 2018.008.P.0482–483; Lake Edward, pelagic catch, open water ± 20 m deep: 0°08'47.4"S 29°43'31.1"E; Exp. HIPE3; 29/01/2018 [n=2 (2); 78.3, 92.4 mm SL]. RMCA 2018.008.P.0484–489; Lake Edward, pelagic catch, open water ± 30 m deep: 0°21'34.8"S 29°43'17.7"E; Exp. HIPE3; 01/02/2018 [n=6 (1); 88.7–105.1 mm SL]. RMCA 2019.002.P.0137; Lake Edward, pelagic catch, open water near border: 0°16'34.5"S 29°42'44.0"E; Exp. HIPE4; 31/03/2019 [n=1 (1); 82.1 mm SL].

Differential diagnosis: Species with an acute snout; acutely pointed oral teeth; very broad interorbital area [IOW 56.8–66.6 (mean 62.3) % HW]; very short predorsal distance [PrD 31.7–34.4 (33.3) % SL]; dominant males light blue with yellow snout, cheeks, and chest; found in upper water layers of deepwater regions of Lake Edward.

Small specimens can be mistaken for *H. pappenheimi* or *H. pelagicus* sp. nov., but differ from both by a deeper body [BD 30.7–33.5 (32.9) vs. 25.4–31.0 (27.7–29.3) % SL]; longer upper jaw [UJL 29.3–35.6 (32.9) vs. 26.5–29.4 (27.7–28.3) % HL]; fewer gill rakers [GR (GRc+1+GRe) 12–14 vs. 13–18].

Resembles *H. mentatus* in habitus and a slight overlap in habitat (*H. mentatus* mostly restricted to littoral regions), differs by a shorter lower jaw [LJL 41.1–46.4 (43.2) vs. 43.9–51.0 (48.5) % HL], more and smaller upper outer teeth [UOT 48–65 vs. 28–46], and dominant males light blue with yellow cheeks and chest vs. uniformly yellow-green with red flanks.

Etymology: specific name from Latin '*aureus*', golden; referring to yellow chest, cheeks, and snout in dominant males and yellow pelvic fins in females.

Description: based on 37 specimens (49.8–116.5 mm SL); body oval and shallow; caudal peduncle shallow. Head short and narrow with a straight to very weakly convex dorsal outline; snout acute in lateral view with an inclination of 32–37°, and acute in dorsal view. Eye average in size; interorbital area very broad; lacrimal deep; cheek shallow. Oral jaws average in length, narrow, relatively slim, and with a gentle gape inclination of 26 –31°; maxilla extends to vertical through anterior margin of orbit; lips thin.

Outer oral teeth many, average in size, not embedded in oral mucosa. Necks slender, cylindrical, and straight; crowns weakly recurved, acutely pointed, bicuspid with some uni- and tricuspid teeth in small specimens (< 90 mm SL), unicuspid teeth in large specimens (> 90 mm SL). Bicuspid teeth acutely pointed and with a protracted major cusp with a very small flange, a small and rounded minor cusp that points straight up, and a narrow cusp gap. Dental arcades rounded; outer teeth closely and regularly set with neck-distances of 1/2 neck-width; outer teeth decrease slightly and gradually in size posteriorly; 2–7 posteriormost premaxillary outer teeth small and uni- or tricuspid in small specimens (< 90 mm SL), unicuspid in large specimens (> 90 mm SL). Inner teeth small, recurved, uni- or tricuspid, and acutely pointed. Tooth bands very slender crescent-shaped with 2–3 rows of inner teeth, narrowing posteriorly until only outer row remains past 3/4 length of tooth band. Inner rows closely and regularly set on 1 neck-width from outer row in both jaws, implantation erect; anteriormost teeth in first row slightly larger than remaining.

Lower pharyngeal bone short, average in width, slim, and shallow over entire length. Pharyngeal teeth, very slender, and recurved; major cusps acutely pointed; minor cusp gap straight; minor cusps very small; cusp protuberances very small to absent. Teeth in two median longitudinal rows equal in size and form to lateral teeth, about 11–12 in each row. Posterior transverse row with 22–25 teeth with a weakly recumbent implantation; major cusp bluntly pointed; minor cusp gap straight to concave; minor cusp very small to absent.

Chest scales generalised, transition to flank scales gradual. Minute scales on proximal half of caudal fin. Very rarely 1–3 rows of 3–7 minute scales on proximal parts of dorsal and anal fins.

Caudal fin truncate; dorsal and anal fins reach to vertical through 1–3 scales anterior to caudal-fin base. Pectoral fin reaches to between just anterior to anal opening and first anal fin spine; pelvic fin reaches to anal opening, in dominant males to first anal fin spine; first branched pelvic-fin ray slightly elongated, in dominant males elongated.

Ceratobranchial gill rakers in outer row of first gill arch closely set, acutely pointed, slender, and simple; posteriormost rakers simple, anvil-shaped, or weakly bifid. Epibranchial gill rakers slender and simple.

Live colouration of dominant males (Fig. 6c): body light blue; flank mostly with 5–6 vertical stripes. Snout, lips, cheek, and chest yellow; belly white; dorsum greenish. Nape band faint; lacrimal, vertical preopercular, and supraorbital stripes very faint; eye dark with silver to golden inner ring. Pectoral fin hyaline; pelvic fin black; dorsal fin dusky with black lappets and crimson maculations in posterior part; anal fin dusky with crimson distal part and 2–3 large (twice distance between fin rays) orange egg spots with dusky borders; caudal fin dusky with crimson posteroventral part and faint black maculations in dorsal part.

Live colouration of females and juveniles (Fig. 6d): dorsal parts of body and head, lacrimal, and lips dark green; ventral parts of body and head white; transition gradual. Flank mostly with 5–6 vertical stripes; nape band faint; lacrimal, vertical preopercular, and supraorbital stripes very faint; eye dark with silver to yellow inner ring. Pectoral and anal fins hyaline, anal fin with yellow sheen and 1–2 faint spots resembling egg spots; dorsal fin hyaline to dusky, caudal fin dusky with maculation in dorsal part, pelvic fin yellow.

Preserved colouration (Fig. 6a): in all specimens, dorsal parts of body and head brown; ventral part of body, operculum, and cheek white; transition rather abrupt at horizontal through lower lateral line. Lacrimal, snout and lips dusky. Flank often with 5–6 vertical stripes, sometimes with faint mid-lateral and dorsal-lateral bands. Lacrimal, supraorbital, and vertical preopercular stripes faint; nostril and interorbital stripes very faint; mental blotch present. Pectoral fin hyaline; dorsal fin dusky and with black lappets and black maculations in posterior part; caudal fin dusky. In dominant males; branchiostegal membrane black; pelvic fin black; anal fin dusky and with 2–3 large egg spots. In juveniles and females; branchiostegal membrane light-coloured; pelvic fin hyaline; anal fin hyaline to faint dusky.

Distribution and ecology: only known from Lake Edward, abundant in the upper water layers of deepwater regions (Figs. 1b–d & 2). Five guts (GL 150–169 (161) % SL) were examined and contained emerging midges and winged ants; most probably an insectivorous species that catches aquatic and terrestrial insects from the water surface.

Discussion

The majority of East African cichlids occupy benthic habitats, but some have specialised to a pelagic lifestyle and inhabit the open waters of lakes. The Lake Edward system is inhabited by about 80 species of *Haplochromis*, of which we identified three as deepwater pelagic species: *H. pappenheimi, H. pelagicus* sp. nov., and *H. aureus* sp. nov.

