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The thick-lipped haplochromine cichlids of the Lake Edward system

A morphometric revision

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Summary

The Lake Edward system, consisting of lakes Edward and George, is, like the other African Great Lakes, home to an extraordinary flock of haplochromine cichlids. Only 33 species are currently known while the total flock is estimated to consist of up to 90 species. The cichlid flock of the Lake Edward system is thus largely unknown. In this study, we performed a morphometric revision of the thick-lipped haplochromine cichlids. These can be divided into two trophic groups, the paedophages, that feed on the intra-buccal eggs and young of other mouthbrooding cichlids, and the lobe-lipped insectivores, that feed on insects living between rock-crevices. Of both groups, one species was known*,* respectively *Haplochromis taurinus* and *H. labiatus*. We found an additional four new species of paedophages: *H.* sp. 'curvidens'*, H.* sp. 'longicauda', *H.* sp. 'molossus' and *H.* sp. 'relictidens'. All species were found to have a paedophagous ecology. The last mentioned has the peculiar characteristic of losing its teeth during growth. Within the lobe-lipped insectivores, one new species was discovered, *H.* sp. 'lobatus', with lobed lips and an extremely prognathous lower jaw. Such a diversity in these rare trophic groups was unexpected and let to a new estimation of 75–175 species within the haplochromine cichlid flock of the lake Edward system, thereby largely exceeding previous estimations.

Abbreviations

General

ca.	Circa (approximately)
cf.	Confer (compare)
e.g.,	Exampli gratia (for example,)
ENSO	El Niño-Southern Oscillations
et al.	Et alia (and others)
etc.	Et cetera (and so forth)
KEA	Exploration hydrobiologique des lacs Kivu, Édouard et Albert (1952–1954)
i.a.,	Inter alia (among other things,)
i.e.,	Id est (that is,)
ITCZ	Intertropical Convergence Zone
mtDNA	Mitochondrial DNA
n	Number
NGS	Next generation sequencing
p./pp.	Page/pages
PC	Principal component
PCA	Principal Component Analysis
RAD	Restriction-site-associated DNA
SD	Standard deviation
SST	Sea-surface temperature
f	frequency

Institutions

For each institution, the abbreviation that is used for their collection is added.

NHM	BMNH	Natural History Museum, London, UK
RBINS	IRSNB	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
RMCA	MRAC	Royal Museum for Central Africa, Tervuren, Belgium

Measurements & meristics

Numbers correspond to the numbering in chapter 2 (pp. 17–24), where extended explanations can be found.

AFB	Anal fin base (9)	LatLl	Lower lateral line scales (29)
AFR	Anal fin formula (37)	LatLu	Upper lateral line scales (29)
AFRr	Anal fin soft rays (37)	LJL	Lower jaw length (23)
AFRs	Anal fin spines (37)	LJW	Lower jaw width (24)
BD	Body depth (2)	LongL	Longitudinal line scales (31)
ChD	Cheek depth (19)	LOT	Lower front teeth (40)
ChS	Cheek scales (35)	LTR	Lower tooth rows (41)
ChSa	Anterior cheek scales (35)	PFR	Pectoral fin formula (38)
ChSp	Posterior cheek scales (35)	PL	Pectoral fin length (14)
CPD	Caudal peduncle depth (11)	PPL	Premaxillary pedicel length (16)
CPL	Caudal peduncle length (10)	PrA	Pre-anal distance (5)
CPS	Caudal peduncle scales (34)	PrD	Pre-dorsal distance (4)
DFB	Dorsal fin base (8)	PrP	Pre-pectoral distance (7)
DFR	Dorsal fin formula (36)	PrV	Pre-pelvic distance (6)
DFRr	Dorsal fin soft rays (36)	SL	Standard length (1)
DFRs	Dorsal fin spines (36)	SnL	Snout length (17)
D-ULL	Upper transverse scales (32)	TL	Total length (12)
ED	Eye diameter (20)	UJL	Upper jaw length (22)
GL	Gut length (43)	ULL-A	Lower transverse scales (32)
GR	Gill rakers (39)	U-LLL	Inter-lateral line scales (30)
GRc	Ceratobranchial gill rakers (39)	UOT	Upper front teeth (0
GRe	Epibranchial gill rakers (39)	UTR	Upper tooth rows (41)
HL	Head length (3)	V	Vertebrae (42)
HW	Head width (15)	Va	Abdominal vertebrae (42)
IOW	Interocular width (21)	Vc	Caudal vertebrae (42)
LaD	Lacrimal depth (18)	VL	Pelvic fin length (13)
LatL	Lateral line scales (29)	V-P	Pelvic-pectoral fin scales (33)

1 Introduction

1.1 Cichlidae

Cichlidae are highly evolved fishes. They form one of the most species-rich families of vertebrates, currently consisting of 1703 valid species (Eschmeyer & Fong, 2016). Many remain undescribed so the actual number may well exceed this value, with estimates of over 3000 species (Salzburger & Meyer, 2004). They can be recognized by a single pair of nostrils and a lateral line that is divided in an upper part high on the flank, and a lower part running over the middle of the caudal peduncle (Kullander, 2003).

1.1.1 Haplochromine cichlids

Cichlids reside mainly in freshwater systems of the tropics and the southern hemisphere. They are most abundant in East Africa as a result of the opportunities its geological history provided (Stiassny & Meyer, 1999; Chakrabarty, 2004). After the elevation of the East African plateaus, the East African Rift system developed (fig. 1), forming an eastern and western branch (Danley et al., 2012). The latter started in the north some 25 million years ago (Roberts et al., 2012). The structure of Lake Edward was one of the first to form at ca. 16-13 million years ago (Kampunzu et al., 1998), after which rifting extended south, shaping the basins of lakes Kivu, Tanganyika and Malawi. Between the two rift branches, the relatively shallow Lake Victoria took shape (Danley et al., 2012). To fishes, the formation of the East African Great Lakes provided a transition from riverine to lacustrine conditions, leading to the emergence of many new ecological opportunities. Some cichlid lineages exploited these through their ability for fast adaptive radiation (see chapter 1.2.2, pp. 9–11) (Seehausen, 2006).

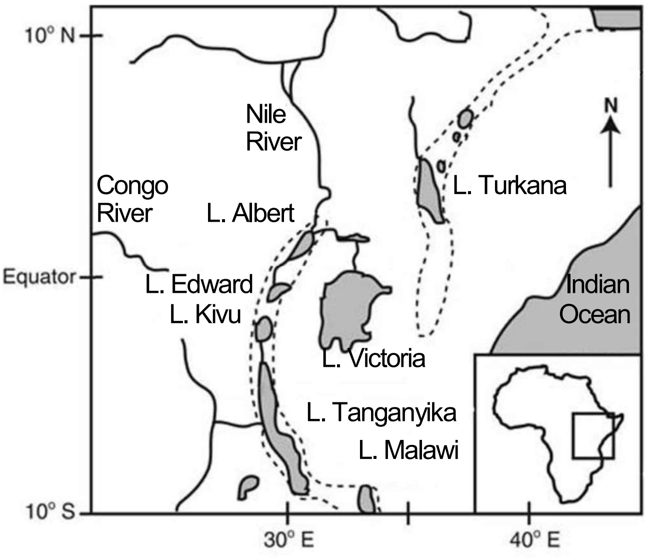

Figure 1 The East African Great Lakes system. The Eastern and Western Rift Branch are indicated by the dotted lines. Modified from Russell & Johnson (2006).

The proto-Lake Tanganyika was first colonised by several ancestral riverine cichlid lineages, 7–9 million years ago (Salzburger et al., 2002). The haplochromines *sensu lato* (fig. 2) form one of these lineages. It is uncertain if they colonised Lake Tanganyika or evolved within its contours (Meyer et al., 2016). The haplochromines *sensu lato* consist of the modern haplochromines, *Pseudocrenilabrus* Fowler, 1934, *Astatoreochromis* Pellegrin, 1904 and a Congolese/South-African lineage. The modern haplochromines, i.e., the haplochromines *sensu stricto*, contain the Tropheini from Lake Tanganyika, the haplochromines that invaded Lake Malawi and those that colonised the East African river

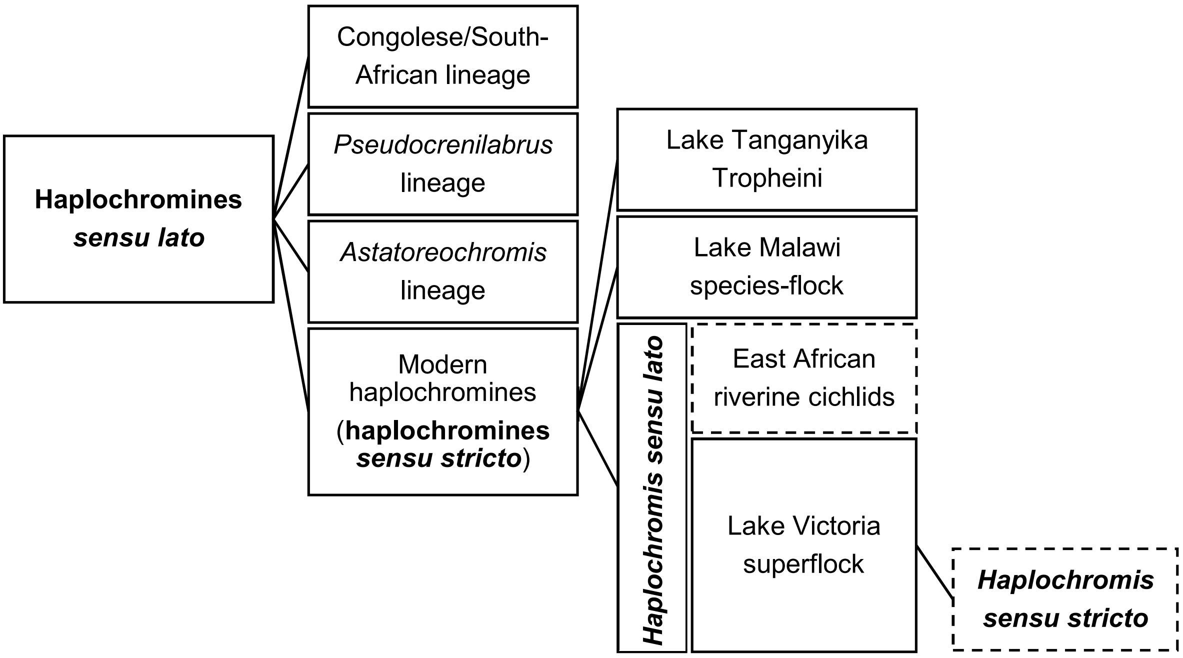

Figure 2 The East African haplochromine cichlids. Boxes drawn in full and dotted lines respectively indicate monophyletic and polyphyletic lineages. Based on Salzburger et al. (2005).

systems 1–2 million years ago. The latter also colonised lakes Kivu, Edward and Victoria (Salzburger et al., 2005). In each lake, they radiated into a presumably endemic species-flock (Stiassny & Meyer, 1999; Takahashi et al., 2001; Verheyen et al., 2003; Salzburger et al., 2005).

Most species in the lineage of the modern haplochromines are classified in the genus *Haplochromis sensu lato* Hilgendorf, 1888 (fig. 2), consisting of the haplochromines of lakes Kivu, Edward, George and Victoria and several East African riverine lineages. This genus is characterised by a '*Haplochromis*'-type of pharyngeal apophysis (van Oijen, 1996), in which the basioccipital of the apophysis strongly contributes to the articulation facet of the upper pharyngeal bone (Greenwood, 1978). They are all maternal mouthbrooders and the feeding apparatus is morphologically very diverse. The teeth on the oral jaws are divided in an outer row, consisting of uni- (fig. 3d-e), bi- (j-m) or tricuspid teeth (f), and at least one inner row of smaller teeth. Within one row, the teeth are usually homodont, i.e., of the same form. The triangular pharyngeal jaws are also very diverse, ranging from thin and slender, set with slender teeth (fig. 3a) to large and stout and containing molariform teeth (c). Sexual dimorphism is usually present. In most species, males display bright colorations in comparison to the dull-coloured females (Barel et al., 1977; Salzburger et al., 2005). Because of their highly adapted feeding apparatus and foraging behaviour, they are represented in a broad range of trophic niches (Witte & Van Oijen, 1990). The species within this genus are very closely related, leading to many phylogenetic uncertainties (Salzburger et al., 2005).

1.1.2 The Lake Victoria superflock

Lakes Victoria, Kivu, Edward, George and Albert (fig. 1) have a rich paleohydrology. During the Holocene, connections formed and disappeared between the distinct waterbodies, hereby causing a lot of uncertainty (Beadle, 1974; Verheyen et al., 2003). The ichthyology of Africa was found to consist of large regions with a similar species composition, that were named ichthyological Provinces. At first, Lakes Edward and Albert were classified in the Nilo-Sudan ichthyological Province (Roberts, 1975). However, it has been found that only Lake Albert has a Nilotic species composition. Greenwood (1979, 1980) saw similarities between the cichlid flocks of lakes George, Edward and Victoria, the latter belonging to the East Coast Province together with Lake Kivu. Consequently, the basins of lakes Edward and George were also classified within this province (Snoeks et al., 1997). The river systems of which are relatively poor in species, although the ichthyofauna of many systems remains to be thoroughly investigated. These rivers possess a high degree of endemic species (Snoeks et al., 2011).

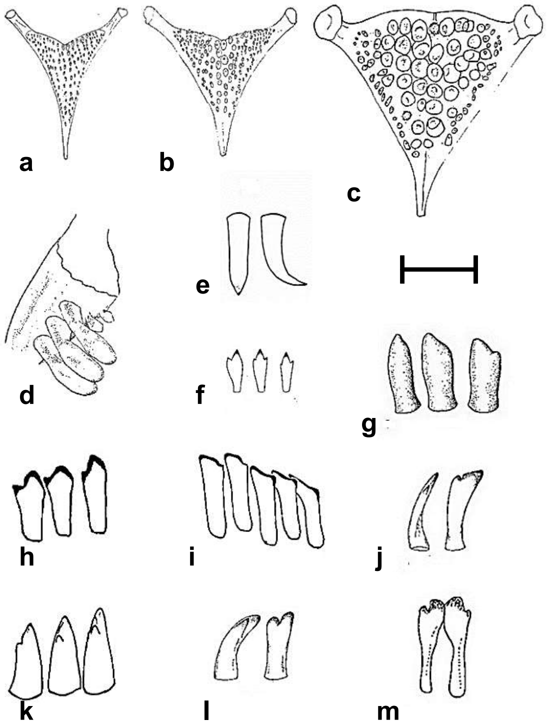

Figure 3 Lower pharyngeal jaws and oral outer teeth of various *Haplochromis sensu lato* species. Pharyngeal jaws (a–c) in occlusal view, teeth in labial (d–i, k, m) or lateral and labial view (e, j, l). (a) *H. angustifrons* and (b) *H. petronius*, insectivores; (c) *H. mylodon* and (g) *H.* 'purple miller', pharyngeal mollusc crushers; (d) *Schubotzia eduardiana*, unknown; (e) *H. dichrourus* "Uganda", piscivore; (f) *H. cryptogramma*, prawn-eater; (h) *H. pappenheimi*, zooplanktivore; (i) *H. limax* and (j) *H. lividus*, epiphytic algae grazers; (k) *H. taurinus*, paedophage; (l) *H. nigricans*, epilitic algae grazer; (m) *H. welcommei*, scale-eater. Scale = (a–c) 2 mm or (d–m) 1 mm. Modified from Greenwood (1973), van Oijen (1991) and Witte & van Oijen (1995).

The haplochromine species flocks of lakes Victoria, Kivu, Edward and George are collectively referred to as the Lake Victoria superflock due to their close and uncertain affinities (Greenwood, 1973, 1980; Verheyen et al., 2003). Greenwood (1979, 1980) hypothesised an evolutionary origin that gave rise to a total of 25 'genera' that he defined by morphological synapomorphies. Greenwood assumed that morphologically resembling species of different lakes have a common ancestry. He suggested that already diversified lineages of morphologically similar species colonised the different lakes and each lineage is represented in several lakes. Hoogerhoud (1984) revisited the 'genera' '*Gaurochromis*' Greenwood, 1980 and '*Labrochromis*' Regan, 1920 *sensu* Greenwood (1980) and found no distinctive characteristics between them. Each character forms a continuous morphocline, i.e., it gradually passes into each other between genera without being able to define a clear distinction. This makes the classification unclear and arbitrary, as is found repeatedly by others (Snoeks, 2000). Phylogenetic studies consistently broke up Greenwood's (1980) 'genera', disproving their monophyly (A. Meyer et al., 1990; Salzburger & Meyer, 2004; Meier et al., 2017). Therefore, for this study the term groups will be used instead of genera to emphasize that they have no phylogenetic meaning. One of these groups, *Haplochromis*, as restricted by Greenwood (1979), will be referred to as *Haplochromis sensu stricto* (fig. 2). To date, this group consists of five lacustrine species of the Lake Victoria superflock (Wamuini et al., 2010). It should be noted that Greenwood expressed his doubts about the phylogenetic meaning of his classification. He examined about 300 species, i.e., all that were known at the time, and based his classification on these, without knowing the full extent of morphological diversity present within the superflock (Greenwood, 1979, 1980). He had no idea of the genetic complexity and rapid speciation of these species. Understanding their evolution is an essential part in understanding the morphological diversity, as will be discussed in the next section.

Another hypothesis about the evolutionary origin of the superflock states a Congolese-Nilotic origin, diverging from the phenotypically-diverse genus *Thoracochromis* Greenwood 1979 (Seehausen et al., 2003). However, phylogenetic analyses that were based on mtDNA found an evolutionary origin in the Lake Kivu species flock (fig. 4) which served as the founding lineage that fed the other lakes of the superflock (Verheyen et al., 2003). This is in agreement with the hydrological connection that existed between the proto-Lake Kivu and Lake Edward until 25 000–11 000 years ago (Beadle, 1974; Pouclet, 1978). When the Virunga Volcanoes erupted (Kampunzu et al., 1998), the basin of Lake Kivu became separated from those of lakes Edward and Victoria (Beadle, 1974), hereby forming the present hydrological system.

Lake Kivu drains off into Lake Tanganyika through the Rusizi river. The flow of this river might have been reversed before the uplifting of the Virunga Volcanoes, feeding the proto-Lake Kivu that could subsequently be colonized by haplochromines originating from Lake Tanganyika (Salzburger et al., 2005). Lake Kivu's cichlid flock possesses a high degree of genetic diversity compared to the other lakes within the superflock due to the older age of its radiation (Machado-Schiaffino et al., 2015). According to this hypothesis, lakes Edward and George were first invaded by derived lineages of Lake Kivu, while others colonised Lake Victoria (Nagl et al., 2000; Verheyen et al., 2003). In each lake these lineages probably radiated independently into a flock of endemic species, although the monophyly of each individual flock cannot be supported (Meyer et al., 1990; Verheyen et al., 2003).

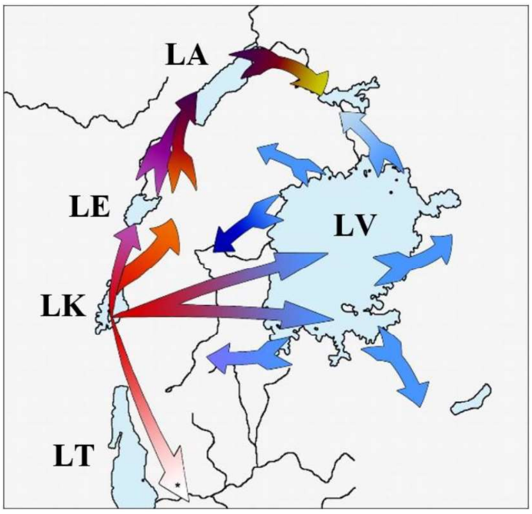

Figure 4 Proposed colonization events between the East African Great Lakes. Notable is Lake Kivu founding lakes Edward and Victoria. LA: Lake Albert; LE: Lake Edward; LK: Lake Kivu; LT: Lake Tanganyika; LV: Lake Victoria. Modified from Verheyen et al. (2003).

Phylogenetic analyses indicate that the species of the

Lake Victoria superflock are monophyletic and very closely related (Verheyen et al., 2003). The flock possesses an extremely diverse morphology although morphological apomorphies, specific for the superflock, have not been discovered (Greenwood, 1979, 1980). For this, the flock is probably too young, as it emerged within the short period of 100 000–400 000 years (Nagl et al., 2000; Seehausen et al., 2003; B. S. Meyer et al., 2016). Phylogenetic analyses based solely on mtDNA are unable to unravel their complex evolutionary history. They give incomplete or incorrect resolutions due to restrictions specific to their speciation process, e.g., hybridisations (See chapter 1.2.2, pp. 9–10) (Stiassny & Meyer, 1999; Verheyen et al., 2003; Manousaki et al., 2013). Whole genome analyses can give a more accurate phylogenetic resolution. A few studies used these techniques and the results so far are promising. Next generation sequencing (NGS) of restriction-site-associated DNA (RAD) markers revealed the distinction between several species in the Lake Victoria flock, although, were unable to provide phylogenetic resolution (Wagner et al., 2012; Keller et al., 2013; Brawand et al., 2014). Meier et al. (2017) was however able to support that Lake Victoria's flock is most likely monophyletic as well as the entire Lake Victoria superflock. For the system of lakes Edward and George, was found that its flock is paraphyletic within the superflock with influences from both the upper Nile and lakes Kivu and Victoria, however not through recent introgression. It currently seems that both the Congolese-Nilotic origin hypothesis of Seehausen et al. (2003) and the Kivu-origin hypothesis of Verheyen et al. (2003) speak part of the truth. To date, many uncertainties remain and the complete evolution of the Lake Victoria superflock has yet to be unravelled.

1.1.2.1 Thick-lipped haplochromines

This study will investigate the haplochromine cichlids with hypertrophied lips of the Lakes Edward and George. Thickened lips were shown to be a vague trait that is difficult to define (Barel et al., 1977) as across numerous species a continuous gradation in hypertrophication of the lip tissue was observed (Greenwood, 1980). Many of these species are, however, not regarded as thick-lipped haplochromines. The classification of Greenwood (1979, 1980) constitutes a solid foundation in classifying the morphological diversity within the Lake Victoria superflock. Therefore, in this study, his classification will be followed to define the groups that delimit the thick-lipped haplochromines. As Greenwood was unable to examine the full extent of the morphological diversity in these lakes, it is possible that species cannot be unambiguously classified within one of his group (Snoeks, 1994). This study will be limited to the species clearly showing the characteristic traits of the groups '*Lipochromis*' and '*Paralabidochromis*'. In what follows, the diagnostic characteristics of each group, according to Greenwood (1980), will be cited shortly. An extended list of characters of the thick-lipped haplochromines of the Lake Victoria superflock can be found in table 3, p. A.2.

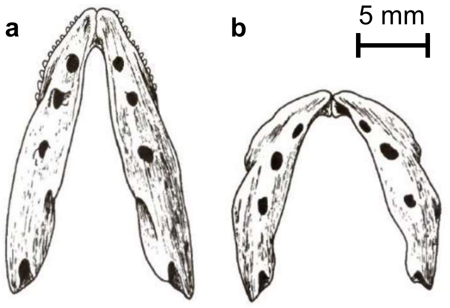

Figure 5 Ventral view of lower jaw morphologies within *Lipochromis*. (a) The parvidens-type in *Haplochromis parvidens* Boulenger 1911 and (b) the obesus-type in *H. obesus* Boulenger 1906. Modified from Greenwood (1980).

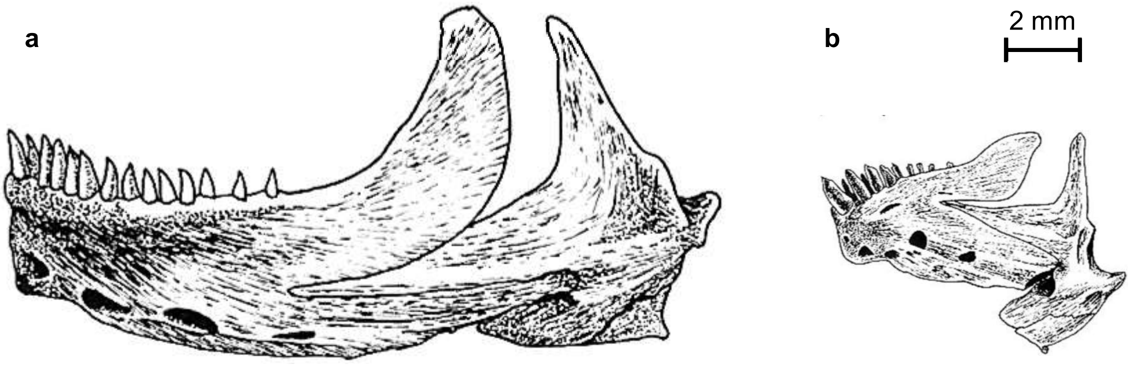

Figure 6 Lateral view of the lower jaws of (a) *Haplochromis obesus* (*Lipochromis*) and (b) *H. crassilabris* (*'Paralabidochromis'*). Modified from Greenwood (1980).

Within the first group, *'Lipochromis'* Regan, 1920, all species have distinctly thickened lips and a specialised paedophagous ecology, i.e., they eat the eggs and young of other cichlids. They are characterised by their long, widely distensible and protractile jaws, set with small teeth that are deeply embedded in the oral mucosa. Two distinct morphologies can be recognised. The obesus-type is characterised by a broad and rounded lower jaw (fig. 5b) with the outer teeth often labially curved (fig. 6a). While the parvidens-type can be identified by its narrow ending lower jaw which has a distinctive 'boat-shape', i.e., resembling the hull of a boat in front view (fig. 5a).

Species within the second group, *'Paralabidochromis'* Greenwood, 1956, possess a dentary with teeth that are deeply implanted in the thick oral mucosa, hence only rendering the tips of the teeth visible. The outer teeth have strong and cylindrical necks. The anterior-most outer teeth on the lower jaw are procumbently implanted, i.e. more horizontally implanted on the dentary (fig. 6b). The number of inner tooth rows reduce posteriorly, until only a single outer tooth row is present. The lower jaw (30–49 % HL) is short and stout, expanding caudally and hereby giving the jaw a chinless appearance. The lips are slightly thickened to lobate. Only species displaying strongly thickened to lobate lips will be investigated within this study. These were named the lobe-lipped haplochromines.

1.2 Evolution of the East African cichlids

East African cichlids display a large phenotypic diversity in morphology, colouration, trophic specialisation and breeding behaviour (Nagl et al., 2000). They obtained this through their large capacity for fast adaptive radiation, mostly in response to new ecological opportunities. In the Great Lakes, cichlid populations adapted to heterogeneous environments, hereby diverging into multiple new lineages. This resulted in the formation of a great variety of closely-related species in a relatively short amount of time (Schluter, 2000).

Species flocks have also evolved within other families of lacustrine fishes through adaptive radiation. For example, *Cyprinodon* Lacépède, 1803 pupfishes have formed a species flock of seven sympatric species, endemic to the lake Laguna Chichancanab in Yucatán, Mexico (Strecker, 2006). This flock is

8 000 years old, indicating a very rapid radiation. It is morphologically adapted to a variety of trophic niches, e.g., detrivores, insectivores and molluscivores (Strecker et al., 1996; Horstkotte & Strecker, 2005; Strecker, 2005). Furthermore, *Bathyclarias* Jackson, 1959 catfishes from Lake Malawi (Agnese & Teugels, 2001) and *Labeobarbus* Rüppell, 1835 species from Lake Tana in Ethiopia (De Graaf et al., 2008) have also formed species flocks. However, the adaptive radiations of Cichlidae are certainly the most extensive and impressive. In what follows, we will discuss the evolutionary mechanisms and some aspects of the adaptive radiations of cichlids in the East African Great Lakes.

1.2.1 Evolutionary mechanisms

The course of evolution is shaped by natural selection, gene flow, genetic drift and mutations. These formed the present phenotypic diversity at an extraordinary fast rate in East African cichlids. A better understanding of these evolutionary mechanisms can be gained by taking a closer look at the biology of haplochromines (Seehausen, 2006). The evolution of the East African cichlid radiations will be conceptualised based on the evolutionary history of the Lake Malawi species flock. The evolutionary history of other systems, including Lake Edward, is largely unknown but we presume that their cichlid flocks evolved in a similar way.

The current hypothesis is that the lacustrine cichlids of Lake Malawi radiated in three distinctive stages (fig. 7). In a first stage, cichlids colonised the lake and probably adapted to either rocky or sandy habitats. During the second stage, they adapted to a variety of ecological niches, coupled with the morphological diversification of the feeding apparatus. Hence, these first two stages were mainly influenced by ecological selection. In a third stage, sexual selection formed the major evolutionary mechanism. Female preference caused the emergence of a variety of isolated species that differed mostly in male colour patterns. These mechanisms will be discussed in more detail below. While each stage was characterised by a distinct selection pressure, other processes still influenced their radiation. The contribution of each mechanism differed in time and space (Danley & Kocher, 2001; Markert et al., 2001).

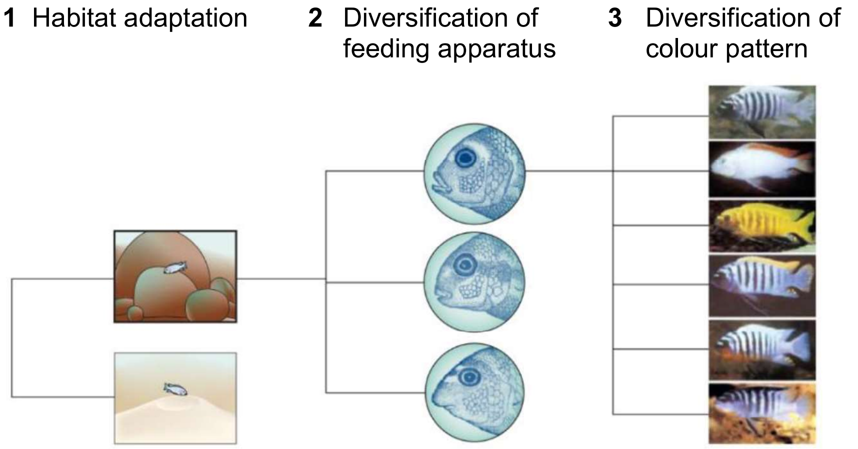

Figure 7 The three-step model, based on the radiation of Lake Malawi's lacustrine cichlids. Cichlids colonised Lake Malawi , followed by their adaptive radiation. An hypothesis states that they evolved through three stages. (1) In a first stage, cichlids diverged in sand-dwelling and rock-dwelling lineages. (2) in the second stage, the feeding apparatus diversified. (3) A third stage is characterised by the emergence of numerous male colouration patterns. Modified from Kocher (2004).

1.2.1.1 Ecological selection

Ecological selection is an important evolutionary mechanism. Transitions from riverine to lacustrine conditions created numerous ecological opportunities through the emergence of unexploited niches. Ecological selection can cause rapid adaptive speciation, allowing species to efficiently occupy these unfilled niches, e.g., in the first two stages of the three-step model (fig. 7). These adaptations mainly consist of a variety of trophic morphological modifications, feeding strategies, habitat preferences and behavioural differences, leading to an extensive radiation of closely-related species (Stiassny & Meyer, 1999; Kocher, 2004).

