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Grasping ecological opportunities: not one but five paedophagous species of *Haplochromis* (Teleostei: Cichlidae) in the Lake Edward system

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Abstract The Lake Edward system in Eastern Central Africa, including Lakes Edward and George and their associated rivers, is home to a species assemblage of endemic haplochromine cichlids. Currently, 36 of these species have been formally described, while it is estimated that the system may harbour a total of 60 species. Species flocks of haplochromine cichlids are morphologically and ecologically very diverse and have radiated into many specialised trophic niches. Paedophagy is the feeding

on eggs and larvae. In *Haplochromis*, most paedophages steal fry and eggs from the buccal cavities of mouthbrooding female cichlids. Hitherto, one formally described species with this diet is known from the Lake Edward system: *Haplochromis taurinus*. We performed a morphometrical revision of all species of *Haplochromis* from this system with a morphology that suggests a paedophagous diet: long oral jaws set with small teeth. Sixty-eight specimens were studied by taking 28 measurements and 20 counts and by performing stomach content observations. We discovered that *H. paradoxus* also had a paedophagous diet. Our analyses further revealed the presence of three new species: *H. gracilifur* sp. nov., *H. molossus* sp. nov., and *H. relictidens* sp. nov. All five of these species were described or redescribed.

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Introduction

Adaptive radiation is the divergence of a lineage or a set of closely related lineages into a multitude of species that are adapted to exploit various ecological niches (Givnish, 2015). The cichlids of the East African Great lakes form the most impressive

examples of adaptive radiations in vertebrates (Seehausen, 1996; Turner, 1996; Snoeks, 2001, 2004; Meier et al., 2017). Although the radiations of lakes Malawi, Tanganyika, and Victoria are well-established models in evolutionary biology (Salzburger et al., 2002; Kocher, 2004; Seehausen, 2006), much less attention has been given to the radiations of the smaller Great Lakes, most notably that of lakes Edward and George.

The Haplochromini

Lake Edward (Fig. 1) is located in Eastern Central Africa, at the border of the Democratic Republic of the Congo and the Republic of Uganda. It is connected with the smaller Lake George through the slow-flowing Kazinga Channel. Both lakes and their associated river systems form a separate hydrographic unit and share a similar ichthyofauna. Hence, we will refer to both lakes as the Lake Edward system. The system's ichthyofauna includes an assemblage of Haplochromini, a lineage of mouthbrooding cichlids that had its origin in Lake Tanganyika (Verheyen

et al., 2003; Salzburger et al., 2005). After colonising the other Great Lakes, Haplochromini underwent explosive speciation and gave rise to the species flock of Lake Malawi and the Lake Victoria region super-flock (LVRS). The latter consists of the haplochromines from the Lake Edward system and lakes Victoria, Kivu, Albert, and their associated rivers and smaller water bodies (Greenwood, 1980; Verheyen et al., 2003). This radiation shows an extensive diversity in morphology, habitat preference, behaviour, and most notably trophic adaptation (Greenwood, 1980; Witte & Van Oijen, 1990; Verheyen et al., 2003; Salzburger et al., 2005). Although the mechanisms that allowed Great Lake cichlids to radiate remain to be fully uncovered (Seehausen, 2006), potential key factors include their large adaptive genetic potential, divergent female mate choice, introgressive hybridisation, and ecological opportunity provided by the lacustrine environment (Greenwood, 1980; Kocher, 2004; Seehausen, 2006; Machado-Schiaffino et al., 2015). In addition, most models postulate that trophic adaptations play a key role.

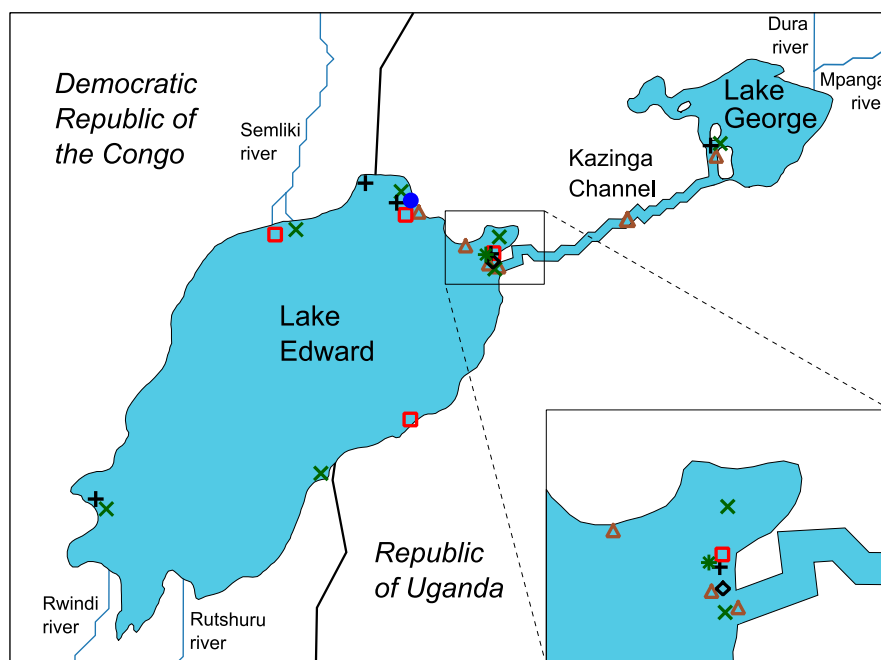


Fig. 1 The Lake Edward system, consisting of lakes Edward and George, and their associated river systems. Both lakes are connected through the Kazinga Channel. The sampling localities of the specimens examined are indicated: *H. sp.* 'gracilifur' (holo- and paratypes: filled circle; $n = 3$); *H. sp.* 'molossus'

(\times , holotype: asterisk; $n = 13$); *H. paradoxus* (open square; $n = 17$); *H. sp.* 'relictidens' (+, holotype: open diamond; $n = 8$); and *H. taurinus* (open triangle; $n = 19$). The holotype of *H. taurinus* and three specimens of *H. paradoxus* stem from an unknown location in Lake Edward

Not all radiations from the Great Lakes are taxonomically equally well known. Lake Tanganyika has an assemblage of approximately 250 cichlid species, of which 207 are considered valid. Lake Malawi is probably inhabited by a flock of 800 species, including 399 valid species. The cichlid flock of Lake Victoria counts approximately 500–600 species, 178 of which are valid, and many others are only known by their cheironyms (Seehausen, 1996; Snoeks, 2001; Froese & Pauly, 2018). The cichlid fauna of the Lake Edward system has hitherto remained largely unstudied. Decades ago, some expeditions have, however, explored this fauna. Important collections were made during the Cambridge expedition to the East African Lakes under supervision of E. B. Worthington in 1930 (Trewavas, 1933), and during the hydrological exploration of lakes Kivu, Edward, and Albert (mission KEA) performed by A. Capart in 1952–1954 (Verbeke, 1957). But a thorough examination of the collected specimens was, at the time, not performed. A few haplochromine species from the Lake Edward system have been described, mainly by Boulenger (1914), Regan (1921), and Trewavas (1933). Some decades later, they were succeeded by Greenwood (1973), who investigated the *Haplochromis* Hilgendorf, 1888 of Lake George. Hitherto, up to 36 formally described species of *Haplochromis* have been listed to inhabit the Lake Edward system (Boulenger, 1914; Regan, 1921; Trewavas, 1933; Poll, 1939a, b; Hulot, 1956; Greenwood, 1973; Lippitsch, 2003; Lippitsch & Kaufman, 2003). However, some of these probably result from misidentifications as the list contains species that are known to be endemic to other systems. For example, several museum specimens from the Lake Edward system were identified as *H. guiarti* (Pellegrin, 1904) and *H. serranus* (Pfeffer, 1896) although these species are known to be endemic to Lake Victoria (Greenwood, 1962). A similar situation holds for *H. paucidens* Regan, 1921, which is endemic to Lake Kivu (Snoeks, 1994). These examples, and the fact that current estimates mention the presence of 60 species of cichlids in the system (Greenwood, 1991; Snoeks, 2000), illustrate that the haplochromine species of the Lake Edward system are in need of a taxonomic revision.

Generic classification of the Lake Victoria region superflock

Greenwood (1980) classified the cichlid species from the LVRS in 20 genera, based on supposed synapomorphies (Greenwood, 1979, 1980). However, phylogenetic analyses showed some of these genera to be paraphyletic (Salzburger et al., 2005; Wagner et al., 2013; Meier et al., 2017), and morphologically, the definitions of these genera often overlap (Hoogerhoud, 1984; van Oijen, 1991; Snoeks, 1994). The complex evolutionary history of *Haplochromis* and the regular occurrence of convergent evolution and hybridisation further complicate the classification of these species into separate genera (Greenwood, 1980; Schluter & Nagel, 1995; Machado-Schiaffino et al., 2015; Meier et al., 2017). Hence, we prefer to classify the haplochromine cichlids of the LVRS within the genus *Haplochromis* following Hoogerhoud (1984), Meyer et al. (1990), Snoeks (1994), van Oijen (1996), and de Zeeuw et al. (2010).

Nevertheless, Greenwood's (1980) classification constitutes a practical framework to classify the morphological diversity that is present within the LVRS. Diet is strongly related to morphology in *Haplochromis* (Greenwood, 1980; Witte & Van Oijen, 1990), and trophic groups have proven to be a practical way to classify the haplochromines of highly species-rich and recently formed radiations (Fryer & Iles, 1972; Greenwood, 1980; Meyer et al., 1990; Witte & van Oijen, 1995; Stiassny & Meyer, 1999; Nagl et al., 2000; Snoeks, 2001). Therefore, species with a similar niche are often placed in the same genus sensu Greenwood (1980), e.g. most piscivores in *Harpagochromis* Greenwood, 1980 and *Prognathochromis* Greenwood 1980; most detritivores in *Enterochromis* Greenwood 1980; most pharyngeal mollusc crushers in *Labrochromis* Regan 1920; most epiphytic algae scrapers in *Haplochromis*; and most paedophages, the topic of this study, in *Lipochromis* Regan 1920. So, for this study, all specimens that were investigated were selected based on a *Lipochromis* sensu Greenwood (1980) morphology, which presumes that they have a paedophagous diet. However, some species cannot be classified into the genera sensu Greenwood 1980, e.g. *H. cronus* Greenwood 1959, a paedophage from Lake Victoria, and the trophic niches of some species remain unknown, e.g. *H. paradoxus* (Lippitsch & Kaufman, 2003) from Lake Edward. Therefore,

species that show some characteristics that suggest a paedophagous ecology were also included in this study.

Paedophages

Paedophagous cichlids *sensu lato* feed on the eggs, embryos, and/or larvae of other cichlids (Greenwood, 1959, 1973, 1980; van Oijen, 1996). For some time, it was unknown how paedophagous species acquired their food. All species of *Haplochromis* are maternal mouthbrooders. After spawning, females will take up their eggs in their buccal cavities where these will be incubated for several weeks. By doing so, they protect their fry by keeping it safe from predators. For several days after incubation, the mothers will keep guarding their juveniles (Seehausen, 1996). These occasionally leave the safety of the buccal cavities of the females but return to it when in danger. After haplochromine cichlids were observed to voluntarily abandoned their fry in aquaria, Fryer & Iles (1972) hypothesised that paedophages might feed on abandoned broods. This has, however, been criticised by McKaye & Kocher (1983) and Ribbink & Ribbink (1997) who argued that cichlids probably do not abandon their young frequently, as this represents an evolutionary unstable strategy. Moreover, breeding females have also been observed to keep their broods in stressful conditions (Ribbink & Ribbink, 1997). Observations of paedophagous behaviour gave an idea of the strategies that can be used to exploit separate phases of mouthbrooding behaviour. *Haplochromis barbarae* Greenwood, 1967, endemic to Lake Victoria, was observed in aquarium conditions to exploit the spawning phase. This species quickly snatched the eggs of a female immediately after spawning, before she got the chance to pick them up (Witte-Maas, 1981). Another species, *Champsochromis spilorhynchus* (Regan, 1922), was seen in Lake Malawi to prey on free-swimming juveniles that were guarded by their mothers. Hereby, this species exploits the final phase of mouthbrooding behaviour, i.e. the guarding phase (Ribbink & Ribbink, 1997).

We define paedophagy *sensu stricto* as related to the behaviour of some haplochromines that exploit the strictly buccal phases of mouthbrooding. During these stages, eggs and embryos are kept continuously in the buccal cavities of females. McKaye & Kocher (1983) observed in underwater observations how the

paedophagous *Caprichromis orthognathus* (Trewavas, 1935), *Caprichromis liemi* (McKaye & MacKenzie, 1982), and an undescribed species, all from Lake Malawi, rammed the heads of breeding female cichlids. Hereby, these females lost parts of their broods, which were quickly snatched by the paedophage. Greenwood (1959) studied paedophages *sensu stricto* from the LVRS and hypothesised that these species followed a strategy of engulfing the snouts of breeding females to suck out the fry. This hypothesis was later supported by aquarium observations of two species from Lake Victoria: *Haplochromis parvidens* (Boulenger, 1911) and an undescribed species (Greenwood, 1974; Wilhelm, 1980). These species also showed head-ramming behaviour. Hence, both strategies seem to occur within the LVRS.

Most paedophagous species from the LVRS have been placed in the strictly paedophagous genus *Lipochromis* *sensu* Greenwood (1980) which is characterised by a thick-lipped and widely distensible mouth with long jaws and small teeth that are deeply embedded in the oral mucosa (Greenwood, 1980). Although only one species of *Lipochromis* *sensu* Greenwood (1980) is known from the Lake Edward system, *Haplochromis taurinus* Trewavas, 1933 (Greenwood, 1980), additional observations pointed to the presence of more species with a paedophagous ecology in the system. For example, when revising the species of *Haplochromis* from Lake Kivu, Snoeks (1994) also investigated some specimens from Lake Edward that strongly resembled *H. occultidens* Snoeks, 1988, a paedophagous species from Lake Kivu. He concluded that these specimens were not conspecific with *H. occultidens* but belonged to undescribed species (i.e. *H. molossus* sp. nov. & *H. relictidens* sp. nov., see below). He mentioned that *H. occultidens* differed from these specimens by its more slender body, smaller interorbital width, shorter premaxillary pedicel, and shallower lachrymal bones. The strong resemblance of these specimens to *H. occultidens* indicated that they probably had a paedophagous diet.

The aim of this study is to perform a systematic revision of the *Haplochromis* species from the Lake Edward system with a paedophagous ecology.

Material and methods

Specimens examined

Sixty-eight specimens were examined (see species descriptions). These include 18 specimens from the Royal Belgian Institute for Natural Sciences, Brussels (IRSNB), 49 from the Royal Museum for Central Africa, Tervuren (MRAC), and one, the holotype of *H. taurinus*, from the Natural History Museum, London (BMNH). Specimens were selected based on traits that suggest a paedophagous diet: long jaws with a broad gape, firmly thickened lips, bullate maxillae, and small teeth that are deeply embedded in the thickened oral mucosa (Greenwood, 1980; Witte & van Oijen, 1990). Specimens that only showed some of these characteristics but could possibly have a paedophagous diet were also included in this study.