Eco-morphology

Haplochromis pappenheimi and *H. pelagicus* sp. nov. strongly resemble each other in morphology. Both species have a very shallow body with a long and shallow caudal peduncle, many gill rakers, a short oral upper jaw set with small teeth, and the posterior ~1/4–1/5 of the premaxilla is edentulous in some specimens. This morphology is mostly consistent with that of deepwater pelagic species of zooplanktivores from Lake Victoria (Witte & Witte-Maas, 1987; van Rijssel et al., 2015) and with the definition of '*Yssichromis*' *sensu* Greenwood (1980): a shallow body [BD 23–30 (modal range 27–29) % SL], a long and shallow caudal peduncle [CPL 17–25 (modal range 19–22) % SL; CPL/CPD 1.7–2.1 (modally 1.8–2.0) = CPD 47.6–58.8 (50.0–55.6) % CPL], and edentulous premaxilla over the posterior 1/4–1/3 of its dentigerous arms. Some of our measurements of *H. pappenheimi* and *H. pelagicus* sp. nov. deviate slightly from '*Yssichromis*' and *H. pappenheimi sensu* Greenwood (1973), which could be partially due to differences in measuring technique. Furthermore, in both species, not all specimens have an edentulous posterior part of the premaxillary dentigerous arm and when this trait is present only the posterior ~1/5–1/4 is edentulous. This has also been observed in other species that would otherwise correspond to '*Yssichromis'*, namely *H. tanaos* Oijen & Witte 1996, *H. laparogramma* Greenwood & Gee 1969 and the type species of '*Yssichromis'*, *H. fusiformis* Greenwood & Gee 1969, all from Lake Victoria, and *H. kamiranzovu* from Lake Kivu (Greenwood & Gee, 1969; Witte & Witte-Maas, 1987; Snoeks, 1994; van Oijen & Witte, 1996). Therefore, it appears that '*Yssichromis' sensu* Greenwood (1980) has been defined too narrowly with regard to this trait.

The third deepwater pelagic species found, *H. aureus* sp. nov., differed morphologically from *H. pappenheimi* and *H. pelagicus* sp. nov. Within the Lake Edward system, *H. aureus* sp. nov. bears some morphological resemblance to *H. mentatus*. Both species have a shallow body with a long caudal peduncle, an acute snout, and oral jaws set with acutely pointed teeth. While *H. mentatus* has a typical piscivorous morphology (Vranken *et al.*, 2022), that of *H. aureus* sp. nov. is more generalised with a shorter head, shallower cheeks, and shorter jaws. Hereby, *H. aureus* sp. nov. seems to have a morphology intermediate between that of piscivores and insectivores, reminiscent of that of the insecti-piscivorous *H. guiarti* (Pellegrin 1904) from Lake Victoria (Greenwood, 1962; Witte & van Oijen, 1990; Vranken *et al.*, 2022). While the morphology of *H. aureus* sp. nov. is mostly consistent with '*Prognathochromis',* its upper oral jaw is not beaked and a mental protuberance of the lower jaw is absent. The more generalised morphology of *H. aureus* sp. nov. leans towards '*Astatotilapia'*, a group of generalised species that is characterised by the lack of specialised morphological traits and is often used as a catch-all taxon (Greenwood, 1980; van Oijen, 1996).

Besides the three known deepwater pelagic species from the Lake Edward system, the piscivorous *H. mentatus* and *H. latifrons* might also be presumed to be pelagic species as both have a morphology similar to that of pelagic piscivores from Lake Victoria with a shallow body, a long caudal peduncle, and a broad interorbital area (Vranken *et al.*, 2022). However, only one specimen of *H. mentatus* and none of *H. latifrons* were found in our pelagic catches, which might be due to these species being more rare than the three known deepwater pelagic species.

Morphology of pelagic species

All pelagic species of *Haplochromis* from the Lake Edward system share several morphological traits. All have an elongated body (*i.e.*, a shallow body with a long and shallow caudal peduncle and a relatively short head in comparison to other species with a similar diet), a very broad interorbital area, many gill rakers, and many vertebrae in comparison to other species of *Haplochromis* from the Lake Edward system (Table 3).

The most extremely elongated bodies are represented by the zooplanktivorous *H. pappenheimi* and *H. pelagicus* sp. nov., which share some additional morphological traits that distinguish them from most other species of *Haplochromis* from the Lake Edward system, such as shorter pre-dorsal and pre-pelvic distances, shallower cheeks, narrower oral jaws of which the upper jaw is shorter compared to the lower jaw, and more gill rakers (Table 3).

Sexual dimorphism

All species of *Haplochromis* are female mouth-brooders in which a female takes her eggs into her mouth and incubates them until they develop into free-living juveniles. Hence, a female can increase her reproductive potential by having a larger buccal cavity (van Oijen & Witte, 1996; Okuda *et al.*, 2002). Many species of *Haplochromis* are known to display a sexual dimorphism in traits that can be associated to buccal cavity size. Most frequently, females have a longer head than males (Snoeks, 1994; tkint *et al.*, 2012), which would give them a longer buccal cavity. In females of many deepwater pelagic zooplanktivores and similar species (*e.g.*, *H. pyrrhocephalus* Witte & Witte-Maas 1987, *H. heusinkveldi* Witte & Witte-Maas 1987, *H. tanaos*, and *H. thereuterion*, all from Lake Victoria), the depth rather than the length of the buccal cavity seems to be larger than in males. These females have deeper cheeks and smaller eyes than males (Witte & Witte-Maas, 1987; van Oijen & Witte, 1996; van Rijssel et al., 2013). Similarly, females of both *H. pappenheimi* and *H. pelagicus* sp. nov. have deeper lacrimals and cheeks than males, and females of *H. pappenheimi* have smaller eyes than males. Given the very shallow cheeks and short heads of deepwater pelagic zooplanktivorous species in comparison to most other species of *Haplochromis* (Table 3), an increased buccal cavity volume might be more efficiently acquired through an increase in buccal cavity depth rather than length. While this pattern is found in most deepwater pelagic zooplanktivorous species, females of *H. kamiranzovu* from Lake Kivu have a longer and narrower head than males and a clear sexual dimorphism in cheek depth or eye size was not observed (Snoeks, 1994).

In *H. pappenheimi* and *H. pelagicus* sp. nov., indications of sexual dimorphism are also present in body shape, more specifically in caudal peduncle length (♂<♀). Similarly, females of *H. tanaos*, *H. laparogramma*, and *H. heusinkveldi* Witte & Witte-Maas 1987, all from Lake Victoria, and *H. kamiranzovu* from Lake Kivu have a longer or larger caudal peduncle than males (Snoeks, 1994; van Oijen & Witte, 1996; van Rijssel et al., 2013). This could indicate an additional sexual difference in ecology, habitat preference, and/or behaviour. However, gut contents of both species from Lake Victoria showed no sexual differences (van Oijen & Witte, 1996), contradicting possible differences in diet. Similarly, specimens of both sexes of *H. pappenheimi* and *H. pelagicus* sp. nov. were nearly always caught sympatrically, which seems to contradict a sexual difference in habitat preference. An exception was observed in littoral catches around the mouth of the Kazinga Channel, where females of *H. pelagicus* sp. nov. were more abundant than males. While these locations might represent brooding areas, mouth brooding females were absent from all catches. We hypothesise that the longer caudal peduncle in females of some pelagic species of *Haplochromis* might represent a female trade-off between buccal cavity volume and an elongated body shape. All these species have a very shallow and streamlined body, a morphology that is considered adaptive for swimming efficiently in open waters (Feilich, 2016). The deeper anterior region of the head in females of these species gives them a less-streamlined body compared to males, especially during incubation when the buccal cavity is expanded to facilitate the eggs. This less-streamlined shape is possibly compensated by a longer caudal peduncle. Hereby, it is unlikely that sexual dimorphism in body shape evolved as a sexually selected trait or through initial niche divergence between both sexes. Instead, it could have evolved as a functional trade-off between ecology present in both sexes and mouth brooding behaviour present in females only (Ronco *et al.*, 2019).

No clear morphological difference in measurements or counts were found between the sexes of *H. aureus* sp. nov., with the exception of females that tend to have a deeper caudal peduncle than males.