Cichlids possess two sets of jaws, the oral- and pharyngeal jaws. The latter are modified gill arches, posterior in the branchial basket. The pharyngeal jaws of cichlids are functionally decoupled from the oral jaws. This enables them to adapt to a variety of food sources, creating an extensive diversity of trophic adaptations (Seehausen, 2006). Multiple tooth rows are implanted on both the oral and pharyngeal jaws (Streelman et al., 2003). The morphology of the teeth on both jaws can be very diverse, extending their adaptability even further. For example, piscivores have large, unicuspid teeth (fig. 3e) whereas molluscivores have stout and molariform teeth (c). The amount, size and implantation of the teeth is specialised in function of their trophic niche (Stiassny & Meyer, 1999). These can range from piscivores, phytophages, molluscivores, algae grazers to scale- or parasite eaters (Witte & Van Oijen, 1990). Furthermore, the feeding apparatus of cichlids is regulated by only a few genes. Hence, small genetic changes can have a large morphological effect, allowing the phenotype to respond quickly to ecological selection (Albertson et al., 2003).

But ecological selection is not the mechanism that shapes the trophic morphology of cichlids. The environment also plays an important role in the establishment of variation. Cichlids have been shown to possess a significant diversity in phenotypic plasticity, enabling a quick change in the expression of traits (Pfennig et al., 2010). For example, insectivorous thick-lipped cichlids that are reared in captivity are unable to feed in a natural way, i.e., they will be unable to use their thickened lips to suck insects out of their hiding places due to the absence of this niche in captivity. Consequently, they will develop a reduced lip thickness in comparison to their natural phenotype (Machado-Schiaffino et al., 2014). A change in feeding behaviour can induce a plastic change in morphology. This will promote fast adaptive radiations by stimulating, i.a., the appearance of new phenotypes and the divergence of species (Stauffer & Gray, 2004; Pfennig et al., 2010; Machado-Schiaffino et al., 2014).

1.2.1.2 Sexual selection

All haplochromines *sensu lato* are maternal mouthbrooders. Females lay only a small number of eggs that they immediately take up in their mouths. Here, these will be fertilised and incubated at least until they develop into free-swimming juveniles. This enables the female to gather food for her young and protect them from predation, hereby displaying a high degree of maternal care (Keenleyside, 1991; Stiassny & Meyer, 1999; Salzburger et al., 2002; Kocher, 2004). Females invest a lot of energy in raising a limited number of offspring. Males on the other hand display no paternal care, leading to an asymmetry in reproductive investment between the sexes. Therefore, females can become picky when choosing a mate. They do this by choosing males with attractive colour patterns (Stiassny & Meyer, 1999; Kocher, 2004). Females can display varying preferences in these male colourations. This leads to disruptive sexual selection, forming distinct lineages according to female preference (Kocher, 2004). Males of reproductively isolated, sympatric species often display opposing colourations. Such species are often young and lack major genetic incompatibilities. Prezygotic isolation, in the form of female mate preference, will lead to the conservation of the distinct species, e.g., the third stage of the three step model (fig. 7) (Kocher, 2004). For example, in Lake Malawi, females of the genus *Maylandia* Meyer & Förster, 1984 prefer males with either blue or yellow colour patterns. Females with a certain preference will not mate with males displaying an opposing coloration, leading to the sexual isolation of both phenotypes (Seehausen et al., 1997). Such disruptive sexual selection has, however, not been studied in the Haplochromis species flocks of lakes Kivu, George and Edward (Greenwood, 1973; Snoeks, 1994).

Sexual selection in cichlids depends on visual communication and distinctive male colour patterns will only be selected for, if females are able to notice them (Seehausen et al., 1997). During the 20th century, Lake Victoria has known a fast decrease in its water clarity through urbanisation, deforestation and pollution, leading to an increased flow of sediment into the lake. The *Haplochromis* species, could have been unable to recognize each other, leading to the hybridisation of reproductively isolated species (Seehausen et al., 1997). The water of Lake Edward, and to a greater extend Lake George, has a low visibility, possibly limiting the visual communication between individual cichlids (Beadle, 1932). Species with males displaying bright colour patterns do however occur, presumably through sexual selection. Smith (1995) mentions that some authors hypothesize a greater sensory ability through bigger eyes or enlarged lateral line pores. However, no support can be found for either of these hypotheses.

1.2.2 Adaptive radiation

Cichlids display an extensive diversity in morphology in addition to the variety in habitat preference, behaviour and male colour patterns. This variation allows the segregation of a large number of species through niche isolation (Stiassny & Meyer, 1999). Although they can often produce fertile offspring, closely-related species can still occur conspecifically due to pre-zygotic isolation through female mate preference, in addition to ecological specialisation, causing hybrids to have a reduced fitness. (Kocher, 2004). Meanwhile, species from distantly-related lineages can display convergent evolution within the same lake. For example, in the Lake Tanganyika cichlid flock, several species from distantly-related lineages can have similar morphologies and occupy the same niches, indicating a strong link between morphology and ecology. This allows many species to live sympatrically, despite the necessity of an extensive niche diversity (Muschick et al., 2012). These species will not hybridise because of their distant relatedness.

Throughout East Africa, many lakes have their own species flock of cichlids. The species richness is mainly determined by the size of the lake and the ecological opportunities within it. Large areas generally accommodate a greater diversity of niches through the occurrence of heterogeneous habitats that will allow the sorting of numerous species in addition to large areas that favour allopatric speciation through isolation by distance (Seehausen, 2006, 2015). This species richness is formed by their large capacity for rapid adaptive radiation. But which key-innovation enables them to do this? A few hypotheses have been proposed. Galis & Drucker (1996) conceived that the functional decoupling of the pharyngeal jaws gave them the flexibility to adapt to new ecological niches. Salzburger et al. (2005) proposed the origin of female mouthbrooding behaviour and male egg spots on the anal fin to coincide with this ability. Cichlids radiations are however not confined to lineages displaying either of these characters, while other taxa that display these will fail to radiate when the right conditions are met. These innovations are important mediators, but no necessities for a radiation to occur. The ability for fast adaptive radiation has not yet been explained by the acquisition of a morphological trait. Presumably, it is a genetic character that has been acquired throughout the evolutionary history of a few lineages of East African cichlids (Seehausen, 2006).

During the Holocene, the topology, climate and consequently hydrology have known extensive fluctuations (See section 1.3.1, p. 12) (Stiassny & Meyer, 1999; Chakrabarty, 2004; Russell & Johnson, 2005). To cichlids, changing water levels can create or destroy niches within the lakes in addition to connections between separate waterbodies, allowing distinct lineages or different populations to interact with each other. Many East African cichlid species are genetically closely related due to their recent divergence. Consequently, they are often able to produce fertile hybrids (Seehausen et al., 1997). Due to these hydrological changes, hybridisations between populations of cichlids most likely occurred multiple times throughout East Africa, this could explain inconsistencies between phylogenetic analyses of nuclear and mitochondrial DNA (Rüber et al., 2001). Introgression is thought to have occurred in the species flocks of lakes Tanganyika, Malawi and Victoria (Smith et al., 2003; Keller et al., 2013; Meyer et al., 2016). This form of gene flow could lead to genetically diverse populations with an enlarged evolutionary potential (Seehausen et al., 2003; Kocher, 2004; Schwarzer et al., 2012; Keller et al., 2013). Through hybridisation, populations can possibly overcome genetic constraints and hereby promote fast radiations (Seehausen, 2006).

Beside the previously mentioned selection pressures, also neutral processes can shape the complex evolution of East African cichlids. For example, a changing hydrology can allow divided populations to interact and possibly hybridise with each other. Neutral processes form an important part in maintaining genetic variation, whereas selection pressures cause the sorting of this variation (Brawand et al., 2014). Alternations and interactions between both mechanisms could possibly explain the haplochromines' ability for fast adaptive radiation. They can radiate while maintaining much of their adaptive potential. Hybridisations can cause the increase of their genetic diversity. This gives them the ability to feed a successive radiation if an opportunity would present itself (Seehausen, 2006; Brawand et al., 2014).

1.2.3 Convergent evolution

Remarkable in the adaptive radiation of cichlids is the frequent occurrence of convergent evolution.

Species of distinct radiations have a high phenotypic and ecological resemblance, showing similarities in body shapes, feeding apparatus, behaviour and colour patterns (Colombo et al., 2013; Machado-Schiaffino et al., 2015). This implies that the same evolutionary mechanisms independently formed phenotypically-resembling species (Schluter & Nagel, 1995; Rüber & Adams, 2001; Machado-Schiaffino et al., 2015).

An example of convergent evolution is the hypertrophication of the lips, which evolved multiple times in cichlids. Although it's an uncommon phenotype, most of the East African Great Lakes have endemic thick-lipped cichlid species (fig. 8). For example, *Haplochromis chilotes* Boulenger, 1911 in Lake Victoria, *Abactochromis labrosus* Trewavas, 1935 in Lake Malawi and *Lobochilotes labiatus* Boulenger, 1898 in Lake Tanganyika. Furthermore, this phenotype reappears in species of other fresh-water systems in Africa and Central-America, e.g., *Amphilophus labiatus* Günther, 1864 in Lake Nicaragua (Colombo et al., 2013). The repeated independent evolution of this phenotype suggests it's a functional adaptation (Losos, 2011).

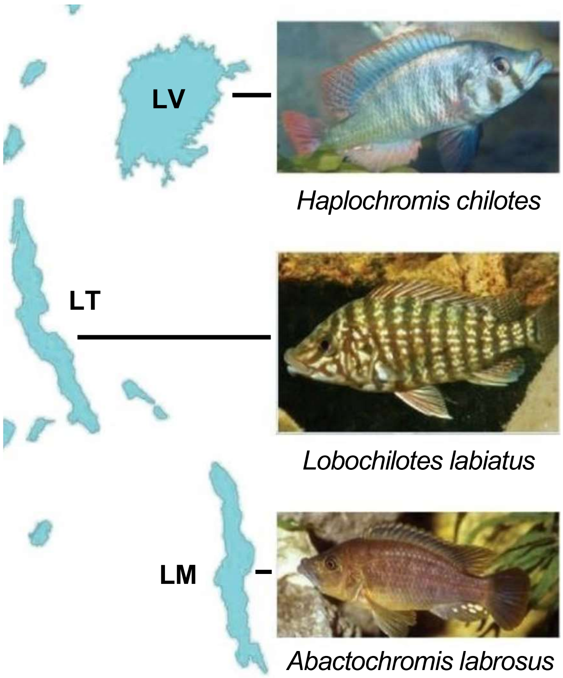

Figure 8 Convergent evolution in East African tick-lipped cichlids. Cichlids of lakes Victoria, Tanganyika and Malawi morphologically resemble each other. All Species possess thickened lips and an elongated and narrowed head. However, phylogenetically, all species independently evolved within its species flock of endemic species. LV: Lake Victoria; LT: Lake Tanganyika; LM: Lake Malawi. Modified from Santos & Salzburger (2012).

1.2.4 Hypertrophication of the lips

Hypertrophied lips cannot be linked to a single trophic adaptation. Some thick-lipped species are molluscivores, crushing molluscs with their strong pharyngeal jaws (Colombo et al., 2013), while others feed on small invertebrates (Elmer et al., 2010; Manousaki et al., 2013). A more peculiar ecological specialisation is paedophagy, in which the eggs and fry of other cichlids are consumed (Greenwood, 1973; van Oijen, 1996).

A few hypotheses regarding the function of thickened lips have been proposed. For example, providing a protection against mechanical shocks, hereby preventing injury when bumping into rocks during feeding (Manousaki et al., 2013). Furthermore, they could increase gustation by enlarging the olfactory surface, and consequently improving prey detection (Arnegard & Snoeks, 2001). This is in coherence with some species expressing a relatively high number of taste buds on their hypertrophied lips (Oliver & Arnegard, 2010). Behavioural experiments have given some insight into the function of thickened lips, e.g., molluscivorous species use their lips to handle prey items. As it is uncertain if specimens display natural behaviour in captivity, some uncertainties remain (Colombo et al., 2013).

The natural environment of thick-lipped insectivores consists mainly of rocky habitats (Kohda et al., 2008; Oliver & Arnegard, 2010). Here they forage by sucking small invertebrates out of crevices in the rocks. Thickened lips have shown to be adaptive for this particular foraging behaviour, as these species have a higher foraging success (Baumgarten et al., 2015). In insectivores, thickened lips are often correlated with a distinctly elongated and narrow head. This provides an easier access to crevices and an increased suction force (Manousaki et al., 2013; Baumgarten et al., 2015).

Paedophagous cichlids exploit the mouthbrooding behaviour of other haplochromines by feeding on their intra-oral eggs and young. Some species do this by both chasing and ramming the brooding female. This will force the female to release her young that will subsequently be snatched by the paedophage (Mckaye & Kocher, 1983). After the victim is exhausted, the paedophage uses its widely-distensible jaws to engulf the mouth of the mouthbrooding female to force her to release her young. The small teeth of paedophages are deeply embedded in the thickened oral mucosa, giving them an edentulous appearance (Ribbink & Ribbink, 1997). Greenwood (1974) hypothesised that this morphology enables them to quickly release the hitherto brooding female after they obtain their meal, without getting their teeth stuck on the victim.

In all examples, thickened lips have shown to be an adaptation for various trophic specialisations. This however does not exclude that other evolutionary forces might have played a role in the development of this exceptional phenotype.

1.3 Lake Edward

1.3.1 Hydrology and climate

Lake Edward (0°20'S, 29°36'E) (fig. 9) is located on the border between the Democratic Republic of the Congo and the Republic of Uganda. It is the smallest of the Large East African Great Lakes, with a surface area of 2 325 km² and a mean depth of 33 m (Lehman, 2002). The smaller (250 km²) and shallower (2.4 m) Lake George, is located northeast of it. These lakes are connected through the wide Kazinga Channel and are collectively regarded as the Lake Edward system. The Kazinga Channel has a length of 36 km and a width ranging between 150–1 000 m (Smith, 1995). Lake George is characterised by green water that flows slowly, through the Kazinga channel, to the clear water of lake Edward. This colour difference is caused by the lower phytoplankton densities of Lake Edward (Beadle, 1932). Furthermore, Lake Edward has a higher salinity and alkalinity. The latter lake is fed by soda-rich water by the Rutshuru river, that flows through volcanic regions of the Virunga Mountains (Beadle, 1932). The visibility of the lake is low, approximately only up to 30 cm (Smith, 1995). Lake Edward has a permanent thermocline, located at a depth of 40–70 m. The saline-rich water that is being fed to the lake has a higher density. In the lake, this water will accumulate in the hypolimnion, below a depth of 50

m. This water layer is rich in H_2S and permanently anoxic, causing it to be inhabitable for fishes (Beadle, 1932). Furthermore, the distinct water layers will not turnover as a result of the density difference between the epi- and hypolimnion (Beadle, 1966).

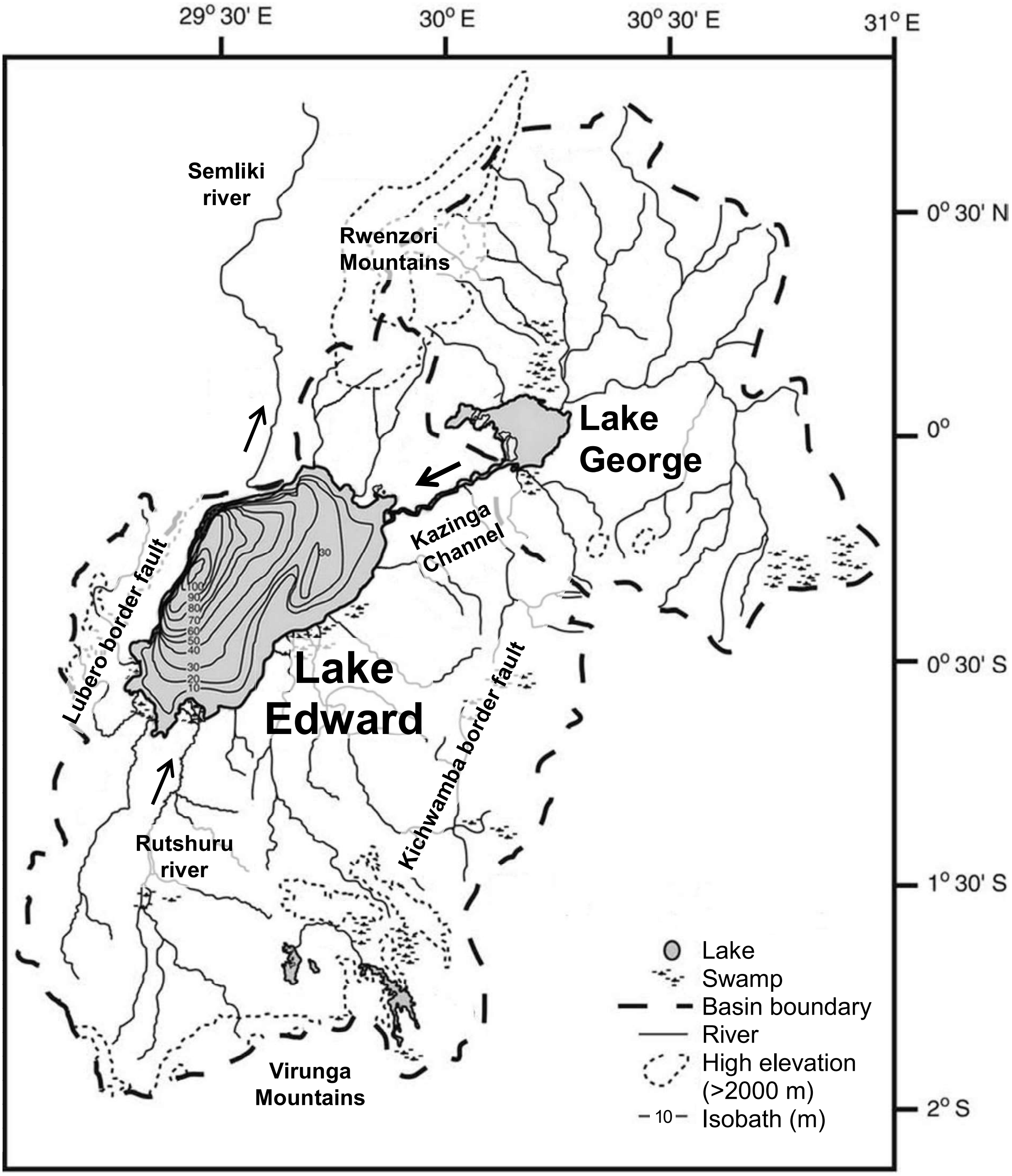

Figure 9 The lake Edward system. Consisting of lakes Edward and George that are connected through the Kazinga Channel. Modified from (Russell & Johnson, 2006).

Although Lake Edward has an outflow through the Semliki river, there is a major water loss through the evaporation of surface water. The evaporation rate is high, at an average of 2 m/year (Russell & Johnson, 2006). Lake Edward has a tropical wet and dry climate with an average rainfall of 0.9 m/year

(Russell & Johnson, 2006). The lake is located just below the equator where the Intertropical Convergence Zone (ITCZ) passes twice a year, exposing it to two wet seasons from October to December and March to May. Fluctuations in precipitation makes the water level of Lake Edward sensitive to changes due to the high evaporation rate (Danley et al., 2012).

During the Holocene, a few dry periods caused major low stands of the water level, probably causing the complete desiccation of the shallow Lake George. These periods were alternated by wetter conditions (Russell & Johnson, 2005). Overall the climate of the Lake Edward system was relatively dry during the Holocene, except for the last few centuries which are characterised by a wetter and stable climate (Russell & Johnson, 2005, 2007; Danley et al., 2012).

1.3.2 Geography

Lake Edward is situated on the Albertine Rift, which is the western branch of the East African Rift (fig. 1, p. 1), at an altitude of 912 m above sea level. At Lake Edward, the rift valley forms a topographic depression to the west, bordered by a single fault, the Lubero Border Fault (fig. 9). This so-called half-graben is occupied by the lake, giving it its distinctive structure (Lehman, 2002; Russell & Johnson, 2005). The deepest part of the lake (117 m) is situated close to the western shore. From here, the fault steeply towers up to 2 000 m above the lake's water level (Lehman, 2002; Russell et al., 2003). To the east, the Kichwamba border fault gently rises, forming hills that separate it from Lake Victoria (Bagalwa et al., 2014). South of Lake Edward, Lake Kivu is situated in the same rift branch. The latter lake drains into Lake Tanganyika and the Congo basin while it is separated from Lake Edward by The Virunga Mountains (Russell et al., 2003). Rivers flowing through these mountains feed, i.a., lakes Kivu and Edward. One of these rivers, the Rutshuru river forms the major inflow of Lake Edward (Beadle, 1932). North of the lake, the Rwenzori Mountains rise, with Lake Albert located behind them in the Albertine Rift. Both lakes are connected through the 160-km long Semliki river, running west around the mountains in the Semliki valley. This river forms the major outflow of Lake Edward. Fish migration from Lake Albert is prevented by the rapids of the Semliki river (Beadle, 1932).

1.3.3 Ichthyofauna

Lakes Edward and George have a similar ichthyofauna, consisting mainly of the same species. Lake Edward is home to several species within the genera *Protopterus* Owen, 1839; *Labeobarbus* van Hasselt, 1823; *Barbus* Cuvier & Cloquet, 1816; *Mormyrus* Linnaeus, 1758; *Clarias* Scopolo, 1777; *Bagrus* Bosc, 1816; *Tilapia* Smith, 1840 etc. (Poll, 1939a; Hulot, 1956). More remarkable are the genera that are lacking from the lake, e.g., *Lates* Cuvier, 1828; *Alestes* Müller & Troschel, 1844; *Citharinus* Cuvier, 1816 and *Hydrocynus* Cuvier, 1816 (Green, 2009). Consequently, niches that are occupied by these genera in other lakes, can be exploited by other species within Lake Edward, most notably haplochromine cichlids.

As many other lakes of East Africa, the Lake Edward system is home to an endemic flock of haplochromines. For a long time, the cichlid radiation of the Lake Edward system has been neglected due to the greater interest in the lake Victoria basin (Smith, 1995). Up to the present day, the ichthyofauna of Lake Edward is largely unknown. The lake is partially situated in the Democratic Republic of the Congo, a country with a lot of political conflicts, impeding the study of its cichlid flock. The limited research that has been done led to the description of a few endemic species (Smith, 1995). Lake George, however, has been investigated by i.a., Regan (1921), Trewavas (1933), Poll (1939a, 1939b), Hulot (1956) and Greenwood (1973). They described a total of 33 species that live in the lake and probably also in Lake Edward, most of which are endemic for the Lake Edward system (Decru, 2016) On the contrary, the estimated number of haplochromine cichlid species that live in the Lake Edward system is assumed to be 60–90 species (Keenleyside, 1991; Snoeks, 2001). According to these estimations, there is still a lot to discover about the haplochromine cichlid flock of the Lake Edward system.

To date, two thick-lipped haplochromine cichlids of the Lake Edward system have been described, namely *H. labiatus* Trewavas, 1933 (*‘Paralabidochromis’*), and *H. taurinus* Trewavas, 1933 (*‘Lipochromis’*).

1.3.4 The HIPE project

HIPE stands for ‘Human impacts on ecosystem health and resources of Lake Edward’. The productivity of the fisheries of Lake Edward has known a drastic decline over the last decades. The objective of the HIPE project is to gain an understanding of the ecosystem functioning and investigate the cause of this disruption. One hypothesis is that this decline is caused by the collapse of the local *Hippopotamus* population during the large-scale poaching activities during decades of civil war in the Democratic Republic of the Congo. This slaughter caused a large decrease in the translocation of nutrients to the lake. The large amount of hippo faeces, that were excreted in the lake, might have fed the lake’s ecosystem in the past, including its high abundance of fish. Within this project, the Royal Museum of Central Africa in Tervuren (RMCA) will study the ichthyofauna of the Lake Edward system, including its haplochromine cichlid flock. Our study was implemented in function of this objective (Decru et al., 2016).

1.4 Aim

The aim of this study is to revise and describe the thick-lipped haplochromine cichlids of Lake Edward. Due to the vague definition of hypertrophied lips, the study will be delimited to two groups of Greenwood’s (1980) classification of the Lake Victoria superflock, namely *‘Lipochromis’* and the lobe-lipped *‘Paralabidochromis’*, both characterised by hypertrophied lips.

Species will be described based on the morphological species concept. It is a practical and widely used way in which species are distinguished by their body size, shape, structure, and colour patterns (Kocher, 2004). Therefore, a detailed comparative morphological study was implemented. On all specimens, 26 measurements and 16 meristics were recorded, in addition to various qualitative observations. We took X-ray scans of 62 specimens and performed basic stomach analysis on 25 ‘*Lipochromis’* specimens.

Principal component analyses were conducted to distinguish between taxa.

2 Material & methods

In this study, 43 specimens from the RBINS collection and 132 specimens from the RMCA collection are studied together with the holotypes of *Haplochromis labiatus* and *H. taurinus* from the NHM collection. Hence, a total of 177 specimens from the Lake Edward system were investigated.

A comparison was made with the species of Lake Kivu that belong to the studied groups. The holotype of *H. occultidens* Snoeks, 1988 (*'Lipochromis'*) and a syntype of *H. paucidens* Regan, 1921 (*'Paralabidochromis'*), were analysed, both from the RMCA collection. The outer teeth of an additional 6 specimens of *H. occultidens* were counted to compare the changes in the number of teeth over different life stages, with the '*Lipochromis'* specimens from the Lake Edward system.

All specimens were carefully investigated. A total of 29 measurements and 15 meristics were taken, following Snoeks (1994) and Barel et al. (1977). Deviations from these methods were indicated and accurately described. All measurements were conducted by a single person to retain consistency and minimize errors, as the interspecific variation between haplochromine cichlids can be very small (Snoeks, 2004). All measurements and counts were performed under a binocular microscope (6.5–50x). All data were consistently collected from the left side of the specimens. If measurements or counts could not be taken due to damages, these were taken on the right side or excluded from the study if this was also impossible.

The sex of a specimen was determined when possible. Some specimens were too young to show gender-specific characters, while other specimens were in a way that damaged the genital region. The dorsal head profile, gape inclination, caudal fin outline, lateral snout outline, maxillary bullation and maxillary posterior extension were described following the terminology of Barel et al. (1977).

2.1 Measurements

On all specimens, 14 body, 10 head and 4 lower pharyngeal jaw measurements (see below) were taken, using a dial calliper (± 0.01 mm). The majority of measurements were conducted between strictly defined bony reference points. Soft tissues were always compressed to the concerned bone, unless otherwise mentioned. Caution was given to prevent the deformation of bony elements, especially in small specimens. All measurements were taken on specimens with a closed mouth and contracted premaxillary pedicel. Specimens with the mouth otherwise, if possible, were forced in this position, if not, they were excluded from all measurements and only the meristics were taken.

2.1.1 Body measurements (fig. 10)

1) Standard length (SL): as defined by Barel et al. (1977). From the anterior point of the premaxilla to the midpoint of the caudal fin base, at the height of the lower lateral line. This point can be determined by articulating the caudal fin.

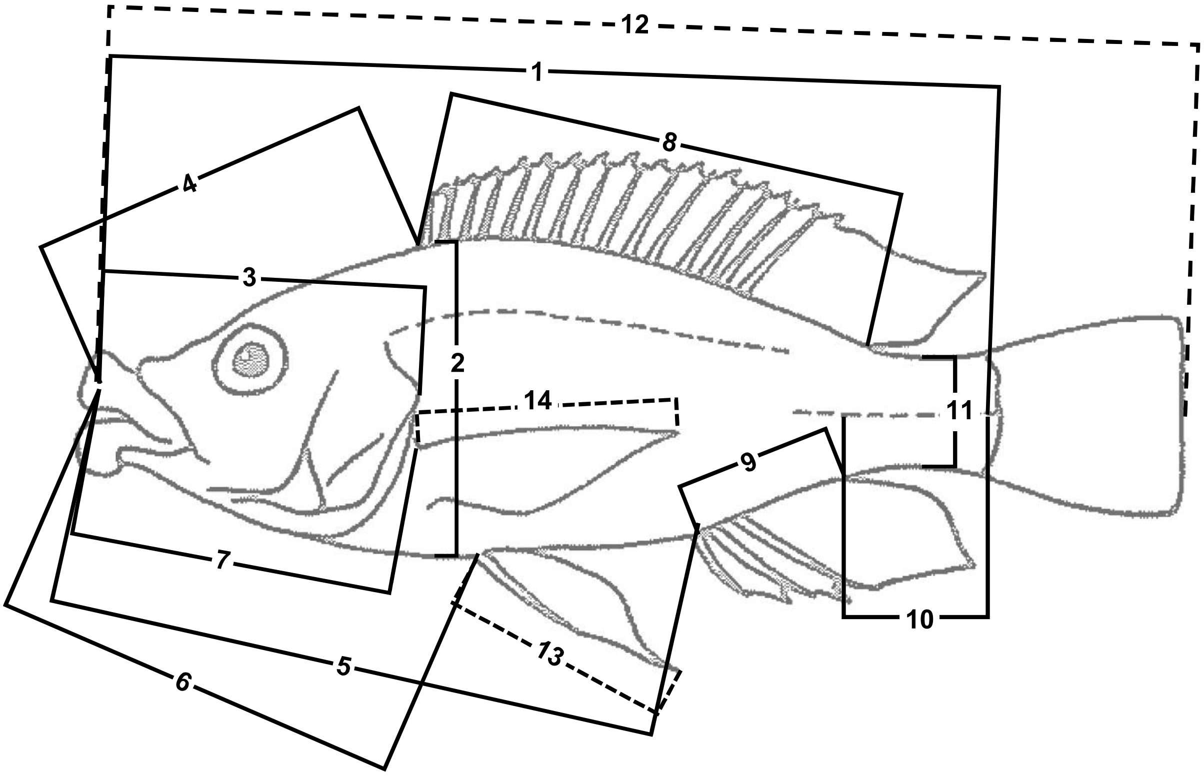

Figure 10 Body measurements taken: numbers are in accordance to the definitions in chapter 2.1.1. Measurements indicated by a dotted line were excluded from all analyses. Figure displaying *Haplochromis chilotes*, endemic to Lake Victoria. Modified from Eccles (1992).

2) Body depth (BD): as defined by Barel et al. (1977). The largest depth of the body anterior of the pelvic fin base. The dorsal reference point was located at the dorsal fin base while excluding the dorsal fin. The body was not compressed for this measurement.

3) Head length (HL): as defined by Barel et al. (1977). From the anterior point of the premaxilla to the posterior point of the operculum, at the height of the opercular blotch.

4) Pre-dorsal distance (PrD): as defined by Snoeks (1994). Distance between the anterior points of the premaxilla and dorsal fin base.

5) Pre-anal distance (PrA): as defined by Snoeks (1994). Distance between the anterior points of the premaxilla and anal fin base.

6) Pre-pelvic distance (PrV): as defined by Snoeks (1994). Distance between the anterior points of the premaxilla and pelvic fin base. The latter was located by articulating the fin.

7) Pre-pectoral distance (PrP): as defined by Snoeks (1994). Distance between the anterior points of the premaxilla and pectoral fin base. The latter was located by articulating the fin.