The holotype and a paratype of *H. occultidens* (MRAC 80.49.P.4502 and 79.31.P.1957, respectively) from Lake Kivu and four specimens of *H. microdon* (Boulenger, 1906) (MRAC 81.30.P.12–13 and 91.02.P.7–8) from Lake Victoria were also examined for comparison (see “Discussion” section).

Morphometrics

All specimens were assigned a priori to five groups: *H. sp.* ‘gracilifur’ (G, $n = 3$; Fig. 2c), *H. sp.* ‘molossus’ (M, $n = 13$; Fig. 2b), *H. cf. paradoxus* (P, $n = 20$; Fig. 2e), *H. sp.* ‘relictidens’ (R, $n = 8$; Fig. 2d), and *H. cf. taurinus* (T, $n = 20$; Fig. 2a). This assignment was done mainly based on the morphology of the anterior outer oral teeth in the lower jaw (Fig. 2, see systematic

account), taking into account a combination of traits that summarise overall tooth morphology (i.e. size, form of neck and crown, and cusp size and shape). Changes in tooth morphology with size, such as abrasion through usage and the tendency towards a larger proportion of unicuspid teeth, have been taken into account in the assignment process.

A total of 48 morphometrics were taken on each specimen, including 28 measurements and 20 counts (Tables S1–S2). All morphometrics, except the counts of vertebrae, were taken under a binocular microscope (6.5–50 \times) using dial callipers (± 0.1 mm). The vertebrae were counted on X-ray scans that were made by the VisiX X-ray system (Medex Loncin SA) at the MRAC. The X-rays were generated using a DeReO WA detector and a GemX-160 generator, which were positioned at 110 cm from each other. All specimens were examined by a single person to retain consistency and minimise errors as advised by Snoeks (1994). All morphometrics were taken from the left side of each specimen. If this was not feasible due to a deformation or damage, the affected morphometric was taken from the right side or excluded if neither was possible. Dissections of the lower pharyngeal bones were performed on 15 specimens (P: 3, G: 2, M: 3, R: 4, T: 3). The dentition of both the oral and pharyngeal jaws were described following the terminology of Barel et al. (1977).

Twenty-three measurements were taken as defined by Snoeks (1994): standard length (SL); body depth (BD); head length (HL); pectoral fin length (PL); caudal peduncle length (CPL) and depth (CPD); snout length (SnL); interorbital width (IOW); lower jaw length (LJL); lachrymal depth (LaD); head width

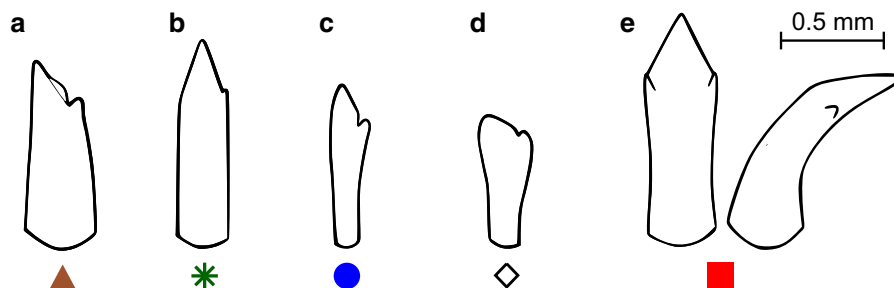


Fig. 2 Labial view of an anterolateral outer tooth in the lower jaw of a specimen of **a** *H. cf. taurinus* (filled triangle; 101.1 mm SL; MRAC 2016.035.P.0002); **b** *H. sp.* ‘molossus’ (asterisk; 104.2 mm SL; MRAC 2016.035.P.0046); **c** *H. sp.* ‘gracilifur’ (filled circle; 102.8 mm SL; MRAC 2017.006.P.0006); **d** *H. sp.*

‘relictidens’ (open diamond; 97.6 mm SL; MRAC 2017.006.P.0009); and **e** *H. cf. paradoxus* (filled square; 96.8 mm SL; MRAC 2016.035.P.0038). For **e**, the lateral view of the tooth was included

(HW); premaxillary pedicel length (PPL); predorsal (PrD), preanal (PrA), prepelvic (PrV) and prepectoral distance (PrP); dorsal (DFB) and anal fin base length (AFB); eye diameter (ED); lower pharyngeal length (LPL, $n = 15$) and width (LPW, $n = 15$); and dentigerous area length (DAL, $n = 15$) and width (DAW, $n = 15$). The definition of cheek depth (ChD) was adapted as the distance between the ventral point of the orbita and the ventral notch on the suspensorium just posterior to the articulation with the lower jaw (i.e. the articulation fossa sensu Barel et al., 1976). Additional measurements were upper jaw length (UJL): taken from the anteromedial point to the posteroventral point of the premaxilla; lower jaw width (LJW): the width of the lower jaw just posterior of the maxillae; pelvic fin length (VL): taken from the anterolateral point of the pelvic fin base to the posteriormost point of the fin; and gut length (GL, $n = 26$): the total, unfolded length of the digestive tract, taken from the anterior point of the oesophagus to the anal opening. Snout and gape inclinations were measured in degrees using a protractor following the terminology of Barel et al. (1977).

Eighteen counts were taken as defined by Snoeks (1994): lateral (LatL), longitudinal (LongL), upper transverse (D-Ull), and lower transverse line scales (ULL-A); scales between pectoral and pelvic fins (P-V); dorsal (DFR: DFRs/DFRb) and anal fin formulas (AFR: AFRs/AFRb), consisting of spine (s) and branched ray counts (b); pectoral fin formula (PFR); gill raker formula (GR: GRc/1/GRe), consisting of ceratobranchial (c) and epibranchial (e) gill raker counts; upper (UOT) and lower outer teeth (LOT); upper and lower inner tooth rows (UTR/LTR); vertebrae (V: Va/Vc), consisting of abdominal (a) and caudal (c) vertebrae counts. Additional counts were the infraorbital and postorbital cheek scales (ChS: ChSi/ChSp), defined as the numbers of scale rows on the cheek ventral to the orbit (i) and on the posterior margin of the preoperculum (p); and the number of teeth in the posterior edge of the lower pharyngeal bone (LPTp).

Qualitative characteristics

All specimens were sexed by investigating the genital papillae (Konings, 2013). The following qualitative characteristics were described following the terminology of Barel et al. (1977): profile of the dorsal part of

the head (i.e. dorsal head profile), lateral snout outline, maxillary bullation, maxillary posterior extension, caudal fin outline, and live (from pictures of freshly caught specimens) and preserved colour patterns. Description of the lateral neurocranial outline (from X-rays) is according to Greenwood (1974).

Stomach content observations

Stomach content observations were performed on 31 specimens (G: 3, M: 5, R: 4, P: 8, T: 11). The digestive tracts were removed under a binocular microscope (6.5–50 \times). The stomachs were dissected, and their contents were identified and quantified. Food items were classified as insects (identified to the rank of order) or eggs, embryos (i.e. a yolk sack was visible) or larvae (i.e. the yolk sack was completely absorbed) of cichlids.

Data analyses

Measurements and counts were analysed separately using principal component analyses (PCA). These were performed on the variance–covariance matrix of the log-transformed data of the measurements, and on the correlation matrix of the raw data of the counts (Zelditch et al., 2004). To allow for comparison, all measurements, except for SL, are expressed as percentages of a reference measurement, mainly of standard length (% SL) or head length (% HL), in the descriptive Tables 1 and 2. Pairwise, inter-group comparisons of these proportions of the measurements, and of the raw data of the counts were performed using Mann–Whitney U (MWU) tests. To avoid size effects, each pairwise test was performed on subsets that consisted of specimens with a similar mean standard length [MWU (SL): $P > 0.5$]. Sequential Bonferroni correction was applied to compensate for multiple testing (Rice, 1989). Measurements of fin lengths, which are often damaged on collection specimens, or measurements and counts that were taken on only a few specimens were excluded from the analyses and the pairwise tests. These were VL, PL, GL, LPL, LPW, DAL, DAW, and LPTp. Angular measurements of snout and gape inclinations were also excluded from all analyses. All statistical analyses were performed in Past 3.13 (Hammer et al., 2001).

Results

Morphometrics

A PCA was performed on the log-transformed measurements of all 68 specimens (Table S3). Principal component (PC) 1, which accounted for 92.4% of the total variance, had large, positive loadings of the same magnitude for all variables, and hence is interpreted as a variable describing size (Zelditch et al., 2004). Lower jaw width and lachrymal depth had high absolute loadings on PC 2, which accounted for 3.7% of the total variance, whereas eye diameter and interorbital width were important contributors to PC 3, which accounted for 1.1% of the total variance. To account for possible size effects, both PC 2 and PC 3 were plotted against PC 1 (Fig. 3a, b). On PC 2 (Fig. 3a), three clusters can be observed. All specimens of *H. cf. paradoxus* clustered in the negative part of PC 2. The second cluster consisted of all specimens of *H. sp. 'relictidens'*. These had higher but still negative values for PC 2. All specimens of *H. sp. 'gracilifur'*, *H. sp. 'molossus'*, and *H. cf. taurinus* formed a cluster with mostly positive values for PC 2. Within this cluster, values on PC 2 become larger with multivariate size (PC 1) for all groups. On PC 3, specimens of *H. cf. taurinus* clustered in the positive part (Fig. 3b), whereas all specimens from *H. sp. 'gracilifur'* and *H. sp. 'molossus'* had negative values for this axis. A PCA restricted to all specimens of the latter two groups was performed (Table S4). Here, both groups were completely separated on PC 2

(Fig. S1), which had the most important loading for caudal peduncle depth.

A PCA was performed on the raw data of the counts (Table S5). The first principal component, which accounted for 18.1% of the total variance, was mainly determined by the numbers of outer teeth in both jaws. One group, *H. cf. paradoxus*, was distinct from all other groups by its higher values for PC 1 (Fig. 3c). For PC 2, which accounted for 13.7% of the total variance, the number of ceratobranchial gill rakers on the outer row of the first gill arch and the numbers of scales in the longitudinal and lower lateral lines were important variables. However, values for all groups overlapped for PC 2 (not shown). Separation was better on PC 3, which accounted for 8.8% of the total variance. Therefore, PC 3 was plotted versus PC 1 (Fig. 3c). The former was mainly determined by the numbers of upper and lower transverse scales, and infraorbital and postorbital cheek scales. The groups *H. sp. 'gracilifur'* and *H. sp. 'molossus'* were completely separated on PC 3 (Fig. 3c). Values for all other groups overlapped. To evaluate possible size effect, the first three axes were also plotted against standard length (not shown) but no further correlations were observed.

The total number of outer teeth (UOT + LOT) was compared for all investigated specimens from the Lake Edward system (Fig. 4). In a plot of teeth counts versus SL, all *H. cf. paradoxus* specimens were completely separated from specimens of the other groups by their large numbers of outer teeth. The specimens of the groups *H. sp. 'gracilifur'*, *H. sp. 'molossus'*, and *H. cf. taurinus* had intermediate

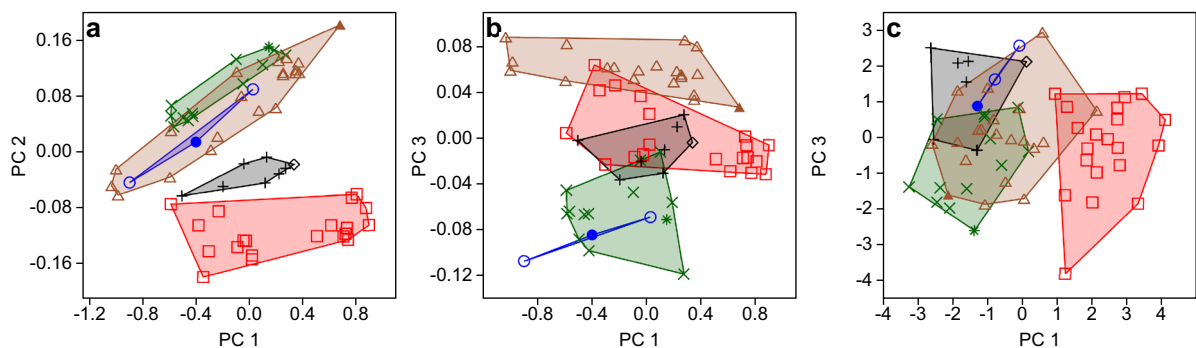


Fig. 3 Principal component analysis plots of **a** PC 2 and **b** PC 3 against PC 1 of 21 log-transformed measurements, and **c** a PCA plot of PC 3 against PC 1 of 20 counts; *H. sp. 'gracilifur'* (open circle, holotype: filled circle; $n = 3$); *H. sp. 'molossus'* (cross,

holotype: asterisk; $n = 13$); *H. cf. paradoxus* (open square; $n = 20$); *H. sp. 'relictidens'* (plus, holotype: open diamond; $n = 8$); and *H. cf. taurinus* (open triangle, holotype: filled triangle; $n = 20$). For PCA loadings, see Tables S3 and S5

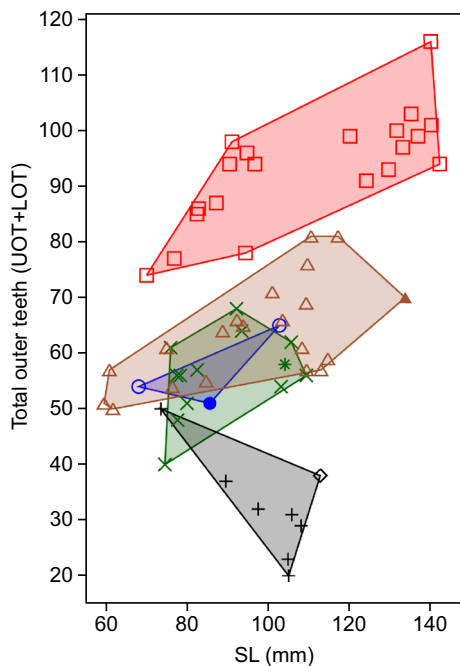


Fig. 4 Total outer tooth numbers, upper and lower jaws added, for *H. sp. 'gracilifur'* (open circle, holotype: filled circle; $n = 3$); *H. sp. 'molossus'* (cross, holotype: asterisk; $n = 13$); *H. cf. paradoxus* (open square; $n = 20$); *H. sp. 'relictidens'* (plus, holotype: open diamond; $n = 8$); and *H. cf. taurinus* (open triangle, holotype: filled triangle; $n = 20$)

numbers of teeth and their tooth counts largely overlapped. The remaining group, *H. sp. 'relictidens'*, had specimens with low numbers of outer teeth that showed a decreasing trend with an increase in body size (statistically not significant). This in contrast to the other groups, in which an increasing trend in tooth number with an increase in body size was seen.