Besides female mouth brooding, the reproductive strategy in *Haplochromis* also includes a strong female assortative mate choice for dominant male colour pattern. In most species, juveniles and adult females are dull-coloured, while dominant males have conspicuous species-specific colour patterns. For example, females of *H. pappenheimi* and *H. aureus* sp. nov. are yellowish or dark-green and have dusky or yellow anal and caudal fins (Figs. 4c & 6c). Dominant males of *H. pappenheimi* are dark-green with crimson anal and caudal fins (Figs. 1a & 4d) and those of *H. aureus* sp. nov. are light blue with a yellow snout and chest and crimson anal and caudal fins (Figs. 1a & 6d). Such a clear pattern was not observed in *H. pelagicus* sp. nov. as adult females and dominant males are both iridescent blue-green and have hyaline anal and caudal fins (Figs. 1a & 5c-d). This could be because of the importance of countershading in pelagic habitats. Whereas dominant males of most species of *Haplochromis* are dark-coloured ventrally (*e.g.*, *H. pappenheimi*; Figs. 1a & 4c), those of *H. pelagicus* sp. nov. are mostly light-coloured ventrally. These patterns were to a lesser degree also present in *H. aureus* sp. nov. The difference in the colour of the ventral part of the body between *H. pappenheimi* and *H. pelagicus* sp. nov. (dark vs. light-coloured) could also contribute to assortative mating in both species. Similar differences in less-conspicuous colour patterns are known for *Diplotaxodon* Trewavas 1935 from the deep waters of Lake Malawi, where they seem to be important for species recognition and assortative mating (Genner *et al*., 2007).

Ecology

Our data suggest that *H. aureus* sp. nov. is mostly restricted to the open waters of deepwater regions where it feeds on pelagic and terrestrial insects (Fig. 1). *Haplochromis pappenheimi* and *H. pelagicus* sp. nov. have very similar diets consisting of zooplankton and midges. While *H. pappenheimi* seems mostly restricted to the open waters of sublittoral and deepwater regions, *H. pelagicus* sp. nov. has a wider distribution. The latter species inhabits the open waters of deepwater regions and also, in low relative abundances, the littoral regions of Lake Edward, the Kazinga Channel, and Lake George.

The differences in morphology and colour pattern between *H. pappenheimi* and *H. pelagicus* sp. nov. discussed above could reflect a differentiation in ecology. Our sampling is restricted to day-catches in the upper and lower 1.5 m of the water column in deepwater regions. Hence, the vertical distribution and diel migration of these species could not be investigated and data on the horizontal distribution are incomplete.

In deepwater pelagic species of zooplanktivores from Lake Victoria, differences in the following ecological parameters were found: diet preference, horizontal and vertical distribution, and diel vertical migration (Goldschmidt *et al.*, 1990; van Rijssel *et al*., 2015). We hypothesise that similar differences might be present between the species from the Lake Edward system. *Haplochromis pappenheimi* might prefer deeper water layers than *H. pelagicus* sp. nov. This is consistent with the larger eyes and non-countershaded dominant males in the former species as Lake Edward is relatively turbid with a strongly decreased visibility in deeper water layers (Levring & Fish, 1956). Such a vertical zonation might also explain its absence from the mouth of the Kazinga Channel, the channel itself, and Lake George (Fig. 1: catches 1–6). Additionally, the larger eyes, longer upper jaw, and more acute oral teeth of *H. pappenheimi* might also indicate a difference in hunting strategy or evolutionary history.*Haplochromis pelagicus* sp. nov. was rarely caught in Lake George and, as stated by Greenwood (1973), most caught specimens are relatively small (< 71 mm SL) (Greenwood, 1973; pers. obs.). However, we also caught three large females from Akika Island and Kashaka Bay in Lake George (74–79 mm SL), so large specimens might just be more rare in Lake George than in the Kazinga Channel and Lake Edward.

Besides deepwater pelagic cichlids, the deepwater regions of Lake Edward are inhabited by *Laciris pelagicus*, a pelagic poecilid species. The distribution and abundance of this species remain unknown as, in our survey, the species was never caught using gill nets of the smallest used mesh size (8 mm). Some specimens were, however, caught in the surface area of deepwater regions of Lake Edward using a scoop net, indicating its presence in the lake, but no estimation of its relative abundance can be made (Decru *et al*., 2022).

Acknowledgements

This research was conducted within the framework of the BELSPO (Belgian Science Policy Office) funded BRAIN projects HIPE (Human impacts on ecosystem health and resources of Lake Edward) and KEAFish (The biodiversity, biogeography and evolutionary history of the northern basins of the Great African Lakes: the enigmatic fish faunas of Lakes Kivu, Edward and Albert revisited) and an FWO (Research Foundation Flanders) funded PhD fellowship to NV (11E0520N). MM benefitted from a FishBase and Fish taxonomy training (2016) through the framework agreement of the RMCA with the Directorate-General for Development Cooperation and Humanitarian Aid. The fieldwork by NV, MVS, and ED was supported by the FWO and fieldwork by MVS by the King Leopold III Fund for Nature Exploration and Conservation. We thank L. Wasswa (Ugandan Fisheries Department) and M. Bifamengo (NaFIRRI, Uganda) for their help in collecting specimens, and W. Okello (NaFIRRI, Uganda) for valuable logistic support. We are grateful to M. Parrent (RMCA), O. Pauwels (IRSNB), J. Maclaine (NHMUK), and E. Aßel (ZMB) for curatorial services, E. Aßel for the provided photograph and X-ray image of the lectotype of *H. pappenheimi*, and support from the SYNTHESYS+ Project, http://www.synthesys.info/, which is financed by European Community Research Infrastructure Action under the H2020 Integrating Activities Programme, Project number 823827.

Data availability

Raw data of all catches generated during this study are provided in Supplementary information (Table S1). Summarised morphometric data are provided in Table 2 and Supplementary information (Table S12); raw morphometric data is available from the corresponding author on reasonable request.

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: 333–380. https://doi.org/10.1163/002829677X00199.

Boulenger, G. A., 1914. Cichlidae In Pappenheim, P. & G. A. Boulenger (eds), Fishe. Wissenschaftliche ergebnisse der Deutschen Zentral-Africa-Expedition, 1907-1908. pp. 253–259.

Buris, M. J., J. P. E. C. Darlington, I. G. Dunn, G. G. Ganf, J. J. Gwahaba & L. M. McGowan, 1973. The biomass and distribution of organisms in Lake George, Uganda. Proceedings of the Royal Society of London. Series B. Biological Sciences 184: 271–298. https://doi.org/10.1098/rspb.1973.0049.

de Zeeuw, M. P., M. Mietes, P. Niemantsverdriet, S. ter Huurne & F. Witte, 2010. Seven new species of detritivorous and phytoplanktivorous haplochromines from Lake Victoria. Zoologische Mededelingen Leiden 84: 201–250.

de Zeeuw, M. P., I. Westbroek, M. J. P. Van Oijen & F. Witte, 2012. Two new species of zooplanktivorous haplochromine cichlids from Lake Victoria, Tanzania. ZooKeys 256: 1–34. https://doi.org/10.3897/zookeys.256.3871.

Decru, E., N. Vranken, P. H. N. Bragança, J. Snoeks & M. Van Steenberge, 2020. Where ichthyofaunal provinces meet: the fish fauna of the Lake Edward system, East Africa. Journal of Fish Biology 96: 1186–1201. https://doi.org/10.1111/jfb.13992.

Decru, E., N. Vranken, H. Maetens, A. Mertens De Vry, A. Kayenbergh, J. Snoeks & M. Van Steenberge, 2022. DNA barcoding the Lake Edward basin: high taxonomic coverage of a tropical freshwater ichthyofauna. Hydrobiologia 849: 1743–1762. https://doi.org/10.1007/s10750-022-04812-0.

Dunn, I. G., 1975. Ecological notes on the *Haplochromis* (Pisces: Cichlidae) species-flock of Lake George, Uganda (East Africa). Journal of Fish Biology 7: 651–666. https://doi.org/10.1111/j.1095-8649.1975.tb04638.x.

Everson, I., A. Taabu-Munyaho & R. Kayanda, 2013. Acoustic estimates of commercial fish species in Lake Victoria: moving towards ecosystem-based fisheries management. Fisheries Research 139: 65–75. https://doi.org/10.1016/j.fishres.2012.09.019.

Feilich, K. L., 2016. Correlated evolution of body and fin morphology in the cichlid fishes. Evolution

70: 2247–2267. https://doi.org/10.1111/evo.13021.

Fryer, G. & T. D. Iles, 1972. The cichlid fishes of the Great Lakes of Africa. Their biology and evolution. Oliver and Boyd, Edinburgh. https://doi.org/10.2307/1442393.

