Similar ecology, different morphology: three new species of oral mollusc shellers from Lake Edward

Nathan Vranken[1,2], Maarten Van Steenberge[1,2,3] & Jos Snoeks[1,2]

[1]Royal Museum for Central Africa, Biology department, Section Vertebrates, Leuvensesteenweg 13, 3080 Tervuren, Belgium

[2]KU Leuven, Ecology, Evolution and Biodiversity Conservation, Charles Deberiotstraat 32, 3000 Leuven, Belgium

[3]Royal Belgian Institute of Natural Sciences, Operational Directorate Taxonomy and Phylogeny, Vautierstraat 29, 1000 Brussels, Belgium

Correspondence

Nathan Vranken, Royal Museum for Central Africa, Biology department, Leuvensesteenweg 13, 3080 Tervuren, Belgium.

Email: nathan.vranken@africamuseum.be;

Tel.: +32 27695632

ABSTRACT

Lake Edward in Eastern Africa harbours a largely understudied assemblage of haplochromine cichlids that displays a range of adaptions to various specialised trophic niches. In this system, we discovered specimens of *Haplochromis* with morphologies similar to those of oral mollusc shellers from Lake Victoria. These morphologies are characterised by short oral jaws with stout teeth that are used either to crush molluscs or to grab the soft bodies of snails and wrench them out of their shells. A morphometric study on 47 specimens from Lake Edward revealed the presence of three new species with an oral shelling morphology, i.e., *H. concilians* sp. nov., *H. erutus* sp. nov., and *H. planus* sp. nov. All three species are formally described. Stomach content observations confirmed an opportunistic oral shelling ecology for *H. concilians* sp. nov. and *H. erutus* sp. nov. Within *H. planus* sp. nov., only large specimens displayed a specialised oral shelling morphology; however, their stomachs were nearly empty, while small specimens consumed mainly Ostracoda and Hydrachnidia. Remarkably, the three species differed considerably in morphology from each other, but they each resembled oral sheller species from Lake Victoria.

Key words:

Hoplotilapia; Lake Victoria region superflock; *Macropleurodus*; molluscivory; *Ptyochromis*; taxonomy

INTRODUCTION

Lake Edward is located in Eastern Africa, on the border between Uganda and the Democratic Republic of the Congo (Fig. 1). It is connected to Lake George through the Kazinga Channel. Both lakes harbour a similar ichthyofauna and are treated as a single system: the Lake Edward system. This system is home to a large assemblage of cichlids of the genus *Haplochromis* Hilgendorf 1888, consisting of an estimated 60–100 species (Greenwood, 1991; Vranken *et al.*, 2019a,b). These species are closely related to the species of *Haplochromis* from Lakes Albert, Kivu, Kyoga, and Victoria and associated lakes and river systems, and, together, form the Lake Victoria region superflock (LVRS) (Verheyen *et. al.*, 2003; Salzburger *et al.*, 2005). The LVRS is a very young radiation of cichlids that evolved over the last 100 000–200 000 years (Verheyen *et al.*, 2003; Bezault *et al.*, 2011). Its species are genetically closely related, but display a broad range in habitat preference, behaviour, trophic morphology, and colour patterns (Bezault *et al.*, 2011; Brawand *et al.*, 2014; Meier *et al.*, 2017).

Greenwood (1979, 1980) proposed a classification of the LVRS based on supposed synapomorphic traits by reclassifying all species into 20 genera. Yet, the morphological definitions of some of these proposed genera overlapped, and several species could not unambiguously be assigned to one of them (Hoogerhoud, 1983; van Oijen, 1991). Therefore, Greenwood's (1980) classification was not universally accepted (Hoogerhoud, 1983; Snoeks, 1994; van Oijen, 1996). Hence, until more is known about the phylogeny of these species, we follow Hoogerhoud (1984), Snoeks (1994), van Oijen

(1996), de Zeeuw *et al.* (2010), and Vranken *et al.* (2019a,b) in retaining all haplochromines of the LVRS in *Haplochromis*. The definitions of most genera *sensu* Greenwood (1980) are largely based on traits associated with the trophic morphologies (e.g., the oral and pharyngeal jaws and dentitions). Hence, a strong link is found between the classification *sensu* Greenwood (1980) and the trophic ecology of these species (Witte & Van Oijen, 1990). Therefore, we will use Greenwood's (1980) classification as a morphological framework that links morphology with ecology in *Haplochromis*. Hence, we will use the genera *sensu* Greenwood (1980) only to describe specific morphologies and mention these genera between single quotation marks to indicate that no nomenclatural value is given to them.

Molluscivory is a common trophic ecology among East African cichlids. Each of the East African Great lakes, and many of the region's river systems are inhabited by molluscivorous species. Examples include *Trematocranus placodon* Regan 1922 from Lake Malawi, *Haplochromis mylergates* Greenwood & Barel 1978 from Lake Victoria, *Astatoreochromis allaudi* Pellegrin 1904 from lakes and rivers of the Lake Victoria region, and *H. mylodon* Greenwood 1973, *H. pharyngalis* Poll & Damas 1939, and *H. placodus* Poll & Damas 1939 from the Lake Edward system. All of these species have hypertrophied pharyngeal jaws with molariform teeth, which are used to crush the shells of molluscs.

Greenwood (1974) recognised a group of molluscivores with a different morphology in *Haplochromis*: the oral shellers. Oral shellers have short and strong oral jaws with stout teeth that some species may use to crush the shells of molluscs, i.e., oral crushing (Greenwood, 1956, 1974). A mollusc crushing strategy is constrained by prey size as large, thick-shelled molluscs are too hard to crush. Whereas this prevents pharyngeal crushers from consuming large molluscs, these can be consumed by oral shellers by using an alternative technique, i.e., oral shelling (Slootweg, 1987). After approaching a moving snail, oral shellers quickly grasp the soft tissue of the snail with their oral jaws and vigorously jerk their heads to wrench the snail from its shell (Slootweg, 1987; Seehausen, 1996).

Within the LVRS, oral shellers are hitherto only known from Lake Victoria. From this lake, 23 biological species with this ecology have been recorded, eight of which are formally described (Greenwood, 1956, 1957; Seehausen, 1996; Seehausen *et al*., 1997; Seegers, 2008). These species are morphologically very diverse, which is exemplified by their classification in five genera *sensu* Greenwood (1980), i.e., ‘*Hoplotilapia*’ Hilgendorf 1888, ‘*Macropleurodus*’ Regan 1922, ‘*Paralabidochromis*’ Greenwood 1956, ‘*Platytaeniodus*’ Boulenger 1906, and ‘*Ptyochromis*’ Greenwood 1980 (Greenwood, 1956; Slootweg, 1987). Three of these are monospecific. *Haplochromis degeni* Boulenger 1906 and *H. retrodens* Hilgendorf 1888 are the sole species with a ‘*Platytaeniodus*’ and a ‘*Hoplotilapia*’ morphology, respectively. Both species have upper jaws set with broad U-shaped tooth bands. They differ in the lower jaw, which is deep and set with two distinct patches of teeth in the former and shallow with a U-shaped tooth band in the latter. *Haplochromis bicolor* Boulenger 1906 is the only known species that has a ‘*Macropleurodus*’ morphology with strongly curved dentigerous arms of the upper jaw, slender tooth bands, and stout outer teeth with recurved major cusps and labially implanted minor cusps. Remarkably, the distantly related *Chilotilapia rhoadesii* Boulenger 1908 from Lake Malawi has a strikingly similar trophic morphology (Greenwood, 1983), hereby representing a clear example of convergent evolution (Salzburger *et al*., 2005). Four valid species have a ‘*Ptyochromis*’ morphology with thickened lips, the anteriormost parts of the lower jaws curving slightly downwards, and strongly recurved and unicuspid oral teeth set in broad tooth bands that narrow laterally.