For each set of comparisons between the groups, except for *H. sp. 'gracilifur'*, at least one variable differed significantly for the MWU tests. Significant differences were most often obtained by UOT and LJW, followed by LOT and ED (Table S6). Because of the low number of specimens ($n = 3$), comparisons involving *H. sp. 'gracilifur'* revealed almost no significant differences.

Qualitative characteristics and angular measurements

Each group showed diagnostic qualitative characteristics. The most notable differences were found in the live colour pattern of mature males, the gape

inclination, the lower jaw morphology, and the lengths of the dental arcades. Specimens of *H. cf. paradoxus* were the only ones that had beaked premaxillae, slender lower jaws, and long dental arcades (Fig. 5c). All other specimens had short dental arcades (Fig. 5a, b). Specimens of *H. sp. 'molossus'* and *H. cf. taurinus* were further distinct by their broadly rounded lower jaws (Fig. 5a), while the lower jaws of specimens of *H. sp. 'gracilifur'* and *H. sp. 'relictidens'* were more slender. They differed from each other by the relatively rounded lower jaws in *H. sp. 'gracilifur'*, while these had an acute outline in specimens of *H. sp. 'relictidens'* (Fig. 5b). The gentle gape inclinations ($20\text{--}30^\circ$) of *H. sp. 'molossus'* distinguished these specimens from all other groups that had moderate to very steep gape inclinations ($> 40^\circ$). Mature males of *H. cf. paradoxus* were yellow (Fig. 6e), whereas in *H. taurinus*, these had blue basic colours and dark red flanks without stripes (Fig. 6a). Males of *H. sp. 'gracilifur'* and *H. sp. 'relictidens'* had a green basic colour and bright red flanks. The former had clear horizontal stripes (Fig. 6c) while the latter bore vague vertical stripes (Fig. 6d). Mature males of *H. sp. 'molossus'* were also green, but they had blue vertical stripes (Fig. 6b). Other notable diagnostics were described in detail in the species descriptions below.

Stomach content observations

The gut lengths of the investigated specimens of *H. sp. 'gracilifur'* (GL 82–126% SL, $n = 3$), *H. sp. 'molossus'* (GL 90–169% SL, $n = 5$), *H. cf. paradoxus* (GL 94–130% SL, $n = 5$), *H. sp. 'relictidens'* (GL 88–158% SL, $n = 3$), and *H. cf. taurinus* (GL 119–222% SL, $n = 10$) were short. The stomachs of five *H. cf. taurinus* specimens contained between 9 and 18 eggs, embryos, or larvae of cichlids. One specimen of *H. cf. taurinus* deviated from this pattern as its stomach contained only Ephemeroptera larvae. Three specimens of *H. sp. 'molossus'* had stomachs that contained 1–5 cichlid embryos, while four specimens of *H. sp. 'relictidens'* had stomachs that held 7–14 cichlid eggs, embryos, or larvae. One specimen of *H. sp. 'gracilifur'* was found with 13 cichlid eggs in its stomach and two specimens of *H. cf. paradoxus* had stomachs that contained 13 and 17 cichlid larvae. All other examined specimens (G: 2, M: 2, P: 6, T: 5) had empty stomachs.

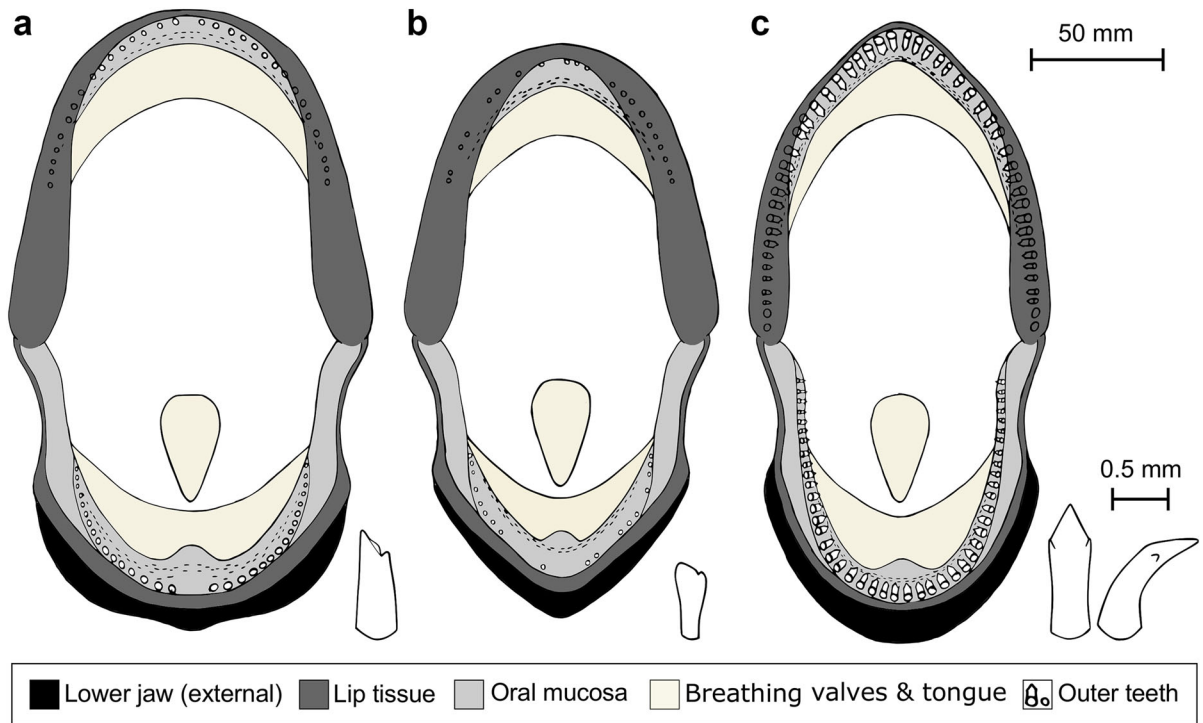


Fig. 5 Schematic representation of the anterior view of the expanded oral jaws of **a** *H. cf. taurinus*, **b** *H. sp. 'relictidens'*, and **c** *H. cf. paradoxus*. The labial view, and in one case (**c**) also the lateral view, of an anterolateral outer tooth in the lower jaw

Species delineation

All five groups that were delineated based on outer tooth morphology (Fig. 2) were also supported by a PCA of the log-transformed data of the measurements (Fig. 3a, b), by angular measurements, and by qualitative characteristics. In addition, a PCA of the counts (Fig. 3c) could distinguish between some of the groups such as between *H. sp. 'gracilifur'* and *H. sp. 'molossus'*, the groups that were less clearly separated in the PCA of the measurement data.

We could confirm that all five groups were distinct species. The group *H. cf. paradoxus* had a morphology that is unique within the Lake Edward system and that corresponded to the original species description of *H. paradoxus* (Lippitsch & Kaufman, 2003). Type specimens could not be measured because they could not be sent due to museum's policy. However, morphometric differences were small (see species description) and presumably result of a divergent methodology. Therefore, the specimens of the group *H. cf. paradoxus* were confirmed as *H. paradoxus*. The group *H.*

of each specimen are included. The teeth are embedded in the firmly thickened oral mucosa. The lips are also firmly thickened, especially the lateral parts of the upper lip, which completely cover all teeth

cf. taurinus included the holotype of *H. taurinus* and was thus confirmed as *H. taurinus*. Diagnostic and qualitative characteristics of each of the species discerned will be mentioned in the species descriptions of *H. gracilifur* sp. nov., *H. molossus* sp. nov., and *H. relictidens* sp. nov. and in the redescription of *H. paradoxus* and *H. taurinus*. Results of the MWU tests were used to determine the most diagnostic traits. The proportions of the measurements and the raw meristic data of each species are given in Tables 1 and 2, respectively. An identification key to the paedophagous species of the *Haplochromis* of the Lake Edward system is presented.

Systematic account

Haplochromis taurinus Trewavas, 1933

(Figures 2a, 5a, 6a, 7, S2, and S3; Tables 1, 2)

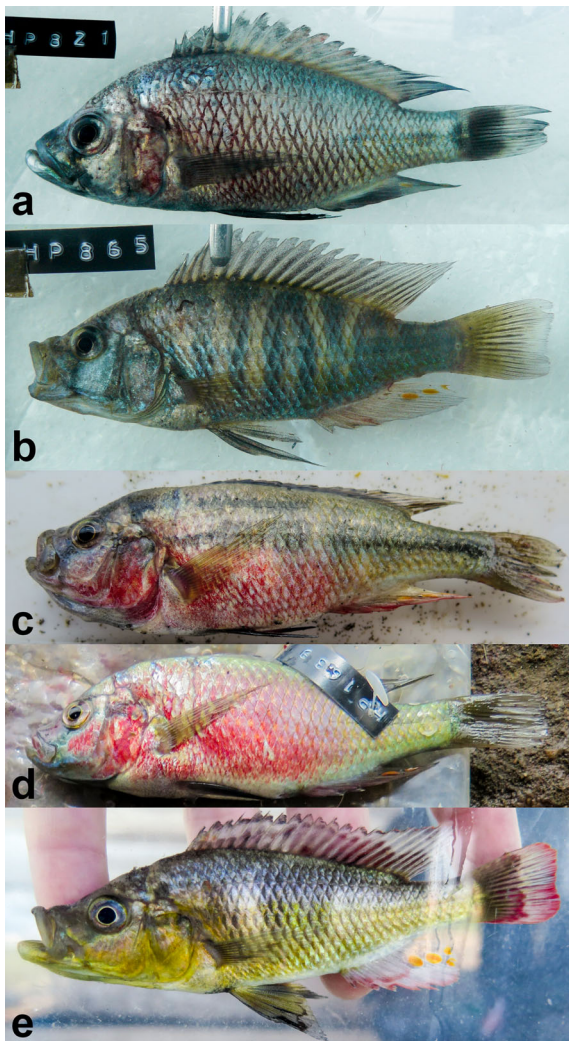


Fig. 6 Life colour patterns of freshly caught mature males of **a** *H. cf. taurinus* [MRAC 2016.035.P.0017 (HP821)]; **b** *H. sp.* ‘molossus’ [MRAC 2016.035.P.0048 (HP865)]; **c** *H. sp.* ‘gracilifur’ [MRAC 2017.006.P.0006]; **d** *H. sp.* ‘relictidens’ [MRAC 2017.006.P.0008]; and **e** *H. cf. paradoxus* [MRAC 2017.006.P.0011]. The contrast was slightly enhanced

Lipochromis taurinus: Greenwood, 1980.

Holotype

BMNH 1933.2.23.406; Lake Edward, Uganda [♀133.8 mm SL].

Other material examined

MRAC 2016.035.P.0001; Lake Edward, 1 km E. of Nyamugasani river, sand substrate: 0°10′22.8″S

29°50′13.2″E; Exp. HIPE 1; 22/10/2016 [$n = 1$; ♀ 88.8 mm SL]. MRAC 2016.035.P.0002–5 & 0006–8; mouth of Kazinga Channel, Lake Edward: 0°12′32.4″S 29°53′06.0″E; Exp. HIPE 1; 24/10/2016 [$n = 6$; ♀ 75.0; ♂ 76.4; ♀ 101.1; ♀ 103.6; ♀ 108.4; ♂ 117.3 mm SL]. MRAC 2016.035.P.0010–12; Akika island, Lake George, Lake Edward system: 0°01′26.7″S 30°09′38.2″E; Exp. HIPE 1; 07/11/2016 [$n = 1$; ♀ 84.8 mm SL]. MRAC 2016.035.P.0013–16; Kazinga Channel, near Queen Elisabeth Bush Lodge, Lake Edward system: 0°08′09.6″S 30°02′27.6″E; Exp. HIPE 1; 04/11/2016 [$n = 3$; ♂ 60.9; ♀ 61.8; ♂ 109.7 mm SL]. MRAC 2016.035.P.0017–19 & 0020; Akika island, Lake George, Lake Edward system: 0°01′26.7″S 30°09′38.2″E; Exp. HIPE 1; 06/11/2016 [$n = 4$; ♀ 59.6; ♂ 109.4; ♂ 109.5; ♂ 114.8 mm SL]. MRAC 2017.006.P.0055 & 0056–58; Kayanja offshore, Lake Edward: 0°05′34.8″S 29°45′28.8″E; Exp. HIPE 2; 31/03/2017 [$n = 2$; ♂ 92.4 mm; ♀ 93.9 mm SL]. MRAC 2017.006.P.0035–40; mouth of Kazinga Channel, hard substrate, Lake Edward: 0°12′14.4″S 29°52′37.2″E; Exp. HIPE 2; 24/03/2017 [$n = 2$; ♀ 110.6; ♂ 113.1 mm SL].

Etymology

Not mentioned in original description. Probably refers to Latin ‘taurus’, bull. Presumably relating to resemblance of head morphology to that of a bull: stout with firmly thickened lips.

Description

Maximum size 133.8 mm SL. Eyes large, head short, snout concave, and slopes at 35–40° (Fig. 7). Jaws iso- to prognathous, long, and broadly rounded; gape inclination 40–45°. Maxillae bullate (i.e. posteriorly enlarged and exposed), reaching posteriorly to vertical through anterior margin of pupil. Lips and oral mucosa firmly thickened. Neurocranium of generalised or nearly generalised *Haplochromis* type; supraoccipital crest high and pyramidal (Fig. S2b). Flank scales ctenoid; chest scales smaller than flank scales, size transition gradual.