Genner, M. J., P. Nichols, G. R. Carvalho, R. L. Robinson, P. W. Shaw, & G. F. Turner, 2007. Reproductive isolation among deep-water cichlid fishes of Lake Malawi differing in monochromatic male breeding dress. Molecular Ecology 16: 651–662. https://doi.org/10.1111/j.1365-294X.2006.03173.x.

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. https://doi.org/10.1007/s10641-006-9180-7.

Greenwood, P. H., 1962. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae), part V. Bulletin of the British Museum (Natural History) Zoology 9: 139–214. https://doi.org/10.5962/bhl.part.16340.

Greenwood, P. H., 1974. The cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. Bulletin of the British Museum (Natural History) Zoology Supplement: 134. https://doi.org/10.5962/p.119071.

Greenwood, P. H., 1979. Towards a phyletic classification of the ‘genus’ *Haplochromis* (Pisces, Cichlidae) and related taxa. Part 1. Bulletin of the British Museum (Natural History). 35: 265–322. https://doi.org/10.5962/bhl.part.20455.

Greenwood, P. H., 1980. Towards a phyletic classification of the “genus” Haplochromis (Pisces, Cichlidae) and related taxa, part II. Bulletin of the British Museum (Natural History) Zoology 39: 1–101. https://doi.org/10.5962/bhl.part.13268.

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

Holm, S., 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6: 65–70.

Kolding, J., P. van Zwieten, F. Marttin, S. Funge-Smith & F. Poulain, 2019. Freshwater small pelagic fish and their fisheries in the major African lakes and reservoirs in relation to food security and nutrition. FAO Fisheries and Aquaculture Technical Paper 642: 124. https://doi.org/10.4060/ca0843en.

Konings, A. F., 2016. Malawi cichlids in their natural habitat. Cichlid Press, El Paso, TX 79913, USA.

Lærdal, T. & M. R. Talbot, 2002. Basin neotectonics of lakes Edward and George, East African Rift. Palaeogeography, Palaeoclimatology, Palaeoecology 187: 213–232. https://doi.org/10.1016/S0031-0182(02)00478-9.

Levring, T. & G. R. Fish, 1956. The penetration of light in some tropical East African waters. Oikos 7: 98–109. https://doi.org/10.2307/3564986.

Malinsky, M., H. Svardal, A. M. Tyers, E. A. Miska, M. J. Genner, G. F. Turner & R. Durbin, 2018. Whole-genome sequences of Malawi cichlids reveal multiple radiations interconnected by gene flow. Nature Ecology & Evolution 2: 1940–1955. https://doi.org/10.1038/s41559-018-0717-x.

Mannini, P., 1998. Ecology of the pelagic fish resources of Lake Tanganyika. PhD thesis, University of Hull.

McGee, M. D., S. R. Borstein, J. I. Meier, D. A. Marques, S. Mwaiko, A. Taabu, M. A. Kishe-Machumu,

B. O'Meara, R. Bruggmann, L. Excoffier & O. Seehausen, 2020. The ecological and genomic basis of explosive adaptive radiation. Nature 586: 75–79. https://doi.org/10.1038/s41586-020-2652-7.

Meier, J. I., D. A. Marques, S. Mwaiko, C. E. Wagner, L. Excoffier & O. Seehausen, 2017. Ancient hybridization fuels rapid cichlid fish adaptive radiations. Nature Communications 8: 14363. https://doi.org/10.1038/ncomms14363.

Moriarty, D. J. W., J. P. E. C. Darlington, I. G. Dunn, C. M. Moriarty & M. P. Tevlin, 1973. Feeding and grazing in Lake George, Uganda. Proceedings of the Royal Society B: Biological Sciences 184: 299–319. https://doi.org/10.1098/rspb.1973.0050.

Murrell, P., 2005. R Graphics. Chapman & Hall/CRC Press.

Okuda, N., M. Miyazaki & Y. Yanagisawa, 2002. Sexual difference in buccal morphology of the paternal mouthbrooding cardinalfish *Apogon doederleini*. Zoological Science 19: 801–807. https://doi.org/10.2108/zsj.19.801.

Regan, C. T., 1921. The Cichlid fishes of Lakes Albert Edward and Kivu. Annals and Magazine of Natural History Series 9: 632–639. https://doi.org/10.1080/00222932108632633.

Ronco, F., M. Matschiner, A. Böhne, A. Boila, H. H. Büscher, A. Indermaur, A. El Taher, M. Malinsky, V. Ricci, A. Kahmen, S. Jentoft & W. Salzburger, 2021. Drivers and dynamics of a massive adaptive radiation in African cichlid fish. Nature 589: 76–81. https://doi.org/10.1038/s41586-020-2930-4.

Ronco, F., M. Roesti & W. Salzburger, 2019. A functional trade-off between trophic adaptation and parental care predicts sexual dimorphism in cichlid fish. Proceedings of the Royal Society B: Biological Sciences 286: 20191050. https://doi.org/10.1098/rspb.2019.1050.

Seehausen, O., 1996. Lake Victoria rock cichlids: taxonomy, ecology, and distribution. Verduyn Cichlids.

Snoeks, J., 1994. The haplochromine fishes (Teleostei, Cichlidae) of Lake Kivu, East Africa: a taxonomic revision with notes on their ecology. Koninklijk Museum voor Midden-Africa, Tervuren, Belgium.

tkint, T., E. Verheyen, B. De Kegel, P. Helsen & D. Adriaens, 2012. Dealing with Food and Eggs in Mouthbrooding Cichlids: Structural and Functional Trade-Offs in Fitness Related Traits. PLoS ONE 7: e31117. https://doi.org/10.1371/journal.pone.0031117.

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

van Oijen, M. J. P. & F. Witte, 1996. Taxonomical and ecological description of a species complex of zooplanktivorous and insectivorous cichlids from Lake Victoria. Zoologische Verhandelingen 0: 3–56.

van Rijssel, J. C., E. S. Hoogwater, M. A. Kishe-Machumu, E. van Reenen, K. V. Spits, R. C. van der Stelt, J. H. Wanink, & F. Witte, 2015. Fast adaptive responses in the oral jaw of Lake Victoria cichlids. Evolution 69: 179–189. https://doi.org/10.1111/evo.12561.

van Rijssel, J. C. & F. Witte, 2013. Adaptive responses in resurgent Lake Victoria cichlids over the past 30 years. Evolutionary Ecology 27: 253–267. https://doi.org/10.1007/s10682-012-9596-9.

Verheyen, E., W. Salzburger, J. Snoeks & A. Meyer, 2003. Origin of the superflock of cichlid fishes from Lake Victoria, East Africa. Science 300: 325–329. https://doi.org/10.1126/science.1080699.

Vranken, N., M. Van Steenberge, A. Balagizi & J. Snoeks, 2020a. The synonymy of *Haplochromis pharyngalis* and *Haplochromis petronius* (Cichlidae). Journal of Fish Biology 97: 1554–1559.

https://doi.org/10.1111/jfb.14455.

Vranken, N., M. Van Steenberge, A. Heylen, E. Decru & J. Snoeks, 2022. From a pair to a dozen: the piscivorous species of *Haplochromis* (Cichlidae) from the Lake Edward system. European Journal of Taxonomy 815: 1–94. https://doi.org/10.5852/ejt.2022.815.1749.

Vranken, N., M. Van Steenberge, A. Kayenbergh & J. Snoeks, 2020b. The lobed-lipped species of *Haplochromis* (Teleostei, Cichlidae) from Lake Edward, two instead of one. Journal of Great Lakes Research 46: 1079–1089. https://doi.org/10.1016/j.jglr.2019.05.005.

Vranken, N., M. Van Steenberge & J. Snoeks, 2019. Grasping ecological opportunities: not one but five paedophagous species of *Haplochromis* (Teleostei: Cichlidae) in the Lake Edward system. Hydrobiologia 832: 105–134. https://doi.org/10.1007/s10750-018-3742-5.

Vranken, N., M. Van Steenberge & J. Snoeks, 2020c. Similar ecology, different morphology: three new species of oral-mollusc shellers from Lake Edward. Journal of Fish Biology 96: 1202–1217. https://doi.org/10.1111/jfb.14107.