‘*Paralabidochromis*’ *sensu* Greenwood (1980) contains mostly insectivorous species. However, one species with this morphology is known to have an oral shelling ecology: *Haplochromis plagiodon* Regan & Trewavas 1928 (Witte, 1980). A ‘*Paralabidochromis*’ morphology is characterised by stout and straight teeth, deep lower jaws with the anteriormost outer teeth procumbently implanted, and slender tooth bands. Although *H. plagiodon* displays these characteristics, it deviates from other species with this morphology by its bicuspid outer oral teeth with obliquely truncated major cusps and horizontally orientated minor cusps vs. uni- to weakly bicuspid teeth with equilateral major cusps and upright minor cusps (Greenwood, 1980). Greenwood (1980) interpreted this tooth morphology as intermediate between ‘*Paralabidochromis*’ and ‘*Macropleurodus*’. Therefore, a ‘*Paralabidochromis*’ morphology does not imply an oral shelling ecology.

The *Haplochromis* assemblage of the Lake Edward system has been poorly studied. Hitherto, no species with an oral shelling ecology has been discovered. The aim of this study is to perform a morphometric study of all species of *Haplochromis* from the Lake Edward system with a morphology that suggests an oral shelling ecology, i.e., corresponding morphologically to *H. plagiodon* or one of the following genera *sensu* Greenwood (1980): ‘*Hoplotilapia*’, ‘*Macropleurodus*’, ‘*Platytaeniodus*’, or ‘*Ptyochromis*’. A taxonomical evaluation is presented.

MATERIALS AND METHODS

Specimens examined

A total of 71 specimens from the Lake Edward system were examined, including 46 from the Royal Museum for Central Africa, Tervuren (MRAC) and 25 from the Royal Belgian Institute of Natural Sciences, Brussels (IRSNB), all unidentified except one (IRSNB 12899: *H. labiatus* Trewavas 1933) (see Taxonomic account). Specimens were selected by their morphologies corresponding to *H. plagiodon* or the following genera *sensu* Greenwood (1980): ‘*Hoplotilapia*’, ‘*Macropleurodus*’, ‘*Platytaeniodus*’, or ‘*Ptyochromis*’ (see Introduction). Specimens that showed small deviations from the genus descriptions were also incorporated. All specimens were assigned *a priori* to three groups based on oral jaw and outer oral tooth morphologies as described following Barel *et al.* (1976, 1977). Specimens of *H.* sp. ‘concilians’ (C, n=36; Fig. 2a) had rounded and stout jaws set with straight, stout, and unicuspid teeth, and with the anterior parts of the lower jaws curving downwards. The lower jaws of *H.* sp. ‘erutus’ (E, n=24; Fig. 2b) were rounded, the upper jaws rectangular with curved dentigerous arms, and both were set with stout and bicuspid teeth. Both jaws of *H.* sp. ‘planus’ (P, n=13; Fig. 2c) were rectangular and posteriorly enlarged, while the lower jaw was anteriorly flattened; the outer teeth were small and unicuspid anteriorly, while large and stout posteriorly in both jaws. Specimens of the first group displayed ‘*Ptyochromis*’ and ‘*Paralabidochromis*’ characteristics. The latter two had ‘*Macropleurodus*’ and ‘*Hoplotilapia*’ morphologies, respectively. Specimens that resembled *H. plagiodon* or that had a ‘*Platytaeniodus*’ morphology were not found within the examined collections.

Specimens of the following species from Lake Victoria were investigated as comparative material: *H. fischeri* Seegers 2008 (MRAC 14870), *H. degeni* (MRAC 91.02.P.1–4), *H. bicolor* (MRAC 81.30.P.9), *H. retrodens* (MRAC 91.16.P.9–10), and *H. crassilabris* Boulenger 1906 (MRAC 14893) with '*Ptyochromis*', '*Platytaeniodus*', '*Macropleurodus*', '*Hoplotilapia*', and '*Paralabidochromis*' morphologies respectively. The holotype of *H. labiatus* (BMNH 1933.2.23.403), which also has a '*Paralabidochromis*' morphology, was examined as well. Additionally, one specimen of *Chilotilapia rhoadesii* (MRAC 99.041.P.1776) from Lake Malawi was investigated because of its strong morphological resemblance to a '*Macropleurodus*' morphology (Greenwood, 1983). Comparisons to all other species of the LVRS were mainly based on data from Greenwood (1979, 1980) and Barel *et al*. (1977).

Data collection

A total of 49 morphometric characters were taken on 47 specimens (C: 20, E: 19, P: 8), consisting of 28 measurements and 21 counts. Vertebrae were counted on X-ray scans made by the VisiX X-ray system (Medex Loncin SA) with a DeReO WA detector and a GemX-160 generator. All other morphometrics were taken under a binocular microscope (6.5–50x) on the left side of each specimen by a single person to retain consistency. All measurements were taken using dial callipers (±0.01 mm). Dissection of the lower pharyngeal bone was performed on 12 specimens (C: 4, E: 4, P: 4). All descriptive terminology used in reference to the generalised *Haplochromis* morphology *sensu* Barel *et al.* (1976, 1977).

Twenty-eight measurements were taken as defined by Vranken *et al.* (2019a): standard length (SL); head length (HL); body depth (BD); predorsal- (PrD), preanal- (PrA), prepectoral- (PrP) and prepelvic distance (PrV); pectoral- (PL) and pelvic fin length (VL); dorsal- (DFB) and anal fin base length (AFB); caudal peduncle length (CPL) and depth (CPD); head width (HW); eye diameter (ED); interorbital width (IOW); snout length (SnL); lacrimal depth (LaD); cheek depth (ChD); premaxillary pedicel length (PPL); upper jaw length (UJL); lower jaw length (LJL) and width (LJW);lower pharyngeal length (LPL; n=12) and width (LPW; n=12); dentigerous area length (DAL; n=12) and width (DAW; n=12); and gut length (GL; n=16). Snout and gape inclinations were measured in degrees using a protractor following the terminology of Barel *et al.* (1977).