8) Dorsal fin base length (DFB): as defined by Snoeks (1994). Distance between the anterior and posterior point of the dorsal fin base. The former was located by articulating the fin while the latter was not compressed.

9) Anal fin base length (AFB): as defined by Snoeks (1994). Distance between the anterior and posterior point of the anal fin base. The former was located by articulating the fin while the latter was not compressed.

10) Caudal peduncle length (CPL): as defined by Barel et al. (1977). Distance between the verticals through the posterior point of the anal fin and the caudal fin base. Determined by articulating the caudal fin.

11) Caudal peduncle depth (CPD): as defined by Barel et al. (1977). Minimal depth of the caudal peduncle. Both points were not compressed while ensuring to exclude the posterior extensions of the dorsal and anal fins from the measurement.

Fin damage is common in preserved specimens causing measurements of their length to deviate from their original length. Therefore, the following three measurements were excluded from the analyses. Nevertheless, they can indicate sexual dimorphisms or inter- and intraspecific variation. Measurements were not recorded if the posterior tip of both the concerned left and right fins were damaged.

12) Total length (TL): from the anterior point of the upper jaw to the posterior tip of the caudal fin. The tip of the longest fin ray was used as reference point.

13) Pelvic fin length (VL): from the most lateral anterior point of the pelvic fin base to the posterior tip of this fin. The former was determined by articulating the fin.

14) Pectoral fin length (PL): as defined by Barel et al. (1977). From the most dorsal anterior point of the pectoral fin base to the most posterior tip of this fin. The former was determined by articulating the fin.

2.1.2 Head measurements (fig. 11)

15) Head width (HW): following Snoeks (1994), head width is defined as the distance between the pterotics. These rigid bony points of the neurocranium are located just dorsal of the dorsal extensions of the preopercula.

16) Premaxillary pedicel length (PPL): as defined by Snoeks (1994). Distance from the medioventral point of the maxilla to the tip of the premaxillary pedicel. The former point located labial of the front row teeth.

17) Snout length (SnL): as defined by Barel et al. (1977). From the anterior point of the maxilla to the anterior point of the orbit. The latter gently compressed to the cartilaginous ring surrounding the orbit.

18) Lacrimal depth (LaD): as defined by Snoeks (1994).

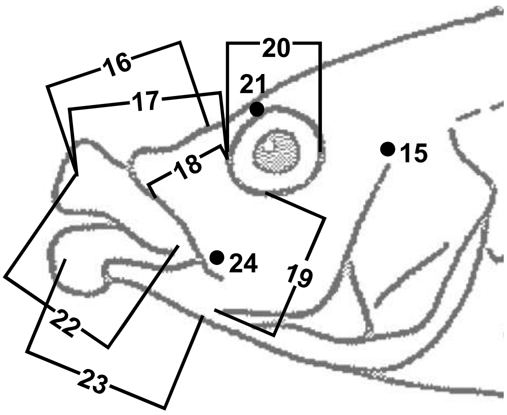

Figure 11 Head measurements taken: numbers in accordance to the definitions in chapter 2.1.2. Displaying *Haplochromis chilotes*, endemic to Lake Victoria. Modified from Eccles (1992).

From the anteroventral point to the anterodorsal point of the lacrima.

19) Cheek depth (ChD): this measurement deviates from Barel et al. (1977) and Snoeks (1994). The suspensorium has anteriorly a ventral notch, just posterior of the articulation with the mandibula, named ‘the articulation fossa’ by Barel et al. (1976). The cheek depth was measured from the articulation fossa to the ventral point of the orbita.

20) Eye diameter (ED): as defined by Snoeks (1994). Distance between the anterior and posterior point of the orbita. Both points gently compressed to the cartilaginous ring around the eye.

21) Interocular width (IOW): as defined by Barel et al. (1977). Minimal distance between the dorsal sides of both orbitae.

22) Upper jaw length (UJL): from the anteromedial point to the posteroventral margin of the maxilla. Caution was given to gently compress the latter point, as the maxilla is flexible.

23) Lower jaw length (LJL): as defined by Barel et al. (1977). From the anteromedial point to the posterolateral margin of the mandibula.

24) Lower jaw width (LJW): as defined by Barel et al. (1977). Width of the mandibula just posteriorly of the posterior margin of the maxilla, when the mouth is closed. The soft tissues were gently compressed without deforming the natural form of the mandibula.

2.1.3 Lower pharyngeal jaw measurements

The lower pharyngeal jaw bone was excised through the gill covers using a scalpel equipped with a #11 surgical blade. Caution was given to prevent damaging the anterior arm of this bone, as it is very brittle. The cartilage on the anterior point of the bone was left intact, all other connective tissue was removed, including the epithelium between the teeth while being careful to not pull the teeth out. The morphology of the lower pharyngeal jaws was described in detail. The dentigerous area was defined and the form of all teeth was noted following Barel et al. (1977). The following measurements were conducted.

25) Lower pharyngeal length (LPL): as defined by Snoeks (1994). From the plain through the posterior tips of the horns to the anterior point of the cartilage, anteriorly on the lower pharyngeal jaw.

26) Lower pharyngeal width (LPW): as defined by Barel et al. (1977). Width between the posterior points of the horns of the lower pharyngeal jaw.

27) Dentigerous area length (DAL): as defined by Barel et al. (1977). Distance between the verticals through the anterior and most posterior points of the dentigerous area of the lower pharyngeal jaw, while being careful to include all teeth and empty tooth sockets.

28) Dentigerous area width (DAW): as defined by Barel et al. (1977). The broadest width of the dentigerous area of the lower pharyngeal jaw, while being careful to include all teeth and empty tooth sockets.

2.2 Meristics

All meristics were counted under a binocular microscope at a magnification of 6.5–50x, using a teasing needle or high precision tweezers. For all specimens, 7 scale, 3 fin ray, 1 gill raker and 3 tooth counts were taken and the vertebrae of 62 specimens were counted.

2.2.1 Scale counts (fig. 12)

Damaged or missing scales were always included in the counts. Furthermore, we ensured that only one scale per row was counted in all except the lateral (meristic 29) and longitudinal scales (meristic 31) counts.

29) Lateral line scales (LatL): as defined by Snoeks (1994). Using the following formula: [LatLu]/[LatLl], the number of scales in the upper (LatLu) and lower lateral line (LatLl). Scales past the caudal fin base were not counted. The fin base can be determined by articulating the fin.

30) Inter-lateral line scales (U-LLL): number of scale rows between upper and lower lateral line, not counting the lateral line scales.

31) Longitudinal line scales (LongL): as defined by Snoeks (1994). The scales of the upper lateral line were counted. The scale just posterior of the upper lateral line was ventroanteriorly followed to the row of the lower lateral line. Including this scale, the count continues posteriorly until the caudal fin base is reached.

32) Transverse line scales (D-ULL/ULL-A): as defined by Snoeks (1994). The upper transverse scales (D-UUL) are the number of scale rows between the first spine of the dorsal fin, counted in a ventroposterior manner, and the upper lateral line. The lower transverse scales (ULL-A) are the number of scale rows between the upper lateral line and the first spine of the anal fin. The lateral line scales were not included. This was a difficult meristic to collect due to the often seemingly random setting of the nape scales, making it difficult to distinguish the rows.

33) Pectoral-pelvic fin scales (P-V): as defined by Snoeks (1994). Number of scales from the first scale dorsal of the anterior point of the pelvic fin base, counted in a dorsoanterior way, to the row just ventral of the pectoral fin base. These scales were often small and embedded which complicates distinguishing them.

34) Caudal peduncle scales (CPS): number of scale rows encircling the caudal peduncle at its narrowest. The rows are counted in a zigzag manner.

35) Cheek scales (ChS): as defined by Barel et al. (1977). Noted down in the following formula: [ChSa]/[ChSp]. The number of scale rows ventral of the orbit

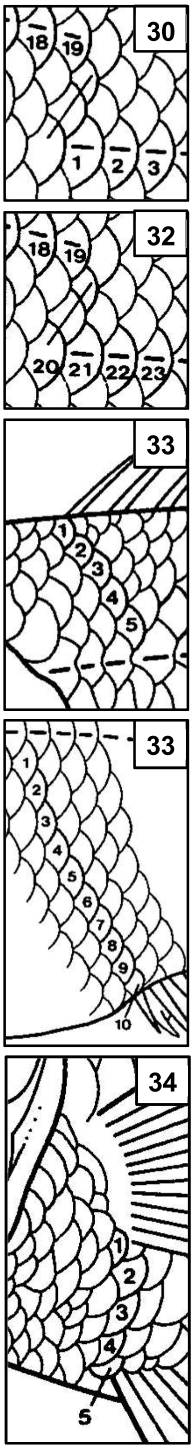

Figure 12 Scale counts taken: numbers are in accordance to the definitions in chapter 2.2.1. Modified from (Snoeks, 1994).

(ChSa) and at the posterior margin of the preoperculum (ChSp).

2.2.2 Fin ray counts

The fins were spread open, using a teasing needle, to ensure no spines or soft rays were overlooked. As convention, the number of spines and soft rays were noted in respectively Roman and Arabic numerals.

36) Dorsal fin formula (DFR): as defined by Snoeks (1994). Noted down in the following formula: [DFRs]/[DFRr] with DFRr and DFRr respectively corresponding to the number of spines and soft rays in the dorsal fin.

37) Anal fin formula (AFR): as defined by Snoeks (1994). Noted down in the following formula: [AFRs]/[AFRr] with AFRr and AFRr respectively corresponding to the number of spines and soft rays in the anal fin.

38) Pectoral fin formula (PFR): as defined by Snoeks (1994). The number of fin rays in the pectoral fin. Small rays dorsally in the fin were not counted.

2.2.3 Gill raker counts

The gill rakers on the outer row of the first gill arch were observed under a binocular microscope at a magnification of 6.5x, using high precision tweezers. Their form was described using the terminology of Barel et al. (1977) and to the following count was conducted.

39) Gill rakers (GR): as defined by Snoeks (1994). Noted using the following formula: [GRc]/1/[GRe] with GRc the number of gill rakers on the outer row of the ceratobranchial and GRe the number of gill rakers on the outer row of the epibranchial, segregated by a ‘1’ that indicates the gill raker that is situated on the cartilaginous plug. The count includes reduced gill rakers, which can be very small.

2.2.4 Oral dentition

The oral teeth of both jaws were examined under a binocular microscope at a magnification of 20–50x. High precision tweezers were used to open the mouth and to gently compress the oral mucosa in order to reveal the whole teeth. All teeth were carefully investigated and described based on the terminology of Barel et al. (1977). The dental arcade, tooth-band, tooth-setting and tooth-form were described in detail. As they display subtle differences between species, these can be important identification characters. Cichlids are generally homodont, i.e., the teeth of the same row are of the same form, although some aberrant teeth may be present. The posterior-most teeth in the front tooth row on the upper jaw can deviate, in some species, in form and size. The possible presence of these inconsistencies was inspected in all specimens. Further peculiar features were likewise described. The following four tooth counts were performed. Counting of the teeth is often difficult due to their small size or deep implantation in the oral mucosa, especially the posterior ones. Emerging and empty teeth sockets were included in all counts.

Some of the terminology of Barel et al. (1977) will be explained. Teeth that have a procumbent implantation, are implanted on the labial slope of the jaw bone. Hence, at least the bases of the teeth slope forwards. Equilateral major cusps have a conical form, with two sloping sides in front view, while subequilateral major cusps have one vertical side and one sloping one. Major cusps can have a flange, this is a small laterally flattened protrusion, laterally on the cusp. the tooth band is defined as the form in which the outer teeth are set. The tooth band can be broad and ‘c’-shaped or narrow and more ‘u’-shaped.

while the dental arcade defines the form in which all the teeth are set. The dental arcade can be thick or slender, depending on the number of tooth rows and their distance from each other. Upper jaw teeth (UOT): as defined by Snoeks (1994). The total number of teeth in the outer row on the premaxilla.

40) Lower jaw teeth (LOT): as defined by Snoeks (1994). The total number of teeth in the outer row on the dentary.

41) Inner tooth rows (UTR/LTR): as defined by Snoeks (1994). The number of inner tooth rows on the (UTR) upper and (LTR) lower oral jaws. Tooth row were defined by at least three teeth in a line, distinct from other tooth rows.

2.2.5 Vertebra counts

The VisiX X-ray system at the RMCA was used to perform X-ray scans of 62 specimens. Images were generated using a DeReO WA detector and a GemX-160 generator, which were set up at 110 mm of each other. The following count was taken on the generated images.

42) Vertebrae (V): counted using the following formula: [Va]/[Vc]. The abdominal vertebrae (Va) counted from the first vertebra distinct from the neurocranium, to and including the vertebra that is in contact with the first spine of the anal fin. The caudal vertebrae (Vc) start from the vertebra that is connected to the second spine of the anal fin, and continue posteriorly, but exclude the urostyle.

2.3 Stomach content analyses

After the comparative morphological analyses. The diet of all *‘Lipochromis’* species was identified to assess their trophic niche. Therefore, basic stomach content analyses were performed under a binocular microscope (6.5–50x). A medioventral incision was made from the medioposterior point of the isthmus, through the pelvic girdle, to the anus, using a scalpel equipped with a #11 surgical blade. The digestive tract of preserved specimens can be fragile, hence, the body cavity was emptied in its entirety by the following method: The anus and genital papilla were detached from the body wall. With the aid of general-purpose tweezers, the peritoneum was cut, laterally between coelom and air bladder over the entire length of the body cavity. The heart was removed and the oesophagus was severed just posterior of the pharyngeal jaws to disconnect the internal organs. After removing them from the body cavity, internal organs were placed in a Petri dish with 70% alcohol to prevent dehydration. The digestive tract was carefully unfolded while removing the connective tissue, using high precision tweezers and dissection scissors. After the gut length (measurement 43) was measured with the unaided eye using a dial calliper (± 0.01 mm), the stomach was dissected. The contents were identified and each of the food items was counted.

43) Gut length (GL): Total length of the digestive tract, from the anterior point of the maxilla to the anus. The digestive tract was dissected and cut off just posterior of the pharyngeal jaws. This part was straightened by placing it on a smooth and dry surface after removing all connective tissue and pulling on the anal end until the whole tract formed a straight line. The length was measured and added to the distance between the anterior point of the maxilla and the posterior point of the pharyngeal jaws. The latter was not compressed and measured through the empty body cavity.

2.4 Data analysis

Measurements and meristics were analysed separately. The analyses of the measurements were performed on the log-transformed raw data of the measurements, to linearize allometric effects. As mentioned before, all body- and head measurements were included except for fin lengths (measurements 12–14). The analyses of the meristics were done on the raw data, as they were assumed to be uncorrelated with size, except for the number of outer teeth on the oral jaws. All the counts were added to the analyses, hereby, LatL (meristic 29), AFR (37), DFR (36), ChS (35) and GR (39) were split up in their individually-counted components, as described above (pp. 20–23).

The multivariate data was analysed by Principal Component Analysis (PCA), implemented in Past 3.13 (Hammer et al., 2001). This method has proven to be useful in comparative morphological analyses of cichlids (Snoeks, 2004; Colombo et al., 2013; Decru et al., 2017). In a PCAs, a principal component (PC) is a linear combination of all the variables (all measurements or all counts). The variance of each PC is maximised with the constraint that it is uncorrelated to all preceding ones. Therefore, PC1 will explain the largest variation, PC 2 the second largest variation that is not explained by all preceding PCs, in this case only PC 1, and so forth. These PCs are determined either on a variance-covariance matrix or a correlation matrix of the data matrix. The former preserves the variance of each variable and is used when all data is on the same scale. The correlation matrix standardises the variance, and is hereby useful if the scale differs between variables. By plotting two PCs on a X-Y graph, the data can be visualised and integrated similarities and differences between specimens can be observed (Ringnér, 2008). All measurements were expressed on the same scale and therefore analysed by PCAs on variance-covariance matrices. The counts were incomparable to each other, hence the PCAs were implemented on correlation matrices. The interpretation of a PCA is not always straightforward as differentiating between intra- and interspecific variation can be difficult in these morphologically resembling species. The values of specimens on PCs that explain a large proportion of the variation were compared between PCAs and the qualitative characters that were observed. If a group of specimens could be supported by PCAs of the measurements and counts, in addition to similar qualitative characters that were distinct from the other specimens, they were presumed to form a species.

Once species were defined, the raw data of all measurements, except standard length were converted to proportions to standardise for size. Following Snoeks (1994), most body and head measurements were respectively expressed as percentages of standard length and head length. The caudal peduncle length and lower jaw width were respectively expressed as percentages of caudal peduncle length and lower jaw length. The lower pharyngeal jaw length was expressed as a percentage of head length, the lower pharyngeal jaw width as a percentage of lower pharyngeal jaw length. The dentigerous length and width are respectively expressed as a percentage of pharyngeal lower jaw length and width. Once species were defined, percentages of each character and the raw data of all meristics were compared between species by performing Mann-Whitney *U*-tests in Past 3.13 (Hammer et al., 2001) (see table8, p. A.7). This nonparametric test analyses if two samples of random values come from the same population. This test does not assume the tested groups to have a normal distribution and can be performed on groups with small sample sizes. All combinations of pairwise comparisons of all species within a group ('*Lipochromis'* or '*Paralabidochromis'*) were performed on samples of specimens with similar body-sizes (MWU p>0.5 for SL). All p-values were corrected with post hoc Bonferroni correction for multiple comparisons.

3 Results

3.1 Preliminary study

For a preliminary study, all supposedly thick-lipped *Haplochromis* specimens from Lake Edward from the Royal Belgian Institute of Natural Sciences (RBINS) were requested. This collection was caught during the Exploration hydrobiologique des lacs Kivu, Édouard et Albert (KEA) in 1953 and consisted of forty specimens. Hulot (1956) identified these as *H. labiatus*, *H. taurinus* and *H. paucidens*. The latter species is currently only known from Lake Kivu. After observing these specimens, Snoeks (1994) concluded that they differed from all Lake Kivu haplochromine species.

All specimens were thoroughly examined to determine which specimens belonged to the thick-lipped haplochromines as defined above. Five specimens had only slightly thickened lips were not included in this study. Each of these will be briefly discussed and their affinities to known species from the Lake Edward system will be postulated.

The first non-thick-lipped specimen (RBINS 13267, fig. 13a) had been identified by Hulot (1956) as *H. labiatus*. It had a slender body (BD 33.6 % SL), with a very short head (HL 30.2 % SL) and big eyes (ED 38.5 % HL). the snout was short (SnL 25.3 % HL) and steep, the premaxillary pedicel sloped at 80°. Both oral jaws were exceptionally short (UJL 22.1 % HL; LJL 23.4 % HL) and almost equally broad (LJW 95.1 % LJL). The outer teeth were numerous and closely set. The major cusps of outer teeth were obliquely truncated and strongly recurved while the large minor cusps had a rather straight orientation. This tooth morphology is characteristic for the group "*Macropleurodus*" *sensu* Greenwood (1980). This group is currently monospecific as only *H. bicolor* Boulenger, 1906, an oral crushing molluscivore from Lake Victoria, has this morphology.

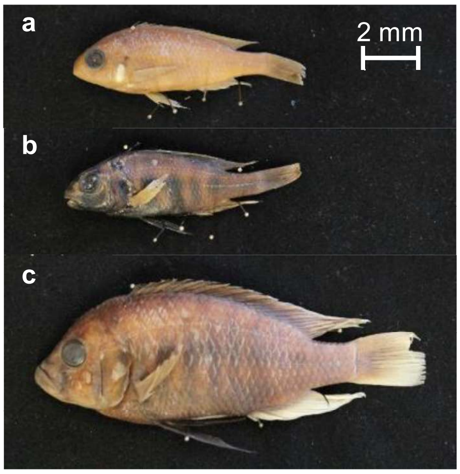

Figure 13 Specimens from the RBINS collection sample not belonging to the thick-lipped groups. (a) RBINS 12899; Lac Edouard: baie de Kasindi; Miss. KEA; 2/06/1953 [♀ SL 66.97 mm]. (b) RBINS 13267; Lac Edouard: Kiavinionge (beach); Miss. KEA; 20/10/1953 [♂ SL 66.83 mm]. (c) RBINS 12901; Lac Edouard: Kiavinionge (pier); Miss. KEA; 28/03/1953 [♂ SL 110.98 mm].

The second specimen (RBINS 13267, fig. 13b) had been identified as *H. taurinus*. It was small (SL 66.83 mm), although it displayed a dominant male colouration, indicating its sexual maturity. Furthermore, it had a slender body (BD 33.4 %SL) and the dentary was severely damaged as its dentition was completely lost. The outer teeth on the premaxilla had long, slender and slightly recurved necks. The crowns were unequally bicuspid with long, slender and isocline major cusps and horizontally orientated minor cusps. The outer teeth on the premaxilla had a very wide setting and seemed recumbently implanted, with the whole teeth pointing buccaly. Although this implantation could be a deformation of the premaxilla and snout. This specimen resembled Greenwood's (1973) redescription of *Haplochromis nigripinnis* Regan, 1921, except for the length of the upper jaw, which was smaller in this specimen (UJL 29.8, vs. 30.6-36.9 (M 34.0) %HL), although this could be a deformation. A comparison with the holotype of *H. nigripinnis*, however, falls beyond the scope of this study.

The last three non-thick-lipped specimens [RBINS 12896 (n = 2/20); ♀ 78.02 mm; ♂ 56.96 mm); 12901, fig. 13c] resembled each other and were considered conspecific. The largest specimen had been identified as *H. paucidens* and the two smaller ones as *H. labiatus*. They had a high body (BD 35.1–39.1 % SL) with a relatively steeply sloping head at 30–40°. The cheeks were high (ChD 17.7–25.8 % HL) and the jaws broadly rounded. The outer teeth were relatively small, numerous and closely set. The necks were laterally compressed and the bicuspid crowns had isocline major cusps with small flanges and acute points. The minor cusps were large and stout with slightly horizontal inclinations. The inner teeth were small and tricuspid. They were set in 2–6 rows. These specimens resembled Greenwood's redescription of *Haplochromis limax* (1973), a species within the genus *Haplochromis sensu stricto* (Greenwood, 1980).

The five specimens discussed above were excluded from all analyses as they were not regarded as thick-lipped species. Hereafter, each of the two groups, namely *'Lipochromis'* and *'Paralabidochromis'* will be analysed and discussed individually.

3.2 ***'Lipochromis'*, the paedophages**

In this section, only specimens that displayed distinctive *'Lipochromis' sensu* Greenwood (1980) characteristics (see section 1.1.2.1, p. 5) were included. This sample consisted of 14 specimens from the RBINS collection, the holotype of *H. taurinus* from the NHM collection and 40 specimens from the RMCA collection. Hereby, a total of 55 specimens from the Lake Edward system were examined. Ten of these specimens do not show any of the distinctive external *'Lipochromis'* characteristics. They had however exceptionally small teeth with recurved necks. These are typical dental characteristics of the group '*Lipochromis'*, together with a strongly thickened oral mucosa. These specimens had only a slightly thickened oral mucosa but the crowns of the outer teeth were strongly recurved horizontally, hereby they still are embedded into the oral mucosa, giving them the characteristic edentulous appearance, which is unique to '*Lipochromis'*. Additionally, the holotype of *H. occultidens* from the RMCA collection was included to make a comparison with the single endemic Lake Kivu species with a *'Lipochromis'* morphology.

Lake Edward specimens were classified into five groups, based on dental characteristics. The form of the outer teeth differed distinctly between all groups (fig. 14). Specimens in the first group had short outer teeth with broad bases, conical necks, subequilateral major cusps with a flange and distinct minor cusps that were slightly horizontally inclined (fig. 14a). As the holotype of *H. taurinus* was assigned to

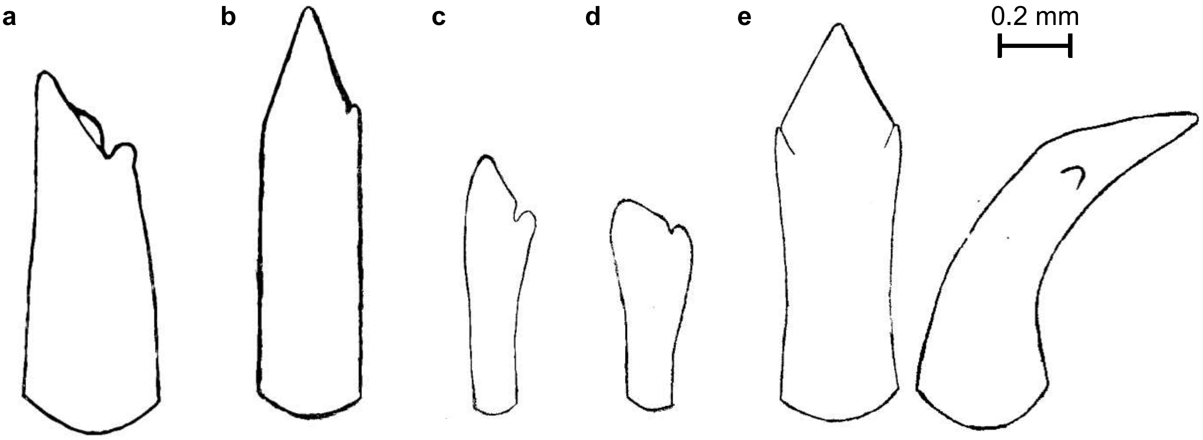

Figure 14 Morphology of the anterior outer teeth on the dentary of the paedophagous haplochromines of the Lake Edward system. All teeth of specimens with a similar size (SL 96.77–103.22 mm). Teeth in frontal view of (a) *H. taurinus*, (b) *H.* sp. 'molossus', (c) *H.* sp. 'longicauda', (d) *H.* sp. 'relictidens', (e) frontal and lateral view of *H.* sp. 'curvidens'. All teeth are drawn on the same scale.

this group, the group will be referred to as *H. taurinus.* The second group has relatively long outer teeth with strong, cylindrical necks, and uni-, weakly bi- or weakly tricuspid crowns with isocline major cusps (b). These specimens were named *H.* sp. 'molossus'. This name referred to the flattened face of the specimens, their broad jaws and shallow gape inclination. This resembles the head of a Molosser (pug), a mastiff-like dog, named after Μολοσσός (Molossos), a figure in Greek mythology. The next group of specimens had very small outer teeth with slender necks, equilateral to subequilateral, acutely-rounded major cusps and distinct minor cusps (c). These specimens were named *H.* sp. 'longicauda, meaning 'long tail', as they had slender and long caudal peduncles. A fourth group was formed by specimens that also had very small teeth with slender necks (d). These teeth were, however, recurved and the weakly bi- to unicuspid crowns were very blunt to sometimes even rounded. As the number of teeth was lower in large specimens, this group was named, *H.* sp. 'relictidens', meaning 'abandoned tooth'. Specimens in the fifth group consist of all specimens that had no external '*Lipochromis'* morphology. Their outer teeth had stout bases, strongly recurved and slightly laterally compressed necks that ended in uni-, weakly bi-, or weakly tricuspid crowns with equilateral major cusps and an almost horizontal orientation (e). This group was named *H.* sp. 'curvidens, meaning 'curved tooth', after their unique tooth morphology. The outer teeth of the holotype of *H. occultidens* from Lake Kivu (not shown on fig. 14) resembled those of *H.* sp. 'relictidens' by their small size, slender necks and the very small number of outer teeth on both jaws. They differed, however, in the form of their teeth that had distinct minor cusps and acutely-rounded major cusps in *H. occultidens*, and blunt, weakly bicuspid teeth in *H.* sp. 'relictidens'. For the analyses, *H. occultidens* was considered a group of its own.

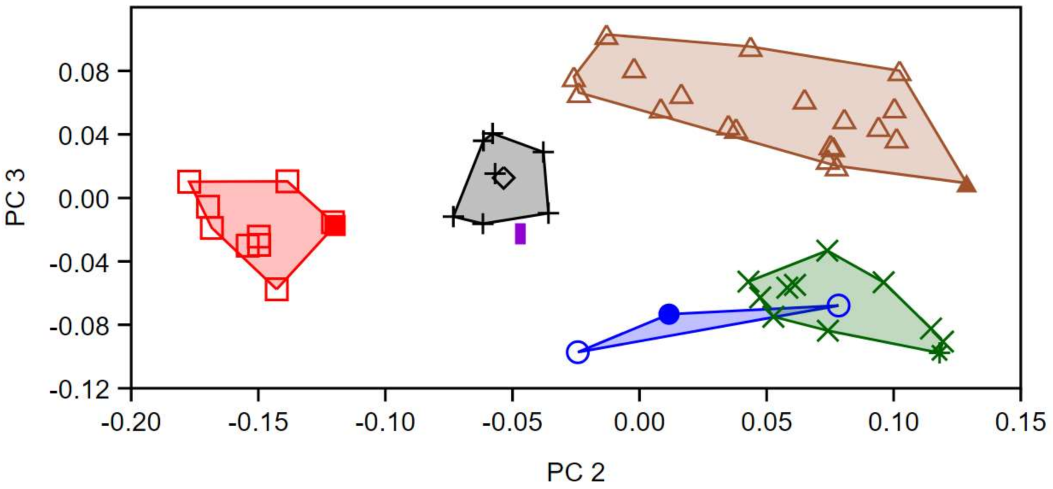

Figure 15 PCA of the logarithmic transformed measurements of 52 specimens from the Lake Edward system with a paedophagous morphology and the holotype of *H. occultidens*, endemic to Lake Kivu. Clusters are based on outer teeth form (fig. 15). *Haplochromis taurinus* (Δ, holotype: ▲), *H.* sp. 'molossus' (×, suggested holotype: ✱), *H.* sp. 'relictidens' (+, suggested holotype: ◇), *H.* sp. 'longicauda' (○, suggested holotype: ●), *H.* sp. 'curvidens' (□, suggested holotype: ■), *H. occultidens* (holotype: ▌). For the PCA loadings, see table 5, p. A.4.

3.2.1 Measurements

Three specimens of the group *H. taurinus* had open mouths with a strongly-protruding premaxilla and could therefore not properly be measured; hence were excluded from all analyses of measurements. A PCA of the log-transformed measurements was performed. Principal component 1 had large, positive loadings for all characters, consequently sorting the specimens by size. Plots of PC 2 and PC 3 on PC 1 showed no effect of size on these PC's. Hence, the effect of size could be filtered out by plotting PC 2 on PC 3 (fig. 15). Lower jaw width, lachrymal depth and snout length had high absolute loadings for PC 2, whereas eye depth and lower jaw width were important for PC 3 (table 5, p. A.4).

A distinction could be made on PC 2, which divided the specimens in small- and large-lacrimal groups (fig. 15). The latter consisted of three groups that were completely situated in the negative part of PC 2, while the small-lacrimal groups were formed by three groups that had mainly positive values for PC 2. The first cluster, *H.* sp. 'curvidens' (fig. 15, □), had much more negative values for PC 2 than the other groups. This group was probably distinct because of its very slender jaws (table 1, p. 35). The other two groups within the large-lacrimal specimens overlapped for PC 2 but *H. occultidens* (▌) and *H.* sp. 'relictidens' (+) were distinct on PC 3. Specimens belonging to *H.* sp. 'relictidens' had higher values. This could be explained by their relatively more slender jaws of *H.* sp. 'relictidens'. Within the small-lacrimal specimens, *H. taurinus* (Δ) was clearly distinct with high values for PC 3, probably because of its larger eyes. The two other groups, *H.* sp. 'molossus' (×) and *H.* sp. 'longicauda' (○) formed a cluster of specimens with high values for PC 2 and low values for PC 3. The former had slightly higher values on PC 2, most likely as their lower jaws were exceptionally broad. When these two groups were analysed seperately, both were clearly distinct from each other. The explaining PC was mainly determined by caudal peduncle depth, most likely due to the more slender caudal peduncle of *H.* sp. 'longicauda'.