Witte, F., T. Goldschmidt, J. H. Wanink, M. J. P. van Oijen, K. Goudswaard, E. L. M. Witte-Maas & N. Bouton, 1992. 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. https://doi.org/10.1007/BF00004782.

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. & E. L. M. Witte-Maas, 1987. Implications for taxonomy and morphology of intra-specific variation in haplochromine cichlids of Lake Victoria, with descriptions of five zooplanktivorous species. From form to fishery, PhD thesis, Rijksuniversiteit Leiden.

Zelditch, M. L., D. L. Swiderski, H. D. Sheets & W. L. Fink, 2004. Geometric morphometrics for biologists: a primer. Elsevier Academic Press, London.

Table 1. Linear measurements and counts with abbreviations.

Morphometric	Abbr.	Morphometric	Abbr.
Anal fin length	AFB	Prepectoral distance	PrP
Body depth	BD	Prepelvic distance	PrV
Cheek depth	ChD	Standard length	SL
Caudal peduncle depth	CPD	Snout length	SnL
Caudal peduncle length	CPL	Upper jaw length	UJL
Dentigerous area length	DAL	Pelvic fin length	VL
Dentigerous area width	DAW	Anal-fin spines and branched-rays	AFR: AFRs/AFRr
Dorsal fin length	DFB	Infra- and postorbital cheek scales	ChS: ChSi/ChSp
Eye depth	ED	Caudal peduncle scales	CPS
Gut length	GL	Dorsal-fin spines and branched-rays	DFR: DFRs/DFRr
Head length	HL	Upper transverse line scales	D-ULL
Head width	HW	Cerato- and epibranchial gill-rakers	GR: GRc/1/GRe
Interorbital width	IOW	Upper and lower lateral line scale	LatL: LatLu/LatLl
Lacrimal depth	LaD	Longitudinal line scales	LongL
Lower jaw length	LJL	Lower outer teeth	LOT
Lower jaw width	LJW	Posterior and medial lower pharyngeal teeth	LPT: LPTp/LPTm
Lower pharyngeal length	LPL	Pectoral-fin branched-rays	PFR
Lower pharyngeal width	LPW	Lower transverse line scales	ULL-A
Pectoral fin length	PL	Upper outer teeth	UOT
Premaxillary pedicel length	PPL	Upper and lower inner tooth rows	UTR/LTR
Preanal distance	PrA	Abdominal and caudal vertebrae	V: Va/Vc
Predorsal distance	PrD	Pelvic-pectoral scales	V-P

Table 2. Measurements and counts of *Haplochromis pappenheimi*, *H. pelagicus* sp. nov., and *H. aureus* sp. nov. All measurements except SL as percentage of the indicated reference measurement.

	H. pappenheimi		***H. pelagicus* sp. nov.**		***H. aureus* sp. nov.**	
	n=27, *=23, **=17, ***=3		n=25, *=15, **=3		n=17, *=16, **=15, ***=2	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
SL (mm)	72.8 ± 4.5	66.9–87.5	76.0 ± 8.9	58.8–101.6	92.4 ± 16.8	58.2–116.5
HL%SL	32.3 ± 0.9	30.9–34.5	32.6 ± 1.0	30.8–34.7	32.9 ± 1.0	30.8–34.4
BD%SL	29.3 ± 1.0	27.2–31.0	27.7 ± 1.4	25.4–30.7	32.1 ± 0.9	30.7–33.5
PrD%SL	33.1 ± 1.0	31.9–35.9	32.9 ± 1.1	30.5–34.8	33.3 ± 0.7	31.7–34.4
PrA%SL	64.3 ± 1.2	62.0–66.8	64.2 ± 0.9	62.2–65.9	64.7 ± 1.4	62.7–67.6
PrP%SL	33.2 ± 0.9	31.3–35.4	33.6 ± 1.0	31.4–35.2	33.4 ± 1.2	31.3–36.1
PrV%SL	38.8 ± 0.8	37.2–40.4	38.4 ± 0.7	37.2–39.7	39.6 ± 1.2	37.6–42.3
PL%SL	28.1 ± 2.2	24.1–30.9*	26.2 ± 1.6	23.1–30.1	28.6 ± 1.3	26.9–31.6*
VL%SL	26.6 ± 3.2	22.4–33.5*	24.5 ± 1.4	21.8–27.0	26.7 ± 2.4	22.6–30.4
DFB%SL	52.6 ± 1.1	51.1–55.0	51.7 ± 1.1	49.7–53.6	53.0 ± 1.2	50.9–55.7
AFB%SL	18.4 ± 0.7	17.3–19.3	18.1 ± 1.0	16.6–19.7	18.9 ± 0.9	17.7–20.7
CPL%SL	18.4 ± 0.7	17.4–19.6	18.6 ± 0.8	17.2–20.1	17.3 ± 0.9	15.8–18.9
CPD%CPL	61.6 ± 3.8	55.0–69.1	58.3 ± 4.2	49.4–66.3	66.5 ± 4.4	59.4–73.2
HW%HL	43.5 ± 0.9	42.2–45.3	42.3 ± 0.9	40.9–44.0	41.6 ± 1.5	38.0–43.8
ED%HL	34.3 ± 0.9	32.5–35.7	32.3 ± 1.9	29.5–35.9	29.4 ± 1.8	26.6–33.8
IOW%HW	59.9 ± 2.4	54.0–63.5	61.7 ± 2.4	58.4–65.6	62.3 ± 2.6	56.8–66.6
SnL%HL	27.9 ± 0.8	26.4–30.2	28.4 ± 0.8	26.9–30.2	31.1 ± 1.7	26.2–33.3
LaD%HL	17.0 ± 0.6	16.1–18.1	17.5 ± 0.8	15.9–19.1	18.5 ± 1.1	16.1–20.2
ChD%HL	18.8 ± 1.1	16.8–21.4	18.3 ± 1.6	15.4–21.3	22.5 ± 2.1	19.5–25.8
PPL%HL	27.0 ± 0.8	24.9–28.2	26.3 ± 0.9	24.3–27.8	26.4 ± 1.1	24.2–27.7
UJL%HL	28.3 ± 0.7	26.8–29.4	27.7 ± 0.8	26.5–29.0	32.9 ± 1.9	29.3–35.6
LJL%HL	41.1 ± 1.0	39.3–43.4	40.8 ± 1.1	38.7–42.3	43.2 ± 1.6	41.1–46.4
LJW%LJL	37.5 ± 1.9	33.8–40.4	33.9 ± 1.6	31.1–36.5	39.5 ± 3.6	34.4–47.0
LPL%HL	28.5 ± 0.9	27.9–29.5***	27.2 ± 0.4	26.9–27.8**	28.7 ± 1.3	27.7–29.6***
LPW%LPL	85.1 ± 2.9	82.3–88.1***	84.8 ± 1.4	83.7–86.3**	87.3 ± 3.5	84.8–89.8***
DAL%LPL	50.2 ± 0.5	49.6–50.6***	47.9 ± 2.2	46.5–50.4**	52.8 ± 4.8	49.4–56.2***
DAW%LPW	70.3 ± 2.2	68.0–72.4***	73.4 ± 1.3	72.1–74.6**	69.5 ± 2.0	68.1–70.9***
	Number (frequency)		**Number (frequency)**		**Number (frequency)**	
UOT	33–54 (median 46)**		36–57 (median 41)*		48–65 (median 58)**	
LOT	30–48 (median 38)**		33–47 (median 42)*		34–52 (median 43)**	
UTR/LTR	1/1 (5); 1/2 (1); 2/1 (11)		1/1 (3); 1/2 (2); 2/1 (8); 2/2 (2)		2/2 (14); 3/2 (1)	
LPT	29/10 (1); 30/9 (1); 34/12 (1)		27/10 (1); 34/12 (1); 37/10 (1)		22/11 (1); 25/12 (1)	
DFR	XV/9 (2); XV/10 (6); XVI/10 (6); XVII/9 (3)		XV/9 (1); XV/10 (5); XV/11 (1); XVI/9 (4); XVI/10 (3); XVI/11 (1)		XIV/10 (1); XV/8 (1); XV/9 (1); XV/10 (3); XVI/9 (6); XVI/10 (3)	