Twenty-one counts were taken as defined by Vranken *et al.* (2019a): upper- (UOT) and lower (LOT) outer teeth; upper and lower inner tooth rows (UTR/LTR); dorsal- (DFR: DFRs/DFRr), anal- (AFR: AFRs/AFRr), and pectoral fin formula (PFR), consisting of spine and branched-ray counts; gill raker formula (GR: GRc/1/GRe), consisting of cerato- and epibranchial gill raker counts; abdominal and caudal vertebrae (V: Va/Vc); longitudinal line scales (LongL); lateral line scales (LatL: LatLu/LatLl), consisting of upper and lower lateral line scale counts; upper- (D-UUL) and lower transverse line scales (ULL-A); scales between pectoral and pelvic fins (P-V); infraorbital and postorbital cheek scales (ChS: ChSi/ChSp); and lower pharyngeal teeth in the posterior row (LPTp; n=12).

The following qualitative characteristics were described following the terminology of Barel *et al.* (1977): lateral neurocranial outline (observed on X-rays), dorsal head profile, lateral snout outline, maxillary bullation, maxillary posterior extension (in reference to a line perpendicular to the body axis instead of to the anterior margin of the vertical preoperculum limb), caudal fin outline, dentition of the oral and pharyngeal jaws, and colouration in vivo (from pictures) and in alcohol. A distinction was made between terms that refer to positions, e.g., lateral and dorsal, and terms that refer to directions, e.g., laterad and dorsad, following the terminology proposed by Barel *et al*. (1976). Specimens were sexed by investigating the genital papillae.

Stomach content observations were performed on 23 specimens (C: 6, E: 7, P: 10). Digestive tracts were removed, stomachs were dissected, and their contents identified and counted under a binocular microscope (6.5–50x).

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 measurements, and on correlation matrices of the raw data of the counts (Zelditch *et al*., 2004). To allow for comparison, all measurements, except for SL, were expressed as percentages of a reference measurement. Possible diagnostic traits were determined by pairwise inter-group comparisons of these proportions of the measurements and of the raw data of the counts by Mann-Whitney *U* (MW*U*) tests with sequential

Bonferroni correction (Rice, 1989). For all data, size effects were avoided by performing the MW*U* tests on subsets of specimens of a similar standard-length class [MW*U* (SL): $P > 0.5$]. Measurements with fin tips as reference points (i.e., TL, VL, and PL), measurements and counts taken on a subset of the specimens (GL, LPL, LPW, DAL, DAW, and LPTp), and angular measurements (i.e., snout and gape inclinations), were excluded from all analyses. All statistical analyses were performed in Past 3.13 (Hammer *et al*., 2001).

RESULTS

A PCA was performed on the variance-covariance matrix of the log-transformed measurements of all 47 specimens (Table S1). The first principal component (PC 1; 69.7% of variance) had large, positive loadings of similar magnitude for all variables, and hence was interpreted as a variable describing size (Zelditch *et al*., 2004). On PC 2 (10.7% of variance), PPL and UJL, followed by ChD and IOW had the highest absolute loadings, while LJW, PPL, IOW, and UJL were important contributors to PC 3 (8.5% of variance). In a plot of PC 3 against PC 2, three distinct clusters could be observed (Fig. 3a), each formed by all specimens of the three *a priori* defined groups. All specimens of *H.* sp. 'erutus' had positive values on PC 3, while these of *H.* sp. 'concilians' and *H.* sp. 'planus' all had negative values. The latter two clusters were completely separated on PC 2, with the groups situated completely in its negative and positive parts respectively. Both PC 2 and PC 3 were also plotted against PC 1 as a multivariate proxy of size, which confirmed that these separations were not due to allometric effects (not shown).

A PCA was performed on the correlation matrix of the raw data of the counts (Table S2). All dental characters (i.e., UOT, LOT, UTR, and LTR), followed by Vc, were important contributors to PC 1 (15.1% of variance), whereas ULL-A was the major variable for PC 2 (11.9% of variance). All specimens of *H.* sp. 'planus' formed a cluster with high positive values on PC 1 (Fig. 3b), while specimens of *H.* sp. 'erutus' and *H.* sp. 'concilians' overlapped completely in the negative side of PC 1. No further patterns could be observed in subsequent axes. An additional PCA was conducted, restricted to counts that were directly linked to trophic morphology: the tooth counts (Table S3). All variables had large, positive loadings on PC 1 (61.9% of variance), whereas the number of teeth contributed positively, and the number of teeth rows negatively on PC 2 (18.4% of variance). On a plot of the first two PCs, the three *a priori* defined groups were almost fully separated (Fig. 3c). All specimens of *H.* sp. 'planus' clustered in the positive part of PC 1, while all specimens of *H.* sp. 'erutus' and *H.* sp. 'concilians' had mainly negative, overlapping scores for PC 1. Yet, the latter two groups were almost completely separated on PC 2, with specimens of *H.* sp. 'erutus' having mainly positive scores, while all specimens of *H.* sp. 'concilians' had negative values.

The MW*U* tests revealed several variables that differed significantly between the *a priori* formed groups (Table S4). *Haplochromis* sp. 'concilians' differed highly significantly (*P* < 0.01) from *H.* sp. 'erutus' by HW, SnL, ChD, PPL, LJW, and LOT, while they differed completely in LPL and DAL (not tested by MW*U*) (Table 1). *Haplochromis* sp. 'concilians' and *H.* sp. 'planus' were significantly different (*P* < 0.05) in DFB, HW, UJL, LJW, UTR, PPL, ChD, IOW, UOT, and LOT, and they were fully separated in the latter five and LPL (not tested by MW*U*). A comparison between *H.* sp. 'erutus' and *H.* sp. 'planus' revealed a highly significant difference in UTR and significant differences in LaD, IOW, UJL, and UOT. The latter three, UTR, and DAL (not tested by MW*U*) were revealed as non-overlapping characteristics.

The above results confirmed the distinction between all three *a priori* defined groups. Comparisons to the comparative material and the literature revealed that these constitute hitherto undescribed species (see Differential diagnoses below). Hence, *H. concilians* sp. nov., *H. erutus* sp. nov., and *H. planus* sp. nov. are formally described in taxonomic account. For each species, the proportions of the measurements and the raw data of the counts are summarised in Table 1.

TAXONOMIC ACCOUNT

***HAPLOCHROMIS CONCILIANS* SP. NOV.**

(Figs. 2a, 4, 5, and 6; Table 1)

Holotype

MRAC 2017.006.P.0063; Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; 30/03/2017 [♂ 76.0 mm SL].