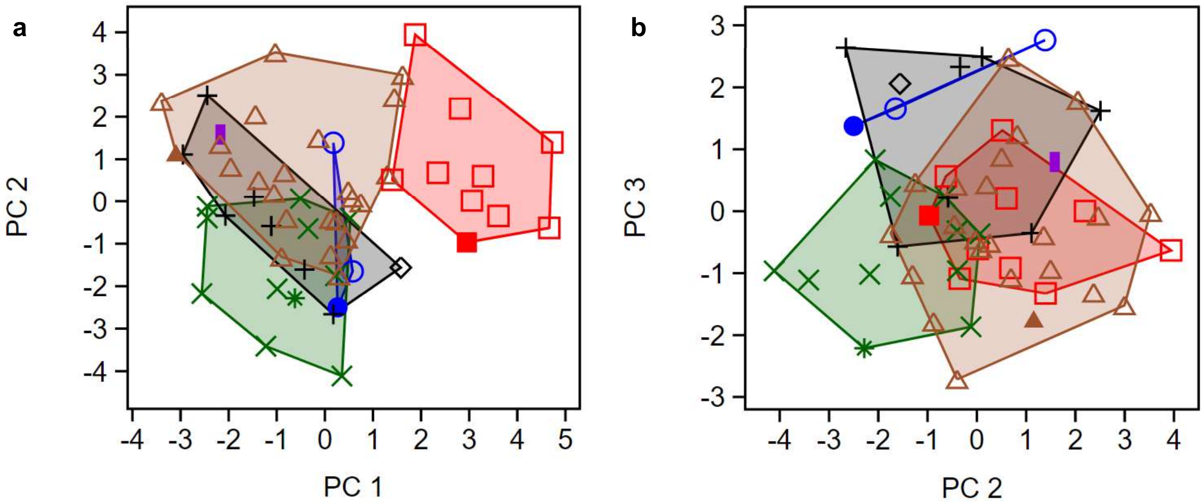

Figure 16 PCA of the meristics of 56 specimens from the Lake Edward system with a paedophagous morphology and the holotype of *H. occultidens*, endemic to Lake Kivu. Groups are based on the form of the outer teeth anteriorly on the dentary (fig. 15). Two plots were made: (a) PC 2 on PC 1 and (b) PC 3 on PC2. *Haplochromis taurinus* (Δ, holotype: ▲), *H.* sp. 'molossus' (×, suggested holotype: ✱), *H.* sp. 'relictidens' (+, suggested holotype: ◇), *H.* sp. 'longicauda' (○, suggested holotype: ●), *H.* sp. 'curvidens' (□, suggested holotype: ■), *H. occultidens* (holotype: ▌). For PCA loadings, see table 5, p. A4

3.2.2 Meristics

As all specimens had two inter-lateral line scales and 16 caudal peduncle scales, these counts were excluded from all analyses on the raw meristics. In a PCA performed on all specimens, PC 1 was mainly determined by the number of upper and lower outer teeth and upper inner tooth rows, whereas PC 2 was mostly determined by the number of caudal vertebrae, lower transversal scales and lower inner tooth rows (table 5, p. A.4). When the first two PCs were plotted against each other (fig 16a), *H.* sp. 'curvidens' (□) was shown to be completely distinct from all other groups. For this group, all specimens had positive values for PC 1. This could be explained by the high counts of outer teeth on both jaws and tooth rows on the upper jaw. *Haplochromis* 'molossus' has low values on PC 2. This group was partially distinct from all other groups because of its relatively low number of lower transversal scales.

When PC 3 and PC 1 of the same analysis (table 5, p. A.4) were plotted on each other, except for *H.* sp. 'curvidens', all groups overlapped. The only distinction was between *H.* sp. 'longicauda' and *H.* sp. 'molossus'. So, a second plot was made, in which PC 3 was plotted against PC 2 (fig. 16b). As in the first plot, *H.* sp. 'molossus' was separated by low values for PC 2. On PC 3, *H.* sp. 'longicauda' had exceptionally high values, probably caused by its few lower lateral line scales. In addition, *H.* sp. 'relictidens' is almost completely located in the possitive values of PC 3, partially distinct from all other groups. This could be explained by its relatively high number of lower transversal scales. *Haplochromis taurinus* showed a huge variation on PC 3 and overlaps with all other groups on this axis.

A PCA with the exclusion of all size-dependant counts, i.e. the tooth counts, was performed. The separation between all groups but one, was slightly worse and a lot worse for *H.* sp. 'curvidens', in

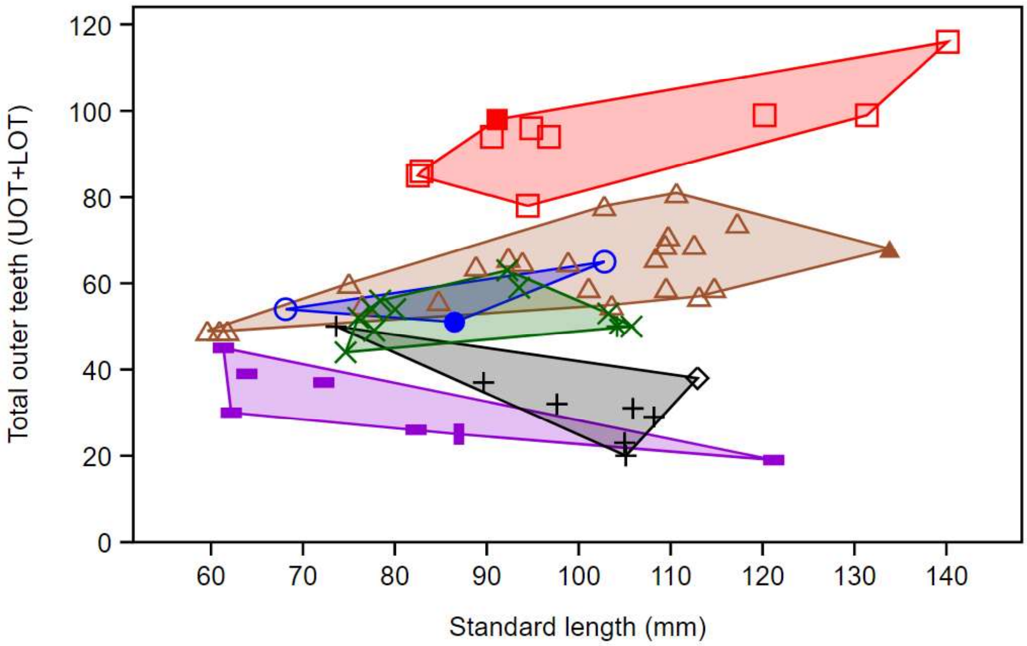

Figure 17 Total number of outer teeth of all paedophagous haplochromine species of the Lake Edward system. *Haplochromis taurinus* (Δ, holotype: ▲), *H.* sp. 'molossus' (×, suggested holotype: ✱), *H.* sp. 'relictidens' (+, suggested holotype: ◇), *H.* sp. 'longicauda' (○, suggested holotype: ●), *H.* sp. 'curvidens' (□, suggested holotype: ■), *H. occultidens* (holotype: ▌).

comparison with the previous analysis. The exception was *H.* sp. 'longicauda'; this group could be completely distinguished from all others with the number of upper and lower lateral line scales as most important variables.

The number of total outer teeth, i.e. the summation of upper and lower outer teeth, was plotted against standard length (fig. 17). In this figure, an additional 5 specimens of *H. occultidens* were added. *Haplochromis* 'curvidens' has a high number of outer teeth and was completely distinct from all other groups. Three groups, *H.* 'longicauda', *H. taurinus* and *H.* sp. 'molossus' had an intermediate number of teeth and overlapped severely. Two groups, *H. occultidens* and *H.* sp. 'relictidens' had a low number of outer teeth. An interesting observation was the number of teeth declining with size in these last two groups, while it generally increased in all other groups.

The most striking characteristic of *H. occultidens* is the similarity it has with *H.* sp. 'relictidens' in dental characteristics. Both species have a lower number of outer teeth as the specimens become larger. They have a similar mouth morphology with an anteriorly narrowing lower jaw and more rounded upper jaw.
Haplochromis occultidens

The most peculiar characteristic of this species is the decrease in the number of teeth in the outer rows as specimens are larger (UOT, LOT; fig. 17, +), giving this species a smooth oral mucosa.

3.2.3 Stomach content analyses

Exploratory stomach content analyses were performed on specimens from each group. In total, 30 specimens were investigated. As this is an invasive technique, only specimens from the RMCA collection could be studied, except for one specimen of *H.* sp. 'curvidens' from the RBINS collection. This low number was due to the limited availability of specimens for all groups, except for *H. taurinus* and *H.* sp. 'curvidens'. Of these groups, 11 and 8 specimens were investigated respectively. All three *H.* sp. 'longicauda' specimens were studied and 4 specimens of both *H.* sp. 'molossus' and *H.* sp. 'relictidens'.

A striking observation was the relatively long digestive system (GL) of *H. taurinus* compared to all other examined species. Furthermore, all species had a distinctive muscular structure that can be defined as the stomach, except for *H.* sp. 'curvidens', its stomach was either small or indefinable. The digestive system of this last group has a muscular region in its anterior part but a distinct bulge was absent in most specimens.

Stomachs of five specimens of *H. taurinus* contained numerous cichlid eggs and larvae. One specimen deviated from this pattern as only several Ephemeroptera larvae were found. Three specimens of *H.* sp. 'molossus', and four of *H.* sp. 'relictidens' had stomachs that contained cichlid eggs and/or larvae while one specimen of *H.* sp. 'longicauda' was found with 13 cichlid eggs in its stomach. Two specimens from *H.* sp. 'curvidens' consumed solely cichlid larvae. All other examined specimens had no food items in their stomachs. This confirms that all five Lake Edward species are paedophages.

In the next sections, all paedophage species will be discussed individually while mentioning their diagnostic characteristics that distinguish them from all other investigated species. Percentages of the mentioned measurements and numbers of the counts are given in table 1, p. 35.

3.2.4 Haplochromis taurinus

Haplochromis taurinus (fig. 18a) has a slightly concave head and long (LJL, UJL, table 1, p. 35), rounded and slightly prognathous jaws that are widely distensible. The maxilla are strongly bullate, i.e. posteriorly enlarged and distinctly visible. The lips and oral mucosa are firmly thickened but the crowns of the outer teeth are mostly still visible on the lower jaw. The outer teeth are small, short and conical (fig. 14a). The crowns have major cusps with a laterally compressed flange and distinct minor cusps. The outer teeth on the dentary are sometimes distinctly anteriorly curved, a character that is absent in all other paedophages. All inner and outer teeth are very closely set, almost against each other. It can be distinguished from all other paedophages by a combination of large eyes (ED), a long upper jaw (UJL) and a broadly rounded lower jaw that is slightly prognathous.

Haplochromis taurinus is further distinct from *H.* sp. 'molossus' by its smaller interorbital (IOW) and lower jaw width (LJW), from *H.* sp. 'longicauda' by its deeper body (BD) and higher caudal peduncle (CPD). It is distinct from both species by a longer premaxillary pedicel (PPL). For a complete species description, see p. A.8, for additional pictures, see fig. 22, p. A.29.

3.2.5 Haplochromis *sp. ‘molossus’*

Haplochromis sp. ‘molossus’ (fig. 18b) has a relatively slender body with distinctly broad (LJW, table 1, p. 35) and long jaws (UJL, LJL). The gape inclination is shallow, sloping at 20–30°. The premaxillary pedicel is short (PPL), the snout stout and blunt giving it a ‘pug-head’. The outer teeth are relatively long, compared to the other paedophagous species (fig. 14b), at least the crowns protrude the thickened oral mucosa but the teeth are hidden in large specimens (SL > 100 mm) due to the firmly thickened and relatively high lips covering them. The necks of the teeth are stout, straight and cylindrical. The crowns are bicuspid in small specimens (SL < 90 mm), uni- to weakly tricuspid in large specimens (SL > 100 mm). The outer teeth anteriorly on the dentary have tips that are straight or very slightly anteriorly curved. *Haplochromis* sp. ‘molossus’ has a relatively low number of lower transversal scales (ULL-A), although values overlap with all other paedophagous species.

Haplochromis sp. ‘molossus’ differs from all other paedophages by its exceptionally broad and rounded lower jaw (LJW). It is further distinct from *H. taurinus* by its smaller eyes (ED) and shorter jaws (LJL, UJL). It differs from *H.* sp. ‘longicauda’ by a longer premaxillary pedicel (PPL), snout (SnL) and anal fin base (AFB). It has a shallower gape inclination (20–30°, vs. 40–55°), more anterior cheek scales (ChS), more upper transversal scales (D-ULL) and distinctly fewer lower transversal scales (ULL-A). Dominant males can be distinguished by their body markings. The flanks of *H* sp. ‘molossus’ show

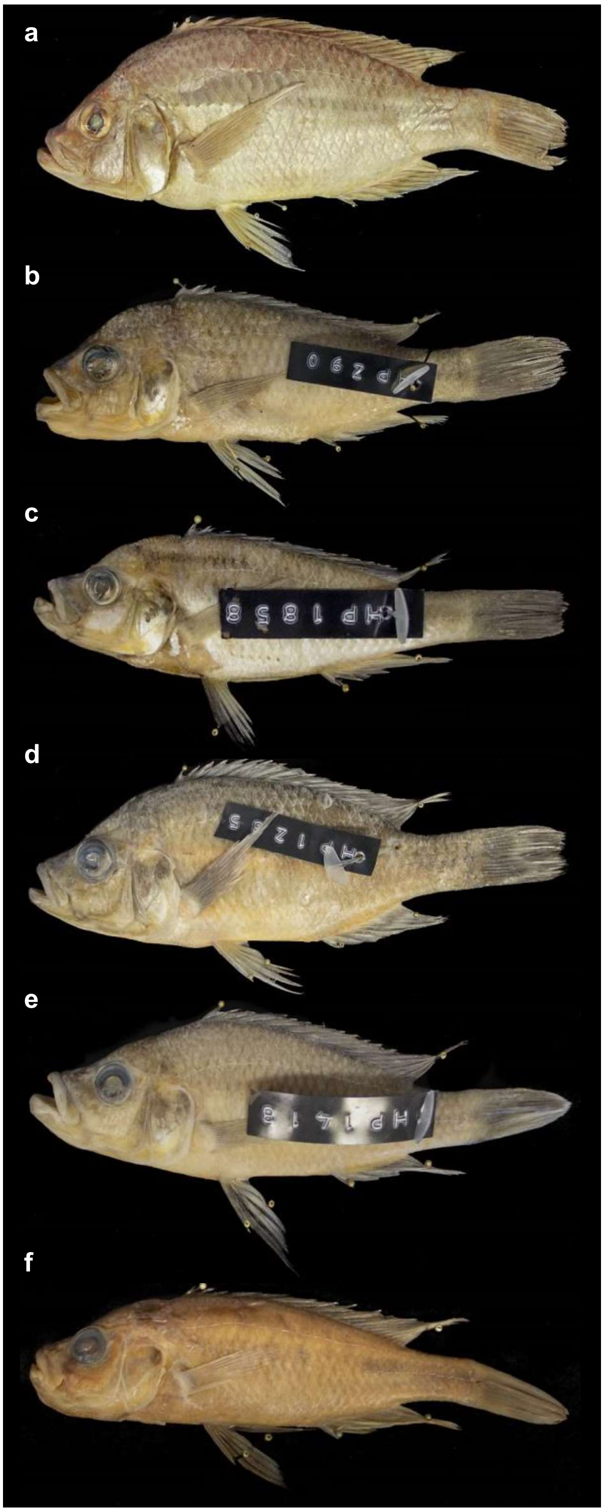

Figure 18 Paedophagous haplochromines from lakes Edward, George and Kivu. (a) *H. taurinus*, holotype [♀ SL 133.82 mm]; (b) *H.* sp. 'molossus', holotype [♀ SL 104.17 mm]; (c) *H.* sp. 'longicauda', holotype [♂ SL 85.67 mm]; (d) *H.* sp. 'relictidens', holotype [♀ SL 112.93 mm] and (e) *H.* sp. 'curvidens', holotype [♂ SL 91.13 mm]; all endemic to the Lake Edward system. (f) *H. occultidens*, holotype [♂ SL 86.97 mm]; endemic to Lake Kivu.

vertical stripes, while *H.* sp. ‘longicauda’ has two very distinct longitudinal lines that run just above the upper and lower lateral line. For a complete species description, see p. A.10, for pictures, see fig. 23, p. A.29.

3.2.6 Haplochromis *sp. ‘longicauda’*

Haplochromis sp. ‘longicauda’ (fig. 18, c) has a very slender body (BD, table 1, p. 35) with a concave head, short snout (SnL) and very short premaxillary pedicel (PPL). The gape has a steep inclination of 40–55°. The anal fin base is short (AFB) while the caudal peduncle is relatively long (CPL) and thin (CPD). The outer teeth are small and bicuspid with distinct minor cusps (fig. 14c). The slender necks are deeply embedded in the oral mucosa so that they are hardly visible. *Haplochromis* sp. ‘longicauda’ has a very low number of lower lateral line scales (LatL). Dominant males have two distinct horizontal lines running just above the upper and lower lateral lines which are absent in all other species of paedophages.

Haplochromis sp. ‘longicauda’ is distinct from *H.* sp. ‘relictidens’ by its rounded lower jaw that is set with more outer teeth (UOT, LOT) instead of an acutely pointed one. For a complete species description, see p. A.13, for additional pictures, see fig. 24, p. A.29.

3.2.7 Haplochromis *sp. ‘relictidens’*

Haplochromis sp. ‘relictidens’ (fig. 18d) distinguishes itself by its large lacrima (LaD, table 1, p. 35) and relatively slender lower jaw (LJW) of which the anterior half suddenly narrows anteriorly, hereby giving it an acute outline. At this point the lower jaw closes within the more rounded upper jaw, which is clearly visible from ventral view. The most peculiar characteristic of this species is the decrease in the number of teeth in the outer rows as specimens are larger (UOT, LOT; fig. 17, +), giving this species a smooth oral mucosa. Small specimens (SL < 75 mm) have small, slightly recurved and bicuspid teeth with acutely-rounded major cusps. Large specimens (SL > 90 mm) have very small, slightly recurved and weakly bicuspid to unicuspid teeth with slender necks and very bluntly pointed to rounded major cusps (fig. 14d).

Haplochromis sp. ‘relictidens’ resembles *H.* sp. ‘curvidens’ most of all paedophagous species but it can be easily distinguished by its shorter head (HL) and bigger eyes (ED). Additionally, it has fewer outer teeth (UOT, LOT) which are set in short dental arcades (2/3 the dentigerous area), in comparison to the very long arcades in *H.* sp. ‘curvidens’. The species differs from *H.* sp. ‘longicauda’ by a higher caudal peduncle (CPD), larger lacrima (LaD), longer premaxillary pedicel (PPL) and a higher number of lower-lateral line scales (LatL). For a complete species description, see p. A.17, for additional pictures, see fig. 25, p. A.29.

Table 1 Synopsis of the distinguishing measurements and counts of all paedophagous haplochromines of the Lake Edward system, i.e. *H. taurinus*, *H.* sp. 'molossus', *H.* sp. 'longicauda', *H.* sp. 'relictidens' and *H.* sp. 'curvidens'. The holotypes and suggested holotypes of all species are included. For all morphometrics, see table 10, p. A.22 and table 11, p. A.28.

	H. taurinus			***H.* sp. 'molossus'**			***H.* sp. 'longicauda'**			***H.* sp. 'relictidens'**			***H.* sp. 'curvidens'**			***H. occultidens***
Measurements			n = 20, *10			n = 11, *4			n = 3			n = 8, *4			n = 10, *4	n = 1
	Mean	Range		Mean	Range		Mean	Range		Mean	Range		Mean	Range		Value
SL (mm)	96.2	59.6	133.8	87.6	74.6	105.8	85.5	68.1	102.8	99.8	73.6	112.9	90.5	82.5	96.8	86.97
HL % SL	31.8	30.5	33.7	30.9	29.5	32.0	30.3	29.8	30.7	31.6	29.6	33.0	34.3	32.8	36.2	31.2
BD % SL	36.0	33.9	40.1	34.9	33.5	38.6	32.4	30.2	34.8	36.3	34.6	38.7	33.6	30.3	36.4	28.2
AFB % SL	20.7	19.7	22.0	20.8	19.3	22.0	17.5	15.9	19.1	20.2	19.0	21.4	18.0	16.6	19.7	18.5
CPL % SL	15.7	14.5	16.9	16.2	14.9	19.0	17.3	16.3	18.2	16.6	15.5	17.7	16.1	15.1	16.7	15.8
CPD % CPL	79.6	73.9	88.1	75.5	65.5	83.6	65.0	62.9	66.4	75.8	68.6	83.3	69.8	62.3	76.9	60.8
GL % SL	196.0	147.6	249.7*	159.0	118.7	197.3*	127.1	108.6	152.9	155.8	115.8	184.8*	139.3	123.1	159.9*	-
HW % HL	51.9	47.1	55.1	53.2	50.9	55.2	51.1	48.1	54.6	50.4	47.7	54.7	43.2	41.7	45.7	47.0
PPL % HL	25.1	23.5	26.2	23.5	21.6	25.8	20.3	18.1	21.6	26.1	24.3	27.5	25.0	23.5	26.8	25.1
SnL % HL	26.7	23.2	31.4	28.0	25.1	30.7	25.2	24.0	26.7	28.6	24.8	30.6	31.1	29.8	33.6	28.0
LaD % HL	14.1	11.5	16.4	14.4	13.3	16.3	14.0	13.7	14.3	17.4	15.8	18.4	16.5	15.4	17.5	15.8
ED % HL	35.7	32.9	40.2	32.3	29.8	33.9	31.0	29.0	32.3	31.7	30.5	34.7	28.8	27.7	30.4	32.6
IOW % HL	24.6	21.2	28.2	28.1	24.1	30.8	26.8	25.9	28.2	26.0	24.3	27.3	22.0	18.8	24.8	21.6
UJL % HL	39.2	34.0	43.5	44.0	41.3	46.4	35.3	33.4	37.0	35.9	34.2	37.5	34.3	31.2	36.6	37.8
LJL % HL	47.7	44.5	51.3	36.7	34.4	39.7	43.5	42.4	44.7	45.0	41.6	47.0	46.5	43.6	48.6	42.3
LJW % LJL	60.9	51.4	72.7	77.1	67.0	87.0	64.9	61.9	69.4	54.7	50.1	59.7	49.6	46.4	55.7	67.5

	H. taurinus	***H.* sp. 'molossus'**	***H.* sp. 'longicauda'**	***H.* sp. 'relictidens'**	***H.* sp. 'curvidens'**	***H. occultidens***
Meristics	n = 23	n = 11	n = 3	n = 8	n = 10	n = 1
	Number & frequency (f)	Number & frequency (f)	Number & frequency (f)	Number & frequency (f)	Number & frequency (f)	Number
UFT	23–39 (median 32)	22–34 (median 30)	26–35 (median 26)	16–26 (median 18)	36–65 (median 53)	14
LFT	25–42 (median 32)	16–34 (median 28)	25–30 (median 28)	7–25 (median 17)	33–51 (median 45)	11
UTR/LTR	1/1 (f 1); 1/2 (f 4); 2/1 (f 1); 2/2 (f 16); 2/3 (f 1)	1/1 (f 4); 1/2 (f 3); 2/1 (f 2); 2/2 (f 2)	1/2 (f 1); 2/1 (f 1); 2/2 (f 1)	2/2 (f 7); 2/1 (f 1)	2/2 (f 3); 3/2 (f 7)	2/2
GR	8/1/2 (f 3); 9/1/2 (f 7); 9/1/3 (f 5); 10/1/2 (f 6); 10/1/3 (f 2)	8/1/1 (f 1); 8/1/2 (f 2); 9/1/2 (f 7); 9/1/3 (f 1)	8/1/2 (f 1); 9/1/2 (f 2)	7/1/3 (f 1); 8/1/2 (f 1); 8/1/3 (f 1); 9/1/2 (f 3); 9/1/3 (f 1); 10/1/2 (f 1)	7/1/3 (f 1); 8/1/2 (f 1); 8/1/3 (f 3); 9/1/2 (f 1); 9/1/3 (f 2); 10/1/3 (f 2)	10/1/2
LatL	19/13 (f 1); 20/11 (f 3); 20/12 (f 5); 21/9 (f 2); 21/10 (f 1); 21/11 (f 2); 21/12 (f 2); 21/13 (f 3); 22/11 (f 1); 22/12 (f 2)	20/12 (f 1); 21/9 (f 1); 21/10 (f 2); 21/12 (f 5); 21/14 (f 1); 22/11 (f 1)	21/7 (f 1); 21/8 (f 1); 22/9 (f 1)	20/9 (f 1); 20/12 (f 1); 21/11 (f 1); 21/12 (f 1); 21/13 (f 1); 22/11 (f 1); 22/12 (f 1); 22/13 (f 1)	19/12 (f 1); 20/10 (f 1); 20/11 (f 1); 20/12 (f 1); 20/13 (f 1); 21/9 (f 1); 21/10 (f 2); 21/11 (f 1); 21/15 (f 1)	21/12
D-ULL	5 (f 11); 6 (f 12)	5 (f 8); 6 (f 3)	6 (f 2); 7 (f 1)	5 (f 3); 6 (f 5)	5 (f 2); 6 (f 7); 7 (f 1)	6
ULL-A	9 (f 6); 10 (f 7); 11 (f 6)	8 (f 1); 9 (7)	10 (f 3)	10 (f 7); 12 (f 1)	9 (5); 10 (f 3); 11 (f 1)	10
ChS	2/7 (f 2); 2/9 (f 2); 3/7 (f 5); 3/8 (f 8); 3/9 (f 5); 4/8 (f 1)	3/7 (f 4); 3/8 (f 4); 3/9 (f 2); 4/9 (f 1)	2/7 (f 1); 2/8 (f 2)	2/6 (f 1); 2/8 (f 2); 3/7 (f 1); 3/8 (f 1); 3/9 (f 1); 3/10 (f 1)	2/8 (f 1); 2/9 (f 4); 3/7 (f 1); 3/8 (f 3); 3/9 (f 1);	3/9

3.2.8 Haplochromis *sp. 'curvidens'*

Haplochromis sp. 'curvidens' has a long and slender lower jaw (LJL, LJW, table 1, p. 35). The gape slopes steeply at 45–55°, the maxilla are bullate, i.e. posteriorly enlarged and distinctly visible, and the premaxilla beaked. These characteristics give it a piscivorous *sensu stricto* appearance. However, the outer teeth in both jaws are strongly recurved horizontally with a conical neck and acutely-rounded, strongly recurved crowns that are embedded in the slightly thickened oral mucosa (fig. 14e). The outer teeth are numerous on both jaws (UOT, LOT; fig. 17, ☐), closely set and implanted in very long dental arcades in comparison to the short arcades in all other paedophagous species. *Haplochromis* sp. 'curvidens' (fig. 18e) differs from all paedophages by its slender head (HW). From all except *H. taurinus* and *H.* sp. 'relictidens', by a longer head (HL) with a more slender lower jaw (LJW). It has much smaller eyes (ED) than *H. taurinus*. From *H.* sp. 'relictidens', it differs by a lower jaw that is equally rounded as the upper jaw instead of narrower, and by the number of outer teeth which are exceptionally few in *H.* sp. 'relictidens'. For a complete species description, see p. A.19, for additional pictures, see fig. 26, p. A.29.

3.2.9 Haplochromis occultidens

Haplochromis occultidens (fig. 18, f), endemic to Lake Kivu, has lips and an oral mucosa that are firmly thickened. The upper lip is anteriorly thin, laterally quickly thickening and hereby completely engulfing the outer teeth. In both jaws, the teeth are set in short dental arcades (2/3 dentigerous area). This trophic morphology is strikingly similar to all paedophagous species from the Lake Edward system, except for *H.* sp. 'curvidens'.

Haplochromis occultidens has a very similar body form to *H. sp.* 'longicauda' (c). Both have a very slender build (BD, table 1, p. 35) with a slender caudal peduncle and a steeply sloping gape inclination. The outer teeth of both species are very small and have distinct cusp-gaps and large minor cusps. They are however clearly distinct by the longer premaxillary pedicel (PPL) and snout (SnL) of *H. occultidens*. The most striking characteristic of *H. occultidens* is the similarity it has with *H.* sp. 'relictidens' in dental characteristics. Both species have a lower

number of outer teeth as the specimens become larger. They have a similar mouth morphology with an anteriorly narrowing lower jaw and more rounded upper jaw. *Haplochromis occultidens* and *H.* sp. 'relictidens' are, however, distinct by the former having a smaller lacrima (LaD), shorter anal fin base (AFB), a narrower interorbital width (IOW) and a more slender caudal peduncle.

3.3 ***'Paralabidochromis'*, the insectivores**

For this study, 90 specimens with *'Paralabidochromis'* characteristics from the Lake Edward system were analysed. This sample consists of 21 specimens from the RBINS collection, 68 from the RMCA collection and the holotype of *H. labiatus* from the NHM collection. A syntype of *H. schoutedeni* Poll, 1932 (RMCA 21483), a synonym of *H. paucidens* (Snoeks, 1988), was analysed in order to make a comparison with the sole species from Lake Kivu that has a *'Paralabidochromis'* morphology.

The characteristics defining *'Paralabidochromis'*, i.e. thickened lips and few strong outer teeth that are procumbently implanted on the short lower jaw, were hard to define and seemed present in a lot of specimens, some of which clearly belonged to different species. "Thickened lips" was a difficult character to define. This character could not be reliably expressed as a measurement as the lips were often deformed in preserved specimens; in addition, lip thickness presumably displays a certain amount of phenotypic plasticity, making it unreliable for morphometric research. The aim of the study on '*Paralabidochromis'* specimens was therefore twofold. First and foremost, we aimed at identifying and describing the species that display all the specific characteristics of '*Paralabidochromis'* and have strongly thickened to lobate lips, i.e. the lobe-lipped species. In these species, the large majority of specimens display thickened lips. Hence, in this study, all groups of specimens that were considered conspecific and have a few aberrant specimens with hypertrophied lips, will be excluded as these groups, will not be considered to consist of thick-lipped specimens. The second aim will be to determine the morphological differences that separate the lobe-lipped species from these other groups of Lake Edward specimens with a resembling morphology.