AFR	III/8 (11); III/9 (6)	III/8 (5); III/9 (10)	III/8 (2); III/9 (12); III/10 (1)
PFR	12 (15); 13 (2)	12 (10); 13 (5)	12 (13); 13 (2)
GR	9/1/3 (1); 10/1/2 (3); 10/1/3 (5); 10/1/4 (1); 11/1/2 (1); 11/1/3 (3); 12/1/3 (1); 12/1/4 (1); 13/1/3 (1)	10/1/3 (1); 11/1/2 (1); 11/1/3 (5); 11/1/4 (2); 12/1/2 (2); 12/1/3 (1); 12/1/4 (1); 12/1/5 (1); 14/1/3 (1)	9/1/2 (5); 9/1/3 (1); 10/1/2 (7); 10/1/3 (2)
V	14/16 (4); 14/17 (6); 14/18 (2)	14/16 (2); 14/17 (7); 14/18 (3)	13/17 (1); 13/18 (1); 14/16 (1); 14/17 (12)
LongL	31 (1); 32 (2); 33 (4); 34 (9); 35 (1)	32 (2); 33 (6); 34 (4); 35 (3)	32 (2); 33 (10); 34 (3)
LatL	20/12 (3); 21/12 (2); 21/13 (2); 22/12 (4); 22/13 (1); 22/14 (1); 23/9 (1); 23/11 (2); 23/12 (1)	20/10 (1); 20/12 (1); 21/11 (1); 21/12 (1); 21/13 (1); 21/14 (2); 21/15 (1); 22/11 (1); 22/13 (3); 22/14 (1); 22/15 (1); 24/9 (1)	20/11 (1); 21/8 (1); 21/10 (1); 21/12 (3); 21/13 (2); 22/10 (1); 22/11 (1); 22/12 (3); 22/14 (1); 23/11 (1)
D-ULL	5 (12); 6 (5)	4 (1); 5 (12); 6 (2)	5 (9); 6 (6)
ULL-A	9 (8); 10 (9)	8 (1); 9 (5); 10 (8); 11 (1)	10 (8); 11 (6); 12 (1)
CPS	16 (10); 17 (3); 18 (4)	16 (8); 17 (6); 19 (1)	16 (5); 17 (3); 18 (6); 19 (1)
V-P	4 (2); 5 (9); 6 (6)	4 (5); 5 (10)	3 (1); 4 (1); 5 (9); 6 (4)
ChS	2/7 (1); 2/8 (4); 2/9 (2); 2/10 (1); 3/8 (1); 3/9 (4); 3/10 (3); 3/12 (1)	2/8 (3); 2/9 (6); 2/10 (3); 3/9 (2); 3/10 (1)	2/8 (1); 2/9 (3); 2/10 (1); 3/8 (2); 3/9 (5); 3/10 (1); 3/11 (1); 4/10 (1)

Table 3. Average values of morphometrics for all pelagic species of *Haplochromis* and the range of average values for other species of *Haplochromis*, all from the Lake Edward system. All measurements as percentage of the indicated reference measurement. Data for *H. mentatus*, *H. latifrons*, and other species based on Vranken *et al.* (2019, 2020a, 2020b, 2020c, 2022).

	H. pappenheimi	***H. pelagicus* sp. nov.**	***H. aureus* sp. nov.**	***H. latifrons***	***H. mentatus***	**Other *H.* spp.**
HL%SL	32.3	32.6	33.0	35.0	35.1	30.3–38.2
BD%SL	29.3	27.7	32.1	28.6	31.2	30.8–37.5
PrD%SL	33.1	32.9	33.3	35.9	35.3	33.2–39.5
PrV%SL	38.8	38.4	39.6	41.8	42.4	40.2–45.7
DFB%SL	52.6	51.7	53.0	49.0	52.3	51.3–56.4
AFB%SL	18.4	18.1	18.9	15.7	18.0	17.5–21.1
CPL%SL	18.4	18.6	17.3	17.0	16.6	14.4–17.3
CPD%CPL	61.6	58.3	66.5	65.2	69.6	65.0–87.9
HW%HL	43.5	42.3	41.6	41.8	40.8	39.2–53.2
IOW%HW	59.9	61.7	62.3	60.0	55.5	41.8–53.8
ChD%HL	18.8	18.3	22.5	27.7	26.4	19.0–31.1
UJL%HL	28.3	27.7	32.9	38.2	37.0	24.1–40.7
LJL%HL	41.1	40.8	43.2	47.8	48.5	30.8–52.7
UJL/LJL	69.0	67.9	76.2	79.9	76.3	70.5–92.2
LJW%LJL	37.5	33.9	39.5	43.5	39.3	37.2–85.7
LPTp	30	34	24	16	18	15–32
LongL	33	34	33	33	33	31–35
V–P	5	5	5	7	6	5–9
GRc	11	11	10	9	9	7–10
GR	14	16	13	13	13	10–13
Vc	17	17	17	16	17	15–16
V	31	31	31	30	31	29–30

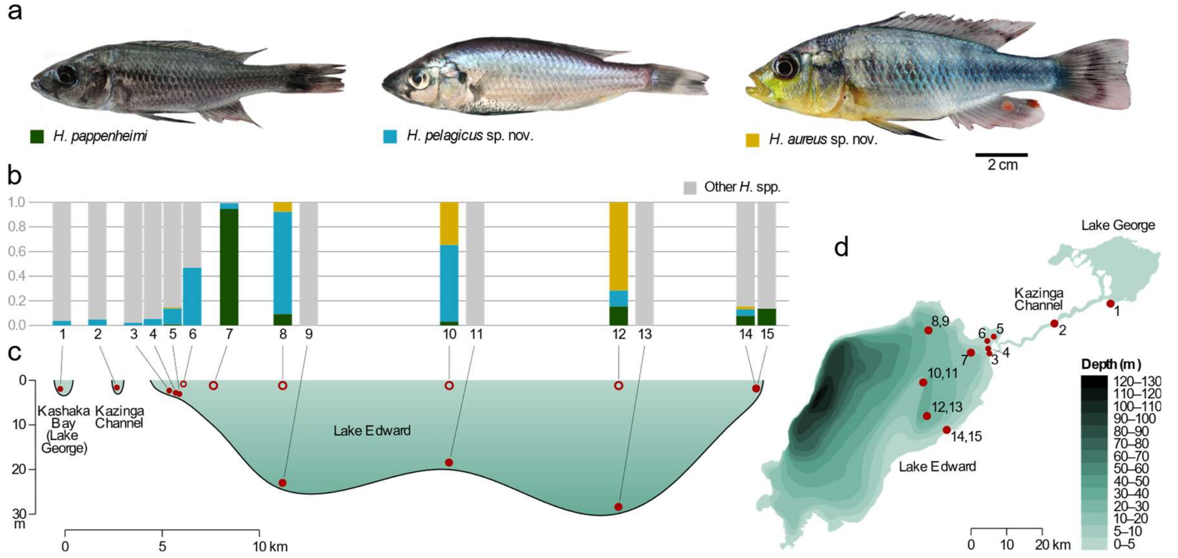

Fig. 1. (a) Dominant males of the deepwater pelagic species of *Haplochromis* from the Lake Edward system scaled to their maximum known size. (b) The relative abundance of the deepwater pelagic species is given for 15 non-standardised gill-net catches from the Lake Edward system: in four deepwater pelagic catches (catches 7, 8, 10 & 12) and eight littoral catches (1–6, 14 & 15), they represented at least 2% of the total number of specimens, while in three deepwater benthic catches (9, 11 & 13), they were absent; specimens of other species of *Haplochromis* are collectively indicated in grey. (c) All catches are plotted on a schematic representation of lake depth, catch depth, and closest distance to the shore with an indication of surface (○) or bottom (●) gill nets. (d) The locations of these 15 catches are indicated on a bathymetric map of the Lake Edward system; map based on Lærdal & Talbot (2002). See Table S1 for raw data of all catches.