Paratypes

MRAC 2016.035.P.0050; Lake Edward, sand substrate, 1 km east of Nyamugasani river: 0°10'22.8"S 29°50'13.2"E; 28/10/2016 [n=1; 70.8 mm SL]. MRAC 2016.035.P.0051–52; 'Coral Reef', hard substrate at mouth of Nyamugasani river, Lake Edward: 0°10'08.4"S 29°49'37.2"E; 21/10/2016 [n=2; 74.8, 75.4 mm SL]. MRAC 2017.006.P.0064–73; Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; 30/03/2017 [n=10; 64.4–76.9 mm SL]. MRAC 2017.006.P.0074; Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; 31/03/2017 [n=2; 74.5, 77.2 mm SL]. MRAC 2018.008.P.0107–108; Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; 20/01/2018 [n=2; 65.0, 60.4 mm SL]. MRAC 2018.008.P.0109–110; Rwenshama, offshore, Lake Edward: 0°24'14.4"S 29°45'57.0"E; 24/01/2018 [n=2; 67.1, 83.1 mm SL]. RBINS 903–918; Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; 21/03/2019 [n=16; 62.0–72.8 mm SL; no morphometrics taken].

Differential diagnosis

Haplochromis concilians sp. nov. differs from all species of *Haplochromis* by skin covering snout thickened and usually (in ca. 80% of specimens) merged with upper lip, by which snout and lip form an uninterrupted surface, and anterior outer teeth in lower jaw located distinctly buccally, hereby leaving labialmost part of lower jaw edentulous. Within Lake Edward system, it shares with *H. erutus* sp. nov., *H. planus* sp. nov., *H. eduardianus* (n=8), and *H. labiatus* (n=46) short and stout jaws and large or more strongly developed lips. It differs from all by a shorter premaxillary pedicel [16.1–21.6 (19.1) vs. 21.4–24.0 (22.6), 21.9–24.4 (23.0), 21.8–26.4 (23.1), and 24.0–27.6 (25.6) % HL, respectively], and hypertrophied pharyngeal jaws set with molariform teeth vs. more slender jaws set with, at most, stout teeth. It differs further from *H. erutus* sp. nov. by straight and unicuspid vs. recurved and bicuspid outer teeth. It differs from *H. eduardianus* by mostly pro- vs. retrognathous jaws, and straight and conical vs. recurved and spoon-shaped outer teeth. It differs from *H. labiatus* by a steeper head (60–75° vs. 40–55°), mostly pro- vs. iso- to retrognathous jaws, and anteriormost outer teeth in lower jaw implanted upright vs. procumbent.

Etymology

Specific name noun in apposition from Latin ‘conciliāre’, to join or knit together, in reference to the part of the skin covering the snout that is fused with the upper lip.

Description

Small species (< 83.1 mm SL) with a relatively slender body. Head blunt and strongly convex, snout short and steep, sloping at 60–75°, eyes relatively large, and cheeks deep. Jaws short, nearly horizontal with a gape inclination of 10–20°, and pro- to rarely isognathous. Maxilla extends to region between anterior margin of orbit and pupil. Dentary, premaxilla, and maxilla thickened and stout; dentary deep over entire length, and with anteriormost part slightly curving downwards. Premaxilla weakly protrusible; premaxillary pedicel short and at an angle of 90–115° to dentigerous arms. Ventralmost part of maxilla over entire length uncovered by lacrimal bone when mouth closed. Snout tissue above upper lip thickened and, in ca. 80% of specimens, fused with upper lip to form an uninterrupted surface. Lips and oral mucosa strongly thickened, thereby often concealing the prognathous lower jaw. Neurocranium with strongly compressed anterior part and a wedge-shaped supraoccipital crest (Fig. 5b). Chest scales small; size transition to flank scales gradual.

Outer oral teeth large, stout, and blunt. Necks long, cylindrical, and straight. Crowns in large specimens (> 65 mm SL) unicuspid with rarely some (weakly) bicuspid teeth posteriorly. In small specimens (< 65 mm SL) crowns (weakly) bicuspid. Major cusps conical, stout, and blunt. If present, minor cusps small, stout, and upright. Dental arcades long and more broadly curved in upper than in lower jaw. Relatively few outer teeth with straight implantations, deeply embedded in the oral mucosa, closely set with an inter-tooth distance of half a tooth width, and outer teeth strongly decrease in size posteriad; posteriormost outer teeth very small in both jaws. In lower jaw, anterior outer teeth located distinctly buccally, thereby leaving anteriormost part of lower jaw edentulous, and lower lip seems to extend relatively deep into buccal cavity. Tooth bands in both jaws crescent shaped, anteriorly with 2–3 rows of inner teeth, well separated from outer rows by distances of 1–2 outer tooth widths. Inner tooth rows abruptly narrow posterolaterally; as such only outer rows remain over posterior quarters in both jaws. Inner teeth relatively large, stout, and blunt; anteriormost inner teeth unicuspid, more posterior inner teeth small and tricuspid.

Lower pharyngeal bone broad, stout, deep, and with keel slightly deeper than posterior part of bone (Fig. 6). Teeth set in 19–22 rows (n=4), four medial tooth rows with molariform teeth, all other teeth stout with blunt major cusps and reduced to absent minor cusps, except for slender postero-lateralmost teeth.

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

Caudal fin weakly emarginate. Dorsal and anal fins reach level between caudal fin base and one scale anterior to this point. Pectoral fins reach level between anus and first anal fin spine; pelvic fins between second spine and first branched ray of anal fin in males, between anus and third anal fin spine in females.

Colouration in vivo

Dominant males (> 70 mm SL): body silver-blue, ventral part of body dusky turquoise, except chest whitish (Fig. 5c). Flank with 4–6 vertical stripes, 2–3 anteriormost stripes dark and extend to dorsal part of body, remaining stripes iridescent turquoise and fainter. An interrupted and faint mid-lateral stripe may be present on flank. Head pale turquoise, snout light blue, dorsal part of head with a purple sheen, and branchiostegal rays black. Nostril-, interorbital-, supraorbital-, and lacrimal stripes, and a nape band well-defined. Dorsal fin hyaline and with a dusky base, crimson lappets (i.e., extensions of membrane between spines), and a crimson and maculated posterior part. Caudal and anal fins crimson, dorsal fin with a maculated posterior part, anal fin with a black posterior margin and 2–3 large orange egg spots that each span two fin rays. Pelvic fins black and pectoral fins hyaline.

Females and juveniles: flanks faint beige-gold; ventral part of body beige-white; snout and dorsal part of head grey with a slight blue hue (Fig. 5d). In some specimens 4–6 faint stripes on flanks. Caudal fin dusky with hints of yellow, orange, or crimson; dorsal fin dusky with black lappets. Dorsal part of caudal fin and posterior part of dorsal fin maculated. Pelvic-, pectoral-, and anal fins hyaline, anal fin with 2–3 small yellow spots resembling egg spots.

Colouration in alcohol

Body brown dorsally, grey ventrally. Nostril-, interorbital-, supraorbital-, and lacrimal stripes, and a nape band distinct and clearly delineated (Fig. 5a). Flanks with 4–6 well-defined vertical stripes in dominant males, faint to absent in females and juveniles. Dorsal fin dusky and with a dark base and dark lappets in anterior part. Posterior part of dorsal fin and, in some specimens, dorsal part of caudal fin maculated. Pectoral-, anal-, and caudal fins yellowish, anal fin in dominant males with dark posterior margin and 2–3 large egg spots. Pelvic fins black in dominant males, yellowish in females.