All specimens were briefly investigated and groups were defined based on trophic morphology, mainly their dental characteristics. Four groups were formed, the first had very narrow, acutely pointed tooth bands, set with unicuspid and cylindrical outer teeth that had distinctly straight crowns. Anteriorly on the lower jaw, the teeth were very long, widely set and procumbently implanted on the anterior margin of the dentary. All other outer teeth were closely set. The inner teeth were small, unicuspid and anteriorly implanted on a distinct space from the outer rows. This group was named *H.* sp. 'lobatus', in reference to its distinctly lobed lips. A second group was defined by all specimens having relatively narrow but rounded tooth bands that were closely set with unicuspid, cylindrical outer teeth with slightly recurved crowns. The anterior teeth on the dentary were also very long and procumbently implanted but closely set. The anterior-most inner teeth are slightly larger and implanted very close to the outer rows. As this group included the holotype of *H. labiatus,* it will be referred to as *H. labiatus.* A few specimens showed slightly thickened lips in combination with a more general *Haplochromis* morphology. The outer teeth were stout with bicuspid crowns consisting of relatively acute major cusps, often a distinct flange, and of minor cusps that were relatively large. The teeth were set in rounded, relatively broad tooth bands. The inner teeth were uni- or tricuspid and always small. As these characteristics are common in generalistic species, this group was named 'the generalists'. The last group was formed by specimens that had an intermediate morphology between *H. labiatus* and the generalists. Many of these specimens had dental characteristics similar to those of the group *H. labiatus* but differed as the outer teeth were more widely set or a wider space between outer and inner rows was present. Some specimens had outer teeth with a relatively straight implantation anteriorly on the dentary or they had clearly broader tooth bands. Although there could be more than one species present in this group, we do not consider

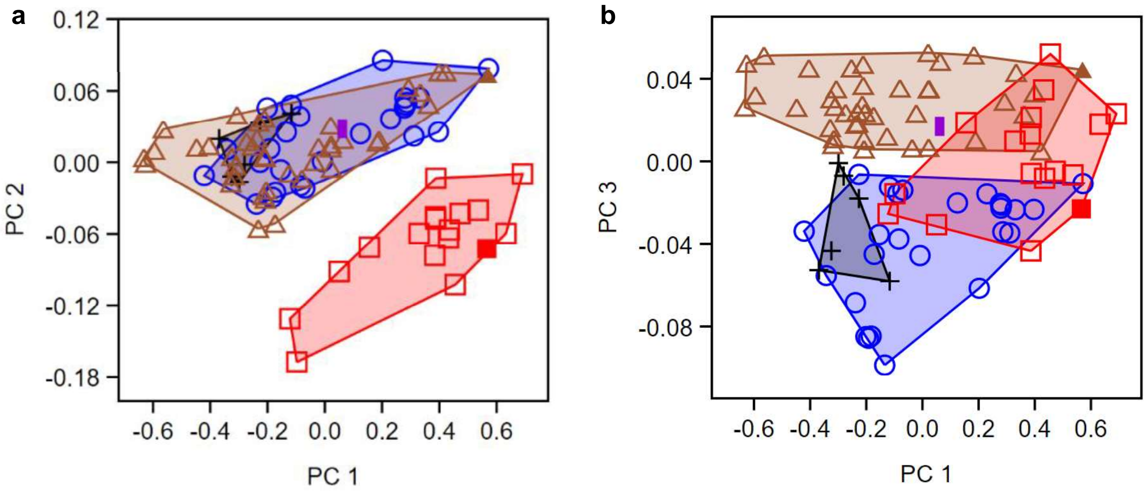

Figure 19 PCA of the log-transformed measurements of 90 specimens from the Lake Edward system with *'Paralabidochromis'* characteristics and a syntype of *H. paucidens*, endemic to Lake Kivu. Groups are based on dental characteristics. Two plots were made, both (a) PC 2 and (b) PC 3 were plotted on PC 1. *H. labiatus* (Δ, holotype: ▲), *H.* sp. 'lobatus' (☐, holotype: ■), fleshy-lipped haplochromines (○), generalists (+), *H. paucidens* (syntype: ▌). For PCA loadings, see table 6, p. A.5.

them at the core of the '*Paralabidochromis'* group. This group was named 'the fleshy-lipped generalists' due to their slightly thickened to thickened lips.

3.3.1 Measurements

A PCA of the log-transformed measurements of all specimens was performed (table 6, p. A.5). All characters got large, positive loadings on PC 1, hereby sorting specimens by body size. Principal component 2 was mainly determined by lower jaw length and lower jaw width. Principal component 3 also had high absolute loadings for lower jaw length and lower jaw width, in addition to upper jaw length and to a lesser extent cheek depth and premaxillary pedicel length.

The analysis was presented by plotting PC 2 and PC 3 *versus* PC 1 (fig. 19). Contrary to the situation in the paedophages, there was a size effect. The group *H.* sp. 'lobatus' (☐) was distinct from all other groups on a plot of PC 2 on PC 1. This could be explained by the long and slender jaws of these specimens. All other groups strongly overlapped with each other in this plot. In a second plot, PC 3 was plotted on PC 1 (fig. 19b). Here, the groups *H. labiatus* and *H. paucidens* had positive values for PC 3. They cannot be distinguished from each other on PC 2 or PC 3, indicating a large morphological similarity, presumably both had a short lower jaw. A clear distinction could be made on PC 7 (explained 0.433% variance), which was mainly determined by upper jaw length, anal fin base length and slightly less by eye depth. The generalists and the fleshy-lipped generalists were situated completely in the negative part of PC 3. Hence, this axis completely separated them from *H. labiatus* and *H. paucidens*. Specimens belonging to the generalists and the fleshy-lipped generalists presumably had long and broad oral jaws. They could, however, not be distinguished from each other in this analysis. This could be caused by both groups containing several species that are morphologically distinct from each other.

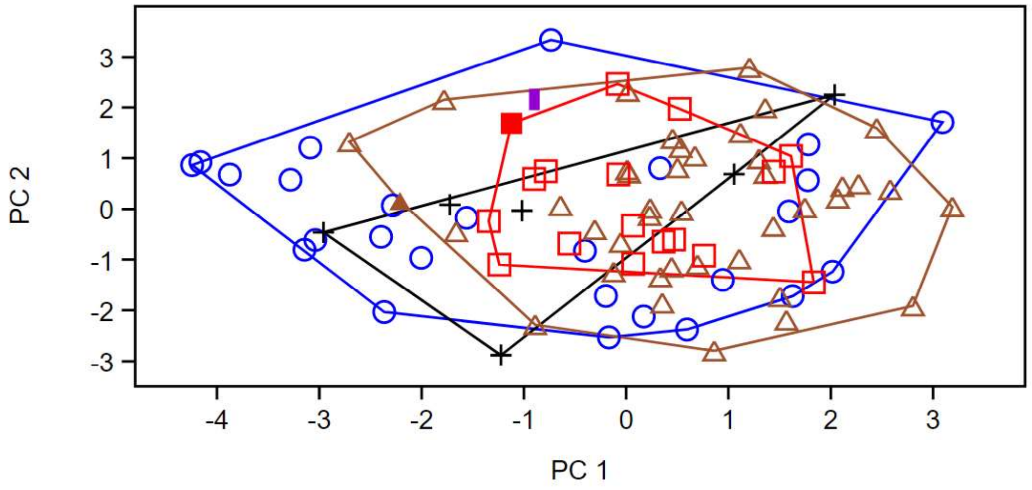

Figure 20 PCA of the meristics of 90 specimens from the Lake Edward system with *"Paralabidochromis"* characteristics and a syntype of *H. paucidens*, endemic to Lake Kivu. *H. labiatus* (Δ, holotype: ▲), *H.* sp. 'lobatus' (□, holotype: ■), fleshy-lipped haplochromines (○), generalists (+), *H. paucidens* (syntype: ▮). For PCA loadings, see table 7, p. A.6.

Consequently, interspecific variation could be included in each group.

3.3.2 Meristics

All specimens had two inter-lateral line and 16 caudal peduncle scales. These counts were excluded from the analysis as no variation was present. Radiographs were only taken from a limited number of specimens. Hence, vertebral counts were also excluded from this analysis. The analysis of all 18 remaining meristics was performed, in which PC 1 was mainly determined by the number of inner teeth rows in both the upper and the lower jaw, and the numbers of pelvic-pectoral and upper transversal scales. The number of branched dorsal and anal-fin rays were important for PC 2, as were the number of posterior cheek scales and the number of inner tooth rows on the upper jaw. Values for all groups overlapped substantially. *Haplochromis paucidens* had a slightly deviant value for PC 2 that was higher than the majority of *H. labiatus* specimens but all meristics seemed to overlap completely. A PCA of only the groups *H. labiatus* and *H.* sp. 'lobatus', i.e. the lobe-lipped specimens, was performed but the results were similar. Hence, distinctions could not be made.

Each group will be discussed separately with the emphasis on the diagnostic characters that distinguish them from all other groups. A synopsis of the most distinctive measurements and meristics of all species with *'Paralabidochromis'* characteristics from the Lake Edward system are summarised in table 2, p. 42.

3.3.3 Haplochromis labiatus

Haplochromis labiatus had a rounded but narrow tooth band, set with stout, unicuspid outer teeth with slightly recurved crowns. The outer teeth of small specimens (SL < 80 mm) were bicuspid. The anterior outer teeth were very long while they, laterally, they abruptly decrease in size. Anteriorly on the dentary, the outer teeth are distinctly procumbently inclined. The dental arcades look compact due to the close setting of the outer teeth and the lack of a space between inner and outer tooth rows. The most labially inner teeth are stouter than teeth that are more buccally implanted. The lips are strongly thickened to very slightly anteriorly lobate.

Haplochromis labiatus has a distinctly short lower jaw (LJL, table 2, p. 42), certainly compared to *H.* sp. 'lobatus'. It differs further from *H.* sp. 'lobatus' by a slightly longer upper jaw (UJL), a broader head (HW) and bigger eyes (ED). The jaws of *H. labiatus* are often retrognathous while *H.* sp. 'lobatus' has often prognathous jaws, although both species can have an isognathous mouth too. The snout of *H.* sp. 'lobatus' is slender and elongated while *H. labiatus* has a broader and stouter snout (LJW). The male nuptial colouration is also somewhat different with *H. labiatus* having an yellowish body colour and orange caudal fin, whereas *H.* sp. 'lobatus' has a greenish body colour and a red caudal fin (fig. 27c, vs. fig. 28c, pp. A.29–A.29). This difference is however not always clear due to the occurrence of specimens with intermediate colouration.

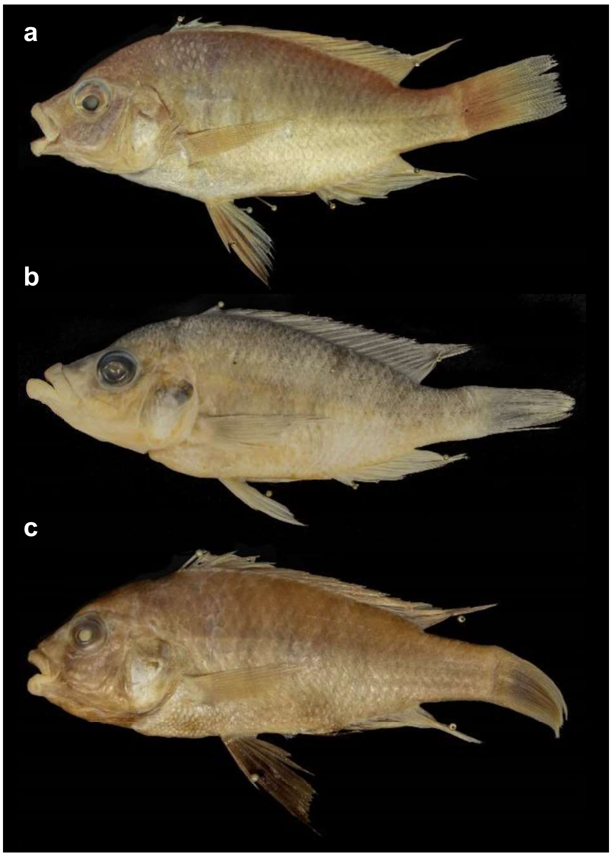

Figure 21 Thick-lipped haplochromines from lakes Edward, George and Kivu. (a) *H. labiatus*, holotype [♀ 104.33 mm] and (b) *H.*sp. 'lobatus', holotype [♀ 104.56 mm]; endemic to the Lake Edward system. (c) *H. paucidens*, syntype of *H. schoutendeni* [♂ 85.42 mm], endemic to Lake Kivu.

Haplochromis labiatus differs from the fleshy-lipped haplochromines by its much shorter lower jaw (LJL) and longer premaxillary pedicel (PPL) and higher neural crest. The outer teeth are set in broader tooth bands in the fleshy-lipped generalists. Laterally, the outer teeth decrease more gradually in size in comparison to the abrupt decrease in *H. labiatus*. These distinctions are all general patterns within the fleshy-lipped generalists, some specimens could still belong to *H. labiatus*. For a complete species description, see p. A.23. For additional pictures, see fig. 27, p. A.29.

3.3.4 Haplochromis *sp. 'lobatus'*

Haplochromis sp. 'lobatus' is completely distinct from all other '*Paralabidochromis'* specimens by its very slender head (HW, table 2, p. 42) and jaws (LJW). The snout is long (SnL), slender and acute, which is most visible dorsally. The upper jaw is short (UJL), the lower jaw slender (LJW) and distinctly long (LJL). The mouth is isognathous to extremely prognathous with all inner teeth rows visible when the mouth is closed. The outer teeth are completely straight and closely set, except for the anterior-most teeth on the lower jaw, which are more widely set. Furthermore, the anterior-most teeth have a strongly procumbent implantation on the anterior margin of the dentary, pointing forward, in the extension of the dentary. The inner teeth are unicuspid, small and form a band, anteriorly set at a distinct distance from the outer row, only laterally closely set to the outer row, from which point they quickly decrease posteriorly until only the outer row remains. The lips are distinctly thickened and often medially strongly lobate. For a complete species description, see p. A.23. For additional pictures, see fig. 28, p. A.29.

3.3.5 The fleshy-lipped generalists

As already mentioned earlier, these specimens share some distinctive characters of *H.* labiatus. Most of them can however be distinguished by their relatively longer upper jaw (UJL, table 2, p. 42), broader lower jaw (LJW) and a shorter premaxillary pedicel (PPL). The outer teeth are implanted in more rounded tooth bands with the anterior outer teeth on the lower jaw having a slightly procumbent implantation. The variation in lip thickness was huge, ranging from no hypertrophication of the lip tissue in some deviant specimens, to possessing lips that were clearly thicker than those of some specimens belonging to *H. labiatus* or *H.* sp. 'lobatus'. We assume that this group includes several species. Some small males (SL 70**–**75 mm) had a distinct dominant colouration that was most likely different from the nuptial colouration of *H. labiatus* although no live pictures of these small males were available. Other specimens in this group had teeth that were similar in shape to the outer teeth of *H. labiatus,* although the specimens had only slightly thickened lips and widely set outer teeth. Although they could be completely separated by PCA, the possibility that some specimens belong to *H. labiatus*, cannot be excluded completely.

3.3.6 The generalists

These specimens strongly resemble some specimens of the fleshy-lipped generalists. They do however, have a steeper sloping head caused by their large neural crest, a character that is also present in *H.* labiatus. The generalists are however clearly distinct by their more acutely pointed, bicuspid outer teeth. Although these teeth have sometimes stout necks, the crowns have slender major cusps, often bearing a flange and/or a distinct cusp gap, that separate them from the minor cusps. The inner teeth are unicuspid or distinctly tricuspid with the minor cusps reaching almost as high as the major cusp. At least two distinct species seem to be present within this cluster as similar-sized specimens had either unicuspid or distinctly tricuspid inner teeth.

3.3.7 Haplochromis paucidens

In both the analysis of the measurements and the meristics, *H. paucidens* could not be distinguished from *H. labiatus*. It differs however by a distinctly shorter head (HL, table 2, p. 42). Also, the lower jaw (LJL), premaxillary pedicel (PPL) and eyes (ED) are smaller in *H. paucidens.* The lacrima is larger (LaD) and the upper jaw is relatively long (UJL). The dental morphology is mainly different by the outer teeth having a less procumbent implantation.

Table 2 Synopsis of the distinguishing measurements and counts of all groups displaying '*Paralabidochromis*' characteristics of the Lake Edward system, i.e. *H. labiatus*, *H.* sp. 'lobatus', the *fleshy-lipped haplochromines* and the generalists. The holotype is included for *H. labiatus* and *H.* sp. 'lobatus', for all morphometrics of these last two species, i.e. the lobe-lipped species, see table 11, p.28.

	H. labiatus		***H.* sp. 'lobatus'**		**Fleshy-lipped haplochromines**		**Generalists**		***H. paucidens***
Measurements		n = 41		n = 17		n = 26		n = 6	n = 1
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Value
SL (mm)	75.3	60.0 104.3	94.8	75.2 110.0	80.0	62.1 105.3	70.0	67.7 74.6	85.42
HL % SL	33.7	32.0 35.8	34.2	32.6 36.7	34.6	32.2 37.4	33.7	33.0 34.1	31.6
HW % HL	49.5	46.9 51.9	47.5	45.4 49.1	48.4	43.8 51.4	48.7	46.2 50.7	46.5
PPL % HL	25.5	23.6 27.5	26.0	24.2 28.5	24.0	20.5 26.5	23.3	22.3 23.6	24.1
SnL % HL	28.0	26.1 32.5	30.6	24.9 34.3	28.6	26.3 31.4	26.4	25.0 29.3	28.8
LaD % HL	15.0	12.9 16.3	15.7	13.0 17.2	14.7	12.9 16.5	14.1	13.2 14.9	16.2
ChD % HL	20.3	16.5 24.1	20.9	16.1 23.0	19.8	15.1 23.5	19.8	18.2 20.9	20.8
ED % HL	34.6	32.1 36.8	31.1	29.1 33.6	34.2	30.9 36.3	35.5	34.2 36.9	29.2
UJL % HL	25.8	23.9 29.0	25.1	20.8 27.8	27.5	24.0 31.1	26.4	25.7 27.7	29.4
LJL % HL	31.0	27.1 33.6	37.2	34.2 40.7	32.7	27.7 36.4	34.5	32.4 36.4	31.2
LJW % LJL	79.8	67.8 93.9	61.6	48.5 70.5	81.0	69.7 99.0	73.0	65.8 83.6	81.7

Meristics	n = 41	n = 17	n = 26	n = 6	n = 1
	Number & frequency (f)	Number & frequency (f)	Number & frequency (f)	Number & frequency (f)	Number
UFT	18–35 (median 26)	21–30 (median 26)	20–33 (median 27)	25–33 (median 27)	33
LFT	12–34 (median 24)	18–33 (median 25)	12–33 (median 24)	24–28 (median 26)	26
UTR/LTR	2/2 (f 13); 2/3 (f 3); 3/2 (f 8): 3/3 (f 15); 4/3 (f 1); 4/4 (f 1)	2/2 (f 5); 2/3 (f 1); 3/2 (f 3); 3/3 (f 5); 4/2 (f 1); 4/3 (f 1); 4/4 (f 1)	1/2 (f 1); 2/2 (f 6); 2/3 (f 1); 3/2 (f 3); 3/3 f (4); 3/4 (f 2); 4/3 (f 3); 4/4 (f 6)	2/2 (f 2); 3/2 (f 1); 3/3 (f 1); 4/3 (f 1)	3/3
DFR	XV/8 (f 1); XV/9 (f 6); XV/10 (f 14); XV/11 (f 1); XVI/8 (f 2); XVI/9 (f 9); XVI/10 (f 8)	XV/8 (f 1); XV/6 (f 3); XV/10 (f 3); XVI/9 (f 9); XVI/10 (f 1)	XV/9 (f 2); XV/10 (f 14); XVI/8 (f 1); XVI/9 (f 6); XVI/10 (f 2); XVII/10 (f 1)	XV/9 (f 2); XV/10 (f 2); XVI/9 (f 2)	XVI/9
AFR	III/7 (f 1); III/8 (f 2); III/9 (f 33); III/10 (f 5)	III/9 (f 16); III/10 (f 1)	III/8 (f 5); III/9 (f 19); III/10 (f 2)	III/8 (f 1); III/9 (f 5)	III/8
D-ULL	5 (f 5); 6 (f 17); 7 (f 9); 8 (f 3)	5 (f 4); 6 (f 11); 7 (f 1); 8 (f 1)	5 (f 11); 6 (f 12); 7 (f 3)	5 (f 4); 7 (f 2)	6
P-V	6 (f 2); 7 (f 6); 8 (f 24); 9 (f 7); 10 (f 2)	5 (f 2); 6 (f 3); 7 (f 5); 8 (f 6); 9 (f 1)	5 (f 2); 6 (f 5); 7 (f 5); 8 (f 5); 9 (f 5); 11 (f 1)	5 (f 1); 6 (f 1); 7 (f 2); 9 (f 1); 10 (f 1)	9
ChS	2/9 (f 1); 3/7 (f 2); 3/8 (f 6); 3/9 (f 11); 3/10 (f 7); 4/8 (f 1); 4/9 (f 11); 4/10 (f 1); 4/11 (f 1)	2/9 (f 3); 2/10 (f 1); 3/9 (f 5); 3/10 (f 4); 4/8 (f 3); 5/10 (f 1)	2/7 (f 2); 2/8 (f 2); 3/7 (f 1); 3/8 (f 9); 3/9 (f 5); 3/10 (f 1); 4/7 (f 1); 4/8 (f 2); 4/9 (f 1); 4/11 (f 1)	3/7 (f 1); 3/9 (f 4); 3/11 (f1)	3/9

4 Discussion

A morphometric revision of the Lake Edward system haplochromines belonging to the groups '*Lipochromis'* and '*Paralabidochromis' sensu* Greenwood (1980), i.e. the thick-lipped *Haplochromis*, was performed. The aim of this study was to delineate the species within these groups by identifying and describing all species with their distinctive morphologies. Two thick-lipped haplochromines from the Lake Edward system were already described, i.e. *H. taurinus* and *H. labiatus*. Within this study, an additional five new species, namely*, H.* sp. 'curvidens', *H.* sp. 'lobatus', *H.* sp. 'longicauda', *H.* sp. 'molossus' and *H.* sp. 'relictidens' have been discovered and preliminarily described. *Haplochromis labiatus* and *H.* sp. 'lobatus' make up the lobe-lipped species within the group '*Paralabidochromis'* but some problems with the delineation of the species remain. The other four of these newly discovered species and *H. taurinus* have a '*Lipochromis'* morphology.

4.1 '*Lipochromis'*, the paedophages

4.1.1 Characteristics

All '*Lipochromis'* species from the Lake Edward system have firmly thickened lips and small outer oral teeth that are deeply embedded in the, at least slightly, thickened oral mucosa. In *H.* sp. 'relictidens', teeth are so deeply embedded that, at most, only their tips are visible. In all other species, the crowns generally protrude the oral mucosa. The outer teeth are, however, anteriorly inclined in *H. taurinus* and strongly recurved in *H.* sp. 'curvidens', two tooth morphologies which are present in '*Lipochromis'* (Greenwood, 1980). The teeth on the dentary of *H.* sp. 'molossus' and *H.* sp. 'longicauda' protrude the oral mucosa but are completely covered by the relatively high and firmly thickened lower lip. Small specimens (SL ± < 85 mm) of all species have relatively larger teeth with the entire crown often protruding the oral mucosa, but this is most likely the general condition in small specimens. All species, except *H.* sp. 'curvidens' (which will be commented below), have slender and very short dental arcades, reaching to 2/3 of the dentigerous length. Laterally in the upper jaw, the outer teeth are strongly engulfed by the firmly thickened lips, making these outer teeth hard to observe. Greenwood described two characteristic jaw morphologies for '*Lipochromis'* (fig 5, p. 5), the parvidens-type, as can be observed in *H.* sp. 'relictidens', is a lower jaw which anteriorly narrows causing it to close within the more rounded upper jaw. The other jaw morphology is the obesus-type that is present in *H. taurinus*, *H.* sp. 'molossus' and *H.* sp. 'longicauda', is a very broadly rounded jaw.

Hoogerhoud (1984) and Snoeks (2000) demonstrated that the genera defined by Greenwood (1980) are not completely distinct from each other. Many species cannot be linked to any of these groups, form intermediates between two groups or show deviations from a morphology, typical for the group. Some paedophagous species from the Lake Edward system also deviate from '*Lipochromis'*. *Haplochromis taurinus* and *H.* sp. 'longicauda' both have bicuspid outer teeth in specimens of all sizes while '*Lipochromis'* has unicuspid teeth in large specimens (SL > 100 mm). All other dental characteristics, i.e. the size and implantation of the teeth, the shape of the tooth bands and the length of the dental arcades are however of a typical '*Lipochromis*'-type. More extraordinary is the strongly deviating morphology of *H.* sp. 'curvidens'. Only its slightly thickened oral mucosa and relatively small and strongly recurved teeth can be linked to '*Lipochromis*'. *Haplochromis* sp. 'curvidens' deviates by its obliquely inclined mouth, a lower jaw with a mental protuberance and distinctly beaked premaxilla. Furthermore, the outer oral teeth are numerous, 33–65 (median 45) on each jaw, and set in long tooth bands. The snout has a shallow inclination and the supraoccipital crest is low and wedge-shaped, giving it an elongated head. All these characters are present in the group "*Prognathochromis*" Greenwood, 1980, a group of piscivorous species. In conclusion, H. sp. 'curvidens' has a typical "*Prognathochromis*" morphology with some '*Lipochromis'* dental characteristics.

4.1.2 Ecology

'*Lipochromis*' *sensu* Greenwood comprises only species with a paedophagous ecology. This is also the case for the Lake Edward system, all species with a '*Lipochromis*' morphology have a paedophagous ecology. Stomachs of each '*Lipochromis*' species contained cichlid eggs and/or larvae. The possibility that fry and eggs were swallowed while mouthbrooding can be disproved as for each species at least one male was found with this stomach content. Stomachs containing partially-digested food items or larvae of different sizes, were present for all species, supporting the presumption that these eggs and larvae were forcefully acquired from mouthbrooding females. In conclusion, *H. taurinus, H.* sp. 'molossus', *H.* sp. 'longicauda', *H.* sp. 'relictidens' and *H.* sp. 'curvidens' were confirmed to have a paedophagous ecology. The stomach content of a single specimen of *H. taurinus* deviated from this pattern by containing several Ephemeroptera larvae. Probably indicating that this species has a more mixed diet. This can be supported by *H. taurinus* being caught in a higher abundance than the other paedophagous species during the RMCA 2017–06: HIPE 2 expedition (Van Steenberge, pers. comm.).

4.1.3 Convergence

Snoeks (1994), during his revision of the Lake Kivu haplochromines, examined the Lake Edward specimens from the RBINS collection that were identified as *H. paucidens* by Hulot (1956). This species was only known from Lake Kivu but could possibly also occur in the poorly known system of Lake Edward. Snoeks has verified that at least all these specimens were not conspecific with *H. paucidens.* He did however recognise several specimens [ISNB 12902 (n=3) and 12905 (n=1)] that slightly resembled *H. occultidens* but belonged to different, unknown species (Snoeks 1994). These specimens could however be identified as *H.* sp. 'relictidens'. An in-depth comparison was made with the inclusion of the holotype of *H. occultidens* and these Lake Edward specimens. A very strong resemblance to *H.* sp. 'relictidens' was indeed found. The latter had, however, a relatively deeper body, a higher caudal peduncle, a larger interorbital width, a longer premaxillary pedicel and a deeper lachrymal bone than *H. occultidens* (for values, see table 1, p. 35). Most of these characters are linked to the deeper body of *H.* sp. 'relictidens'. The morphology of the jaws is however strikingly similar, both with a parvidens-type lower jaw.

The apparent strong link between ecology and morphology has also been observed with *Haplochromis* species from other lakes of the Lake Victoria superflock. Although their phylogenetic relationships remain largely unknown, morphologically similar species of different flocks probably radiated independently (Meyer 1990, Verheyen 2003). *Haplochromis* sp. 'relictidens' has a higher morphological resemblance to *H. occultidens* and *H. microdon*, from lakes Kivu and Victoria respectively, than to any other species occurring in the Lake Edward system (pers. obs.). This strong morphological resemblance could form an example of the extraordinary extend of convergent evolution that has taken place within the Lake Victoria superflock.

A strong resemblance can also be found in the peculiar dental characteristics of *H*. sp. 'relictidens' and *H. occultidens.* Large specimens of both species have a lower number of outer teeth on both jaws than smaller specimens (fig. 17, p. 31). This indicates that these species lose their outer teeth as the fish grow, while the teeth will not be replaced by new ones. Within the Lake Victoria superflock, this has only been documented in these two species. Snoeks (1994) postulated that this trait forms a specialised dental characteristic of the paedophagous ecology of *H. occultidens* as this species probably has no need of its outer teeth. *Haplochromis* sp. 'relictidens' most likely has the same feeding mechanism and its trophic morphology has most likely a similar function. Hereby, the hypothesis of Snoeks (1994) can be supported by these findings. This trophic morphology could be acquired through convergent evolution or common descent. In face of the hybridisation hypothesis, there is also the possibility that it evolved through a mixture of convergence and common descent.

4.1.4 The species richness of Lake Edward

The Lake Victoria superflock includes several flocks that are endemic to the lakes Kivu, Edward and Victoria. Lake Kivu is home to 15 endemic haplochromine cichlids (Snoeks, 1994) while it is estimated that, before the introduction of *Lates niloticus* Linnaeus, 1758, Lake Victoria possessed a flock of 500–700 species (Snoeks, 2001; Turner et al., 2001). Two assumptions will be made in order to make an estimation of the species richness of Lake Edward. The first is that the currently known or estimated richness of lakes Kivu and Victoria is representative for the real situation. The second one assumes that the diversity of trophic niches are represented by a similar ratio of haplochromine species within the different lakes of the Lake Victoria superflock. If these are correct, a rough estimation of the number of haplochromine species within the Lake Edward system can be made by linking the number of paedophages that are present in this system to the numbers in the other lakes. The current estimation of species within the Lake Edward system flock is 60–90 species (Keenleyside, 1991; Snoeks, 2001). Lake Kivu has one species with a paedophagous ecology while the Lake Victoria flock is known to have had at least 20 species, of which many undescribed, paedophages (Greenwood, 1980; Seehausen, 1996). By extrapolating these numbers to the total number of species, 1/15–1/35 species are presumed to have a paedophagous ecology in the lakes of the Lake Victoria superflock. The lake Edward system has a total of five paedophagous species, resulting in an estimation of 75–175 haplochromine cichlid species inhabiting the system. This is in accordance with the current hypothesis of Snoeks (2001), to even twice as many species than was previously thought. This is however a rough estimation, solely based on the species richness within a single ecological niche. The ecosystem of Lake Edward is more similar to that of Lake Victoria. Hence, a comparison with this lake is more meaningful ecologically. But the size of the Lake Edward system is more similar to that of Lake Kivu, so the species richness of this lake was included to reduce allopatric effects that should be lower in the Lake Edward system than in Lake Victoria.