Outer oral teeth small, stout, and bicuspid. Rarely, some uni- or tricuspid teeth laterally and posteriorly in outer rows. Necks cylindrical to conical, and with straight implantations (Fig. 2a). Major cusps

Table 1 Measurements of the paedophagous *Haplochromis* from the Lake Edward system

	<i>H. cf. taurinus</i>			<i>H. sp. 'molossus'</i>		
	Holotype	Mean \pm SD	<i>n</i> = 20, *2 Range	Holotype	Mean \pm SD	<i>n</i> = 13, *3 Range
SL (mm)	133.8	96.2 \pm 20.9	59.6 133.8	104.2	88.9 \pm 13.0	74.6 109.4
HL % SL	30.5	31.8 \pm 0.8	30.5 33.7	30.3	30.7 \pm 1.0	29.5 32.0
BD % SL	38.5	36.0 \pm 1.7	33.9 40.1	33.5	35.1 \pm 1.4	33.5 38.6
PrD % SL	34.0	35.2 \pm 1.0	33.4 36.4	33.6	33.7 \pm 1.2	32.3 36.0
PrA % SL	66.1	66.3 \pm 1.3	64.0 69.4	64.7	65.2 \pm 2.0	64.0 66.3
PrP % SL	32.7	32.8 \pm 1.3	31.2 36.1	31.7	31.4 \pm 1.5	30.3 33.1
PrV % SL	41.4	40.6 \pm 1.6	38.4 45.0	40.2	39.6 \pm 2.3	37.2 42.4
PL % SL	30.1	31.2 \pm 1.3	28.1 32.9	28.7	30.4 \pm 1.4	28.0 32.8
VL % SL	27.4	27.6 \pm 3.0	22.8 34.6	29.2	29.4 \pm 1.2	26.9 31.2
DFB % SL	58.8	54.4 \pm 1.7	51.4 58.8	56.3	55.8 \pm 1.8	52.7 59.2
AFB % SL	21.0	20.7 \pm 0.6	19.7 22.0	21.0	20.6 \pm 0.8	19.0 22.0
CPL % SL	14.9	15.7 \pm 0.7	14.5 16.9	16.6	16.2 \pm 0.5	14.9 19.0
CPD % CPL	88.1	79.6 \pm 4.4	73.9 88.1	72.8	75.2 \pm 3.5	65.5 83.6
HW % HL	55.1	51.9 \pm 1.8	47.1 55.1	55.2	53.7 \pm 2.2	50.9 57.0
ED % HL	33.0	35.7 \pm 2.1	32.9 40.2	32.6	32.3 \pm 1.5	29.8 33.9
IOW % HL	28.2	24.6 \pm 1.9	21.2 28.2	30.1	28.5 \pm 2.6	24.1 33.5
SnL % HL	31.4	26.7 \pm 2.4	23.2 31.4	30.7	28.0 \pm 1.6	25.1 30.7
LaD % HL	15.0	14.1 \pm 1.2	11.5 16.4	16.3	14.6 \pm 1.2	13.3 17.0
ChD % HL	25.8	22.1 \pm 1.8	19.0 25.8	23.4	23.2 \pm 2.0	20.3 28.0
PPL % HL	25.6	25.1 \pm 0.7	23.5 26.2	23.5	23.4 \pm 0.9	21.6 25.8
UJL % HL	43.5	39.2 \pm 2.7	34.0 43.5	39.1	36.8 \pm 2.2	34.4 39.7
LJL % HL	48.0	47.7 \pm 2.0	44.5 51.3	45.9	44.2 \pm 2.3	41.3 49.4
LJW % LJL	72.7	60.9 \pm 5.9	51.4 72.7	87.0	76.6 \pm 6.4	67.0 87.0
LPL % HL	–	31.4 \pm 1.5	30.2 32.4*	30.5	28.7 \pm 1.5	27.7 30.5*
LPW % LPL	–	91.1 \pm 5.3	87.1 94.6*	106.2	103.2 \pm 2.9	100.4 106.2*
DAL % LPL	–	51.6 \pm 0.7	51.3 52.3*	42.2	45.4 \pm 3.4	42.2 49.0*
DAW % LPW	–	66.1 \pm 0.8	64.6 67.9*	63.4	62.0 \pm 1.4	60.6 63.4*

Table 1 continued

	<i>H. sp. 'gracilifur'</i>			<i>H. sp. 'relictidens'</i>			<i>H. cf. paradoxus</i>		
	Holotype	Mean ± SD	<i>n</i> = 3, *2 Range	Holotype	Mean ± SD	<i>n</i> = 8, *4 Range	Mean ± SD	<i>n</i> = 20, *3 Range	
	SL (mm)	85.7	85.5 ± 17.3	68.1	102.8	112.9	73.6	109.8 ± 25.2	70.1
HL % SL	30.2	30.3 ± 0.5	29.8	30.7	32.2	29.6	34.3 ± 0.8	32.2	36.2
BD % SL	32.2	32.4 ± 2.3	30.2	34.8	36.3	34.6	36.0 ± 2.7	30.3	42.1
PrD % SL	33.1	33.2 ± 0.3	33.0	33.5	34.4	33.5	34.4 ± 1.0	32.7	36.0
PrA % SL	67.7	66.9 ± 0.7	66.4	67.7	66.2	66.2	68.7 ± 1.4	65.7	73.3
PrP % SL	31.0	31.6 ± 0.7	31.0	32.3	34.2	31.4	36.1 ± 0.9	34.6	37.8
PrV % SL	40.6	40.8 ± 1.3	39.6	42.3	42.9	41.3	43.9 ± 1.1	41.7	46.1
PL % SL	28.9	28.5 ± 0.4	28.1	28.9	29.0	29.0	30.4 ± 1.3	28.4	32.9
VL % SL	27.5	25.9 ± 2.2	23.4	27.5	25.2	25.2	28.1 ± 1.8	24.4	31.2
DFB % SL	53.9	54.3 ± 0.4	53.9	54.6	52.7	52.1	53.9 ± 1.3	51.0	58.0
AFB % SL	17.6	17.5 ± 1.6	15.9	19.1	19.9	19.0	18.2 ± 0.8	16.6	19.7
CPL % SL	18.2	17.3 ± 1.0	16.3	18.2	17.2	15.5	16.2 ± 0.8	14.4	17.3
CPD % CPL	62.9	65.0 ± 1.8	62.9	66.4	72.6	68.6	72.0 ± 5.2	62.3	82.4
HW % HL	50.5	51.1 ± 3.3	48.1	54.6	52.4	47.7	44.9 ± 2.0	41.7	51.2
ED % HL	29.0	31.0 ± 1.8	29.0	32.3	30.5	30.5	28.2 ± 2.0	25.3	32.1
IOW % HL	25.9	26.8 ± 1.2	25.9	28.2	26.2	24.3	23.7 ± 2.3	18.8	28.9
SnL % HL	25.0	25.2 ± 1.4	24.0	26.7	29.7	24.8	32.2 ± 1.7	28.7	36.0
LaD % HL	14.1	14.0 ± 0.3	13.7	14.3	16.7	15.8	17.7 ± 1.8	14.7	21.5
ChD % HL	21.6	22.2 ± 2.6	20.0	25.1	24.5	20.1	23.6 ± 1.9	19.5	26.8
PPL % HL	21.1	20.3 ± 1.9	18.1	21.6	27.0	24.3	26.2 ± 1.5	23.5	29.1
UJL % HL	35.4	35.3 ± 1.8	33.4	37.0	34.5	34.2	33.9 ± 1.3	30.8	37.7
LJL % HL	43.5	43.5 ± 1.2	42.4	44.7	46.1	41.6	46.5 ± 1.4	43.6	50.8
LJW % LJL	63.4	64.9 ± 2.0	61.9	69.4	51.4	50.1	48.6 ± 4.2	42.0	59.7
LPL % HL	28.1	28.8 ± 1.0	28.1	29.5*	—	25.9	28.0 ± 0.5	27.5	28.4*
LPW % LPL	104.3	106.7 ± 3.5	104.3	109.2*	—	93.0	95.0 ± 2.8	91.9	97.0*
DAL % LPL	49.4	45.2 ± 5.9	41.0	49.4*	—	47.0	49.6 ± 2.2	47.4	51.8*
DAW % LPW	68.3	66.6 ± 2.4	64.9	68.3*	—	62.9	66.9 ± 0.9	66.3	68.0*

n number, *SD* standard deviation

Asterisks indicate an alternate number of observations for this measurement or count

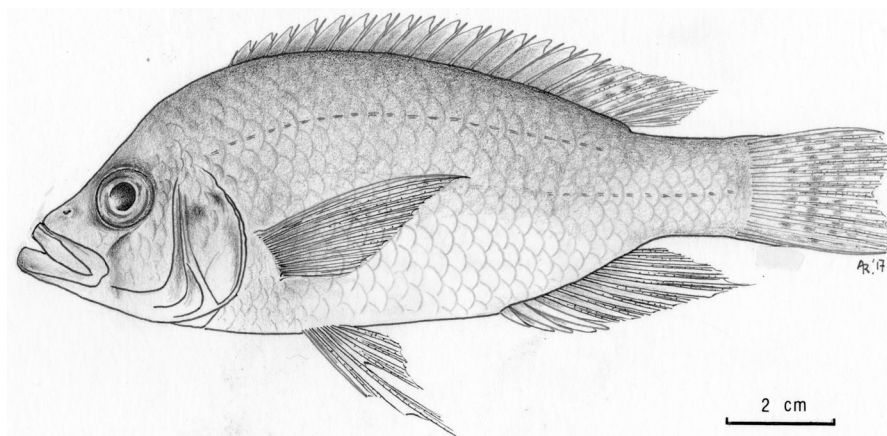
Table 2 Counts of the paedophagous *Haplochromis* from the Lake Edward system

	<i>H. cf. taurinus</i> <i>n</i> = 20, *Holotype Number (frequency)	<i>H. sp. 'molossus'</i> <i>n</i> = 13, *Holotype Number and (frequency)	<i>H. sp. 'gracilifur'</i> <i>n</i> = 3, *Holotype Number (frequency)	<i>H. sp. 'relictidens'</i> <i>n</i> = 8, *Holotype Number (frequency)	<i>H. cf. paradoxus</i> <i>n</i> = 20, *Holotype Number and (frequency)
UOT	23–39 (median 32; IQR 6)	22–34 (median 29; IQR 7)	26–35 (median 26; IQR 5)	16–26 (median 18; IQR 5)	36–65 (median 51; IQR 7)
LOT	25–42 (median 32; IQR 6)	16–34 (median 28; IQR 2)	25–30 (median 28; IQR 3)	7–25 (median 17; IQR 6)	33–51 (median 44; IQR 5)
UTR/LTR	1/1 (1); 1/2 (4); 2/1 (1); 2/2 (14*)	1/1 (5*); 1/2 (3); 2/1 (2); 2/2 (3)	1/2 (1); 2/1 (1*)	2/2 (7*); 2/1 (1)	2/2 (5); 3/2 (15)
GR	8/1/2 (2); 9/1/2 (7); 9/1/3 (3); 10/1/2 (6*); 10/1/3 (2)	8/1/1 (1); 8/1/2 (3); 9/1/1 (2); 9/1/3 (1*)	8/1/2 (1); 9/1/2 (2*)	7/1/3 (1); 8/1/2 (1); 8/1/3 (1*); 9/1/2 (3); 9/1/3 (1); 10/1/2 (1)	7/1/3 (2); 8/1/2 (1); 8/1/3 (4); 9/1/2 (3); 9/1/3 (5); 10/1/2 (3)
DFR	XV/8 (1); XV/9 (10); XV/10 (4); XVI/8 (2); XVI/9 (1); XVI/10 (1); XVII/8 (1*)	XV/9 (6*); XV/10 (1); XVI/9 (6)	XV/9 (2*); XV/10 (1)	XV/7 (1); XV/9 (5*); XV/10 (1); XVI/9 (1)	XIV/10 (1); XV/9 (4); XV/10 (12); XV/11 (1); XVI/9 (2)
AFR	III/8 (10); III/9 (9*); III/10 (1)	III/8 (8*); III/9 (5)	III/8 (2*); III/9 (1)	III/8 (4*); III/9 (4)	III/8 (15); III/9 (5)
PFR	13 (19*); 14 (1)	12 (7*); 13 (6)	12 (2*); 13 (1)	12 (3*); 13 (5)	12 (14); 13 (6)
V	13/16 (4); 14/15 (13); 14/16 (3*)	14/14 (1); 14/15 (11*); 14/16 (1)	14/15 (2*); 14/16 (1)	13/16 (2); 14/15 (6*)	14/15 (10); 14/16 (10)
LongL	31 (4); 32 (12*); 33 (4)	30 (2); 31 (3); 32 (7*); 33 (1)	31 (1); 32 (1*); 33 (1)	31 (4*); 32 (3); 33 (1)	30 (2); 31 (5); 32 (11); 33 (2)
LatL	19/13 (1); 20/11 (3); 20/12 (5); 21/9 (2); 21/11 (2); 21/12 (1*); 21/13 (2); 22/11 (1); 22/12 (2)	20/12 (1); 20/13 (1); 21/9 (1); 21/10 (2); 21/12 (6); 21/14 (1*); 22/11 (1)	21/7 (1*); 21/8 (1); 22/9 (1)	20/9 (1*); 20/12 (1); 21/11 (1); 21/12 (1); 21/13 (1); 22/11 (1); 22/12 (1)	19/10 (1); 19/12 (1); 20/10 (1); 20/11 (1); 20/12 (1); 20/13 (2); 20/14 (1); 20/15 (1); 21/9 (1); 21/10 (2); 21/7 (1); 21/11 (3); 21/12 (1); 21/15 (1); 22/11 (1); 22/12 (1)
D-UllL	5 (10*); 6 (10)	5 (8*); 6 (5)	6 (2*); 7 (1)	5 (3); 6 (5*)	4 (1); 5 (9); 6 (9); 7 (1)
ULL-A	9 (7); 10 (5*); 11 (8)	8 (2*); 9 (8); 10 (3)	10 (3*)	10 (7*); 12 (1)	9 (7); 10 (9); 11 (2); 12 (1)
P-V	5 (9*); 6 (8); 7 (3)	5 (4*); 6 (5); 7 (4)	5 (1*); 6 (2)	5 (4); 6 (3*); 7 (1)	4 (2); 5 (2); 6 (9); 7 (7)
ChS	2/7 (2); 2/9 (2); 3/7 (4); 3/8 (6*); 3/9 (5); 4/8 (1)	3/7 (4*); 3/8 (5); 3/9 (3); 4/9 (1)	2/7 (1*); 2/8 (2)	2/6 (1); 2/8 (2*); 3/7 (1); 3/8 (1); 3/9 (1); 3/10 (1)	2/8 (1); 2/9 (4); 3/7 (1); 3/8 (7); 3/9 (5); 3/10 (1); 4/7 (1)

IQR interquartile range, *n* number

Asterisks indicate an alternate number of observations for this measurement or count

Fig. 7 *Haplochromis taurinus*, holotype; 133.8 mm SL; BMNH 1933.2.23.406



subequilateral, bluntly pointed, and with a clear flange (i.e. a thin and flat protrusion, laterally implanted on cusp). Minor cusps stout and slightly horizontally inclined. In upper jaw, necks slightly recurved and posteriormost teeth tricuspid. In lower jaw, necks straight and both major and minor cusps often anteriorly curved. Tooth bands in both jaws broadly rounded and short (i.e. posterior thirds of premaxillae bear no teeth). Dental arcades narrow with 1–3 (mostly 2) rows of small and tricuspid inner teeth; one outer tooth width spacing between inner and outer rows. Number of inner tooth rows quickly diminish posteriorly, until only outer row remains. Teeth in all rows closely and consistently set, bases of outer teeth almost touching each other. Necks of all teeth deeply embedded in oral mucosa. In lower jaw, crowns of all teeth mostly visible (Fig. 5a) and lower lip uniformly thickened but not dorsally enlarged; hence lip reaches same height as oral mucosa. Anterior part of upper lip thin and crowns visible. Laterally, upper lip quickly thickens and covers teeth completely.

Lower pharyngeal bone 1.1 times longer than broad ($n = 4$) and shallow (Fig. S3). Keel narrows anteriorly in lateral view, giving it an acute outline. Pharyngeal teeth with straight and cylindrical necks and bicuspid crowns. Major cusps straight and pointed with blunt tips, cusp gaps slightly concave, and minor cusps very small. Teeth posteriorly in two median rows slightly stouter. Posterior edge of bone set with 23–27 stout and bluntly pointed teeth with slightly hooked major cusps and reduced minor cusps.

Ceratobranchial gill rakers on outer row of first gill arch unifid, short, and pointed anteriorly, becoming longer, blunt, and in some specimens bi- to quadrid

posteriorly. Epibranchial gill rakers unifid, slender, and pointed.