Distribution and ecology

Endemic to Lake Edward. Gut short (GL 72–139 % SL, n=4), diet mainly molluscivorous. We examined the gut contents of six specimens. Four were dominated by remains of Gastropoda, consisting of opercula (2–4 mm) and small complete snails (shells 2–4 mm). Two guts had no remains of Gastropoda, but one contained a small fish and one was empty. All five filled guts also contained some sand or gravel and various small Arthropoda, Ostracoda, and/or Hydrachnidia.

HAPLOCHROMIS ERUTUS SP. NOV.

(Figs. 2b, 7, 8, and 9; Table 1)

Holotype

MRCA 2018.008.P.0111; Kagoro fishing ground, open water, Lake Edward: 0°12'50.1"S 29°49'19.7"E; 4/02/2018 [♂ 73.9 mm SL].

Paratype

IRSNB 12899; Lac Edouard: Baie de Kasindi: 0°04'35"S 29°42'31"E; Miss. KEA; 2/06/1953 [n=1; 66.97 mm SL]. MRAC 2016.035.P.0053; Lake Edward, sand substrate, 1 km east of Nyamugasani river: 0°10'22.8"S 29°50'13.2"E; 22/10/2016 [n=1; 73.0 mm SL]. MRAC 2017.006.P.0077–78; Rwenshama, rocky shore, Lake Edward: 0°24'05.7"S 29°46'35.1"E; 26/03/2017 [n=2; 65.8, 72.1 mm SL]. MRAC 2017.006.P.0079; Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; 30/03/2017 [n=1; 80.1 mm SL]. MRAC 2018.008.P.0112–113; Kayanja, offshore, Lake Edward: 0°05'31.2"S 29°45'30.3"E; 20/01/2018 [n=2; 62.4, 63.2 mm SL]. MRAC 2018.008.P.0114-0119; Rwenshama, offshore, Lake Edward: 0°24'14.4"S 29°45'57.0"E; 24/01/2018 [n=6; 64.7–77.7 mm SL]. MRCA 2018.008.P.0120–124; Kagoro fishing ground, open water, Lake Edward: 0°12'50.1"S 29°49'19.7"E; 4/02/2018 [n=5; 72.9–83.4 mm SL]. RBINS 895–897; Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; 21/03/2019 [n=3; 62.3–65.1 mm SL; no morphometrics taken].

Etymology

Specific name noun in apposition from Latin ‘erutus’, torn out. Refers to its oral shelling ecology, in which soft bodies of snails are wrenched or torn out of their shells.

Differential diagnosis

Haplochromis erutus sp. nov. differs from all other species of *Haplochromis*, except *H. bicolor* from Lake Victoria, by a small and rectangular mouth with a short upper jaw that curves downwards halfway its length, in combination with blunt, bicuspid, and recurved outer oral teeth and, in lateral part of upper jaw, more stout inner teeth (mostly more distinct in dextral side). It differs from *H. bicolor* (data taken from Greenwood, 1956) by much larger eyes [35.4–40.7 (38.1) vs. 21.4–32.0 (27.0) % HL], slightly more slender interorbital width [22.5–26.1 (24.1) vs. 25.8–34.5 (30.8) % HL], and slightly shorter snout [23.2–27.1 (25.7) vs. 26.5–34.2 (31.5) % HL]. Differs further by a shallower supraoccipital crest, dominant males with beige-silver vs. red flanks, and piebald colouration seemingly absent in *H. erutus* sp. nov., while frequently observed in females of *H. bicolor.*

Within Lake Edward system, it shares with *H. concilians* sp. nov., *H. labiatus*, *H. eduardianus*, and *H. planus* sp. nov. stout jaws and large or more strongly developed lips. It differs from *H. labiatus* (n=46) by a shorter snout [22.4–25.4 (23.9) vs. 26.5–30.2 (28.1) % HL] and large vs. lobed lips, from *H.*

eduardianus (n=8) and *H. planus* sp. nov. by a shorter upper jaw [20.9–26.0 (24.1) vs. 27.5–33.8 (31.3) and 27.6–32.1 (30.8) % HL, respectively], and from *H. concilians* sp. nov. by large vs. strongly thickened lips, a longer premaxillary pedicel [21.4–24.0 (22.6) vs. 16.1–21.6 (19.1) % HL], and beige-silver vs. silver-blue dominant males.

Description

Small species (< 83.4 mm SL) with a relatively slender body. Head short and convex, snout short, steep, and sloping at 55–70°, and eyes large and almost entering the dorsal outline of head. Jaws isognathous and with a rectangular outline and a gentle gape inclination of 20–35°. Maxilla extends to anterior margin of orbit. Lower jaw short, stout, deep posteriorly, and more shallow anteriorly. Upper jaw short and with dentigerous arms that curve gently downwards halfway their lengths, mostly more distinct in dextral part of jaw. Lips and oral mucosa large and lateral parts of lower lip expand laterad, hereby accentuating rectangular outline of jaws. Opercular breathing valves large (i.e., clearly visible posterior of operculum). Neurocranium slightly compressed anteriorly and with a relatively low and wedge-shaped supraoccipital crest (Fig. 8b). Chest scales small; size transition to flank scales gradual.

Outer teeth large and relatively few in both jaws. Necks stout, cylindrical and slightly inclined mediad (i.e., pointing towards adjacent teeth in same row). Crowns stout, bicuspid, and often slightly abraded. Major cusps large, blunt, truncated, and recurved; minor cusps stout and blunt. Outer teeth of large specimens (> 70 mm SL) with strongly recurved and slightly protracted major cusps, and reduced and labially implanted minor cusps. Dental arcades rectangular in upper jaw, rounded in lower jaw (in contrast to rectangular outline of lower lip). Dental arcades long, outer teeth closely set with crowns touching each other. Outer teeth decrease in size posteriad in the lower jaw, while all teeth in upper jaw equally large. Inner teeth stout, relatively small, and tricuspid. In lateral part of upper jaw (i.e., where jaw curves strongest), inner teeth more densely set, larger, bi- to tricuspid, and more similar in form to outer teeth (mostly more distinct in dextral part of tooth band). Tooth bands slender with 1–2 rows of inner teeth on 1–2 outer tooth widths from outer row. In upper jaw, outer and one inner row remain in posteriormost part; in lower jaw, inner rows narrow gradually posteriad, only outer row remains over posterior quarter.

Lower pharyngeal bone slightly longer than broad and equally deep over entire length (Fig. 9). Pharyngeal teeth slender, major cusps acute, minor cusps reduced to absent, and cusp gaps concave. Teeth in posteriormost transversal row stout, and with blunt major cusps and distinct, small, and horizontally inclined minor cusps. Teeth set in 23–26 rows (n=4); two median rows set with more stout teeth, no molariform teeth.