4.2 *'Paralabidochromis'*, the insectivores

4.2.1 Characteristics

The lobe-lipped species from the Lake Edward system have a typical '*Paralabidochromis'* morphology. Two species are known, *H. labiatus* and a newly discovered species: *H.* sp. 'lobatus'. The premaxilla is anteriorly bullate and has a premaxillary pedicel that is as long or longer than the dentigerous arms. The outer teeth are unicuspid, long, relatively stout and cylindrical with an acutely rounded, conical cusp. The line, formed by the implantations of the outer teeth on the dentary, slopes anteriorly downwards because the teeth are implanted on the dorso-anterior surface of the dentary. Additionally, these anterior outer teeth are implanted perpendicular to the bone, hence they have a distinct procumbent implantation. The lateral outer teeth abruptly decrease in size compared to the anterior outer teeth on both jaws. The tooth bands are relatively narrow and 'u'-shaped in *H. labiatus* while they are very narrower and acute ('v'-shaped) in *H.* sp. 'lobatus'. The lips are strongly thickened to lobate in both species. The lower jaw is stout with the anguloarticular ventrally enlarged, giving the head ventrally a distinct slope. All these characters are distinct for '*Paralabidochromis'*. Typically, species of this group have jaws that are anteriorly equal, this is however not the case in both species from the Lake Edward system. Generally, *H.* sp. 'lobatus' has prognathous jaws while *H. labiatus* has a retrognathous mouth. *Haplochromis labiatus* further deviates by a slightly shorter lower jaw than the general condition in *'Paralabidochromis'* [27.1–33.6 (mean 31.0), vs. 30–49 (modal range 33–35) % HL].

4.2.2 Niche segregation

The divergent trophic morphologies between *H. labiatus* and *H.* sp. 'lobatus' could be an example of niche segregation. Both species are sympatric and have a similar morphology, except for the respectively pro- and retrognathous mouths of *H.* sp. 'lobatus' and *H. labiatus.* Thickened lips have proven to be an adaptation in order to prey on insects living on hard substrates (Baumgarten et al., 2015). Possible explanations for the nature of these lips are that they are used to seal off crevices in order to suck out insects more efficiently or that the lips form a protection for the procumbently implanted teeth (Arnegard & Snoeks, 2001). *Haplochromis* sp. 'lobatus' could use its more slender snout to reach for insect larvae between rock crevices, as has been observed in *H. chilotes*, an endemic of Lake Victoria with a similar morphology. Many specimens of *H. labiatus* show strongly abraded teeth, anteriorly on both jaws. This, in combination with the more evenly thickened lips, could indicate that they look for prey on top of hard substrates, against which the teeth wear off faster. This could explain how both species can exploit similar food sources without entering in direct competition with each other. This difference in trophic morphology is not known in species of Lake Kivu. In Lake Victoria, Seehausen (1996) mentions two species with lobed lips to coexist, i.e. *H. chilotes and H.* sp. 'short head chilotes', but does not comment on a possible difference in ecology.

In this study, the lobe-lipped haplochromines from the Lake Edward system were compared to the generalist species with a similar morphology, i.e. the fleshy-lipped haplochromines, from the same lakes. The lobe-lipped species have a more slender lower jaw and a shorter upper jaw in combination with a longer premaxillary pedicel. These characteristics give them smaller mouths that are less distensible but more protrusible than the generalistic species (Greenwood, 1980). Probably as an adaptation to efficiently catch insects out of small rock crevices, as has been found in other lakes (Kohda et al., 2008). The meristics show not much species-specific variation in the identification of these species as would be expected because of the young age of their radiation (Wamuini et al., 2010).

4.2.3 Phenotypic variation

In haplochromines, intraspecific variation can in some cases exceed interspecific variation (Van Steenberge, 2014). This seems to be the case between *H. labiatus* and the fleshy-lipped species. With the available data, defining a trait to unequivocally separate the lobe-lipped and non-lobe-lipped species was infeasible. The intraspecific variation is larger than the interspecific variation. The extensive variation could be explained due to phenotypic variation as lip thickness has shown to be in some haplochromine species of other lakes (Machado-Schiaffino et al., 2014). The large diversity in lip thickness that is present in *H. labiatus* and the fleshy-lipped generalists suggests that these species also have lips that show a large phenotypic variation. However, this should be regarded with caution. Barel et al. (1977) and Greenwood (1959) noted that there is a huge phenotypic variation present within the head morphology and lip-thickness of *H. chilotes*, an endemic species of Lake Victoria with thickened to lobate lips. This has however been corrected by Seehausen (1996), who recognised two distinct species, i.e. *H. chilotes* and *H.* sp. 'short head chilotes', that were presumably both present within the sample that Greenwood (1959) examined for his redescription of *H. chilotes*. This could also be the case in *H. labiatus* of Lake Edward. Describing similar Haplochromis species has shown to be difficult.

4.2.4 Evolutionary implications

The polyphyletic origin of the Lake Edward system flock (Meier et al., 2017) could have contributed to its high species diversity. This contributes to the genetic diversity within the flock and different lineage can contribute to the species diversity within the different trophic niches. For example, contact between different lineages could give rise to another species of paedophage with a slightly different niche that could exploit. For example, another strategy could arise to catch already partly free-swimming larvae than to catch eggs. The evolution of the haplochromine cichlids of Lake Edward is however unknown. Through convergent evolution are unrelated species able to display very similar phenotypes; therefore, relations between the different species cannot be deduced from morphological resemblance. Next generation sequencing has proven to be a promising tool in resolving these hypotheses (Wagner et al., 2012; Keller et al., 2013; Brawand et al., 2014).

5 Conclusion

We performed a morphometric revision of the thick-lipped haplochromine cichlids of the Lake Edward system. This group can be divided in two specific ecologies.

The first is the paedophages, they were found to consist of five species, namely *H. taurinus* and the newly discovered *H.* sp. ‘curvidens’*,* *H.* sp. ‘longicauda’, *H.* sp. ‘molossus’ and *H.* sp. ‘relictidens’. all five were found to have a paedophagous ecology. We found a large morphological resemblance between *H.* sp. ‘relictidens’ and *H. occultidens* and *H. microdon*, the last two respectively from lakes Kivu and Victoria. *H.* sp. ‘relictidens’ is morphologically similar to these two species than it is to any other species within the Lake Edward system. Whether this resemblance is acquired through convergent evolution or common descent is however unknown.

The second ecology is the lobe-lipped insectivores. These consist of two species, *H. labiatus* and the newly discovered *H.* sp. ‘lobatus’. These two species have a divergent trophic morphology. *Haplochromis labiatus* mostly has a retrognathous lower jaw, while *H.* sp. ‘lobatus’ mostly has a prognathous one. As both species occur sympatrically, this we assume this to be an example of convergent evolution.

Both these rare trophic groups show a large diversity that was unexpected. Based on the diversity of the paedophagous haplochromines, we made an estimation of 75–175 species within the haplochromine cichlid flock of the lake Edward system, thereby largely exceeding previous estimations.

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7 Addendum

7.1 Risk assessment

The safety regulations of the institution, the RMCA, were read and signed before the start of this study. Only specimens that are preserved on 70% isopropanol were examined. Specimens from new collections were fixated in 10% formalin on the field. They were first thoroughly rinsed in water for a few days to remove excess of formalin. When the formalin-smell was completely gone, they could be transferred to 70% isopropanol, and investigated. Formalin is a toxic component that can irritate the eyes. when inhaled, it can cause headaches and a burning sensation in the throat. When it comes in contact whit the skin, irritation can occur. Be taking these precautions, these toxic effects were prevented. Windows were regularly opened to provide access to fresh air and remove potential accumulation of evaporating substances, mainly isopropanol. All jars were kept shut to prevent the evaporation of alcohol. Other substances were not present in the workspace. Latex gloves were available to handle the specimens to prevent skin irritation after long-term exposure to the isopropanol. Caution was taken in handling specimens as the teeth and the spines in pelvic, dorsal and anal fins were sharp and able to puncture the skin. The specimens were dried with a towel before incisions with a scalpel were made to prevent slippage and cuts. Scalpels were always used with care and the surgical knives were renewed when they became dull to ensure that they were used in a safe and controlled manner. Radiographs were only taken under supervision of qualified staff.

7.2 Introduction

Table 3 General characters of the groups *'Lipochromis'* and *'Paralabidochromis'* according to Greenwood (1980). In this study cumulatively defined as the thick-lipped cichlids of the Lake Victoria superflock. Distinctive characters are indicated in bold. Figures modified from (Greenwood, 1973, 1980).

		***'Lipochromis'* Regan, 1920**	***'Paralabidochromis'* Greenwood, 1956**
	Bones		
Neurocr.	Supraoccipital crest	Tall, expansive	High
	Preorbital region	-	Deep (33–37 % NL), steeply sloping
Upper jaw	Premaxilla	Ventral margin distinctly thickened	Dentigerous arms somewhat inflated
	Posterior bullation	Obvious	Not strong
	Premaxillary pedicel	-	Equally long as dentigerous arms
	Maxilla	Bullate	Maxilla foreshortened
Lower jaw	Side view shape	-	Short, deep (foreshortened appearance)
	Top view shape	(A) Obesus type: broadly rounded (B) Parvidens type: narrow & acute	Narrow, bluntly V-shaped outline
	Symphysial region	-	Expanded
	Ramus	Posterior bullation	Posterior bullation
	LJL (% HL)	**Long**: 38–56 (mean 42–48)	30–49 (mean 33–35)
	External		
Body	Maximum size	130–170 mm SL	70–150 mm SL
	Body form	Variable	-
Head	Head profile	Heavy-blunt to slender-subacute	Straight or concave, steeply sloping
	Mouth	Slightly prognathous, wide lateral gape	Isognathous
	Mouth: inclination	Slightly oblique	Horizontal
	Lips	Thick, upper lip covers the teeth	Somewhat thickened to lobate
	Dentary		
Outer teeth	Neck form	Embedded in the oral mucosa	Stout, long, recurved, cylindrical
	Crown form	**Reflected labially (A)**, recurved (B)	Unicuspid: conical, robust Bicuspid: major cusp equilateral, minor cusp reduced OR major cusp more compressed, minor cusp at an angle
	Crown type	100 mm SL: < bicuspid, > unicuspid	65–70 mm SL: < bicuspid, > unicuspid
	Size	**Short teeth**	Anterior teeth longer than lateral ones
	Implantation	**Deeply embedded in thick oral mucosa**, at most only crown visible	**Lower jaw: anterior procumbently**, upper jaw: vertically
	# in upper jaw	Few teeth: 30–62 (generally ±40)	Few teeth: 16–48 (mean 30–35)
Inner teeth	Crown type	> 80–100 mm SL: unicuspid	>90 mm SL: uni- & tricuspid
	Size	-	Outer inner tooth row anteriorly slightly larger teeth than in other inner rows
	Implantation	Usually completely buried in oral mucosa	-
	Rows	1–2 rows	2–3 rows
	Relation to outer teeth	-	Separated by a distinct interspace
	Dental arcade	Short, posterior no teeth or widely spaced	Anteriorly narrowing: U-shaped
Pharyn.	Form (lower)	Short & broad	Short & broad
	Dentigerous surface	Long & broad	Long & broad
	Teeth	Fine & weakly bicuspid Posterior coarser than the others	Crown: compressed & bicuspid Median tooth rows: coarse teeth

7.3 Results

7.3.1 PCA Loadings

Table 4 PCA loadings of the logarithmic transformed measurements of 52 specimens from the Lake Edward system with a paedophagous morphology and the holotype of *H. occultidens*, endemic to Lake Kivu. For the plot of PC 2 on PC 3, see fig. 15, p. 29.

	PC 1	**PC 2**	**PC 3**
% variance	91.071	3.896	1.141
log(SL)	0.191	0.020	-0.018
log(BD)	0.225	0.074	0.133
log(HL)	0.204	-0.097	-0.004
log(PrP)	0.212	-0.154	-0.002
log(PrD)	0.190	0.010	0.177
log(PrV)	0.218	-0.071	-0.136
log(PrA)	0.203	-0.015	-0.062
log(DFB)	0.196	0.100	-0.059
log(AFB)	0.192	0.286	0.180
log(CPL)	0.193	-0.027	-0.123
log(CPD)	0.205	0.147	0.134
log(HW)	0.206	0.198	0.049
log(PPL)	0.235	-0.224	0.309
log(SnL)	0.270	-0.309	-0.227
log (LaD)	0.277	-0.471	-0.165
log(ChD)	0.262	-0.074	-0.202
log(ED)	0.164	0.154	0.494
log(IOW)	0.230	0.126	-0.346
log(LJL)	0.227	-0.102	0.286
log(UJL)	0.228	0.145	0.221
log(LJW)	0.218	0.598	-0.383

Table 5 PCAs of the meristics of 56 specimens from the Lake Edward system with a paedophagous morphology and the holotype of *H. occultidens*, endemic to Lake Kivu. For the plot of PC 1 on PC 2, see fig. 16a, p. 30.

	PC 1	**PC 2**	**PC 3**
% variance	18.482	14.290	8.473
LatLu	-0.272	0.007	0.310
LatLl	-0.098	0.231	-0.375
LongL	-0.199	0.282	-0.035
D-ULL	0.141	0.267	0.300
ULL-A	-0.047	0.335	0.302
P-V	0.185	0.129	0.211
ChSa	-0.221	0.093	-0.283
ChSp	0.085	0.185	0.312
GRc	-0.167	0.280	-0.228
GRe	0.241	0.171	0.108
DFRs	-0.293	0.050	-0.247
DFRr	0.236	0.121	0.028
AFRr	-0.238	0.086	0.178
PFR	-0.226	0.178	0.078
UTR	0.330	0.143	0.051
UOT	0.380	0.179	-0.284
LTR	0.078	0.362	-0.002
LOT	0.344	0.174	-0.333
Va	0.159	-0.272	0.013
Vc	-0.164	0.416	-0.034

Table 6 PCA loadings of the logarithmic transformed measurements of 90 specimens from the Lake Edward system displaying '*Lipochromis'* characteristics and a syntype of *H. paucidens*, endemic to Lake Kivu. For the plot of PC 2 on PC 3, see fig. 19, p. 38.

	PC 1	**PC 2**	**PC 3**
% variance	91.187	1.881	1.149
log(SL)	0.204	-0.016	0.051
log(BD)	0.219	0.237	-0.017
log(HL)	0.219	-0.135	-0.138
log(PrP)	0.200	-0.031	0.086
log(PrD)	0.220	-0.098	-0.096
log(PrV)	0.223	-0.025	-0.014
log(PrA)	0.197	0.105	0.160
log(DFB)	0.194	0.197	-0.033
log(AFB)	0.195	-0.027	0.209
log(CPL)	0.195	0.170	0.174
log(CPD)	0.203	0.079	0.047
log(HW)	0.209	-0.082	-0.079
log(PPL)	0.231	-0.191	0.357
log(SnL)	0.250	-0.294	-0.112
log (LaD)	0.253	-0.146	0.133
log(ChD)	0.274	0.090	0.313
log(ED)	0.143	0.080	-0.166
log(IOW)	0.208	0.109	0.313
log(LJL)	0.261	-0.571	-0.428
log(UJL)	0.239	0.314	-0.323
log(LJW)	0.206	0.475	-0.428

Table 7 PCA loadings of the meristics of 90 specimens from the Lake Edward system displaying *'Lipochromis'* characteristics and a syntype of *H. paucidens*, endemic to Lake Kivu. For the plot of PC 1 on PC 2, see fig. 20, p. 39.

	PC 1	**PC 2**	**PC 3**
% variance	16.202	10.325	9.168
LatLu	-0.048	-0.249	0.368
LatLl	0.019	0.241	-0.414
LongL	0.066	0.109	0.300
D-ULL	0.370	0.315	0.118
ULL-A	0.296	0.219	-0.254
P-V	0.346	0.200	0.006
ChSa	0.216	0.051	0.333
ChSp	0.297	0.355	-0.004
GRc	-0.228	0.011	-0.333
GRe	-0.163	0.123	-0.031
DFRs	0.039	0.035	0.296
DFRr	0.093	-0.366	-0.153
AFRr	0.130	-0.372	0.048
PFR	-0.083	0.050	-0.329
UTR	-0.360	0.312	0.096
UOT	-0.209	0.349	0.212
LTR	-0.436	0.198	0.165
LOT	-0.193	0.057	-0.015

7.3.2 Mann–Whitney U*-tests*

Table 8 Statistical p-values obtained from within-group pairwise comparisons of all thick-lipped haplochromine species from the Lake-Edward system by Mann–Whitney *U*-tests and post hoc Bonferonni correction. ^p < 0.1, *p < 0.05, **p < 0.01.

n =	8 3	8 9	10 8	10 20	3 11	3 4	3 19	7 6	11 16	8 20	11 11
	H. sp. ‘curvidens’ *H.* sp. ‘longicauda’	*H.* sp. ‘curvidens’ *H.* sp. ‘molossus’	*H.* sp. ‘curvidens’ *H.* sp. ‘relictidens’	*H.* sp. ‘curvidens’ *H. taurinus*	*H.* sp. ‘longicauda’ *H.* sp. ‘molossus’	*H.* sp. ‘longicauda’ *H.* sp. ‘relictidens’	*H.* sp. ‘longicauda’ *H. taurinus*	*H.* sp. ‘molossus’ *H.* sp. ‘relictidens’	*H.* sp. ‘molossus’ *H. taurinus*	*H.* sp. ‘relictidens’ *H. taurinus*	*H. labiatus* *H.* sp. ‘lobatus’
SL (mm)	0.610	0.532	0.756	0.708	0.756	0.596	0.525	0.617	0.505	0.980	0.580
BD (% SL)	0.262	0.361	0.351	0.262	0.119	0.112	0.026	0.100	0.132	0.629	0.000
HL (% SL)	0.019	0.001	0.002	0.000*	0.161	0.377	0.011	0.943	0.051	0.939	0.148
PrP (% SL)	0.019	0.002	0.001	0.000*	1.000	0.216	0.090	0.134	0.046	0.050	0.013
PrD (% SL)	0.126	0.075	0.505	0.022	0.533	0.052	0.008	0.018	0.002	0.401	0.518
PrV (% SL)	0.032	0.075	0.037	0.000*	0.756	0.216	0.597	0.432	0.941	0.004	0.103
PrA (% SL)	0.185	0.061	0.023	0.001	0.119	0.377	0.341	0.225	0.160	0.031	0.166
DFB (% SL)	0.475	0.024	0.505	0.210	0.119	0.860	0.916	0.520	0.036	0.780	0.003
PL (% SL)	-	-	-	-	0.062	0.052	0.020	0.018	0.032	0.373	-
VL (% SL)	-	-	-	-	0.020	0.377	0.751	0.432	0.011	0.431	0.005
AFB (% SL)	0.759	0.001	0.002	0.000**	0.013	0.052	0.008	0.100	0.570	0.162	0.069
CPL (% SL)	0.185	0.532	0.307	0.037	0.087	0.377	0.026	0.520	0.312	0.014	0.735
CPD (% CPL)	0.185	0.049	0.100	0.002	0.029	0.052	0.008	0.830	0.046	0.134	0.011
HW (% HL)	0.019	0.001	0.003	0.000*	0.436	0.860	0.525	0.134	0.246	0.035	0.000^
PPL (% HL)	0.019	0.014	0.824	0.301	0.019	0.052	0.008	0.012	0.000^	0.057	0.601
SnL (% HL)	0.019	0.002	0.002	0.000*	0.029	0.216	0.459	0.943	0.064	0.079	0.001
LaD (% HL)	0.019	0.005	0.965	0.000*	0.756	0.052	0.916	0.008	0.505	0.000*	0.644
ChD (% HL)	0.759	0.962	0.100	0.082	0.756	0.860	1.000	0.054	0.246	0.703	0.255
ED (% HL)	0.052	0.002	0.000	0.000**	0.276	0.596	0.008	0.617	0.000*	0.000	0.000
IOW (% HL)	0.019	0.001	0.019	0.015	0.436	0.596	0.072	0.284	0.001	0.057	0.001
LJL (% HL)	0.032	0.008	0.120	0.262	1.000	0.377	0.011	0.353	0.000	0.009	0.000*
UJL (% HL)	0.475	0.011	0.056	0.000^	0.533	0.860	0.057	0.353	0.080	0.006	0.013
LJW (% LJL)	0.019	0.001	0.007	0.000*	0.029	0.052	0.341	0.003	0.000*	0.013	0.000*
LatLu	0.120	0.166	0.087	0.137	0.329	0.849	0.196	0.942	0.273	0.259	0.011
LatLl	0.023	0.623	0.468	0.386	0.012	0.072	0.008	0.677	0.631	0.788	0.975
LongL	0.670	0.570	1.000	0.223	0.793	0.554	0.953	0.157	0.674	0.186	0.844
D-ULL	0.152	0.107	0.334	0.081	0.021	0.270	0.042	0.162	0.409	0.576	0.228
ULL-A	0.360	0.069	0.138	0.314	0.011	0.564	0.911	0.004	0.003	0.745	0.632
V-P	0.152	0.301	0.043	0.027	0.864	0.414	0.907	0.833	0.502	0.824	0.048
ChSa	0.099	0.441	0.643	0.087	0.002	0.264	0.015	0.034	0.045	0.310	0.270
ChSp	0.259	0.414	0.636	0.279	0.739	0.578	0.501	0.682	0.674	0.831	0.046
GRc	0.583	0.219	0.925	0.046	0.921	1.000	0.194	0.828	0.041	0.063	0.030
GRe	0.015	0.003	0.083	0.005	0.898	0.264	0.401	0.127	0.184	0.537	1.000
DFRs	0.880	0.122	0.584	0.180	0.190	1.000	0.327	0.058	0.579	0.476	0.059
DFRr	0.724	0.100	0.038	0.039	0.370	0.270	0.604	0.719	1.000	0.771	0.539
AFRr	0.895	0.451	0.211	0.184	1.000	1.000	0.769	0.938	0.801	0.977	0.316
PFR	0.895	0.237	0.083	0.000**	0.591	0.414	0.004	0.334	0.004	0.007	0.543
UTR	0.012	0.001	0.004	0.000*	0.415	0.386	0.947	0.058	0.109	0.135	0.592
UOT	0.018	0.001	0.000	0.000**	1.000	0.050	0.560	0.004	0.373	0.000*	0.780
LTR	0.153	0.043	0.314	0.334	0.591	0.386	0.393	0.245	0.023	0.887	0.353
LOT	0.017	0.001	0.000	0.000*	0.876	0.112	0.098	0.005	0.107	0.000*	0.619
Va	-	-	0.122	0.134	-	0.564	0.480	1.000	0.134	0.854	-
Vc	0.543	1.000	0.853	0.375	0.329	1.000	1.000	0.589	0.100	0.581	-

7.4 Species descriptions

7.4.1 Haplochromis *taurinus Trewavas, 1933*

Studied specimens

Holotype: BMNH 1933.2.23.406; Lake Edward, Uganda [♀133.82 mm SL].

Other specimens:

RMCA 2016–36: HIPE 1; Nyamugasane, Lake Edward: 0°10'23"S 29°50'13"E; 22/10/2016 [♀ 88,83 mm SL]. RMCA 2016–36: HIPE 1 (incl. HP369; HP396; HP398); Mouth of the Kazinga Channel, Lake Edward: 0°12'32"S 29°53'06"E; 24/10/2016 [♀ 75.00; ♂ 76.44; ♀ 101.08; ♀ 103.59; ♀ 108.39; ♂ 117.25 mm SL]. RMCA 2016–36: HIPE 1 (HP706; HP707; HP770; HP773); Kasenji, Lake George: 0°01'55"S 30°09'00"E; 4/11/2016 [♂ 60.92; ♀ 61.79; ♂ 109.73; ♀ 112.56 mm SL]. RMCA 2016–36: HIPE 1 (incl. HP802; HP821; HP882); Kasenji, Lake George: 0°01'55"S 30°09'00"E; 6/11/2016 [♀ 59.60; ♂ 109.40; ♂ 109.51; ♀ 114.75 mm SL]. RMCA 2016–36: HIPE 1 (HP870; HP882); Kazinga Channel near Bush lodge, Lake Edward: 0°08'10"S 30°02'28"E; 7/11/2016 [♀ 84.76; ♂ 102.78 mm SL]. RMCA 2016–36: HIPE 1; Rwenshama, Lake Edward: 0°24'14"S 29°46'26"E; 8/11/2016 [♀ 98.85 mm SL]. RMCA 2017–06: HIPE 2 (HP1796, HP1829); Kayanja, Lake Edward; 31/03/2017 [♀ 93.88; ♂ 92.35 mm SL]. RMCA 2017–06: HIPE 2 (HP1286, HP1294); Mweya, hard substrate at mouth of Kazinga channel; 24/03/2017 [n=2/4, ♀ 110.63; ♂ 113.09 mm SL].

Etymology

The original description of *H. taurinus* by Trewavas (1933) does not mention its etymology. It probably refers to the Sanskrit 'sthura-', meaning 'thick, compact' or the Latin 'taurus', meaning 'bull'. Hereby probably referring to the stout head morphology, like a bull, with firmly thickened lips.

Description

Haplochromis taurinus is endemic to the Lakes Edward and George. It has a relatively deep body (table 9, p. A.16, BD) with a slightly concave head, sloping at 35–40°. The eyes are large (ED), the snout relatively short (SnL) and the jaws slightly prognathous with a gape inclination of 40–45°. The jaws are long (LJL; UJL), anteriorly rounded and widely distensible. The maxilla reach vertically to the anterior point of the pupil and they are bullate, i.e., posteriorly enlarged and distinctly visible with the mouth closed. The lips and oral mucosa are firmly thickened.

The caudal fin has an emarginate outline and is scaled on 50–60% its length. Dorsal and anal fins almost reach the caudal fin base in females and juveniles, can extend up to the first quarter of the caudal fin in males. The pelvic fins reach between the anus and second spine of the anal fin in females and juveniles, up to the second branched ray of this fin in males. The pectoral fins to between the genital opening and second spine of the anal fin.

The outer teeth are distinctly small, short and bicuspid with occasionally uni- or tricuspid teeth intercalated. The teeth posteriorly on the premaxilla are smaller and tricuspid. Outer teeth have short and stout necks with a circular cross-section, commonly with a stouter base, giving them a conical appearance. The necks are straight on the dentary, straight to recurved on the premaxilla, always with an erect implantation. The crowns are short and unequally bicuspid. The subequilateral major cusp has a broad base with a laterally-compressed and acutely-pointed tip and a small flange. The minor cusp is relatively stout, bluntly-pointed and labially implanted with a somewhat horizontal orientation. The crowns of outer teeth are distinctly anteriorly curved medially on the dentary. The inner teeth are set in 1–3, mostly 2 rows of small, broad and tricuspid teeth with a straight implantation. The tooth band is narrow, rounded and very short in both jaws, to 2/3 the dentigerous area. Inner tooth rows quickly diminish until posteriorly only the outer row remains. The teeth of all rows are very closely and consistently set. The upper lip is anteriorly thin, laterally quickly thickening, hereby engulfing the teeth.

The lower pharyngeal bone is relatively slender (LPW), fine and shallow. The teeth are slender with straight necks and bicuspid crowns. The major cusps are straight and acutely-pointed with blunt tips. The minor cusp is very small and the cusp gap slightly concave. Teeth are set in 23–27 rows (n=4) with stouter teeth in the median 2 rows. Posteriorly, the teeth have stout, bluntly pointed and slightly hooked major cusps and reduced minor cusps.

The gill rakers of the first gill arch are anteriorly short, stout and acutely pointed. The posterior rakers are relatively long and slender, unifid and acutely to bluntly pointed or bi- to tetrafid.

Colouration in live

Dominant males: The dorsum, chest, dorsal snout, lips and lower jaw are blue-green. The belly and flank are yellow with over the length of the pectoral fins a deep-red colouration at the borders of the scales. The flank and dorsum colouration extends over the caudal peduncle. The suboperculum has a deep-red colour, the eyes white-yellow. Lachrymal stripes are clearly visible. The nostril, interorbital and vertical preopercular stripes are faint. Blotches are present on the operculum and chin. The pelvic fins are black, pectoral fins dusky to black. The dorsal fin is grey-blue with maculated branched rays, i.e. dotted lines running between the rays. The anal fin is grey-blue with 5–7 large orange-brown egg spots between the third and eighth branched fin ray. The caudal fin is maculated with centrally a dusky horizontal stripe.

Females and juveniles: The dorsum is blue-green, the flank yellow-green and ventrally they are white. The lips are yellow-green. The caudal fin is yellowish with centrally a dusky horizontal stripe. The pectoral fins are yellow-green; the dorsal, pelvic and anal fins hyaline to yellow. The anal fin has vague orange spots between the branched fin rays, resembling egg spots. A chin blotch and faint nostril, interocular and lachrymal stripes are present.

Colouration in alcohol

Lachrymal and preopercular vertical stripes are clearly defined. Interorbital, nostril and a vertical stripe high on the dorsal head are very faintly visible. a chin blotch is always present. The branched rays of the dorsal fin and the upper part of the caudal fin are maculated. The anal fin of males with 3–7 faint large egg spots between the third and eight branched fin rays.

Ecology

Haplochromis taurinus has a paedophagous ecology, feeding on the eggs and larvae of other cichlids. The stomachs of one specimen contained invertebrate remains, which lets us presume that they have an opportunistic feeding habit. The digestive tract is short (GL), in coherence with a predatory lifestyle.

Diagnosis

The mean percentages are indicated in brackets.

Haplochromis taurinus is endemic to the lakes Edward and George. It has a slightly concave head and long [LJL 44.5–51.3 (47.7) % HL; UJL 34.0–43.5 (39.2) % HL], rounded and slightly prognathous jaws that are widely distensible. The maxilla are strongly bullate, i.e. posteriorly exposed and distinctly visible; the lips and oral mucosa firmly thickened with the crowns of the outer teeth visible. The dental arcades are short (2/3 dentigerous area) and closely set with bicuspid outer teeth and 1–3, mostly 2, rows of tricuspid inner teeth. The outer teeth are short, stout and conical, with a broad base, subequilateral major cusp with a thin flange and a relatively stout minor cusp. It is the only species within the Lake Edward system with distinctly anteriorly curved outer teeth on the dentary.

Haplochromis taurinus differs from *H.* sp. ‘molossus’ sp. nov. (m) and *H.* sp. ‘longicauda’ sp. nov. (l) by its higher body [BD 33.9–40.1 (36.0), vs. m: 33.5–38.6 (34.9), l: 30.2–34.8 (32.4) % HL), larger eyes [ED 32.9–40.2 (35.7), vs. m: 29.8–33.9 (32.3), l: 29.0–32.3 (31.0) % HL] and longer lower jaws [LJL 44.5–51.3 (47.7), vs. m: 34.4–39.7 (36.7), l: 42.4–44.7 (43.5) % HL]. From *H.* sp. ‘molossus’ sp. nov. by its gentler sloping head, steeper gape and slenderer lower jaws [LJW 51.4–72.7 (60.9), vs. m: 67.0–87.0 (77.1) % LJL]. From *H.* sp. ‘longicauda’ by a thicker caudal peduncle [CPD 73.9–88.1 (79.6), vs. l: 62.9–66.4 (65.0) % CPL], longer premaxillary pedicel [PPL 23.5–26.2 (25.1), vs. l: 18.1–21.6 (20.3) % HL] and steeper gape. From both by its distinct teeth form. *Haplochromis* sp. ‘molossus’ has longer teeth with a straighter neck, equilateral major cusp without flange and no to very small minor cusps in large specimens; *H.* sp. ‘longicauda’ very small teeth with a slender, slightly recurved neck and no anteriorly curved tips.