Caudal fin emarginate. Dorsal and anal fins almost reach caudal fin base in females, extend to between caudal fin base and first quarter of caudal fin in males. Pelvic fins extend to between anus and second spine of anal fin in females, up to second branched ray of anal fin in males. Pectoral fins extend to between genital opening and second spine of anal fin in both sexes.

Live colour pattern

Mature males (> 100 mm SL): Body with a metallic shine (Figs. 6a, S2c). Dorsum, dorsal part of caudal peduncle, snout, and chest blue. Belly, posterior part of flanks, and ventral half of caudal peduncle gold-yellow. Opercula and anterior part of flanks dark red. Lachrymal stripes and a mental blotch present, while vertical preopercular, nostril, and interorbital stripes only faintly visible. Pectoral fins hyaline to dusky, pelvic fins black, and dorsal and anal fins grey-blue. Anal fin with 3–7 orange-brown small egg spots (i.e. size equal to distance between adjacent fin rays). Branched rays of dorsal and caudal fins often weakly maculated (i.e. dotted lines on membranes between fin rays).

Females and juveniles (< 85 mm SL): Dorsum blue-green, flanks yellow-green, and belly white (Fig. S2d). Caudal fin yellowish, pectoral fins yellow-green, and dorsal, pelvic, and anal fins hyaline to yellow. Anal fin with vague, orange spots that resemble egg spots. Lips yellow-green and a mental blotch and faint nostril, interorbital, and lachrymal stripes present.

Preserved colour pattern in alcohol

Body grey-brownish, dorsally darker (Fig. S2a). Belly whitish in females and juveniles, blackish in mature males. A mental blotch, vertical preopercular, and lachrymal stripes present. Interorbital and nostril stripes and a nape band faintly visible. Posterior part of dorsal fin and upper part of caudal fin often weakly maculated. Anal fin of mature males with 3–7 faint egg spots.

Distribution and ecology

Endemic to the Lake Edward system. It has a paedophagous diet. The stomachs of five specimens contained fry of other cichlids. One specimen had only Ephemeroptera larvae in its stomach, implying an at least occasional opportunistic feeding habit. The gut is short (119–222% SL, $n = 10$), in accordance with its predatory ecology.

Differential diagnosis

Haplochromis taurinus differs from all *Haplochromis* species of Lake Edward system by its anteriorly curved outer teeth in the lower jaw. Distinct from all other known paedophagous species within these lakes by its larger eyes [32.9–40.2 (35.7) vs. 29.0–34.7% HL] and outer teeth with conical necks and bicuspid crowns with major cusps that bear a clear flange versus cylindrical to constricted necks and uni-, bi-, or weakly tricuspid crowns that, in large specimens (> 100 mm SL), bear no flange. Similar to *H. molossus* sp. nov. and *H. gracilifur* sp. nov. by its rounded jaws and small lachrymal bones. Distinct from *H. gracilifur* sp. nov. by its deeper caudal peduncle [73.9–88.1 (79.6) vs. 62.9–66.4 (65.0) % CPL] and longer premaxillary pedicel [23.5–26.2 (25.1) vs. 18.1–21.6 (20.3) % HL]; from *H. molossus* sp. nov. by its more slender jaws [51.4–72.7 (60.9) vs. 67.0–87.0 (76.6) % L JL], more gentle sloping snout [35–40 vs. 45–55°], and steeper gape inclination [40–45 vs. 20–30°]. Easily separated from *H. relictidens* sp. nov. and *H. paradoxus* by its smaller lachrymal bones [11.5–16.4 (14.1) vs. 15.8–18.4 (17.4) and 14.7–21.5 (17.7) % HL, respectively] and broadly rounded lower jaw versus anteriorly slender lower jaw. In addition, it has more outer teeth in the upper jaw than *H. relictidens* sp. nov. and fewer than

H. paradoxus [23–39 (median 32) versus 16–26 (18) and 36–65 (51), respectively]. Mature males of *H. taurinus* have metallic-blue bodies with dark red flanks versus colour pattern different in all other paedophagous species.

Haplochromis molossus sp. nov.

(Figures 2b, 6a, 8, S4, and S5; Tables 1, 2)

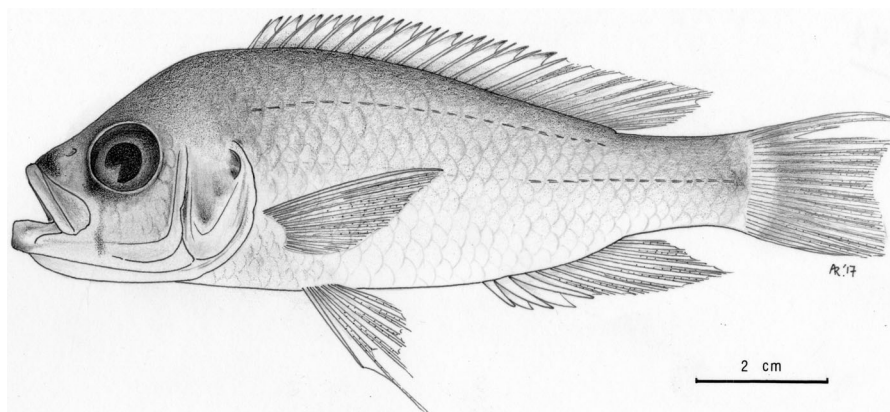
Holotype

MRAC 2016.036.P.0046; Mukutu Kihinga, rocky offshore of Mweya, Lake Edward: 0°11'31.2"S 29°52'26.4"E; Exp. HIPE 1; 23/10/2016 [♀ 104.2 mm SL].

Paratypes

IRSNB 12898; Lac Edouard: au large de la riv. Kigera: 0°29'42"S 29°38'14"E; Miss. KEA; 25/04/1953 [$n = 1$; ♂ 74.6 mm SL]. IRSNB 12902; Lac Edouard: au large de la riv. Talia: 0°31'05"S 29°20'26"E; Miss. KEA; 23/04/1953 [$n = 1$; ♂ 76.0 mm SL]. IRSNB 12903; Lac Edouard: au large de la riv. Talia: 0°31'05"S 29°20'26"E; Miss. KEA; 23/04/1953 [$n = 1$; ♀ 77.5 mm SL]. IRSNB 12904; Lac Edouard: au large de la riv. Kigera: 0°29'42"S 29°38'14"E; Miss. KEA; 25/04/1953 [$n = 1$; ♀ 80.0 mm SL]. IRSNB 12906; riv. Semliki: baie Copile: 0°08'27"S 29°36'04"E; Miss. KEA; 11/08/1953 [$n = 1$; ♂ 102.3 mm SL]. MRAC 2016.035.P.0045; Katoko breeding ground, soft substrate offshore of Katwe, Lake Edward: 0°09'43.2"S 29°53'16.8"E; Exp. HIPE 1; 20/10/2016 [$n = 1$; ♀ 105.8 mm SL]. MRAC 2016.035.P.0047; mouth of Kazinga Channel, Lake Edward: 0°12'32.4"S 29°53'06.0"E; Exp. HIPE 1; 24/10/2016 [$n = 1$; ♂ SL 77.8 mm]. MRAC 2016.035.P.0048–49; Akika island, Lake George, Lake Edward system: 0°01'26.7"S 30°09'38.2"E; Exp. HIPE 1; 07/11/2016 [$n = 2$; ♂ 92.2; ♂ 93.5 mm SL]. MRAC 2017.006.P.001; Rwenshama, rocky shore, Lake Edward: 0°24'05.7"S 29°46'35.1"E; Exp. HIPE 2; 25/03/2017 [$n = 1$; ♂ 82.6 mm SL]. MRAC 2017.006.P.002; Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; Exp. HIPE 2; 30/03/17 [$n = 1$; ♀ 109.4 mm SL]. MRAC 2017.006.P.0003; Kayanja offshore, Lake Edward:

Fig. 8 *Haplochromis molossus* sp. nov., holotype; 104.2 mm SL; MRAC 2016.035.P.0046



0°05'34.8"S 29°45'28.8"E; Exp. HIPE 2; 31/03/2017 [$n = 1$; ♂ 78.4 mm SL].

Etymology

Specific name derived from the Latin ‘molossus’ and used in apposition. It relates to the ‘pug-head’ habitus (i.e. flat face and broad, rounded jaws with a gentle gape inclination) of the species. Pugs belong to mastiff-like dogs, also called Molossus dogs due to their ancestral origin as dogs of Molossians. This ancient Greek tribe got its name from Μολοσσός (Molossos), a figure in Greek mythology.

Description

Maximum size 109.4 mm SL. Body relatively slender, head short and concave, snout steeply sloping (45–55°) (Fig. 8). Jaws long, very wide, broadly rounded, isognathous, and with a gentle gape inclination (20–30°). Maxillae bullate (i.e. posteriorly enlarged and exposed) and reach posteriorly to vertical through anterior margin of pupil. Lips and oral mucosa firmly thickened. Neurocranium of generalised *Haplochromis* type; supraoccipital crest high and slightly convex (Fig. S4b). Flank scales ctenoid; chest scales smaller than flank scales, size transition gradual.

Outer oral teeth small, deeply embedded in oral mucosa, and hidden behind lower lip, which extends dorsally over oral mucosa (Fig. 2b). Necks stout, straight, cylindrical, and with straight implantations. Major cusps isocline; minor cusps point straight up. In large specimens (> 100 mm SL) outer teeth weakly bi- to unicuspid with an intercalation of some weakly tricuspid teeth anteriorly and laterally; anterior in

lower jaw major cusps straight to very slightly anteriorly curved, minor cusps implanted slightly labially on necks. Outer teeth of small specimens (< 80 mm SL) unequally bicuspid. In all specimens, posteriormost outer teeth in both jaws very small and tricuspid. All outer teeth closely set; inter-tooth distance of one tooth width. Dental arcades slender; 1–2 tooth widths between outer and inner rows. Inner teeth small, tricuspid, and irregularly set in 1–2 rows that diminish posteriorly, until only outer row remains. Tooth bands short (i.e. posterior thirds of premaxillae bear no teeth).

Lower pharyngeal bone deep, and 1.0–1.1 times broader than long ($n = 3$; Fig. S5). Pharyngeal teeth slender and bicuspid; major cusps acute and straight, cusp gaps absent to small, and minor cups small. Teeth posteriorly in two median rows stouter. Posterior edge of bone set with 24–28 enlarged teeth with blunt and slightly recurved major cusps and reduced minor cusps.

Ceratobranchial gill rakers on outer row of first gill arch anteriorly stout, short, unifid, and pointed; posteriorly becoming longer, but still rather short, slightly anvil-shaped, and in some specimens bi- to quadrid. Epibranchial gill rakers stout, short, unifid, and pointed.

Caudal fin emarginate. Dorsal and anal fins reach to just before caudal fin base in females, maximally just exceeding this point in males. Pectoral fins extend to genital opening; pelvic fins reach to between genital opening and second spine of anal fin in all specimens.

Live colour pattern

Mature males (> 90 mm SL): Flanks, dorsum, snout, and caudal and pectoral fins olive-green (Figs. 6b,

S4c). On flanks, 6–8 black-turquoise vertical stripes present. Belly and caudal peduncle dark-turquoise. Cheeks, opercula, and lower jaw turquoise. Anal fin hyaline with a reddish hue over spines, and three small, orange egg spots (i.e. size equal to distance between adjacent fin rays) on straight line. Dorsal fin dusky, lappets black (i.e. extensions of membranes between spines); caudal fin maculated (i.e. dotted lines on membranes between fin rays). Eyes olive-green and black. Mental blotch, lachrymal stripes, and nape band present.

Females and juveniles (< 75 mm SL): Body with vertical colour-gradient from olive-green dorsally to white ventrally (Fig. S4d). Dorsal part of head blueish, cheeks white, and snout dusky. Mental blotch present, nape band and lachrymal stripes faintly visible. Lappets of dorsal fin and eyes dark. Pectoral fins olive-green, all other fins hyaline-green, and posterior tips of dorsal, caudal, and pelvic fins hyaline.

Colour pattern in alcohol

Body brownish (Fig. S4a), in mature males, flanks with 6–8 vertical stripes, caudal fins maculated, and anal fins bearing three small egg spots on a straight line. Pelvic fins hyaline in females and black in males. In all specimens, pectoral fins dusky, lappets of dorsal fin black, and anal fin uniformly hyaline. Nostril and interorbital stripes faint and clear mental blotch present. Lachrymal stripes clear in males, faint in females, and in all specimens, these continue, over eyes, into faint supraorbital stripes.

Distribution and ecology

Endemic to the Lake Edward system. It has a paedophagous diet. The stomachs of three dissected specimens contained solely cichlid embryos. The gut is short (90–169% SL, $n = 5$), in accordance with its predatory lifestyle.

Differential diagnosis

Haplochromis molossus sp. nov. differs from all other known paedophagous *Haplochromis* within these lakes by its broader oral jaws [67.0–87.0 (76.6) vs. 42.0–72.7 (48.6–64.9) % L JL], steeper snout (45–55 vs. 10–40°), and more gentle gape inclination (20–30° vs. 40–55°). Similar to *H. taurinus* and *H. gracilifur*

sp. nov. by its rounded jaws and small lachrymal bones. Further distinct from *H. taurinus* by its smaller eyes [29.8–33.9 (32.3) vs. 32.9–40.2 (35.7) % HL] and from *H. gracilifur* sp. nov. by its deeper caudal peduncle [65.5–83.6 (75.2) vs. 62.9–66.4 (65.0) % CPL], longer premaxillary pedicel [21.6–25.8 (23.4) vs. 18.1–21.6 (20.3) % HL], and higher numbers of infraorbital cheek scales [3–4 vs. 2] and lower lateral line scales [9–14 vs. 7–9]. In addition, it has more outer teeth in upper jaw than *H. relictidens* sp. nov. and fewer than *H. paradoxus* [22–34 (median 29) vs. 16–26 (18) and 36–65 (51), respectively]. Distinct from both by smaller lachrymal bones [13.3–17.0 (14.6) vs. 15.8–18.4 (17.4) and 14.7–21.5 (17.7) % HL, respectively]. Further separated from *H. relictidens* sp. nov. by its broadly rounded lower jaw versus, pointed lower jaw. Mature males of *H. molossus* have green bodies and flanks with 6–8 vertical stripes versus different colour patterns in all other paedophages.

Haplochromis gracilifur sp. nov.

(Figures 2c, 6c, 9, S6, and S7; Tables 1, 2)

Holotype

MRAC 2017.006.P.0004; Kayanja offshore, Lake Edward: 0°05′34.8″S 29°45′28.8″E; Exp. HIPE 2; 31/03/2017 [♂ 85.7 mm SL].

Paratypes

MRAC 2017.006.P.0005–6; Kayanja offshore, Lake Edward: 0°05′34.8″S 29°45′28.8″E; Exp. HIPE 2; 31/03/2017 [$n = 2$; ♂ 68.1; ♂ 102.8 mm SL].