Gill rakers on outer row of first gill arch short, stout, unifid, and triangular. No rakers on anteriormost part of ceratobranchial.

Caudal fin emarginate. Dorsal and anal fins reach level between two scales anterior to and one scale posterior to caudal fin base. Pelvic fins reach level between first and second anal fin spine; pectoral fins between one scale anterior to anus and first anal fin spine.

Colouration in vivo

Dominant males (> 73 mm SL): body beige-silver; cheeks and ventral half of body whitish (Fig. 8c). Flanks with 3–4 faint vertical stripes; caudal peduncle with faint mid-lateral stripe. Nostril-, interorbital-, lacrimal-, supraorbital-, and vertical preopercular stripes, and a nape band present. Dorsal fin dusky with anteriorly black and posteriorly red lappets; anal fin yellow with dusky base and two large orange egg spots (i.e., size of twice distance between rays). Caudal fin red with dark base, pectoral fins hyaline, and pelvic fins black. Posterior part of dorsal fin and dorsal part of caudal fin maculated.

Females and juveniles: body beige-silver; belly and cheeks whitish (Fig. 8d). Flanks with 4–5 faint vertical stripes and a faint mid-lateral stripe. Dorsal fin dusky, pectoral and pelvic fins hyaline, anal and caudal fins yellow, and anal fin with two small yellow-orange spots resembling egg-spots.

Colouration in alcohol

Body dorsally brown-yellow and ventrally grey-yellow (Fig. 8a). Flanks of dominant males with 2–5 faint vertical stripes and faint mid-lateral stripe, while all stripes absent or faint in females. Dominant males with nostril-, interorbital-, lacrimal-, supraorbital-, and vertical preopercular stripes, and a nape band. Dorsal fin dusky and with dark lappets and weakly maculated posterior part. Caudal fin ventrally hyaline-yellow, while dorsally dusky and weakly maculated. Pectoral and anal fins hyaline; anal fin with two faint egg-spots in dominant males. Pelvic fins black in dominant males and hyaline in females.

Distribution and ecology

Endemic to Lake Edward. Gut short (GL 119–153 % SL, n=5), diet mainly molluscivorous. Guts of seven specimens examined; four guts dominated by remains of Gastropoda, consisting of isolated snail tissues, opercula (2–5 mm), and small complete snails (shells 1.5–3.5 mm), each of these guts also contained 100–500 small Chironomidae larvae. Guts of two specimens only contained few Chironomidae pupae, Hydrachnidia, and/or Ostracoda, and one gut was empty. Small amounts of sand were occasionally found.

HAPLOCHROMIS PLANUS SP. NOV.

(Figs. 2c, 10, 11, and 12; Table 1)

Holotype

MRAC 2017.006.P.0060; Rwenshama, rocky shore, Lake Edward: 0°24'05.7"S 29°46'35.1"E; 26/03/2017 [♂ 76.6 mm SL].

Paratype

MRAC 2017.006.P.0059; Mouth of Kazinga Channel, hard substrate, Lake Edward: 0°12'14.4"S 29°52'37.2"E; 23/03/2017 [n=1; 60.4 mm SL]. MRAC 2017.006.P.0061; Rwenshama, rocky shore, Lake Edward: 0°24'05.7"S 29°46'35.1"E; 26/03/2017 [n=1; 82.0 mm SL]. MRAC 2017.006.P.0062; Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; 25/03/2017 [n=1; 60.0 mm SL]. MRAC 2018.008.P.0103; Kayanja, offshore, Lake Edward: 0°05'31.2"S29°45'30.3"E; 20/01/2018 [n=1; 67.4 mm SL]. MRAC 2018.008.P.0104; Kayanja, offshore, Lake Edward: 0°05'31.2"S 29°45'30.3"E; 21/01/2018 [n=1; 61.8 mm SL]. MRAC 2018.008.P.0105–106; Rwenshama, offshore, Lake Edward: 0°24'14.4"S 29°45'57.0"E; 24/01/2018 [n=2; 64.6, 71.0 mm SL]. RBINS 898–902; Kayanja offshore, Lake Edward: 0°05'34.8"S 29°45'28.8"E; 21/03/2019 [n=5; 58.0–62.7 mm SL; no morphometrics taken].

Etymology

Specific name from Latin ‘planus’, flat. Refers to its flat, shovel-like lower jaw.

Differential diagnosis

Haplochromis planus sp. nov. differs from all other species of *Haplochromis*, except *H. retrodens* from Lake Victoria, by a shallow, broad, and rectangular lower jaw with ascending arms steeply sloping upwards, enlarged, and distinctly visible intrabuccally. Oral tooth bands U-shaped and, in large specimens (> 75 mm SL), set posteriorly with large and stout inner and outer teeth, especially in upper jaw. All oral mucosa in lower jaw at same height and oral breathing valves strongly reduced to narrow, rectangular skin folds. Distinct from *H. retrodens* (data taken from Greenwood, 1956) by larger eyes [35.7–41.6 (38.2) vs. 23.8–29.6 (26.9) % HL], correlated shorter snout [24.6–28.8 (26.1) vs. 29.0–36.8 (32.5) % HL] and more slender interorbital width [19.1–22.1 (20.4) vs. 24.2–33.8 (28.7) % HL], and dominant males with scarlet to red vs. dark grey-green flanks.

It differs from *H. concilians* sp. nov. and *H. erutus* sp. nov. by a shallow vs. deep lower jaw, a more narrow interorbital region [19.1–22.1 (20.4) vs. 22.5–26.4 (24.2) and 23.4–27.2 (25.1) % HL, respectively], and dominant males with scarlet to red vs. blue-silver and silver-beige flanks, respectively. It differs further from *H. concilians* sp. nov. by a longer premaxillary pedicel [21.9–24.4

(23.0) vs. 16.1–21.6 (19.1) % HL] and from *H. erutus* sp. nov. by a longer upper jaw [27.6–32.1 (30.8) vs. 20.9–26.0 (24.1) % HL].

Description

Small species (< 82.0 mm SL) with a relatively slender body. Head straight to slightly convex, snout relatively acute and sloping at 40–55°. Eye large, interorbital distance small, and jaws broad, isognathous, and with a gape inclination of 15–25°. Upper jaw enlarged posteriorly, and maxilla extends to just past anterior margin of pupil. Lower jaw very shallow anteriorly and laterally, with a square outline and ventral margin of dentigerous arm horizontal in rostral view, hereby jaw somewhat resembles a shovel. Ascending arm of lower jaw (i.e., coronoid wing) steeply sloping upwards and enlarged (i.e., clearly visible intrabuccal). In lower jaw, intrabuccal oral mucosa at same height as dentigerous area of jaw and oral breathing valve reduced to a narrow and rectangular skin fold. Lips and oral mucosa large. Neurocranium generalised with a low and convex occipital crest (Fig. 11b). Chest scales small; size transition to flank scales gradual.