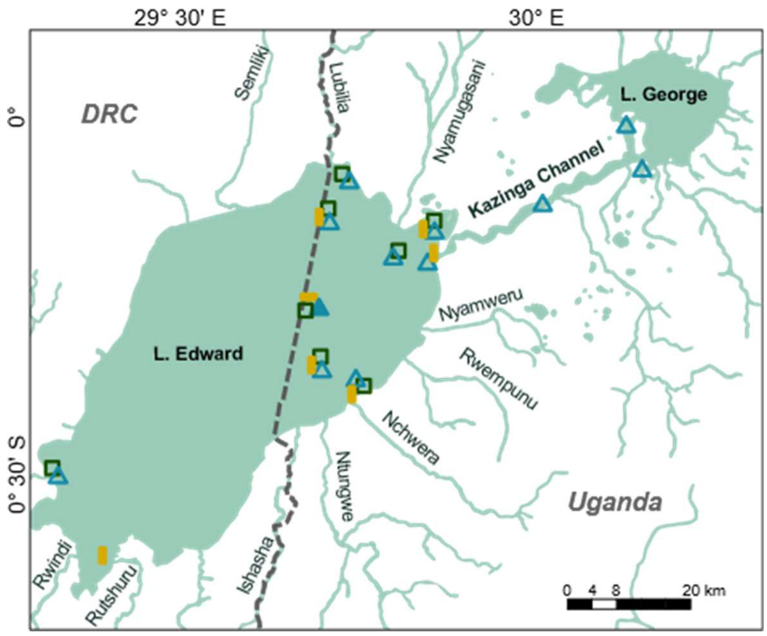

Fig. 2. Catch localities of the deepwater pelagic specimens examined in the taxonomic revision : *Haplochromis pappenheimi* (□), *H. pelagicus* sp. nov. (△, holotype ▲), and *H. aureus* sp. nov. (▮, holotype ▬). Some specimens, including the types of *H. pappenheimi*, were caught from an unknown location in Lake Edward and are not shown. See Taxonomic account for complete specimen lists.

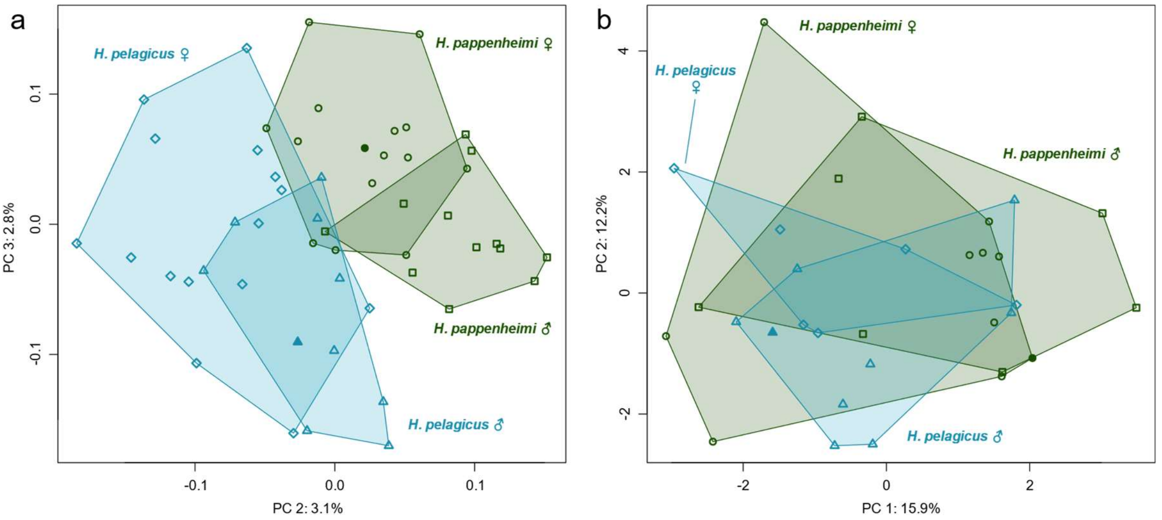

Fig. 3. Plots of (a) PC 2 against PC 3 of a PCA on log-transformed measurements and (b) PC 1 against PC 2 of a PCA on raw counts of *Haplochromis pappenheimi* (♂ □, ♀ ○; lectotype ●) and *H. pelagicus* sp. nov. (♂ △, ♀ ◇; holotype ▲).

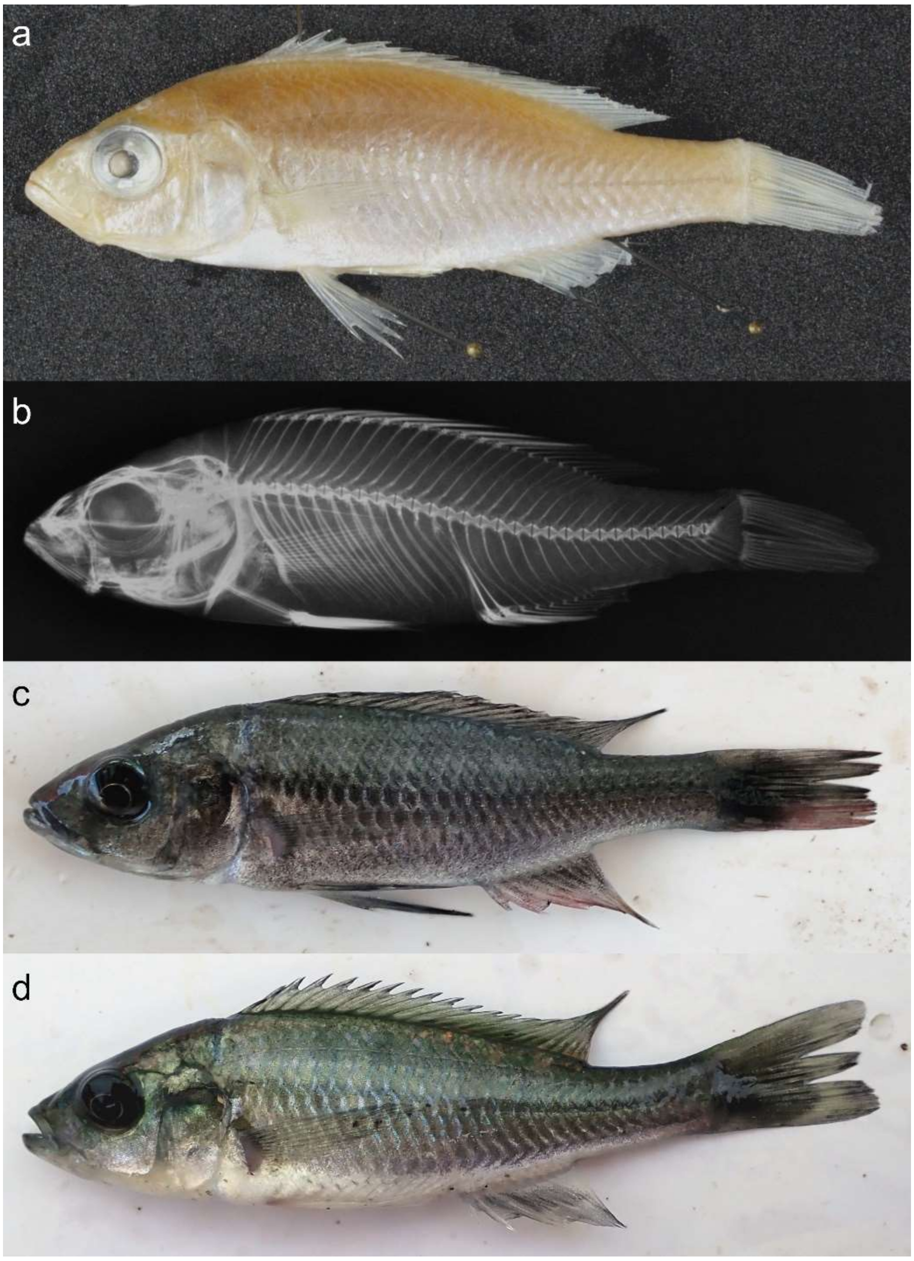

Fig. 4. *Haplochromis pappenheimi* (a) Photograph of the preserved lectotype (ZMB 19110; 71.3 mm SL), (b) an X-ray image of the lectotype, and photographs of freshly caught (c) dominant male (most likely RMCA 2019.002.P.0149; 76.4 mm SL) and (d) female (RMCA 2018.008.P.0517; 68.7 mm SL) to illustrate the live colour patterns. The contrast was slightly enhanced.