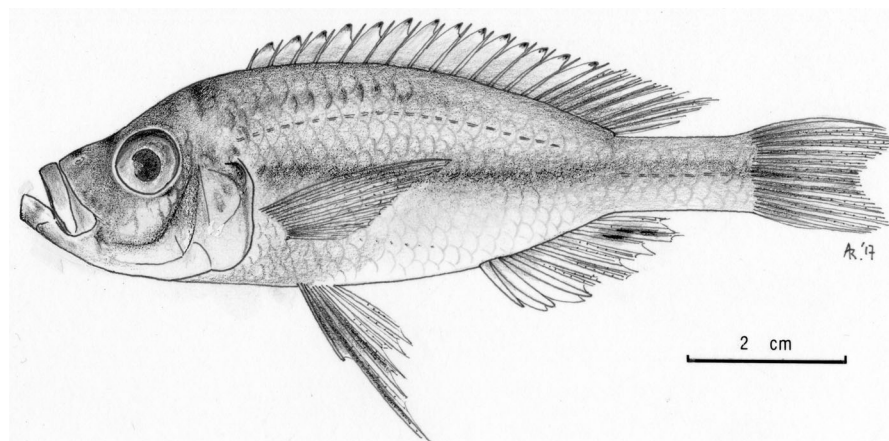
Etymology

Specific name derived from Latin ‘gracilis’, slender, and ‘fur’, thief. In reference to its slender body and paedophagous diet, it steals fry from buccal cavities of mouthbrooding cichlids. Specific name noun in apposition.

Description

Maximum size 102.8 mm SL. Body very slender, caudal peduncle slim, and anal fin base short (Fig. 9).

Fig. 9 *Haplochromis gracilifur* sp. nov., holotype; 85.7 mm SL; MRAC 2017.006.P.0004



Head concave above eyes, snout and premaxillary pedicel short and slope very gently (10–20°), and dorsal part of head steep (40–50°). Oral jaws long, rounded, and isognathous. Maxillae bullate (i.e. posteriorly enlarged and exposed) and reach posteriorly to vertical through anterior edge of eyes. Oral mucosa and lips firmly thickened. Neurocranium of generalised *Haplochromis* type; supraoccipital crest high and slightly convex (Fig. S6b). Lower lateral line scales few; flank scales ctenoid; chest scales smaller than flank scales, size transition gradual.

Outer oral teeth very small, deeply embedded in oral mucosa, and hidden behind lower lip, which extends over oral mucosa. Necks slender, slightly recurved, with a circular cross section, and gradually expanding into the broader crowns (Fig. 2c). Crowns slightly laterally compressed and bicuspid. Posterior-most outer teeth in both jaws tricuspid. Crowns of small specimens (< 70 mm SL) with distinct cusp gaps, major cusps strongly truncated and blunt, and minor cusps long, slender, rounded, point straight up, and reach same height as major cusps. Crowns of large specimens (> 100 mm SL) with major cusps weakly truncated and minor cusps small but relatively long, with slightly horizontal orientations. Tooth bands short (e.g. posterior third of premaxillae bear no teeth). Dental arcades very slender, outer rows separated by one tooth width from 1–2 rows of tricuspid inner teeth. Inner rows diminish posteriorly, until only outer row remains.

Lower pharyngeal bone 1.0–1.1 times broader than long ($n = 2$), relatively shallow posteriorly, and keel equally deep to distinctly deeper than posterior part of bone (Fig. S7). Pharyngeal teeth uni- to weakly

bicuspid and slender. Major cusps acutely pointed, cusp gaps slightly concave, minor cups very small to absent. All rows with similar-sized teeth. Posterior edge of bone set with 30–32 teeth with acutely rounded major cusps and small minor cusps.

All gill rakers on outer row of first gill arch short, stout, and unifid.

Caudal fin emarginate and its posterior margin dorsally and ventrally rounded. Dorsal and anal fins extend to 1–2 scale lengths before caudal fin base. Pectoral fins of all specimens and pelvic fins of juveniles reach to just before anus; pelvic fins extend to anal fin base in males.

Live colour pattern

Mature males (> 100 mm SL): Dorsum, caudal peduncle, and caudal and pectoral fins olive-green (Figs. 6c, S6c). Snout slightly darker with a blue hue dorsally. Eyes dark and flanks, opercula, cheeks, extension of caudal fin, and spines of anal fin bright red. Belly and branched rays of anal fin whitish, latter with three relatively small, bright yellow to orange egg spots (i.e. size slightly larger than distance between adjacent fin rays). Branched rays of dorsal fin hyaline and with black lappets (i.e. extensions of membranes between spines). Two longitudinal stripes just above upper and lower lateral lines. Lower one runs from eye, over opercular blotch, to caudal fin base; upper stripe runs over anterior part of dorsum. Lachrymal, nasal, interorbital, and supraorbital stripes, nape band, and mental notch present.

Females and juveniles (< 70 mm SL): Female colour pattern unknown. Juveniles body and pelvic

fins white-gold. Head and body without distinct markings, except for opercular blotches. Dorsal fin dusky, caudal fin dark-greenish, and anal fin yellow (Fig. S6d).

Colour pattern in alcohol

Body brownish (Fig. S6a), mature males with two longitudinal stripes above upper and lower lateral line. Lachrymal, nasal, interorbital, and supraorbital stripes, nape band, and mental blotch present. Markings of preserved females unknown; juveniles without distinct markings, except opercular blotch.

Distribution and ecology

Endemic to the Lake Edward system, currently only known from Lake Edward proper. It has a paedophagous diet. The stomach of the holotype contained 13 cichlid eggs, and those of two other examined specimens were empty. The digestive tract is short (82–126% SL, $n = 3$), in accordance with its predatory lifestyle.

Differential diagnosis

Haplochromis gracilifur sp. nov. differs from all other known paedophages from these lakes by its shorter premaxillary pedicel [18.1–21.6 (20.3) vs. 21.6–29.1 (23.4–26.2) % HL], smaller number of lower lateral line scales [7–9 vs. 9–15, exceptionally 7], and bicuspid outer teeth with long minor cusps. Resembles *H. molossus* sp. nov. and *H. taurinus* by its rounded jaws and small lachrymal bones. Differs from both by its more slender body [30.2–34.8 (32.4) vs. 33.5–38.6

(35.1) and 33.9–40.1 (36.0) % SL, respectively]. Further distinct from *H. taurinus* by its shorter lower jaws [42.4–44.7 (43.5) vs. 44.5–51.3 (47.7) % HL] and smaller eyes [29.0–32.3 (31.0) vs. 32.9–40.2 (35.7) % HL]; from *H. molossus* sp. nov. by its more slender jaws [61.9–69.4 (64.9) vs. 67.0–87.0 (76.6) % L JL], steeper gape inclination (40–50 vs. 20–30°), and more gentle snout inclination [10–20° vs. 45–55°]. In addition, it has more outer teeth in upper jaw than *H. relictidens* sp. nov. and fewer than *H. paradoxus* [26–35 (median 26) vs. 16–26 (18) and 36–65 (51), respectively]. Clearly distinct from both by its smaller lachrymal bones [13.7–14.3 (14.0) vs. 15.8–18.4 (17.4) % HL and 14.7–21.5 (17.7), respectively]. Further separated from *H. relictidens* sp. nov. by lower jaws rounded, whereas pointed in latter. Males of *H. gracilifur* sp. nov. have bright red flanks with two horizontal stripes versus different colour patterns in all other paedophages.

Haplochromis relictidens sp. nov.

(Figures 2d, 5b, 6d, 10, S8, and S9; Tables 1, 2)

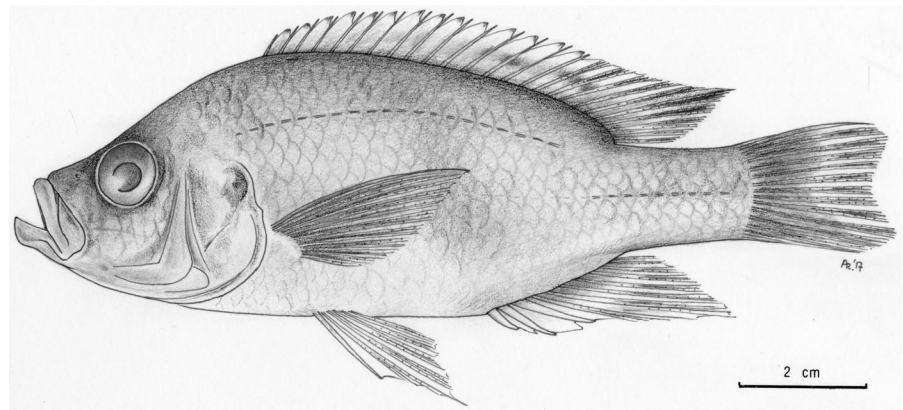
Holotype

MRAC 2017.006.P.0007; Mouth of Kazinga Channel, hard substrate, Lake Edward: 0°12'14.4"S 29°52'37.2"E; Exp. HIPE 2; 24/03/2017 ♀ 112.9 mm SL].

Paratypes

IRSNB 12902; Lac Edouard: au large de la riv. Talia: 0°31'05"S 29°20'26"E; Miss. KEA; 23/04/1953

Fig. 10 *Haplochromis relictidens* sp. nov., holotype; 112.9 mm SL; MRAC 2017.006.P.0007



[$n = 2$; ♂ 105.1; ♂ 108.2 mm SL]. IRSNB 12905; Lac Edouard: Baie de Kasindi: 0°04'35"S 29°42'31"E; Miss. KEA; 2/06/1953 [$n = 1$; ♂ 90.5 mm SL]. MRAC 2016.035.P.0042; Mukutu Kihinga, rocky offshore of Mweya, Lake Edward: 0°11'31.2"S 29°52'26.4"E; Exp. HIPE 1; 23/10/2016 [$n = 1$; ♂ 105.0 mm SL]. MRAC 2016.035.P.0043; mouth of Nyamugasani river, coral reef, hard substrate, Lake Edward: 0°10'08.4"S 29°49'37.2"E; Exp. HIPE 1; 21/10/2016 [$n = 1$; ♂ 105.0 mm SL]. MRAC 2016.035.P.0044; Akika island, Lake George, Lake Edward system: 0°01'26.7"S 30°09'38.2"E; Exp. HIPE 1; 07/11/2016 [$n = 1$; ♀ 73.6 mm SL]. MRAC 2017.006.P.0008; Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; Exp. HIPE 2; 30/03/2017 [$n = 1$; ♂ 105.9 mm SL].

Other material examined

MRAC 2017.006.P.0009; Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; Exp. HIPE 2; 30/03/2017 [$n = 1$; ♂ 97.6 mm SL; excluded from the type series due to a somewhat deformed snout].

Etymology

Specific name of *H. relictidens* sp. nov. derived from Latin 'relinquere', to relinquish, and 'dens', tooth and used in apposition. It refers to the decrease in number of outer teeth in both jaws with size.

Description

Maximum size 112.9 mm SL. Head concave and premaxillary pedicel slopes gently (10–30°) (Fig. 10). Jaws long and isognathous and gape inclination steep (40–50°). Jaws with a unique morphology; lower jaw relatively broad but anteriorly pointed and upper jaw rounded (Fig. 5b). Hence, upper jaw anteriorly broader than lower jaw, rendering anterolateral part of upper jaw visible in ventral view. In small specimens (< 85 mm SL), both jaws rounded. In all specimens, maxillae bullate (i.e. posteriorly enlarged and exposed) and extend posteriorly to between verticals through anterior margins of orbita and pupils. Lips and oral mucosa firmly thickened. Neurocranium of generalised *Haplochromis* type; supraoccipital crest high and pyramidal (Fig. S8b). Flank scales ctenoid; chest scales smaller than flank scales, size transition gradual.

All oral teeth very small and deeply embedded in thickened oral mucosa, at most, only tips of outer teeth visible (Fig. 2d). Especially upper lip laterally thickened, covering all teeth (Fig. 5b). Necks slender, cylindrical, slightly recurved, and gradually expanding into crowns. Crowns broad, slightly laterally compressed, and stout. Outer teeth of small specimens (< 80 mm SL) bicuspid; crowns equilateral, acutely rounded, and with a small flange (i.e. a small, very thin, lateral protrusion on major cusp); minor cusps relatively large and rounded. Outer teeth of large specimens (> 90 mm SL) uni- to weakly bicuspid; both major and minor cusps subequilateral to equilateral, very short, stout, and blunt to rounded. Outer teeth in both jaws of all specimens few and reduce in number with size (Fig. 3). Especially in largest specimens (> 100 mm SL), anterior teeth in outer rows missing and empty tooth sockets often absent. Outer teeth widely and very irregularly set; inter-tooth distance at least one tooth width. Inner teeth small and tricuspid; distinct space of 1–3 tooth widths between inner and outer rows. Tooth bands short (e.g. posterior thirds of premaxillae bear no teeth), inner teeth diminish posteriorly, until only outer rows remain.

Lower pharyngeal bone 1.0–1.1 times longer than broad ($n = 3$) (Fig. S9). Pharyngeal teeth slender, major cusps acute, cusp gap straight, and minor cusps reduced or absent. Teeth posteriorly in two median rows stout with blunt major cusps. Posterior edge of bone set with 24–26 enlarged and stout teeth with blunt major cusps and reduced minor cusps.

Gill rakers on outer row of first gill arch short, slender, unifid, and acute. Antermost gill rakers very short, posteriormost ceratobranchial gill rakers with a slight anvil-like shape.

Caudal fin weakly emarginate to almost subtruncate. Dorsal and anal fins reach to between a scale length before and past caudal fin base. Pectoral fins extend to between anus and second spine of anal fin. Pelvic fins extend maximally to first spine of anal fin in females and between first and second spine in males.

Live colour pattern

Mature males (> 95 mm SL): Flanks, opercula, and cheeks bright red (Figs. 6d, S8c). Dorsal and ventral borders of cheeks and lower jaw blue-green. Dorsal part of body, snout, caudal peduncle, and dorsal and pectoral fins green-gold. Body whitish ventrally and

flanks with 4–5 very faint vertical stripes. Dorsal fin with black lappets (i.e. extensions of membranes between spines). Anal fin reddish between spines, hyaline between branched rays, and with 2–3 bright-orange small egg spots (i.e. size of distance between adjacent fin rays) with black borders. Anterior half of caudal fin black and separated by a vertical, narrow, yellow stripe from hyaline and black-speckled posterior part. Eyes whitish and with bright yellow inner rings. Lachrymal stripes reduced to spots ventrally of eyes.

Females and juveniles (< 75 mm SL): Dorsally, body green-gold over its entire length, gradually merging into whitish ventral part (Fig. S8d). Lower jaw and horizontal arms of preopercula blue-green. Eyes whitish and with yellow inner rings. Pectoral, dorsal, and anal fins hyaline and with yellowish bases. Anterior part of caudal fin black, separated by a vertical, narrow, yellow stripe from hyaline, black-speckled posterior part.