Outer teeth small, with slender and slightly recurved necks, and broad and strongly recurved crowns. In small specimens (< 65 mm SL): crowns bicuspid; major cusps short and isocline while bearing a small flange to obliquely truncated; minor cusps stout, large, and horizontally inclined. In large specimens (> 70 mm SL): crowns uni- to bicuspid and major cusps isocline, broad, relatively short, and bluntly pointed; minor cusps small, if present. Dental arcades broad and with square outlines. Outer teeth closely set with an inter-tooth distance of 0.5–1 outer tooth width; in anterior part of lower jaw, outer teeth implanted procumbently in anterior margin of bone. Inner teeth small, tricuspid, and set in 2–4 rows without a distinct gap between inner and outer rows. Dental arcades long in upper jaw with 1–4 posteriormost outer teeth large, stout, unicuspid, and buccally orientated; mostly short in lower jaw, reaching to before ascending arm, although, in large specimens (> 70 mm SL), 1–3 stout outer teeth may occur halfway on ascending arm. Tooth bands in both jaws narrow posteriad, until only outer row remains over posterior quarters. In large specimens (< 70 mm SL), outer and one inner row remains posteriorly, and posteriormost part of upper jaw set with inner teeth equal in size and form to the outer teeth (i.e., unicuspid, large, and stout).

Caudal fin emarginate. Dorsal and anal fins reach level between caudal fin base and two scales anterior to this point. Pectoral fins reach level between genital opening and anal fin; pelvic fins between first spine and first branched ray of anal fin in males, between genital opening and anal fin in females.

Gill rakers on the outer row of the first gill arch small, unifid, and stout. Posteriormost ceratobranchial rakers can be bifid.

Lower pharyngeal bone relatively fine, short, broad, shallow posteriorly, and with a slightly deeper keel (Fig. 12). All pharyngeal teeth slender, with concave major cusp gaps, small but distinct minor cusps, and often cusp protuberances. Teeth set in 25–32 rows (n=4), teeth in median two rows at most slightly stouter. Teeth in posteriormost row with blunt major cusps, straight major cusp gaps, and distinct but small minor cusps.

Colouration in vivo

Dominant males (> 58 mm SL): flanks and dorsal part of head scarlet to red, chest white, snout bright blue (Fig. 11c). Cheeks and opercula orange-red; dorsal part of head and anterior half of flanks scarlet to red; branchiostegal rays black. Flanks of dominant males sometimes with 4–5 blueish vertical stripes. Pelvic fins black; dorsal and caudal fins orange-red, and lappets (i.e., extensions of membranes between spines) of dorsal fin black anteriorly and red posteriorly. Pectoral and anal fins hyaline, anal fin with 2–3 large yellow egg spots, each spanning two fin rays. Lacrimal-, preorbital-, and supraorbital stripes and a vague nape band present.

Females and juveniles: body whitish, dorsally with a greenish sheen, snout dusky (Fig. 11d). Pelvic-, anal-, and ventral part of caudal fin yellow; dorsal part of caudal fin dusky; anal fin with 2–3 small spots resembling egg spots. Dorsal fin dusky and pectoral fins hyaline.

Colouration in alcohol

Body dorsally brown-yellow, ventrally brown-white, and branchiostegal membrane black (Fig. 11a). Lacrimal stripes and a nape band present in dominant males, while faint in females; nostril-, interorbital-, and vertical preopercular stripes faint in all specimens. flanks of dominant males with 4–5 faint vertical stripes. All fins hyaline, except dorsal and caudal fins dusky, and dominant males with pelvic fins black and anal fin with dusky posterior margin and 2–3 large egg spots. Anterior part of dorsal fin with black lappets in all specimens.

Distribution and ecology

Endemic to Lake Edward. Gut short (GL 113–170 % SL, n= 7). Gut contents of ten specimens (60.4–82.0 mm SL) examined; six guts dominated by Ostracoda and/or Hydrachnidia, while three were nearly empty. All these guts contained few Arthropoda (i.e., mainly Heteroptera or Diptera larvae), small amounts of sand, and some detritus. Remaining gut completely empty.

DISCUSSION

All three species, *H. concilians* sp. nov., *H. erutus* sp. nov., and *H. planus* sp. nov., differ strongly in their habitus from all other described species from the Lake Edward system. Although they also differ from each other, all show clear morphological similarities to oral mollusc shelling species from Lake Victoria. Therefore, the three newly discovered species were compared to the species from Lake Victoria, taking into account the definitions of the corresponding genera *sensu* Greenwood (1980).

Haplochromis concilians sp. nov. shows characteristics of '*Paralabidochromis*', '*Ptyochromis*', and '*Labrochromis*' but cannot unequivocally be assigned to any of these genera *sensu* Greenwood (1980). It shares with the former two a short and deep lower jaw, thickened lips, and stout unicuspid oral teeth (Fig. 2a), while it deviates from both by the straight vs. procumbent implantation of the anterior outer teeth in the lower jaw, and the molariform vs. stout pharyngeal teeth. In *H. concilians* sp. nov., the anterior part of the lower jaw curves slightly downwards, as found in a '*Ptyochromis*' but not in a '*Paralabidochromis*' morphology. A '*Labrochromis*' morphology is characterised by hypertrophied pharyngeal jaws with molariform teeth. These are also present in *H. concilians* sp. nov., but the specialised oral dentition is very different from the generalised dentition in '*Labrochromis*'. Unique to *H*. *concilians* sp. nov. are the tissue of the snout that is usually merged with the upper lip (in ca. 80% of specimens) and the anterior teeth in the lower jaw that are implanted distinctly buccally, hereby leaving the anteriormost part of the jaw edentulous. These morphological traits are unknown for any other species within the LVRS (Barel *et al*., 1977; Greenwood, 1980; Seehausen, 1996).

The trophic morphology of *H. erutus* sp. nov. is different from all other Lake Edward species but strongly resembles one other species within the LVRS, *H. bicolor* from Lake Victoria. Both species have a '*Macropleurodus*' morphology with a short upper jaw in which the dentigerous arms curve laterally downwards. Both outer and inner teeth are large and stout with recurved major cusps and labially implanted minor cusps (Fig. 2b). In both species, a handedness is observed in the degree of the development of the trophic morphology, i.e., the curvature of the upper jaw and the stoutness of the teeth were larger in either the dextral or the sinistral side (Greenwood, 1956). While very similar in their trophic morphology, *H. erutus* sp. nov. deviates from *H. bicolor* by a shallower supraoccipital crest, much larger eyes [35.4–40.7 (38.1) vs. 21.4–32.0 (27.0) % HL], and the beige-silver vs. red flanks of dominant males (a more elaborate diagnosis is presented in the species description of *H. erutus* sp. nov.). In addition, *Chilotilapia rhoadesii* from Lake Malawi has a strikingly similar morphology to *H. erutus* sp. nov. and *H. bicolor* (Greenwood, 1983). Since the Lake Malawi flock evolved independently from the LVRS (Salzburger *et al*., 2005, Meier *et al*., 2017), this similarity forms a clear example of convergent evolution.