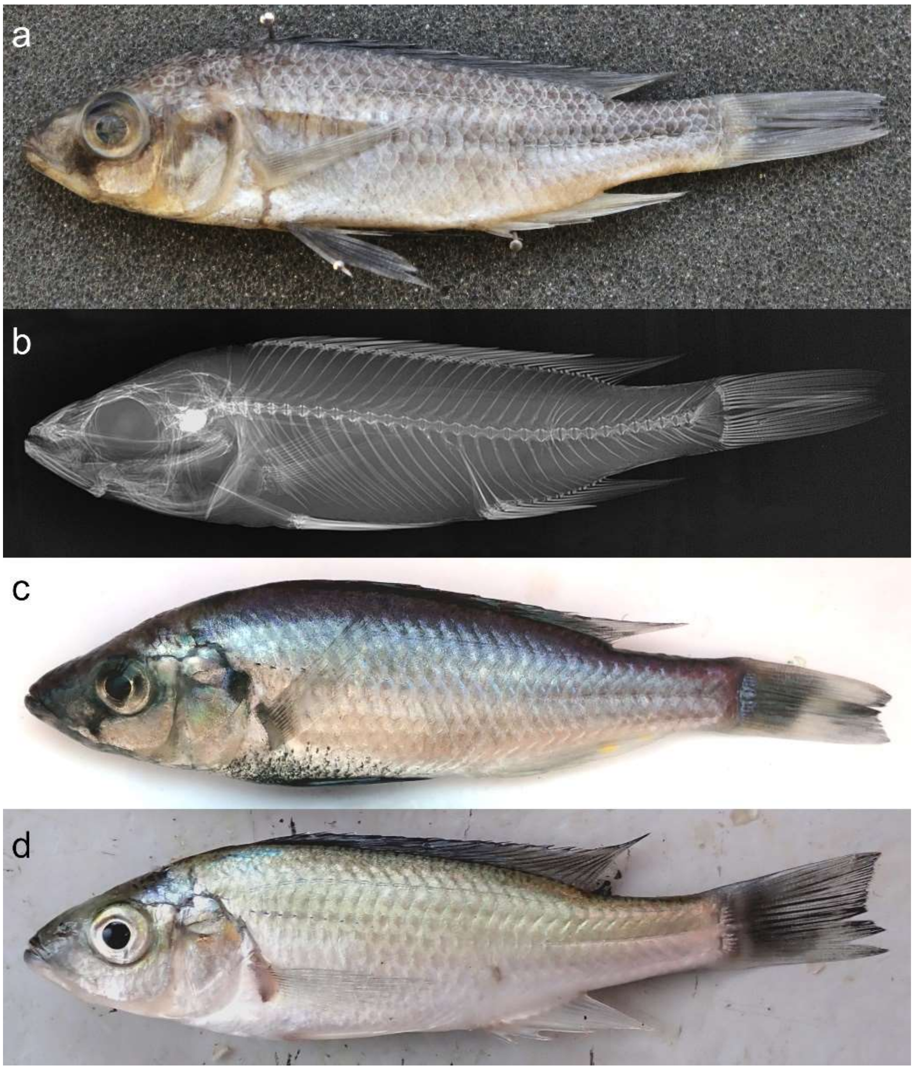

Fig. 5. *Haplochromis pelagicus* sp. nov. (a) Photograph of the preserved holotype (RMCA 2019.002.P.0138; 76.0 mm SL), (b) an X-ray image of the holotype, and photographs of freshly caught (c) dominant male (RMCA 2018.008.P.0495; 74.6 mm SL) and (d) female (RMCA 2019.002.P; same catch as holotype; 67.2 mm SL) to illustrate the live colour patterns. The contrast was slightly enhanced.

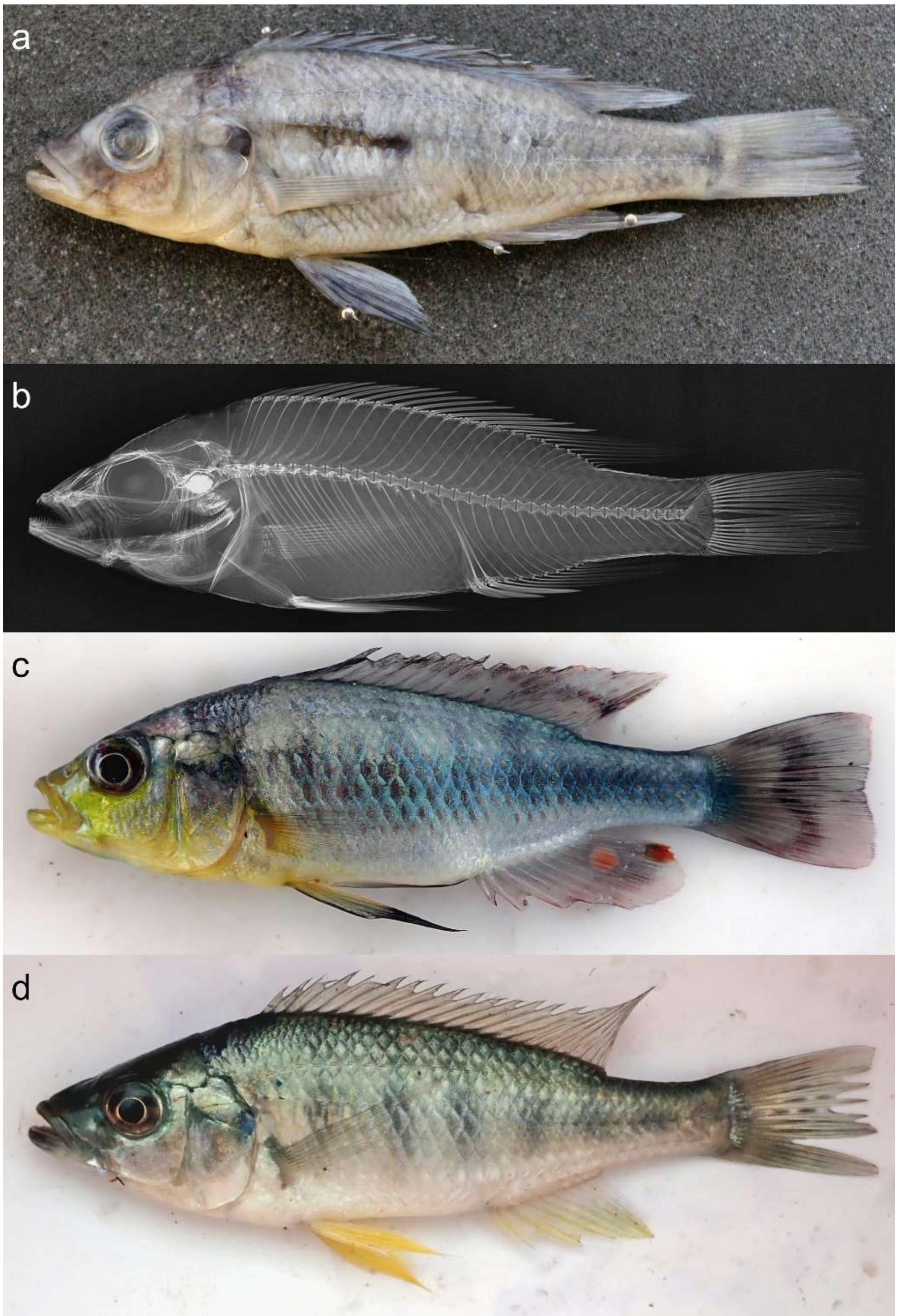

Fig. 6. *Haplochromis aureus* sp. nov. (a) Photograph of the preserved holotype (RMCA 2019.002.P.0136; 90.0 mm SL), (b) an X-ray image of the holotype, and photographs of freshly caught (c) dominant male (from same catch as holotype) and (d) female (IRSNB 967; 87.4 mm SL) to illustrate the live colour patterns. The contrast was slightly enhanced.