7.4.2 Haplochromis sp. ‘molossus’

Studied specimens

Holotype: RMCA 2016–36: HIPE 1 (HP290); Mukutu Kikinga, Lake Edward: 0°11'31"S 29°52'26"E; 23/10/2016 [♀ SL 104.17 mm].

Paratypes: RBINS 12898; Lac Edouard: au large de la riv. Kigera: 0°29'42"S 29°38'14"E; Miss. KEA; 25/04/1953 [♂ SL 74.64 mm]; RBINS 12902; Lac Edouard: au large de la riv. Talia: 0°31'05"S 29°20'26"E; Miss. KEA; 23/04/1953 [n=1/3, ♂ SL 76.01 mm]; RBINS 12903; Lac Edouard: au large de la riv. Talia: 0°31'05"S 29°20'26"E; Miss. KEA; 23/04/1953 [♀ SL 77.53 mm]; RBINS 12904; Lac Edouard: au large de la riv. Kigera: 0°29'42"S 29°38'14"E; Miss. KEA; 25/04/1953 [♀ SL 80.04 mm]; RBINS 12906; Lac Edouard: riv. Semliki (bae Copile. d'nids de Tilapia): 0°08'27"S 29°36'04"E; Miss. KEA; 11/08/1953 [♂ SL 102.28 mm]; RMCA 2016–36: HIPE 1 (HP22); Offshore of Katoko, Lake Edward: 0°09'43"S 29°53'17"E; 20/10/2016 [♀ SL 105.75 mm]; RMCA 2016–36: HIPE 1 (HP400); Mouth of Kazinga Channel, Lake Edward: 0°12'32"S 29°53'06"E; 24/10/2016 [♂ SL 77.53 mm]. RMCA 2016–36: HIPE 1; Kasenji, Lake George; 7/11/2016 [♂ 92.24; ♂ 93.52 mm SL]. RMCA 2017–06: HIPE 2; Kayanja, Lake Edward; 31/03/2017 [♂ 78.39 mm SL].

Etymology

The specific name, molossus, relates to the 'pug-head', i.e. flat face and broad, rounded jaws with a shallow inclination. Pugs belongs to the mastiff-like dogs, also called Molossers due to their ancestral origin to Molossian dogs. Derived from the Greek Μολοσσός (Molossos), a figure in Greek mythology who gave his name to the Molossians.

Description

Haplochromis sp. 'molossus' sp. nov. has a relatively slender body (table 9, p. A.16, BD) with a slightly concave and steep head, sloping at 45–55° and a large interocular width (IOW). The jaws are distinctly broad (LJW), rounded, long (LJL) with a shallow gape inclination of 20–30°, resulting in a 'pug-head', i.e. resembling a pug in frontal view. The jaws are isognathous, the maxilla bullate, i.e. posteriorly enlarged and distinctly exposed, and extend vertically to the anterior margin of the pupil. The lips and oral mucosa are firmly thickened and it has few lower transversal scales (ULL-A).

The caudal fin is emarginate and scaled to 50–75% its length. The dorsal and anal fins reach to just before the caudal fin base in females, maximally just exceeding it in males. The pelvic fins extend to between the genital opening and second spine of the anal fin. The pectoral fins to the genital opening.

The outer oral jaw teeth are relatively small with their lower half deeply embedded in the oral mucosa. The outer teeth on the dentary are not visible because the high, thickened lower lip covers them. The necks are stout and completely straight, in one specimen slightly recurved, with a circular cross-section. Small specimens (< 80 mm SL) have bicuspid outer teeth, large specimens (> 100 mm SL) unicuspid teeth with weakly bi- or tricuspid teeth intercalated. Posteriorly in both jaws of all specimens, the outer teeth are tricuspid. The major cusps of all crown types are isocline and slightly laterally compressed. In the lower jaw ending in a straight to very slightly anteriorly curved major cusp, straight in the upper jaw. Minor cusps are small, slightly labially implanted on the neck and point straight up. All outer teeth have a straight implantation and close setting. Inner teeth are small, tricuspid and irregularly set in 1–2 rows that gradually diminish laterally until posteriorly only the outer row remain. The dental arcades are slender, short (2/3 the dentigerous area) and have an almost straight, bracket shape: "(".

The lower pharyngeal bone is slightly broader than long (LPW) and has a fine form with a short dentigerous area (DAL). The teeth are fine, the major cusp acute and straight, with no to a small gap between the major and small minor cusps. The posterior teeth are enlarged with blunt, slightly recurved major cusps and reduced minor cusps. The teeth are set in 24–28 rows (n=3), the median two with stouter teeth.

All gill rakers of the first gill arch are stout and short, the posterior ones usually with a bi- to tetrafid form. Gill rakers of small specimens (SL < 80 mm) are slender and rather long.

Colouration in live

Dominant males: the body has an olive-green ground colouration with 6–8 relatively broad black-turquoise vertical stripes. The ventral body and caudal peduncle are dark turquoise. The cheeks, operculum and lower jaw are lighter turquoise. The snout, pectoral fins and caudal fin are olive-green. The dorsal fin dusky. The anal fin hyaline with a reddish flush over the spines and three orange egg spots on a straight line between the fifth and eighth branched rays. Lachrymal and vertical dorsal head stripes are clearly present and the caudal fin is maculated, i.e. dotted lines running between the rays. The eyes are olive-green and black.

Females and juveniles: the olive-green dorsal body gradually merges into the ventrally white colouration. The dorsal head is blueish, the cheeks white and the snout darker. A mental blotch is clearly present, lachrymal and vertical dorsal head stripes faint. The eyes and lappets of the dorsal fin are dark. The pectoral fins are olive-green, all other fins a lighter shade. The posterior ends of the dorsal, caudal and pelvic fins are hyaline.

Colouration in alcohol

The pectoral fins are dusky, the pelvic fins hyaline in females, black in males. The lappets of the dorsal fin are black and the anal fin is uniformly hyaline without clear egg spots. The caudal fin is maculated. Faint nostril and interorbital stripes and a clear chin blotch is present. The lachrymal stripe is distinct in males, faint in females, in all specimens continuing over the eyes into a faint supraorbital stripe. Dominant males have 6–8 vertical stripes on their flank.

Ecology

Haplochromis sp. 'molossus' sp. nov. has a paedophagous ecology. Three specimens with a filled stomach were found, all containing solely *Haplochromis* larvae. The gut is short (GL), in coherence with its predatory lifestyle.

Diagnosis

The mean percentages are indicated between brackets

Haplochromis sp. 'molossus' has a flattened, concave frontal head profile, sloping at 45–55°, with distinctly broad and rounded jaws [LJW 67.0–87.0 (77.1*) % LJL], gently sloping at 20–30°. The body is relatively slender [BD 33.5–38.6 (34.9) % SL] with few lower transversal scales [ULL-A 8–9]. The oral outer teeth are small but strong with a straight and circular neck, bicuspid crown in small specimens (SL

< 80 mm), weakly tricuspid to unicuspid in large specimens (> 100 mm) with an isocline and straight to slightly anteriorly curved major cusp. They are set in slender and short dental arcades (2/3 dentigerous area). The lips and oral mucosa are firmly thickened, the maxilla bullate, i.e. posteriorly enlarged and distinctly exposed.

Haplochromis sp. 'molossus' differs from *H. taurinus* (t) *and H.* sp. 'longicauda' (l) by broader jaws, a steeper sloping head (45–55, vs. t: 35–40, l: 35–45°) and gentler gape inclination (20–30°, vs. t: 40–45, l: 40–50°). *Haplochromis* sp. 'molossus' has longer outer teeth with a straight neck and weakly tricuspid to unicuspid crown in comparison to respectively a conical or slender neck, both with a clearly bicuspid crown. From *H. taurinus* by its smaller eyes [ED 29.8–33.9 (32.3*), vs. 32.9–40.2 (35.7) % HL] and broader interorbital width [IOW 24.1–30.8–(28.1), vs.21.2–28.2 (24.6) % HL], from *H.* sp. 'longicauda' by its thicker caudal peduncle [CPD 62.9–66.4 (65.0), vs. 65.5–83.6 (75.5) % CPL], longer premaxillary pedicel [PPL21.6–23.5 (25.8), vs. l: 18.1–21.6 (20.3) % HL], more cheek scales [ChS 3–4/7–9 vs; l: 2/7–8] and lower-lateral line scales [LatL 20–22/9–14, vs.l: 21–22/7–9] and different male nuptial colouration, i.e. flank with 6–8 faint vertical stripes vs. 2 clear longitudinal ones.

Haplochromis sp. 'molossus' differs from an undescribed species of phytophage [RMCA 2017-06: HIPE 2: HP1393 (♀ 82.55 mm SL)] by its more thickened lips. Both have broad jaws but *H.* sp. 'molossus' has a slenderer head [HW 50.9–55.2 (53.2*) % HL], causing the jaws to be very distinct when looking at the head in front view in comparison to a spherical head.

7.4.3 Haplochromis *sp. 'longicauda'*

Examined specimens

Holotype: RMCA 2017–06: HIPE 2 (HP1797, HP1858); Kayanja, Lake Edward; 31/03/2017 [n=1/3; ♂ 85.67 mm SL].
Paratypes: RMCA 2017–06: HIPE 2 (HP1797, HP1858); Kayanja, Lake Edward; 31/03/2017 [n=2/3; ♂ 68.12; ♂ 102.81 mm SL].

Etymology

The species-specific name of *H.* sp. 'longicauda' is derived from the Latin 'longus', long, and 'cauda', tail, referring to the distinctive long and slender caudal peduncle of this species.

Description

Haplochromis sp. 'longicauda' is endemic to the Lake Edward system. It has a very slender body (table 9, p. A.16, BD) with a long and slim caudal peduncle (CPL, CPD) with a low number of lower lateral line scales (LatL). The head concave above the eyes, the premaxillary pedicel sloping at 10–20°. The snout and premaxillary pedicel are distinctly short. The interorbital region is broad (IOW) and the rounded jaws are long (UJL, LJL) with a steep gape inclination of 40–50°. The maxilla are bullate, i.e. posteriorly enlarged and distinctly visible, and reach to the anterior margins of the eyes. The oral mucosa and lips are firmly thickened.

The dorsal and anal fins reach to 1–2 scale lengths anterior of the caudal fin base. The caudal fin is emarginate with very rounded edges and scaled to 50% of its length. The pectoral fins are short, reaching together with the pelvic fins of females to just before the anus. The latter extending to the anal fin base in males.

The outer teeth are very small, strongly embedded in the oral mucosa and completely covered by the lips. The crowns of the outer teeth can be visible in small specimens (SL < mm) due to their relatively larger size. The outer teeth are bicuspid, posteriorly in both jaws tricuspid. They have a very slender, straight neck with a circular cross-section that gradually expands into a broader, slightly laterally compressed crown. The major cusp of large specimens (SL > mm) is equilateral and relatively slender with an acutely-rounded tip and a stout flange. The distinct minor cusp is rounded with a straight to slightly horizontal orientation and is separated from the major cusp by a small cusp-gap. Small specimens (SL < mm) have outer teeth with a subequilateral major cusp, the flange is even stouter and the minor cusp larger with a straight orientation. The inner teeth resemble the outer ones except for their tricuspid crowns. They are implanted very close to the outer tooth row. The dental arcade is very slender and short (2/3 the dentigerous area), occasionally a tooth can be present past this point.

The lower pharyngeal jaw is slightly wider than long (LPW). One large specimen was observed and had a distinctly expanded ventral crest on the anterior extension of the jaw. This was not present in the lower pharyngeal jaw of the holotype so the significance is unknown. All teeth are slender and acutely pointed with a slightly concave cusp gap. A minor cusp is absent or reduced to a remnant. The posterior-most teeth have an acutely-rounded major cusp and a small minor cusp. The teeth are implanted in 30–32 rows (n=2).

The outer gill raker on the first gill arch are unifid, short and stout in all observed specimens.

Colouration in live

Dominant males: the dorsum, caudal peduncle and pectoral and caudal fins are olive green. The snout has a slightly darker colouration and some blue showing through dorsally on the head. Dark horizontal stripes run just above the upper and lower lateral lines. The lower one runs from the eye, over the opercular blotch, to the caudal fin base; the upper one over the anterior part of the dorsum. The flanks, opercula, cheeks, extension of the caudal fin and spines of the anal fin are bright red. The ventral body and the branched rays of the anal fin are whitish, except for the bright yellow-orange egg spots on this fin. The eyes are mainly dark. The lappets of the dorsal fin are black, the branched rays hyaline.

Females and juveniles: the female colouration of this species is unknown. One small juvenile (SL 68.12 mm) has a white-gold ground-colour and pelvic fins. The head or body have no notable markings. The dorsal fin is dusky, the caudal fin dark moss-greenish and the anal fin is yellow.

Colouration in alcohol

Two longitudinal lines run over the body just above upper and lower lateral line. The upper line runs over the anterior part of the flank, the lower line from the eye to the caudal fin base. lachrymal, nasal, interorbital, supraorbital and vertical dorsal head stripes and a chin and opercular blotches are clearly present in dominant males. The posterior part of the dorsal fin and the upper part of the caudal fin are faintly maculated.

Ecology

Haplochromis sp. ‘longicauda’ has a paedophagous ecology. The stomach of the holotype contains 13 cichlid eggs, but was empty in all other specimens. The digestive tract is short (GL) as expected in a predatory species.

Diagnosis

The mean percentages are indicated between brackets.

Haplochromis sp. ‘longicauda’ has a slender body [BD 30.2–34.8 (32.4) % SL] with a long and slender caudal peduncle [CPL 16.3–18.2 (17.3) % SL; CPD 62.9–66.4 (65.0) % CPL] with few lower lateral lines scales [LatL 21–22/7–9]. The head is concave above the eyes, the snout and premaxillary pedicel distinctly short [SnL 24–26.7 (25.2) % HL; PPL 18.1–21.6 (20.3) % HL] and has a steeply sloping gape at 40–50°. The jaws are relatively long [LJL 42.4–44.7 (43.5) % HL] and rounded; the lips and oral mucosa firmly thickened. The outer teeth are very small and slender with a bicuspid crown and are deeply embedded in the oral mucosa. The inner teeth are slightly smaller and implanted very closely to the outer row. The dental arcades are short (2/3 dentigerous area). Dominant males have striking longitudinal stripes running just above both the upper and lower lateral line.

Haplochromis sp. ‘longicauda’ differs from *H.* sp. ‘molossus’ (m) and *H. taurinus* (t) by its slenderer caudal peduncle [CPD 62.9–66.4 (65.0), vs. m: 65.5–83.6 (75.5), t: 73.9–88.1 (79.6) % CPL] and much shorter premaxillary pedicel [PPL 18.1–21.6 (20.3), vs. m: 21.6–25.8 (23.5), t: 23.5–26.2 (25.1) % HL]. Large specimens (SL > 100 mm) can be distinguished further by their smaller bicuspid teeth with the neck slenderer than the crown instead of equally broad (m) or broader (t). From *H.* sp. ‘molossus’ a steeper gape inclination [40–50, vs. m: 20–30].

Haplochromis sp. ‘longicauda’ differs from *H.* sp. ‘relictidens’ by their slenderer body [BD 30.2–34.8 (32.4), vs. 34.6–38.7 (36.3) % SL]) and smaller lachrima [LaD 13.7–14.3 (14.0), vs. 15.8–18.4 (17.4) % HL].

Table 9 Summary of the broad-jawed paedophagous haplochromine species of the Lake Edward system; *H. taurinus*, *H.* sp. 'molossus' sp. nov. and *H.* sp. 'longicauda' sp. nov.

	H. taurinus			***H.* sp. 'molossus'**			***H.* sp. 'longicauda'**		
Measurements		n = 20, *10, **3			n = 11, *4, **3			n = 3, *2	
	Mean	Range		Mean	Range		Mean	Range	
SL (mm)	96.2	59.6	133.8	87.6	74.6	105.8	85.5	68.1	102.8
TL (mm)	119.8	75.3	161.3	110.5	95.4	133.6	106.6	86.3	127.1
Body measurements (% SL)									
Head length (HL)	31.8	30.5	33.7	30.9	29.5	32.0	30.3	29.8	30.7
Body depth (BD)	36.0	33.9	40.1	34.9	33.5	38.6	32.4	30.2	34.8
Pre-pectoral length (PrP)	32.8	31.2	36.1	31.5	30.3	33.1	31.6	31.0	32.3
Pre-dorsal length (PrD)	35.2	33.4	36.4	33.9	32.6	36.0	33.2	33.0	33.5
Pre-pelvic length (PrV)	40.6	38.4	45.0	39.6	37.2	42.4	40.8	39.6	42.3
Pre-anal length (PrA)	66.3	64.0	69.4	65.2	64.0	66.3	66.9	66.4	67.7
Dorsal fin base (DFB)	54.4	51.4	58.8	55.5	52.7	59.2	54.3	53.9	54.6
Pectoral fin length (PL)	31.2	28.1	32.9	30.1	28.0	32.8	28.5	28.1	28.9
Pelvic fin length (VL)	27.6	22.8	34.6	29.5	26.9	31.2	25.9	23.4	27.5
Anal fin base (AFB)	20.7	19.7	22.0	20.8	19.3	22.0	17.5	15.9	19.1
Caudal peduncle length (CPL)	15.7	14.5	16.9	16.2	14.9	19.0	17.3	16.3	18.2
Caudal ped. depth (CPD % CPL)	79.6	73.9	88.1	75.5	65.5	83.6	65.0	62.9	66.4
Gut length (GL % SL)	196.0	147.6	249.7*	159.0	118.7	197.3*	127.1	108.6	152.9
Head measurements (% HL)									
Head width (HW)	51.9	47.1	55.1	53.2	50.9	55.2	51.1	48.1	54.6
Premaxillary pedicel length (PPL)	25.1	23.5	26.2	23.5	21.6	25.8	20.3	18.1	21.6
Snout length (SnL)	26.7	23.2	31.4	28.0	25.1	30.7	25.2	24.0	26.7
Lachrymal depth (LaD)	14.1	11.5	16.4	14.4	13.3	16.3	14.0	13.7	14.3
Cheek depth (ChD)	22.1	19.0	25.8	22.7	20.3	25.0	22.2	20.0	25.1
Eye depth (ED)	35.7	32.9	40.2	32.3	29.8	33.9	31.0	29.0	32.3
Interorbital width (IOW)	24.6	21.2	28.2	28.1	24.1	30.8	26.8	25.9	28.2
Upper jaw length (UJL)	39.2	34.0	43.5	44.0	41.3	46.4	35.3	33.4	37.0
Lower jaw length (LJL)	47.7	44.5	51.3	36.7	34.4	39.7	43.5	42.4	44.7
Lower jaw width (LJW % LJL)	60.9	51.4	72.7	77.1	67.0	87.0	64.9	61.9	69.4
Pharyngeal length (LPL % HL)	31.4	30.2	32.4**	28.7	27.7	30.5**	28.8	28.1	29.5*
Pharyngeal width (LPW % LPL)	91.1	87.1	94.6**	103.2	100.4	106.2**	106.7	104.3	109.2*
Dentigerous length (DAL % LPL)	51.6	51.3	52.3**	45.4	42.2	49.0**	45.2	41.0	49.4*
Dentigerous width (DAW % LPW)	66.1	64.6	67.9**	62.0	60.6	63.4**	66.6	64.9	68.3*
Meristics		n = 23, *22			n = 11			n = 3	
	Number & frequency (f)			Number & frequency (f)			Number & frequency (f)		
Upper jaw teeth (UFT)	23–39 (median 32)			22-34 (median 30)			26-35 (median 26)		
Lower jaw teeth (LFT)	25–42 (median 32)			16-34 (median 28)			25-30 (median 28)		
Inner teeth rows (UTR/LTR)	1/1 (f 1); 1/2 (f 4); 2/1 (f 1); 2/2 (f 16); 2/3 (f 1)			1/1 (f 4); 1/2 (f 3); 2/1 (f 2); 2/2 (f 2)			1/2 (f 1); 2/1 (f 1); 2/2 (f 1)		
Gill rakers (GR)	8/1/2 (f 3); 9/1/2 (f 7); 9/1/3 (f 5); 10/1/2 (f 6); 10/1/3 (f 2)			8/1/1 (f 1); 8/1/2 (f 2); 9/1/2 (f 7); 9/1/3 (f 1)			8/1/2 (f 1); 9/1/2 (f 2)		
Dorsal fin formula (DFR)	XV/8 (f 1); XV/9 (f 11); XV/10 (f 6); XVI/8 (f 2); XVI/9 (f 1); XVI/10 (f 1); XVII/8 (f 1)			XV/9 (f 5); XV/10 (f 1); XVI/9 (f 5)			XV/9 (f 2); XV/10 (f 1)		
Anal fin formula (AFR)	III/8 (f 12); III/9 (f 10); III/10 (f 1)			III/8 (f 7); III/9 (f 4)			III/8 (f 2); III/9 (f 1)		
Pectoral fin formula (PFR)	13 (f 22); 14 (f 1)			12 (f 5); 13 (f 6)			12 (f 2); 13 (f 1)		
Vertebrae (V)	13/16 (f 4); 14/15 (f 15); 14/16 (f 3)*			14/14 (f 1); 14/15 (f 9); 14/16 (f 1)			14/15 (f 2); 14/16 (f 1)		
Longitudinal line scales (LongL)	31 (f 4); 32 (f 15); 33 (f 4)			31 (f 3); 32 (f 7); 33 (f 1)			31 (f 1); 32 (f 1); 33 (f 1)		
Lateral line scales (LatL)	19/13 (f 1); 20/11 (f 3); 20/12 (f 5); 21/9 (f 2); 21/10 (f 1); 21/11 (f 2); 21/12 (f 2); 21/13 (f 3); 22/11 (f 1); 22/12 (f 2)			20/12 (f 1); 21/9 (f 1); 21/10 (f 2); 21/12 (f 5); 21/14 (f 1); 22/11 (f 1)			21/7 (f 1); 21/8 (f 1); 22/9 (f 1)		
Interlateral line scales (U-LLL)	2 (f 23)			2 (f 11)			2 (f 3)		
Upper transversal scales (D-ULL)	5 (f 11); 6 (f 12)			5 (f 8); 6 (f 3)			6 (f 2); 7 (f 1)		
Lower transversal scales (ULL-A)	9 (f 6); 10 (f 7); 11 (f 6)			8 (f 1); 9 (7)			10 (f 5)		
Pectoral-pelvic Scales (P-V)	5 (f 7); 6 (f 10); 7 (f 2)			5 (f 4); 6 (f 3); 7 (f 1)			5 (f 3); 6 (f 1); 7 (f 1)		
Caudal peduncle scales (CPS)	16 (f 23)			16 (f 11)			16 (f 3)		
Cheek scales (ChS)	2/7 (f 2); 2/9 (f 2); 3/7 (f 5); 3/8 (f 8); 3/9 (f 5); 4/8 (f 1)			3/7 (f 4); 3/8 (f 4); 3/9 (f 2); 4/9 (f 1)			2/7 (f 1); 2/8 (f 2)		

7.4.4 Haplochromis sp. ‘relictidens’

Studied specimens:

Holotype: RMCA 2017–06: HIPE 2 (HP1285); Mweya, hard subrate at mouth of Kazinga channel; 24/03/2017 [♀ 112.93 mm SL].

Paratypes: RBINS 12902 (n=2/3); Lac Edouard: au large de la riv. Talia: 0°31'05"S 29°20'26"E; Miss. KEA; 23/04/1953 [♂ 105.13, ♂ 108.19 mm SL]; RBINS 12905; Lac Edouard: Baie de Kasindi (en face de l’ane.vill.Kasindi–50 m au large): 0°04'35"S 29°42'31"E; Miss. KEA; 2/06/1953 [♂ 90.50 mm SL]; RMCA 2016–36: HIPE 1; Mukutu Kikinga, Lake Edward: 0°11'31"S 29°52'26"E; 23/10/16 [♂ 104.99 mm SL]; RMCA 2016–36: HIPE 1 (HP 907); Kasenji, Lake George: 0°01'55"S 30°09'00"E; 7/11/2016 [♀ 73.62 mm SL]. RMCA 2017–06: HIPE 2; Kayanja, Lake Edward; 30/03/2017 [♂ 105.90 mm SL].

Other specimens: RMCA 2017–06: HIPE 2; Kayanja, LakeEdward; 30/03/2017 [♂ 97.63 mm SL].

Etymology

The specific name, relictidens, is derived from the Latin ‘relinquo’, to relinquish, and ‘dens’, tooth. It refers to the decrease in the number of oral teeth in the outer rows with body size.

Description

H. sp. 'relictidens’ is endemic to the Lake Edward system. It has a relatively high body (table 10, p. 22, BD) and concave head, the snout slopes at 10–30°, the dorsal head at 35–45°. The jaws are isognathous with a gape inclination of 40–50°. The snout is acutely-rounded and the lacrima relatively large (LaD). The maxilla are bullate, i.e. posteriorly enlarged and distinctly visible, and reach vertically to between the anterior margins of the orbita and pupils. The lips and especially the oral mucosa are firmly thickened. The jaws are long (UJL; LJL) and posteriorly relatively slender (LJW). Halfway its length, the lower jaw suddenly narrows anteriorly, ending acutely and hereby resembling the hull of a rowing boat. The lower jaw anteriorly closes within the more rounded upper jaw which is clearly visible in ventral view. The lower jaw of small specimens (SL < mm) is more rounded, like the upper jaw.

The dorsal and anal fins reach to the caudal fin base with a deviation of a scale length. The caudal fin is weakly emarginate, almost subtruncate. The pelvic fins reach maximally to the first spine of the anal fin in females, between the first and second spine in males; the pectoral fins to between anus and second spine of the anal fin.

All teeth are small and deeply embedded in the thick oral mucosa, at most only the tips are visible. The base of the recurved neck is slender with a circular cross-section. The neck expands in a broad, slightly laterally compressed but stout uni- to bicuspid crown. The major cusp is isocline to subequilateral, acutely pointed in the smallest specimen (SL 73.62 mm), very short and distinctly blunt in larger specimens (SL > 90 mm). The minor cusp is small and bluntly pointed. The few outer teeth (UFT; LFT) even reduce in number with body size. Inner teeth are small and tricuspid, with a distinct space between outer and inner tooth rows. The dental arcade is very short (2/3 dentigerous area).

The lower pharyngeal bone is relatively slender. The teeth are slender with an acute major cusp. a straight cusp-gap separates it from the reduced or absent minor cusp. The teeth are set in 24–26 (n=3) rows, the median two have stouter teeth with a bluntly pointed major cusp. Teeth posterior on the bone are larger and stout, the major cusp is blunt and minor cusp reduced.

The gill rakers on the first gill arch are anteriorly unifid, relatively short and slender. The posterior ones are more flattened, stout and slightly bifid.

Colouration in live

Dominant males: The flanks, opercula, and cheeks are bright red. the dorsal and ventral border of the cheeks and the lower jaw is blue-green. The rest of the head, the dorsum, upper part of the caudal peduncle, pectoral and dorsal fins moss-green-gold. The dorsal fin with black lappets. The ventral body is whitish over its whole length. The anal fin has reddish spines and hyaline branched rays with large bright orange, black bordered egg spots. The anterior half of the caudal fin is distinctly black, parted by a slender yellow border from the hyaline, black speckled posterior end. The eyes are whitish with a bright yellow inner ring. The lachrymal stripes are restricted to black spots beneath the eyes.

Females: dorsally, the whole body and head are moss-green-gold, gradually passing into the whitish ventral body. The lower jaw and horizontal arms of the preopercula are blue-green. The eye is whitish with a yellow inner ring. The pectoral, dorsal and anal fins are hyaline with a yellowish basal part and randomly occurring dark specks. The caudal fin is anteriorly distinctly black, divided by a narrow vertical yellow band from the hyaline and speckled posterior end.

Colouration in alcohol

Preserved specimens have faint interorbital, nostril and dorsal head stripes. the lachrymal stripes are reduced to spots beneath the eyes. The dorsal and caudal fins are dark with an abrupt transition to the hyaline posterior ends. Males have at least two vague egg spots on the anal fin between the third and eighth branched ray.

Ecology

Haplochromis sp. 'relictidens' has a paedophagous ecology. The stomachs of three specimens were observed, all containing numerous cichlid eggs and/or larvae, even of different sizes within one specimen. The digestive system was very short (GL) in conjugation with a predatory ecology.

Diagnosis

Haplochromis sp. 'relictidens' sp. nov. differs from all other haplochromine cichlids of the Lake Edward system by very short (2/3 the dentigerous area) and slender dental arcades. The few outer teeth [UFT 16–26 (median 18); LFT 7–25 (median 17)] decrease further in number with body size. They are deeply embedded in the oral mucosa, at most the tips are visible. The outer teeth are small with slender, recurved necks and broader, bicuspid and very blunt crowns. Furthermore, the head is concave and the jaws relatively long [ULJ 34.2–37.5 (35.9) ´% HL; LJL 41.6–47.0 (45.0) % HL]. The anterior half of the lower jaw narrows anteriorly into an acute boat-shape, hereby closing within the more rounded upper jaw (visible in ventral view). The maxilla are bullate, i.e., posteriorly enlarged and distinctly exposed. The lips and oral mucosa firmly thickened. The body is relatively high [BD 34.6–38.7 (36.3) % SL], the lacrima large [LaD 15.8–18.4 (17.4) % HL] and the head concave with a relatively broad interorbital region [IOW 24.3–27.3 (26.0) % HL].

7.4.5 Haplochromis *sp. 'curvidens'*

Studied specimens

Holotype: RMCA 2017–06: HIPE 2 (HP1418); Rwenshama, landingsite, Lake Edward 26/03/2017 [♂ 91.13 mm SL].

Paratypes: RBINS 13432 [n=3/17; ♀ 120.23; ♂ 131.35; ♀ 140.15 mm SL]. RMCA 2016–36: HIPE1; Mukutu Kikinga; 23/10/2016 [n=3/17; ♂ 71.97; ♂ 82.50; ♂ 96.77 mm SL]. RMCA 2016–36: HIPE1; Mukutu Kikinga; 24/10/2016 [♂ 82.90 mm SL]. RMCA 2017–06: HIPE 2; Rwenshama, landingsite, Lake Edward; 25/03/2017 [♀ 94.46 mm SL]. RMCA 2017–06: HIPE 2 (HP1859, 1864); Kayanja, Lake Edward; 31/03/2017 [♀ 90.55; ♀ 94.84 mm SL].

Etymology

The species-specific name, curvidens, is a composition of the Latin 'curvus', curved, and 'dens', tooth. It refers to strongly recurved oral teeth and slightly recurved pharyngeal teeth.

Description

Haplochromis sp. 'curvidens' sp. nov. has a general body form with a circumflex dorsal outline in small specimens (SL < 100 mm), a relatively high body form in large specimens (SL > 120 mm). The head is slender (table 10, p. 22, HW) and dorsally straight to concave with a sharp angle above the eye, sloping at 30–40°. The snout slopes at 10–30°, has an acute outline. the snout and lacrima are long (SnL, LaD), the jaws very slender (LJW), long (LJL) and anteriorly rounded with the gape steeply sloping at 40–55°. These characteristics give this species a piscivorous *sensu stricto* appearance except for the outer teeth morphology (see further). The premaxilla are beaked; the maxilla reach to before the anterior margin of the eye and are bullate, i.e. posteriorly enlarged and distinctly visible. The lips and oral mucosa are slightly thickened. The scales on the cheeks are often vertically elongated.