Haplochromis planus sp. nov. more strongly resembles *H. retrodens* from Lake Victoria than any other known species from the LVRS, including those of the Lake Edward system. Both species have a '*Hoplotilapia*' morphology, which is characterised by flat, broad, and rectangular lower jaws with inflated and nearly vertically orientated ascending arms (Fig. 2c) (Greenwood, 1956). The oral tooth bands are U-shaped and broad over their whole lengths. The outer teeth are small, unicuspid, strongly recurved, and have a procumbent implantation in the anterior part of the lower jaw and, in both jaws,; the posteriormost inner and outer teeth are large and stout. However, both species differ from each other by the larger eyes of *H. planus* sp. nov. [35.7–41.6 (38.2) vs. 23.8–29.6 (26.9) % HL] and the scarlet to red vs. dark grey-green flanks of dominant males ((a more elaborate diagnosis is presented in the species description of *H. planus* sp. nov.).

We confirmed a molluscivorous diet for two of the three new species described. The stomach contents of both *H. concilians* sp. nov. and *H. erutus* sp. nov. consisted mainly of gastropod remains. Primarily opercula (2–5 mm), snail tissue, and small complete shells (1.5–4.0 mm) were found in the stomachs, while shell fragments were absent. The opercula and snail tissue belonged to relatively large snails, which were probably shelled by grabbing their soft bodies and tearing them out of their shells. Nevertheless, we cannot exclude that these species used an oral or pharyngeal crushing technique. Cichlids with similar morphologies from Lake Victoria were observed to use both techniques to prey on snails (Greenwood, 1974; Katunzi, 1982; Slootweg, 1987). The molluscivorous diets of *H. concilians* sp. nov. and *H. erutus* sp. nov. are supplemented with various Arthropoda, Ostracoda, and Hydrachnidia, in accordance to the opportunistic feeding habits of oral shellers from Lake Victoria (Greenwood, 1956; Katunzi, 1982).

We could not confirm a molluscivorous diet for *Haplochromis planus* sp. nov. Large specimens of this species (> 70 mm SL) show a specialised morphology with stout oral jaws that are set with stout teeth. We were able to examine the gut of only one large specimen (82.0 mm SL), but this gut was nearly empty. Meanwhile, small specimens (60.4–71.0 mm SL) were found to consume mainly Ostracoda and/or Hydrachnidia. In aquaria, *H. retrodens* from Lake Victoria was observed to use its shovel-like lower jaw to scoop up the substrate in search of prey (Greenwood, 1956). When molluscs were found, they were crushed by the oral jaws. The similar trophic morphology of *H. planus* sp. nov. suggests that small specimens of this species display a similar scooping behaviour to catch Hydrachnidia and Ostracoda that live in the bottom debris (Gerber & Gabriel, 2002). However, the oral jaw apparatus of small specimens are probably not strongly developed enough to crush molluscs. Greenwood (1956) only observed gut contents of large specimens (75–144 mm SL) of *H. retrodens*, which were found to consume mainly bivalves. Similar to this species, the specialised morphology of large specimens of *H. planus* sp. nov. could be developed enough to display an oral crushing technique.

Although the oral shellers from Lakes Edward and Victoria have similar morphologies, they display clear differences in eye size. All known species from the Lake Edward system have distinctly larger eyes than any formally described oral shellers from Lake Victoria (35.2–41.6 vs. 21.4–33.4 % HL; Fig. 13) (Greenwood, 1956, 1957, 1959; Seegers, 2008). All comparisons include specimens with similar standard lengths. Similarly, a difference in eye size was found between the lobed-lipped insectivores *H. lobatus* Vranken *et al.* 2019b from Lake Edward and *H. chilotes* Boulenger 1911 from Lake Victoria but a possible functional significance of this difference remains unclear (Vranken *et al*., 2019b). For oral shellers from Lake Victoria, behavioural experiments showed that they are highly dependent on their eyesight for detecting snails and catching them using the oral shelling technique (Witte *et al*., 2013). Prior to the recent increased eutrophication of Lake Victoria (Seehausen *et al*., 1997), its transparency was higher than Lake Edward (Levring & Fish, 1956). Oral shellers from Lake Edward may have evolved larger eyes as an adaptation to these relatively low-light conditions. Possibly by increasing the number of light sensitive cones in their eyes, which requires larger eyes (Van Der Meer & Anker, 1984). Furthermore, the requirement of oral shellers to have an accurate visual perception presumably explains why oral shellers prefer sand substrates, where the water is less murky, over muddy substrates (Witte, 1980; Seehausen, 1996; Witte *et al*., 2013), even though snails are more abundant in the latter (Okedi, 1990). Hitherto, no specimens with an oral shelling morphology were collected from the turbid Lake George. The visibility of its water may be too low or sand substrates to scarce to provide suitable habitats for oral shellers.

In low-light conditions, species of oral shellers from Lake Victoria have a lower shelling efficiency, while mollusc crushing is nearly unaffected (Witte *et al*., 2013). *Haplochromis concilians* sp. nov. has a morphology that may be more adapted to crushing molluscs than to shelling them. All bones in the oral jaw apparatus are strongly build; the premaxillary pedicel is short and inclines at a steep angle of 90–115° to the dentigerous arms, and the lower jaw is deep and short with the anteriormost stout outer teeth located distinctly buccally. These traits have been linked to an increased biting force (Barel, 1983; Otten, 1983) and could allow *H. concilians* sp. nov. to crush larger molluscs using the oral crushing technique. Presumably, the stout pharyngeal jaws with molariform teeth are adapted to crush molluscs (Smits *et al*., 1996), and the strongly thickened lips are adapted to the handling of gastropod shells, prior to crushing them (Colombo *et al*., 2013). We hypothesise that *H. concilians* sp. nov. uses primarily oral and pharyngeal crushing techniques and to a lesser extend an oral shelling technique to prey on molluscs.

All three newly described species from Lake Edward each resemble more closely species endemic to Lake Victoria, than any other species within the Lake Edward system. Species of *Haplochromis* from both systems are closely related. However, phylogenetic relationships between species remain largely unknown (Greenwood, 1980; Salzburger *et al*., 2005). Similar-looking species of *Haplochromis* from the Lake Edward system and Lake Victoria might be more closely related to each other than to species from the same lake (Greenwood, 1980). Another possibility is that the cichlids from both lakes evolved independently and that these situations thus represent cases of convergent evolution. Various intermediary scenarios are, however, also probable, given their presumed origin from a hybrid flock (Meier *et al*., 2017). Meier *et al.* (2017) found some support that the species from Lake Victoria form a monophyletic lineage and thatthe assemblage from the Lake Edward system is paraphyletic. Unfortunately, no oral shelling species were included in this study. Further research is necessary to unravel the complex phylogeny of *Haplochromis* from the LVRS. Regardless of how they evolved, it seems that the Lake Edward system has a rich cichlid community that is morphologically and ecologically similar to that of Lake Victoria.

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