Colour pattern in alcohol

Body brownish, flanks of mature males with 4–5 very faint vertical stripes, and anal fin with 2–3 vague egg spots. Nape band, interorbital and nostril stripes faint. Lachrymal stripes reduced to faint spots ventrally of eyes (Fig. S8a). Dorsal and caudal fins dark, with abrupt transitions to their hyaline posterior extensions.

Distribution and ecology

Endemic to the Lake Edward system. It has a paedophagous diet. The stomach contents of four

specimens all consisted of numerous cichlid eggs and/or embryos. The gut is very short (88–158% SL, $n = 3$), in accordance with its predatory ecology.

Differential diagnosis

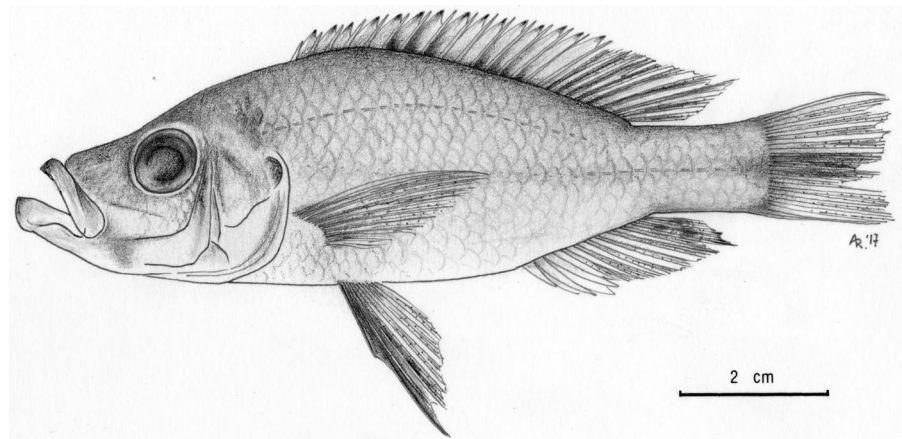
Haplochromis relictidens sp. nov. differs from all other known species from the Lake Edward system by its unique lower jaw morphology in large specimens (> 90 mm SL): lower jaw acute and upper jaw rounded, rendering anterolateral parts of upper jaw visible in ventral view. Outer teeth very small, blunt to rounded, widely and irregularly set, few [16–26 (median 18) vs. 22–65 (29–51)], and decreasing in number with size. Differs further from *H. taurinus*, *H. molossus* sp. nov., and *H. gracilifur* sp. nov. by its more slender and acute lower jaw [50.1–59.7 (54.7) vs. 51.4–72.7 (60.9), 67.0–87.0 (76.6), and 61.9–69.4 (64.9) % L JL, respectively], its larger lachrymal bones [15.8–18.4 (17.4) vs. 11.5–16.4 (14.1), 13.3–17.0 (14.6), and 13.7–14.3 (14.0) % HL, respectively]. Further distinct from *H. paradoxus* by its broader head [47.7–54.7 (50.4) vs. 41.7–51.2 (44.9) % HL]. Mature males green-gold with bright red flanks and very faint vertical stripes versus different colour pattern in all other paedophagous species.

Haplochromis paradoxus (Lippitsch & Kaufman, 2003)

(Figures 2e, 5c, 6e, 11, S10, and S11; Tables 1, 2)

Pyxichromis paradoxus Lippitsch & Kaufman, 2003

Fig. 11 *Haplochromis paradoxus*, male; 91.1 mm SL; MRAC 2017.006.P.0011



Holotype (not examined)

MCZ 135757; Katwe Town, Lake Edward: 0°08'51"S 29°53'01"E; 26/06/1994 [A97365; ♂ 74.5 mm SL].

Paratype (not examined)

MCZ 135757; Katwe Town, Lake Edward: 0°08'51"S 29°53'01"E; 26/06/1994 [$n = 1$, A97364; ♂ 73.6 mm SL].

Material examined

IRSNB 13482; 2–3 km à l'Ouest de Kiavinionge: 0°09'04"S 29°34'37"E; 1/06/1953 [$n = 7$; ♀ 120.2; ♀ 124.3; ♂ 129.7; ♂ 131.4; ♀ 131.8; ♀ 140.2; ♀ 142.4 mm SL]. IRSNB 15644; Lac Edouard; 1952–1953 [$n = 3$; ♂ 133.2; ♀ 135.3; ♀ 140.3 mm SL]. MRAC 2016.035.P.0023–36 & 0037–41; Mukutu Kihinga, rocky offshore of Mweya, Lake Edward: 0°11'31.2"S 29°52'26.4"E; Exp. HIPE 1; 23/10/2016 [$n = 6$; ♂ 70.1; ♂ 76.9; ♂ 82.5; ♂ 82.9; ♂ 87.3; ♂ 96.8 mm SL]. MRAC 2017.006.P.0010; Rwenshama, rocky shore, Lake Edward: 0°24'05.7"S 29°46'35.1"E; Exp. HIPE 2; 25/03/2017 [$n = 1$; ♀ 94.5 mm SL]. MRAC 2017.006.P.0011; Rwenshama, rocky shore, Lake Edward: 0°24'05.7"S 29°46'35.1"E; Exp. HIPE 2; 26/03/2017 [$n = 1$; ♂ 91.1 mm SL]. MRAC 2017.006.P.0012–13; Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; Exp. HIPE 2; 31/03/2017 [$n = 2$; ♀ 90.6; ♀ 94.8 mm SL].

Etymology

Specific name derived from Greek 'παράδοξος', paradoxical, strange, incredible. It refers to its bizarre morphology (i.e. steep gape and gentle premaxillary pedicel inclination) and occurrence in Lake Edward. Lippitsch & Kaufman (2003) recognised its resemblance to *Pyxichromis* sensu Greenwood (1980), only known from lakes Kyoga and Victoria. Its distribution struck them as a biogeographical paradox.

Description

Maximum size 142.4 mm SL. Body slender, dorsal outline slightly caret-shaped (Δ), and head concave in small specimens (< 120 mm SL) (Fig. 11). Body deep, dorsal outline curved, and head straight to

slightly concave in large specimens (> 150 mm SL). Head long and slender; premaxillary pedicel slopes very gentle ($10\text{--}30^\circ$); dorsal part of head slopes steep ($30\text{--}40^\circ$). Snout long and acute, and lachrymal bones deep. Jaws long, slender, acute, and prognathous; gape inclination very steep ($40\text{--}55^\circ$). Premaxillae relatively short and beaked (i.e. anteriormost part enlarged labially) (Fig. 5c). Maxillae bullate (i.e. posteriorly enlarged and exposed) and reach posteriorly to just before vertical through anterior edge of eyes. Neurocranium of generalised or nearly generalised *Haplochromis* type; supraoccipital crest relatively low and slightly wedge-shaped (Fig. S10b). Typical piscivorous sensu stricto sensu Witte & Van Oijen (1990) appearance, except in oral tooth morphology (see further). Lips and oral mucosa slightly and firmly thickened. Flank scales ctenoid; chest scales smaller than flank scales, size transition gradual.

Outer oral teeth small and strongly recurved, giving crowns a horizontal orientation (Fig. 2e). Each tooth lays, over its entire length, pressed against oral mucosa. Bases of necks stout, with straight implantations, and embedded in oral mucosa. Necks slightly constricted halfway their lengths (i.e. hourglass-shaped) and strongly recurved. Crowns with broad bases and horizontal orientations. Outer teeth of large specimens (> 75 mm SL) weakly tricuspid with an intercalation of few unicuspid teeth anteriorly and laterally; major cusps short, equilateral, and bluntly pointed. Outer teeth of small specimens (< 75 mm SL) bicuspid with long minor cusps and equilateral major cusps that bear a flange (i.e. a small and flattened protrusion, laterally on cusp). In all specimens, posteriormost 2–5 teeth in upper jaw enlarged, unicuspid, acutely pointed, and only slightly recurved. Tooth bands long, and all outer teeth closely set and comparable in size (Fig. 5c). Inner teeth small, tricuspid, and strongly recurved. Dental arcades slender and diminishing quickly over anterior thirds of each jaw, until only one inner and outer rows remain posteriorly. A space of one tooth width separates outer and 2–3 inner tooth rows.

Lower pharyngeal bone 1.0–1.1 times longer than broad ($n = 3$) and becomes relatively deep posteriorly (Fig. S11). Pharyngeal teeth with slender necks, expanding into slightly broader bases of crowns. Crowns bi- to weakly bicuspid; major cusps acutely pointed and slightly recurved, cusp gaps large and concave, minor cusps absent to small. Teeth

posteriorly in two median rows stouter. Posterior edge of bone set with 26–28 enlarged and stout teeth, bluntly pointed major cusps, no cusp gaps, and reduced minor cusps.

Gill rakers on outer row of first gill arch unifid, slender, and rather short. Posterior ceratobranchial gill rakers of large specimens (> 150 mm SL) broader and bi- to quadrid.

Caudal fin emarginate. Dorsal and anal fins extend to between caudal fin base and one scale length before this point in females, maximally to first quarter of caudal fin's length in males. In all specimens, pelvic fins extend to between first and third spine of anal fin and pectoral fins extend to between anus and first spine of anal fin.

Live colour pattern

Mature males (> 90 mm SL): Ventrally: body white, and head greenish; dorsally: body and head grey to bluish (Figs. 6e, S10c). Subopercula, opercula, and flanks intense yellow. Flanks of medium-sized specimens (110–120 mm SL) sometimes show 3–5 vague, vertical bars. Mental blotch, opercular blotches, faint vertical preopercular, and lachrymal stripes present. Anal and pectoral fins hyaline, and anal fin dark red ventrally and with 4 small, orange egg spots (i.e. size equal to distance between fin rays) with subtle white borders. Pelvic fins black, and caudal fin and posterior part of dorsal fin dark red. Dorsal fin anteriorly dusky and with black lappets (i.e. extensions of membranes between spines).

Females and juveniles (< 80 mm): Dorsal part of body green-greyish, flanks pale-yellow, and ventral part of body and cheeks white (Fig. S10d). Dorsal part of head and dorsal and caudal fins dusky. Pelvic and anal fins yellowish and pectoral fins hyaline. Opercular and mental blotches present.

Colour pattern in alcohol

Body brownish, flanks with 3–5 faint vertical stripes in large specimens (> 150 mm SL), rarely present in smaller specimens (> 120 mm SL). All fins dusky, except pelvic fins of small specimens (< 80 mm SL) (Fig. S10a). Mental and opercular blotches present; vertical preopercular and lachrymal stripes faint.

Distribution and ecology

It is endemic to the Lake Edward system. A clearly delineated stomach is absent in several specimens; at most, a relatively small and thick-walled bulge in the digestive tract is distinguishable. The digestive tracts of two small specimens (80–95 mm SL) contained 13–17 cichlid larvae (< 10 mm SL), indicating that at least small specimens have a paedophagous diet. The stomachs of seven small and one large specimens (132 mm SL) were empty. The gut is short (94–130% SL, $n = 5$), in accordance with its predatory ecology.

Systematic comment

This redescription corresponds well to the original species description of *Pyxichromis paradoxus* by Lippitsch & Kaufman (2003) and proposes the new generic combination *Haplochromis paradoxus*. We were unable to examine the type specimens (see above) but noticed some small deviations between the data of the original description and ours: a shorter prepelvic distance (38.3–38.9 vs. 41.7–46.1% SL), a shorter premaxillary pedicel (16.2–18.4 vs. 23.5–29.1% HL), and fewer branched rays in the anal fin (5–7 vs. 8–9). The gape inclination of type specimens also slightly exceeded our range (50–58 vs. 40–55°). These differences are probably the result of a divergent methodology in measurements. We cannot really explain the difference in soft anal fin ray counts, but noticed that our counts fall within the range found for all haplochromines described by Greenwood (1973) from Lake George, which is 8–10, exceptionally 7.

Differential diagnosis

Haplochromis paradoxus differs from all known paedophagous species of *Haplochromis* of the Lake Edward system by its more numerous outer teeth [36–65 (median 51) vs. 16–35 (18–32)] that are strongly recurved and closely set in long tooth bands. Further distinct from *H. gracilifur* sp. nov. and *H. molossus* sp. nov. by a longer snout [28.7–36.0 (32.2) vs. 24.0–26.7 (25.2) and 25.1–30.7 (28.0) % HL, respectively] and longer head [32.2–36.2 (34.3) vs. 29.8–30.7 (30.3) and 29.5–32.0 (30.7) % SL, respectively], from *H. taurinus* by its smaller eyes [25.3–32.1 (28.2) vs. 32.9–40.2 (35.7) % HL], and

from *H. relictidens* sp. nov. by its more slender head [41.7–51.2 (44.9) vs. 47.7–54.7 (50.4) % HL]. Mature males dorsally grey to bluish and ventrally intense yellow versus different colour patterns in other paedophages.

Haplochromis paradoxus can be distinguished from piscivorous sensu stricto species from these lakes (many undescribed) by its small teeth with very strongly recurved necks and short, bluntly pointed, and usually weakly tricuspid crowns versus larger, straight to recurved, and acutely pointed teeth in piscivores. Its lips are slightly thickened, and its maxillae reach posteriorly before vertical through anterior edge of eyes versus lips are not thickened and maxilla generally exceed this point in piscivorous species.

Key to the paedophagous species of *Haplochromis* from the Lake Edward system

- 1A Head relatively short (29.5–33.7% SL) and broad (47.1–57.0% HL); eyes large (29.0–40.2% HL); premaxillae not beaked (Figs. 7–10). Outer oral teeth straight to recurved, few (16–39) in upper jaw, and set in short dental arcades (Fig. 5a–b). Lips firmly thickened, upper lip anteriorly thin, but laterally strongly thickened, making posteriormost teeth hard to observe2
- 1B Head long (32.2–36.2% SL) and slender (41.7–51.2% HL); eyes small (25.3–32.1% HL); premaxillae beaked (Fig. 11). Outer oral teeth very strongly recurved, numerous (36–65) in upper jaw, and set in long dental arcades (Fig. 5c). Lips weakly thickened.....*H. paradoxus*
- 2A Lachrymal bones relatively deep (15.8–18.4% HL); lower jaw pointed; upper jaw rounded (Fig. 5b). Outer oral teeth few (16–26) in upper jaw, often set randomly, and major cusps very blunt to rounded (Fig. 2d).....*H. relictidens* sp. nov.
- 2B Lachrymal bones shallow (11.5–17.0% HL); both oral jaws rounded (Fig. 5a). Outer oral teeth more numerous (22–39) in upper jaw, set regularly, and major cusps acute to blunt (Fig. 2a–c)3
- 3A Oral jaws often prognathous; eyes large (32.9–40.2% HL); lower pharyngeal jaw 1.1 times longer than broad. Outer oral teeth: necks conical, crowns bicuspid, and major cusps anteriorly curved and bear flange (Fig. 2a). Mature males metallic blue and flanks dark red without stripes (Fig. 6a).....*H. taurinus*
- 3B Oral jaws isognathous, eyes relatively small (29.0–33.9% HL); lower pharyngeal jaw 1.0–1.1 times broader than long. Outer oral teeth: necks cylindrical, crowns uni- or bicuspid, and major cusps recurved or straight and, in large specimens (> 100 mm SL), without flange. Mature males green and flanks of variable colour and striped.....4
- 4A Lower jaw very broad (67.0–87.0% LJJ); gape inclination gentle (10–30°); caudal peduncle broad (65.5–83.6% CPL). Outer oral teeth: necks straight and stout, crowns bicuspid (< 80 mm SL) or uni- to weakly tricuspid (> 100 mm SL, Fig. 2b), major cusps equilateral, and minor cusps short. Mature males with olive-green flanks and 6–8 vertical stripes (Fig. 6b).....*H. molossus* sp. nov.
- 4B Lower jaw relatively broad (61.9–69.4% LJJ) and gape inclination steep (40–50°), caudal peduncle slender (62.9–66.4% CPL). Outer oral teeth: necks recurved and slender, crowns bicuspid, major cusps truncated, and minor cusps long (Fig. 2c). Mature males with bright red flanks and 2 longitudinal stripes (Fig. 6c).....*H. gracilifur* sp. nov.

Discussion

Diet

The content of all but one of the investigated stomachs that were not empty, consisted solely of the eggs, embryos, and/or larvae of cichlids. As all *Haplochromis* are maternal mouthbrooders, it cannot be excluded that female specimens might have swallowed their own broods. This is, however, very unlikely to have happened with the investigated specimens as many of the examined stomachs contained fry of different age classes, which were often largely digested. Furthermore, at least one male specimen for each species was found with this particular stomach content. Hence, these broods must have been taken from other cichlids

and it seems unlikely that the presence of fry is the result of an opportunistic feeding regime. Gut contents of specimens with other trophic niches (i.e. insectivores, piscivores, and molluscivores) have also been investigated and no cichlid fry was found. Hence, we can confirm the paedophagous diet of all five species.

Greenwood (1980) made a distinction between species with short and long gut lengths. Species with long guts (GL > 4 times SL) were postulated to have a phytophagous diet, while short gut lengths (GL < 2.5 times SL) were linked to a predatory ecology. All five species discussed here have short guts, in accordance with their predatory lifestyles. Specimens of *H. taurinus* have slightly longer guts than the other paedophagous species from the Lake Edward system (119–222 vs. 82–169% SL). They also have a less specialised trophic morphology (i.e. bicuspid outer teeth with acutely pointed major cusps that protrude the oral mucosa, and a lower lip that did not extend above the oral mucosa, hereby rendering the teeth visible). The stomach of one specimen of *H. taurinus* contained Ephemeroptera, and this species was also caught in higher numbers than the other paedophagous species during recent expeditions (MRAC 2016–35 & 2017–06). Therefore, it seems that *H. taurinus* may have a more generalistic diet than the other four species discussed here.

Comments on the genera sensu Greenwood (1980)

Greenwood (1979, 1980) revised the genus *Haplochromis* and recognised 25 genera that were defined by morphological characteristics that were presumed to be synapomorphies. Within these genera, morphological overlap was observed, and phylogenetic studies suggested that some of them are paraphyletic (Hoogerhoud, 1984; Snoeks, 1994; Salzburger et al., 2005; Meier et al., 2017). Hence, the classification of Greenwood (1980) remains uncertain and has not been generally accepted (Hoogerhoud, 1984; Meyer et al., 1990; Snoeks, 1994; van Oijen, 1996; de Zeeuw et al., 2010). Nevertheless, the publications of Greenwood (1979, 1980) remain a practical reference guide to the morphological and trophic diversity of the LVRs.

All three newly described species (i.e. *H. gracilifur* sp. nov., *H. molossus* sp. nov., and *H. relictidens* sp. nov.) can be assigned to *Lipochromis* sensu Greenwood (1980) on morphological grounds. Greenwood

re-described this genus based on seven species, six from Lake Victoria and *H. taurinus* from the Lake Edward system, all with a paedophagous diet. These species were characterised by a large gape, small teeth, which were deeply embedded in the oral mucosa, and thickened lips. Especially the lateral parts of the upper lip were thickened, which caused the teeth to be well-hidden behind the lips. Other characteristics included a high supraoccipital crest, relatively long and stout jaws, bullate maxillae, and oral teeth that were set in short and slender dental arcades (Greenwood, 1980). All these characteristics are also present in *H. gracilifur* sp. nov., *H. molossus* sp. nov., and *H. relictidens* sp. nov.

Greenwood (1980) distinguished two subgenera within *Lipochromis*. The nominate subgenus, *Lipochromis* (*Lipochromis*), was characterised by broadly rounded jaws (i.e. the ‘obesus’-type) and anteriorly curved outer teeth in the lower jaw. Species of the other subgenus, *Lipochromis* (*Cleptochromis*), had lower jaws that narrowed anteriorly (i.e. the ‘parvidens’-type) and had rounded upper jaws that were set with recurved outer teeth. Both *H. taurinus* and *H. molossus* sp. nov. agreed with the definition of *Lipochromis* (*Lipochromis*). However, *H. molossus* sp. nov. slightly deviates by its straight outer teeth versus anteriorly curved teeth. *Haplochromis relictidens* sp. nov., on the other hand, has a typical *Lipochromis* (*Cleptochromis*) morphology. However, the decreasing trend in the number of teeth with size as seen in *H. relictidens* sp. nov. was not mentioned in the description of this subgenus. Also *H. gracilifur* sp. nov. has very small and recurved teeth but lacks the typical ‘parvidens’-type lower jaw morphology. In this species, both the upper and lower jaws have rounded outlines, but they are not distinctly broad as in the ‘obesus’-type. Therefore, *H. gracilifur* sp. nov. appears to have a morphology intermediate between both subgenera.

Specimens of *H. paradoxus* show some resemblance to *Lipochromis* sensu Greenwood (1980). They have long jaws, slightly thickened lips, small oral teeth, and a paedophagous diet. However, the species deviates from the definition of the genus by its relatively low and wedge-shaped supraoccipital crest (vs. a high and pyramidal crest), beaked premaxillae, an elongate head, and its numerous outer oral teeth [33–65 (median 45)] that are set in long tooth bands in both jaws. Lippitsch & Kaufman (2003) described *H.*

paradoxus within the genus *Pyxichromis*. This was based on a list of 16 synapomorphies, seven of which are non-scale-related features (i.e. gape inclination $> 45^\circ$; premaxillary pedicel inclination $< 25^\circ$; very pronounced concavity before the eyes; lower jaw length $> 44\%$ HL; dental-articular ligament sensu Lippitsch & Kaufman, 2003 hypertrophic and far-forward reaching; angle between anterior and ventral margins of suspensorium $< 90^\circ$; articulation between suspensorium and lower jaw anterior to entopterygoid; and maxillae with a distinctive form: shank process sensu Barel et al., 1976 large and divided from body of bone by a ridge, and anterior part of bone protracted). The scale characters show no features unique to this genus and dental characteristics have not been included in the reassessment of *Pyxichromis* by Lippitsch & Kaufman (2003). The original description of this genus mentioned that the outer teeth are mostly slender and unicuspid, but that also other tooth forms can occur (Greenwood, 1980). This description was based on two species (i.e. *H. orthostoma* Regan, 1922; *H. parorthostoma* Greenwood, 1967), the diet of which is unknown. *Haplochromis paradoxus* has been described on two specimens: the holo- and the paratype (73.6–74.5 mm SL). All small specimens (< 90 mm SL) of *H. paradoxus* indeed have a morphology that corresponds to the definition of *Pyxichromis* sensu Lippitsch & Kaufman (2003). However, large specimens (120.2–142.4 mm SL) do not adhere to the definition of this genus. These have low and wedge-shaped supraoccipital crests, steeper inclinations of their premaxillary pedicels of at least 20° , but more generally 30° , and their head profiles are weakly concave to straight, without pronounced concavities above their eyes. Furthermore, these specimens have beaked premaxillae, elongated heads and long jaws, characteristics that hint towards the genus *Prognathochromis* sensu Greenwood (1980). The outer teeth of *Prognathochromis* species are recurved, unicuspid, and very acutely pointed, while only the posteriormost outer teeth of *H. paradoxus* correspond to this morphology. All other teeth in the outer rows are small, very strongly recurved, weakly tricuspid and bear short and bluntly pointed major cusps. Therefore, *H. paradoxus* seems to have an intermediate morphology between *Pyxichromis* sensu Lippitsch & Kaufman (2003) and *Prognathochromis* sensu Greenwood (1980).

Morphological comparison

Haplochromis species that have the same diet often show strong morphological similarities both within and among lakes (Greenwood, 1979, 1980; Seehausen, 1996; Machado-Schiaffino et al., 2015). Although their intra-lacustrine phylogenetic relationships remain largely unknown, resembling species of different flocks most probably have evolved independently (Meyer et al., 1990; Verheyen et al., 2003; Meier et al., 2017). Paedophagous species are also known from lakes Victoria and Kivu, most of which share the specific *Lipochromis* sensu Greenwood (1980) characteristics (Greenwood, 1980; Snoeks, 1994). For example, *H. relictidens* sp. nov. has a stronger morphological resemblance to *H. occultidens* and *H. microdon*, from lakes Kivu and Victoria, respectively, than to any other known species from the Lake Edward system. All the three species are, however, distinct from each other. *Haplochromis relictidens* sp. nov. differs from *H. occultidens* by its larger lachrymal bones (15.8–18.4 vs. 15.0–15.8% HL) and from *H. occultidens* and *H. microdon* by its broader lower jaw (68.6–83.3 vs. 67.5–68.2 and 43.9–49.1% LJJ, respectively). *Haplochromis microdon* can be distinguished from both by its unicuspid instead of bicuspid outer teeth.

The occurrence of the lower jaw morphology of the ‘parvidens’-type in paedophagous species of different lake systems suggests that this morphology can be linked to a paedophagous diet (Greenwood, 1980; Snoeks, 1994). Greenwood has observed that *H. parvidens* from Lake Victoria displayed snout-engulfing behaviour in captivity, for which this morphology could be an adaptation (Greenwood, 1974). Paedophagous species engulf the snouts of breeding females to suck out their broods. Greenwood (1959) hypothesised that very small teeth that are deeply embedded in the thickened oral mucosa enable paedophages to easily release the breeding females after they have acquired their meals. However, smooth jaws can make it difficult to hold on to their victims for a long enough time to steal the broods of these females. We postulate that the unique lower jaw morphology of *H. relictidens* sp. nov. could function as a lock that fits between the two arms of the lower jaw of a breeding female, providing a better hold and preventing the female from turning her head away in an attempt to escape. Additionally, an acute lower jaw

could push up the basihyal of a breeding female. Hereby, her buccal cavity would be compressed and her fry forced out. The rounded upper jaw, on the other hand, appears to be ideally shaped to seal off the dorsal part of the victim's snout.

A decrease in the number of outer teeth with size can be observed in *H. relictidens* sp. nov. (Fig. 4). Some outer teeth are missing and only a few empty tooth sockets are visible. Within the LVRS, this characteristic has, hitherto, only been described for *H. occultidens* from Lake Kivu. Snoeks (1994) postulated that this species loses its outer teeth as they grow larger, and that the teeth are not being replaced when lost. This could be a specialised dental characteristic of a snout-engulfing hunting habit, as this species may not need functional outer teeth. Given the similar trophic morphology, we assume that *H. relictidens* sp. nov. has a similar hunting strategy.

Haplochromis paradoxus has strongly recurved outer teeth that lay almost flat on top of the oral mucosa or are slightly sunken into it. The oral teeth are small and the jaws have an edentulous appearance, both of which are characters that have been linked to a paedophagous diet (Greenwood, 1980). However, the overall morphology of *H. paradoxus* deviates from all other paedophages from the Lake Edward system but resembles that of a piscivore sensu stricto. Stomach analyses did, however, reveal that at least small specimens (< 120 mm SL) had a paedophagous diet. Other paedophages sensu lato from the LVRS are also known to lack a typical *Lipochromis* morphology, e.g. *H. barbarae*, an egg-snatcher from Lake Victoria. However, of all known paedophages of the LVRS, *H. paradoxus* is the sole known species that has strongly recurved teeth.

Haplochromis paradoxus resembles *Caprichromis orthognathus* from Lake Malawi by its steeply sloping gape and strongly developed lower jaw. The latter species is known to display head-ramming behaviour (McKaye & Kocher, 1983). We presume that *H. paradoxus* could display a similar hunting technique. *Haplochromis taurinus*, *H. molossus* sp. nov., and *H. gracilifur* sp. nov. all have a stout head with rounded and strongly developed jaws and firmly thickened lips. These traits could also be adaptations for head-ramming behaviour to force breeding females to lose their fry (McKaye & Kocher, 1983). On the other hand, their large gapes that can be broadly expanded, the anteriorly curved outer teeth of *H. taurinus*, and the

hidden teeth of the two other species could also facilitate snout-engulfing. The development of the jaws is important for both hunting tactics. In all three species, the lower jaw widths increase proportionally with size, which can explain the size effects that are present on PC 2 in the PCA of the measurements (Fig. 3a).

Interestingly, there is a large variation in gape inclinations within the paedophages from the Lake Edward system. *Haplochromis molossus* sp. nov. has a gentle gape inclination, while it is slightly steeper in *H. taurinus*, followed by *H. relictidens* sp. nov. and *H. gracilifur* sp. nov., whereas a very steep gape inclination is observed in *H. paradoxus*. This divergence in gape inclination has also been observed in Lake Malawi paedophages, which could be linked to their different strategies of head-ramming (Trewavas, 1935; McKaye & MacKenzie, 1982; McKaye & Kocher, 1983). Hence, each species of paedophage from the Lake Edward system could have its own hunting tactics, allowing them to co-occur in this ecosystem.

The species richness of *Haplochromis* from the Lake Edward system

The number of species of *Haplochromis* within the Lake Edward system is unknown. Hence, estimations of its species richness are necessary. A rough estimation could be made by comparing the proportions of paedophagous species between closely related systems. Lake Kivu is home to 15 endemic species of *Haplochromis*, one of which has a paedophagous diet (Snoeks, 1994). Lake Victoria possessed, prior to the introduction of *Lates niloticus* (Linnaeus, 1758), a flock of 500–700 species of *Haplochromis* (Snoeks, 2000), including at least 24 paedophages (Barel et al., 1977; Greenwood, 1980; Witte & Van Oijen, 1990; Seehausen, 1996; Goldschmidt, 2004). Hence, in these two lakes, species with a paedophagous diet take up ~ 3–7% of the species diversity of *Haplochromis*. The Lake Edward system has a total of five paedophagous species. Hence, considering that Lake Edward has a similar ecosystem as Lake Victoria and a comparable size to Lake Kivu, we could make a rough estimate that the system contains about 70–150 species of *Haplochromis* in total. This is a somewhat larger estimate than current estimate of 60 species (Greenwood, 1991; Snoeks, 2000). Although this is

just a rough estimation, it does show that there are still a lot of species of *Haplochromis* that remain to be discovered from the Lake Edward system.

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