The dorsal and anal fins reach to between the caudal fin base and a scale length before this point, to the first quarter of the caudal fin's length in dominant males. The pelvic fins reach to between the first and third spine of the anal fin in both sexes, the pectoral fins to between the anal opening and the first spine of the anal fin. The caudal fin is emarginate and scaled to 45–50% its length.

The outer teeth are small and have a stout base that is embedded in the slightly thickened oral mucosa.

The neck is recurved and slightly laterally compressed. The crown is strongly recurved, hereby laying horizontally, on top of the oral mucosa. It has a weakly tricuspid to unicuspid form. The major cusp is relatively short, equilateral and acute to acutely-rounded. the minor cusps are strongly reduced and often only visible by the slightly broader base of the crown. Bicuspid teeth can be intercalated in the outer rows of small specimens (SL < 90 mm). The crown is slightly broader than the neck and strongly recurved. These have a subequilateral to equilateral, acutely pointed major cusp with a distinct, laterally-compressed flange. The major cusp is separated by a distinct cusp gap from the blunt minor cusp that is to some extend horizontally orientated. All specimens have, posterior on the premaxilla, 4–5 straight unicuspid teeth that are larger and stouter. The inner teeth of all specimens are small, tricuspid and have a straight implantation with a recurved to strongly recurved neck. the dental arcades are long and slender with all tooth rows implanted closely to each other and all teeth closely set.

The lower pharyngeal bone is equally broad as long and relatively slender. It has a shallow form that is equally thin over its whole surface. The teeth have a slender neck and slightly broader crown base. the major cusp is acutely pointed and slightly recurved. A large, concave cusp gap ends in no to a small minor cusp. Posterior teeth are larger and stouter with a bluntly pointed major cusp, no cusp gap and a minor cusp implanted against the base of the major cusp. The teeth are implanted in 26–28 (n=3) rows with the middle two consisting of stouter teeth.

The outer gill rakers on the first gill arch are unifid, anteriorly rather stout and long while the posterior ones are very long and slender, the epibranchial rakers very slender.

Colouration in live

Dominant males: the body and head is dorsally grey-blueish. The suboperculum, operculum and flank are intense yellow. The body is ventrally white; the head ventrally greenish without any clear markings. The pectoral and anal fins are hyaline, the anal is ventrally dark red and has four large orange egg spots with a subtle white border. The dorsal and caudal fins have a dark red colouration, the dorsal fin anteriorly dusky. The pelvic fins are black.

Females and juveniles: dorsally they are green-greyish, the flank pale-yellow and the ventral body and cheeks white. The dorsal head and dorsal and caudal fins are dark. The pelvic and anal fins yellowish, the pectoral hyaline. There are no clear markings except for a small opercular and chin blotches.

Colouration in alcohol

All the fins have a dusky colouration except for the pelvic fin in some juveniles. The upper part of the caudal fin and the posterior-most part of the dorsal fins are maculated. The lappets of the dorsal fin are black. Except for a chin blotch and a faint lachrymal stripe, there are no distinct markings on the body or head.

Ecology

Haplochromis sp. ‘curvidens’ sp. nov. has a paedophagous ecology. The stomachs of two small specimens (SL 80–95 mm) contained numerous cichlid larvae of more than one undetermined species. The ecology of large specimens was not identified. Notable was the absence of a clearly defined stomach in several specimens, at most a relatively small stomach could be distinguished.

Diagnosis

Haplochromis sp. ‘curvidens’ has a piscivorous *sensu stricto* appearance. The head is concave to straight. The snout is long [SnL 29.8–36.0 (32.1) % HL] and acute, the premaxilla are beaked and slope gently at 10–30°, the gape steeply at 45–55°. The head and lower jaws are long and slender [HL 32.2–36.2 (34.2) % SL; HW 41.7–51.2 (44.2) % HL; LJL 43.6–50.8 (46.8) % HL; LJW 45.7–55.7 (48.7) % LJL], the maxilla reach to before the eyes in contradiction to many piscivorous species. *Haplochromis* sp. ‘curvidens’ has a unique outer tooth morphology, they are relatively small and closely set. The neck is circular and stout, the crown strongly recurved horizontally, weakly tricuspid to unicuspid in large specimens (SL > 90 mm), bicuspid in small specimens (SL < 90 mm).

It differs from *H.* sp. ‘relictidens’ by its long dental arcades in comparison to short ones (2/3 dentigerous area). *Haplochromis* sp. ‘curvidens’ has a huge number of acutely-rounded, strongly recurved outer teeth, *H.* sp. ‘relictidens’ few bluntly pointed outer teeth [UFT 36–65 (median 53), vs. 16–26 (median 18)] The lower jaw of *H.* sp. ‘curvidens’ is more rounded and does not close anteriorly within the upper jaw.

Table 10 Summary of the slender-jawed paedophagous haplochromine species of the Lake Edward system; *H.* sp. 'relictidens' sp. nov and *H.* sp. 'curvidens' sp. nov.

	***H.* sp. 'relictidens'**			***H.* sp. 'curvidens'**					
				Small specimens			Large specimens		
Measurements		n = 8, *4, **3			n = 7, *4, **3			n = 3, *1	
	Mean	Range		Mean	Range		Mean	Range	
SL (mm)	99.8	73.6	112.9	90.5	82.5	96.8	130.6	120.2	140.2
TL (mm)	124.0	94.2	138.7	111.5	99.4	119.9	164.0	149.1	171.8
Body measurements (% SL)									
Head length (HL)	31.6	29.6	33.0	34.3	32.8	36.2	34.0	32.2	35.7
Body depth (BD)	36.3	34.6	38.7	33.6	30.3	36.4	39.0	36.7	42.1
Pre-pectoral length (PrP)	33.8	31.4	34.7	36.2	34.6	37.8	36.5	35.7	37.2
Pre-dorsal length (PrD)	34.8	33.5	36.4	34.1	32.7	34.8	34.4	33.8	35.5
Pre-pelvic length (PrV)	42.7	41.3	45.4	43.5	41.7	45.6	45.1	43.8	46.1
Pre-anal length (PrA)	67.1	66.2	68.2	68.5	65.7	71.2	70.4	67.5	73.3
Dorsal fin base (DFB)	54.2	52.1	56.6	53.1	51.0	55.5	54.9	53.0	58.0
Pectoral fin length (PL)	31.6	29.0	33.3	30.6	29.6	31.4	30.4	28.5	32.4
Pelvic fin length (VL)	28.2	25.2	30.2	29.1	27.8	30.2	28.3	28.0	28.6
Anal fin base (AFB)	20.2	19.0	21.4	18.0	16.6	19.7	18.1	17.6	18.6
Caudal peduncle length (CPL)	16.6	15.5	17.7	16.1	15.1	16.7	16.6	16.0	17.3
Caudal ped. depth (CPD % CPL)	75.8	68.6	83.3	69.8	62.3	76.9	74.2	66.4	82.4
Gut length (GL % SL)	155.8	115.8	184.8**	139.3	123.1	159.9*	107.4*	-	-
Head measurements (% HL)									
Head width (HW)	50.4	47.7	54.7	43.2	41.7	45.7	46.6	43.3	51.2
Premaxillary pedicel length (PPL)	26.1	24.3	27.5	25.0	23.5	26.8	27.5	27.0	27.9
Snout length (SnL)	28.6	24.8	30.6	31.1	29.8	33.6	34.2	33.2	36.0
Lachrymal depth (LaD)	17.4	15.8	18.4	16.5	15.4	17.5	20.2	18.9	21.5
Cheek depth (ChD)	21.7	20.1	24.5	22.7	19.5	25.3	25.1	23.1	26.8
Eye depth (ED)	31.7	30.5	34.7	28.8	27.7	30.4	27.9	26.7	29.6
Interorbital width (IOW)	26.0	24.3	27.3	22.0	18.8	24.8	26.1	24.6	28.9
Upper jaw length (UJL)	35.9	34.2	37.5	34.3	31.2	36.6	33.8	30.8	37.7
Lower jaw length (LJL)	45.0	41.6	47.0	46.5	43.6	48.6	47.6	45.5	50.8
Lower jaw width (LJW % LJL)	54.7	50.1	59.7	49.6	46.4	55.7	46.5	45.7	47.7
Pharyngeal length (LPL % HL)	27.7	25.9	29.0*	28.0	27.5	28.4**	-	-	-
Pharyngeal width (LPW % LPL)	97.4	93.0	99.9*	95.0	91.9	97.0**	-	-	-
Dentigerous length (DAL % LPL)	48.6	47.0	50.0*	49.6	47.4	51.8**	-	-	-
Dentigerous width (DAW % LPW)	65.5	62.9	70.7*	66.9	66.3	68.0**	-	-	-
Meristics		n = 8						n = 10	
	Number & frequency (f)			Number & frequency (f)					
Upper jaw teeth (UFT)	16–26 (median 18)			36–65 (median 53)					
Lower jaw teeth (LFT)	7–25 (median 17)			33–51 (median 45)					
Inner teeth rows (UTR/LTR)	2/2 (f 7); 2/1 (f 1)			2/2 (f 3); 3/2 (f 7)					
Gill rakers (GR)	7/1/3 (f 1); 8/1/2 (f 1); 8/1/3 (f 1); 9/1/2 (f 3); 9/1/3 (f 1); 10/1/2 (f 1)			7/1/3 (f 1); 8/1/2 (f 1); 8/1/3 (f 3); 9/1/2 (f 1); 9/1/3 (f 2); 10/1/3 (f 2)					
Dorsal fin rays (DFR)	XV/7 (f 1); XV/9 (f 5); XV/10 (f 1); XVI/9 (f 1)			XIV/10 (1); XV/9 (f 3); XV/10 (f 5); XVI/9 (f 1)					
Anal fin rays (AFR)	III/8 (f 4); III/9 (f 4)			III/8 (f 8); III/9 (f 2)					
Pectoral fin rays (PFR)	12 (f 3); 13 (f 5)			12 (f 8); 13 (f 2)					
Vertebrae (V)	13/16 (f 2); 14/15 (f 6)			14/15 (f 9); 14/16 (f 3)					
Longitudinal line scales (LongL)	31 (f 4); 32 (f 3); 33 (f 1)			30 (f 1); 31 (f 4); 32 (f 3); 33 (f2)					
Lateral line scales (LatL)	20/9 (f 1); 20/12 (f 1); 21/11 (f 1); 21/12 (f 1); 21/13 (f 1); 22/11 (f 1); 22/12 (f 1); 22/13 (f 1)			19/12 (f 1); 20/10 (f 1); 20/11 (f 1); 20/12 (f 1); 20/13 (f 1); 21/9 (f 1); 21/10 (f 2); 21/11 (f 1); 21/15 (f 1)					
Interlateral line scales (U-LLL)	2 (f 8)			2 (f 10)					
Upper transversal scales (D-ULL)	5 (f 3); 6 (f 5)			5 (f 2); 6 (f 7); 7 (f 1)					
Lower transversal scales (ULL-A)	10 (f 7); 12 (f 1)			9 (5); 10 (f 3); 11 (f 1)					
Pectoral-pelvic Scales (P-V)	5 (f 4); 6 (f 3); 7 (f 1)			6 (f 7); 7 (f 3)					
Caudal peduncle scales (CPS)	16 (f 8)			16 (f 10)					
Cheek scales (ChS)	2/6 (f 1); 2/8 (f 2); 3/7 (f 1); 3/8 (f 1); 3/9 (f 1); 3/10 (f 1)			2/8 (f 1); 2/9 (f 4); 3/7 (f 1); 3/8 (f 3); 3/9 (f 1);					

7.4.6 Haplochromis labiatus *Trewavas, 1933*

Studied specimens

Holotype:

Other specimens:

174,175 RMCA 2017-06: HIPE 2 (HP1844); Kayanja, Lake Edward; 31/03/2017 [n=2/26; ♂ 89.71; ♂ 94.96 mm SL].
185 RMCA 2017-06: HIPE2; Rwenshama, landingsite, Lake Edward; 26/03/2017 [n=1/4; ♂ 71.59 mm SL].

Etymology

The original description of *H. labiatus* by Trewavas (1933) does not mention its etymology. It probably refers to the Latin 'labium', meaning 'lip'. Hereby probably referring to the strongly thickened lips.

Description

Haplochromis labiatus has a sturdy body due to its relatively short caudal peduncle (CPL) and high neural crest. The head is weakly convex, sloping at 30°. The cheeks are high (ChD) and the snout rather slender. The mouth is iso- to retrognathous with a short upper jaw (UJL), and a very short (LJL) and relatively broad lower jaw (LJW). The gape inclination is shallow at 10–30°; the lips strongly thickened, sometimes with the medial part slightly lobate. The chest scales are small and slightly embedded in the skin.

The caudal fin is subtruncate to emarginate. The dorsal and anal fins extend to between the caudal fin base and a quarter the length of the caudal fin. The pelvic fins reach to between the genital opening and second spine of the anal fin, maximally to the third spine of this fin in dominant males. The pectoral fins extend to between the anal opening and the second spine of the anal fin.

The outer teeth have long, stout and very straight necks that are circular on cross-section. The crowns are unicuspid that are slightly recurved and have a stout cusp in large specimens (SL > 80 mm). Posterior on both jaws the teeth are smaller and uni- to weakly bicuspid. All teeth are bicuspid in small specimens (SL < 80 mm) with equilateral to subequilateral major cusps and small minor cusps. Anteriorly in both jaws of all specimens, the teeth are often abraded. The outer teeth have a straight implantation except for anteriorly on the lower jaw where they gradually get a distinctly procumbent implantation. The anterior-most teeth are implanted on the anterior margin of the lower jaw in large specimens. In small specimens, these teeth are more buccally implanted with a slightly procumbent and medial orientation. The dentigerous arms of the premaxilla curve posteriorly distinctly downwards with the outer teeth implanted perpendicular to the bone. The 1–3 posterior-most outer teeth on the upper jaw are distinctly stouter. All outer teeth are closely set in all specimens. The first inner tooth row consists of relatively large, stout and unicuspid teeth that are closely set to the outer row. Buccally, the teeth of the following inner rows decrease in size. The inner teeth have a rather random setting, making the rows hard to define. All teeth are deeply embedded in the thickened oral mucosa, at most only the crowns are visible. The tooth bands are relatively narrow but rounded. Anteriorly, the dental arcade consist of 2–4 rows of inner teeth that gradually diminish laterally, until posteriorly only the outer teeth remain.

The lower pharyngeal bone has a generalised triangular form. Anteriorly, the ventral crest is slightly expanded while the bone is posteriorly rather shallow, especially the arms lay horizontally. the teeth are relatively large and closely set. The teeth are slender with a circular neck. the major cusp is acute and separated from the small minor cusp by a concave cusp gap. The teeth of the two median rows are very stout with a blunt major cusp and a reduced minor cusp. the posterior-most teeth are larger with a rounded major cusp and no minor cusp present.

The outer gill rakers on the first gill arch are anteriorly short, stout and acute, posteriorly relatively slender and short with a rounded outline. All gill rakers have a unifid form.

Colouration in life

Dominant males: the body, cheeks and snout have a silverish ground-colour with turquoise and gold. the chest and pelvic fins are black. The ventral body, preoperculum and dorsal and anal fins are white. The dorsal fin with a faint dusky base and lappets and the branched rays maculated red, i.e., a dotted pattern running between the rays. The anal fin has a yellow extension and 3–5 rather large orange-yellow egg spots with a dark border between the forth and ninth branched rays, of which the anterior three on a straight line. The caudal fin is orange to red-orange with a dark base. the pectoral fins are hyaline with a yellowish shine. A nostril and interorbital stripe are present on the head and the eyes are dark

Females and juveniles: the dorsum, flanks and snout are silverish with a yellow glow. The ventral body, cheeks, operculum, eyes, lips and pelvic fins are white. The pectoral fins are hyaline, the anal fin a white base and yellow extension, the dorsal and caudal fins a yellow base and white extension. The rays of the dorsal fin are slightly dusky, those of the anal fin have two yellow-orange egg-spot resembling dots.

Colouration in alcohol

Males have nostril and interorbital stripes, a darkly coloured ventral head and on their anal fin up to five relatively large egg spots with a distinct border between the fourth and ninth rays. The dorsal fin can be faintly maculated posteriorly, the anal fin has a dark base and a light-coloured extension. Five vertical bars can be visible on the body.

Diagnosis

Mean percentages are indicated in brackets.

H. labiatus has distinctly thickened to slightly lobate lips and a relatively slender snout. The mouth is small and iso- to retrognathous with relatively short upper jaws and distinctly short lower jaws. the mouth is strongly protrusible with a long premaxillary pedicel [PPL 23.6–27.5 (25.5) % HL] The lips are strongly thickened to slightly lobate. The outer teeth are long and stout with a straight, cylindrical neck and slightly-recurved, blunt unicuspid crowns. The outer teeth are closely set, anteriorly on the dentary with a distinctly procumbent implantation. The tooth band is relatively narrow but round and the relatively stout, unicuspid inner teeth are implanted closely to the outer row.

Haplochromis labiatus is distinct from *H*. sp. 'lobatus' by its distinctly shorter and broader lower jaw [LJL 23.9–29.0 (25.8), vs. 20.8–27.8 (25.1) % HL; LJW 67.8–93.9 (80.3), vs. 48.5–70.5 (61.6) % HL], slightly longer upper jaw [UJL 27.1–33.6 (30.8), vs. 34.2–40.7 (37.2) % HL], broader head [HW 46.9–51.9 (49.5), vs. 45.4–49.1 (47.5) % HL] and bigger eyes [ED 32.1–36.8 (34.6), vs. 29.1–33.6 (31.1) % HL]. The jaws are retrognathous in comparison to prognathous in H. sp. 'lobatus', although both can be isognathous. The outer teeth of H. sp. 'lobatus' have a distinctly straight crown and are anteriorly on the lower jaw more widely set on a distinct space from the inner tooth rows. The tooth bands are acute and narrower. The lips are equally thickened over their lengths in *H. labiatus*, but can be anteriorly very lobate in *H.* sp. 'lobatus'.

7.4.7 Haplochromis *sp. 'lobatus'*

Studied specimens

Holotype: RMCA 2016–36: HIPE 1 (n = 1/), Mouth of the Kazinga channel, Lake Edward, 24/10/2016 [♀ SL 104.56 mm].

Paratypes:

176-182 RMCA 2017-06: HIPE 2 (HP1795, HP1832); Kayanja, Lake Edward; 31/03/2017 [n=7/20; 75.23; 75.30; 95.36; 96.75; 97.78; 98.13; 104.20 mm SL].
184 RMCA 2017-06: HIPE 2 (HP1735); Kayanja, Lake Edward; 30/03/2017 [n=1/4; ♂ 85.12 mm SL].

Etymology

The species-specific name, lobatus, is derived from the Latin 'lobata', lobbed, in reference to the strongly thickened to distinctly lobbed lips of *Haplochromis* sp. 'lobatus'.

Description

Haplochromis sp. 'lobatus' has a moderate body form with a slender head (HW) that is straight to slightly concave, gently sloping at 25–40°. Both the snout and lower jaw are long (SnL, LJL), acute and slender (LJW), giving them an elongated look. The upper jaw (UJL) is short with the maxilla reaching to between the nostrils and halfway the nostril and eyes. The mouth has a shallow gape inclination of 0–25° and strongly thickened lips with a loosely swollen texture. The chest scales are small and embedded.

Two extreme head morphologies can be recognised within this species with the occurrence of all intermediate forms. The first has a very slender head and snout with a lower jaw that is anteriorly gently curved upwards and extremely prognathous, maximally so that the anterior teeth of each inner tooth row are visible with the mouth closed. The lips are medially distinctly lobed. The second form has a slightly broader head, elongated snout and an isognathous mouth with a straight lower jaw and uniformly thickened lips.

The caudal fin is subtruncate to emarginate and scaled to 35–50% its length. The dorsal and anal fins reach to a scale length from the caudal fin base, maximally to the fin base, in females; to the first quarter of the caudal fin in males. The pectoral fins reach to between the genital opening and the anal fin base, the pelvic fins to between halfway genital opening and anal fin to the third spine of this fin in females, extending to the first branched ray in males.

The outer teeth have a very straight, cylindrical and long neck, ending in a rather acute and straight unicuspid crown. The outer teeth of the lower jaw are anteriorly widely set and very procumbently implanted on the anterior margin of the dentary, i.e. orientated in the extension of the lower jaw. Laterally the teeth strongly decrease in size and are closely set. Posteriorly, the dentary is set with small and unrefined bicuspid-teeth with a stout subequilateral major cusp and a small, slightly horizontally inclined minor cusp. The outer row of the upper jaw consists only of unicuspid teeth with a straight implantation and a close setting. The dentigerous arm of the premaxilla is posteriorly downwards curved, and the teeth implanted on it remain perpendicular to the bone. The inner teeth are relatively small and unicuspid to weakly bicuspid. They are irregularly set with a distinct gap between outer and inner tooth rows. anteriorly on the lower jaw, they reach higher than the outer row teeth due to their unusual implantation. All teeth are deeply embedded in the oral mucosa. Generally, only the tips are visible. The tooth bands of both jaws are very narrow and acutely pointed, relatively broad anteriorly, quickly decreasing until posteriorly only the outer tooth row remains.

The lower pharyngeal jaw has a standard triangular form. The teeth are relatively large and slender with an acutely pointed major cusp, a convex cusp gap and a small minor cusp. The teeth are set in 23–29 (n=2) rows with the middle two consisting of very stout teeth. The posterior-most teeth are large, unicuspid and very bluntly pointed.

The anterior-most 2–3 outer gill rakers on the first gill arch are stout and short, followed by short and slender posterior ones. All rakers have a unifid form.

Colouration in life

Dominant males: the dorsum has a greenish-turquoise colouration, the flank and caudal peduncle is greenish-turquoise, gold and/or beige and the ventral body is white except for the black chest. Up to five vertical bars can be faintly visible on the flank. The cheeks and lateral snout have a bright turquoise colour, the lips beige. The basal part of the dorsal and anal fins are dark, the outer parts hyaline with a thin red line running over the extension of the branched rays. The dorsal fin is has black lappets and is posteriorly maculated red, i.e. dotted lines running between the rays while the anal fin has three orange egg spots with a black border running on a line between the .. and … branched rays. The pectoral fins are hyaline, the pelvic fins. the caudal fin is emarginate, has a dark base while the fin itself is dark orange to red. the eyes are brown with a white-yellow inner ring. Relatively broad nostril and interorbital stripes, faint supraorbital and lachrymal stripes and a chin blotch are present.

Females and juveniles: the dorsum and all fins are yellowish, the caudal one with some red pigmentation and the anal fin with orange spots on the branched rays, resembling egg spots. The flank gently merges into the white ventral body. the lips are yellowish, the eyes brown with a yellow inner ring.

Colouration in alcohol

Females have no distinct markings except for very faint nostril and interorbital stripes. The lower half of the dorsal and caudal fins are dusky. All other fins and the extensions of the dorsal and caudal fins are hyaline. The body of dominant males is ventrally black over its whole length. The lower half of the dorsal, anal and caudal fins are black, their extensions and the pectoral fins hyaline. The anterior branched rays of the dorsal fin are faintly maculated, the posterior ones distinctly so. The pelvic fins and lappets of the dorsal fin are black. Nostril, interorbital, broad lachrymal, vertical dorsal head and vertical preopercular stripes are distinctly visible. The lips have a light colouration with dusky blotches on the upper lip, a chin blotch on the lower lip.

Diagnosis

Mean percentages are indicated in brackets.

Haplochromis sp. ‘lobatus’ is easily recognisable by its strongly thickened to lobate lips in combination with long lower jaws [LJL 20.8–27.8 (25.1) % HL] and very short upper jaws [UJL 34.2–40.7 (37.2) % HL]. The tooth bands are narrow and acute, especially in the lower jaw. the stout, unicuspid teeth have a very long, cylindrical and straight neck, straight and blunt cusp and are implanted strongly horizontally inclined on the anterior margin of the dentary. The outer teeth are widely set anterior, closely posterior with a distinct space between outer and inner rows.

Haplochromis sp. ‘lobatus’ is distinct from *H. labiatus* and several other undescribed species with thickened lips by its long and slender snout [SnL 24.9–34.3 (30.6), vs. 26.1–32.5 (28.0) % HL] and lower jaw [LJW 48.5–70.5 (61.6), vs. 67.8–93.9 (80.3) % HL; LJL 20.8–27.8 (25.1), vs. 23.9–29.0 (25.8) % HL] and its slenderer head [HW 45.4–49.1 (47.5), vs. 46.9–51.9 (49.5) % HL]. The caudal fin of dominant males is mainly red in *H.* sp. ‘lobatus’ and orange in *H. labiatus* although this distinction is not always clear. The crown of the outer teeth on the dentary are anteriorly straight and widely set on a space from the inner teeth in *H.* sp. ‘lobatus’ in comparison to slightly recurved and closely set without a space from the stout anterior inner teeth in *H.* labiatus.

Table 11 Summary of the lobe-lipped species haplochromine species of the Lake Edward system; *H. labiatus* and *H.* sp. 'lobatus'.

	H. labiatus			***H.* sp. 'lobatus'**		
Measurements		n = 41, *39, **29, ***3			n = 17, *10, **2	
	Mean	Range		Mean	Range	
SL (mm)	75.3	60.0	104.3	94.8	75.2	110.0
TL (mm)	94.1	73.9	132.0	116.3	94.2	136.7
Body measurements (% SL)						
Head length (HL)	33.7	32.0	35.8	34.2	32.6	36.7
Body depth (BD)	37.0	33.6	40.1	36.1	34.4	41.0
Pre-pectoral length (PrP)	35.4	33.0	38.3	37.0	34.0	40.0
Pre-dorsal length (PrD)	37.8	35.8	39.6	37.1	35.5	38.8
Pre-pelvic length (PrV)	43.2	40.9	45.3	45.2	40.3	48.6
Pre-anal length (PrA)	67.0	63.0	69.4	68.5	66.0	70.3
Dorsal fin base (DFB)	54.3	51.2	57.0	52.6	48.7	54.7
Pectoral fin length (PL)	32.1	30.0	34.9**	30.2	29.3	31.5*
Pelvic fin length (VL)	26.9	23.8	31.8*	25.9	22.6	30.6
Anal fin base (AFB)	20.0	18.6	22.1	19.2	17.2	20.4
Caudal peduncle length (CPL)	15.1	13.5	16.2	14.9	12.9	15.9
Caudal ped. depth (CPD % CPL)	83.0	73.9	92.2	79.4	72.9	91.8
Head measurements (% HL)						
Head width (HW)	49.5	46.9	51.9	47.5	45.4	49.1
Premaxillary pedicel length (PPL)	25.5	23.6	27.5	26.0	24.2	28.5
Snout length (SnL)	28.0	26.1	32.5	30.6	24.9	34.3
Lachrymal depth (La)	15.0	12.9	16.3	15.7	13.0	17.2
Cheek depth (ChD)	20.3	16.5	24.1	20.9	16.1	23.0
Eye depth (ED)	34.6	32.1	36.8	31.1	29.1	33.6
Interorbital width (IOW)	23.5	21.2	26.3	22.2	18.7	24.0
Upper jaw length (UJL)	25.8	23.9	29.0	25.1	20.8	27.8
Lower jaw length (LJL)	31.0	27.1	33.6	37.2	34.2	40.7
Lower jaw width (LJW % LJL)	79.8	67.8	93.9	61.6	48.5	70.5
Pharyngeal length (LPL % HL)	27.3	25.7	28.9***	26.4	25.9	26.9**
Pharyngeal width (LPW % LPL)	101.9	97.9	104.4***	98.3	98.2	98.5**
Dentigerous length (DAL % LPL)	53.6	50.3	56.1***	51.4	49.0	53.8**
Dentigerous width (DAW % LPW)	72.7	72.2	73.1***	73.2	72.5	74.0**
Meristics			n = 41			n = 17
	Number & frequency (f)			Number & frequency (f)		
Upper jaw teeth (UFT)	18–35 (median 26)			21–30 (medina 26)		
Lower jaw teeth (LFT)	12–34 (median 24)			18–33 (median 25)		
Inner teeth rows (UTR/LTR)	2/2 (f 13); 2/3 (f 3); 3/2 (f 8): 3/3 (f 15); 4/3 (f 1); 4/4 (f 1)			2/2 (f 5); 2/3 (f 1); 3/2 (f 3); 3/3 (f 5); 4/2 (f 1); 4/3 (f 1); 4/4 (f 1)		
Gill rakers (GR)	6/1/2 (f 4); 6/1/3 (f 1); 7/1/1 (f 3); 7/1/2 (f 17); 7/1/3 (f 1); 8/1/2 (f 11); 8/1/3 (f 1); 9/1/3 (f 1)			5/1/2 (f 1); 6/1/2 (f 2); 7/1/2 (f 6); 7/1/3 (f 1); 8/1/2 (f 5); 9/1/2 (f 2)		
Dorsal fin formula (DFR)	XV/8 (f 1); XV/9 (f 6); XV/10 (f 14); XV/11 (f 1); XVI/8 (f 2); XVI/9 (f 9); XVI/10 (f 8)			XV/8 (f 1); XV/6 (f 3); XV/10 (f 3); XVI/9 (f 9); XVI/10 (f 1)		
Anal fin formula (AFR)	III/7 (f 1); III/8 (f 2); III/9 (f 33); III/10 (f 5)			III/9 (f 16); III/10 (f 1)		
Pectoral fin formula (PFR)	12 (f 24); 13 (f 17)			12 (f 6); 13 (f 11)		
Vertebrae (V)	14/15 (f 6); 14/16 (f 1)			-		
Longitudinal line scales (LongL)	30 (f 1); 31 (f 10); 32 (f 19); 33 (f 11)			30 (f 1); 31 (f 3); 32 (f 7); 33 (f 4); 34 (f 1)		
Lateral line scales (LatL)	20/11 (f 6); 20/12 (f 2); 20/13 (f 4); 21/11 (f 9); 21/12 (f 6); 21/13 (f 5); 21/14 (f 1); 22/11 (f 3); 22/12 (f3); 22/13 (f 1); 23/12 (f 1)			19/12 (f 1); 20/13 (f 1); 21/10 (f 1); 21/11 (f 2); 21/12 (f 2); 22/10 (f 1); 22/12 (f 4); 22/13 (f 3); 22/14 (f 1); 23/12 (f 1)		
Interlateral line scales (U-LLL)	2 (f41)			2 (f 17)		
Upper transversal scales (D-ULL)	5 (f 5); 6 (f 17); 7 (f 9); 8 (f 3)			5 (f 4); 6 (f 11); 7 (f 1); 8 (f 1)		
Lower transversal scales (ULL-A)	9 (f 4); 10 (f 20); 11 (f 16); 12 (f 1)			10 (f 9); 11 (f 8)		
Pectoral-pelvic Scales (P-V)	6 (f 2); 7 (f 6); 8 (f 24); 9 (f 7); 10 (f 2)			5 (f 2); 6 (f 3); 7 (f 5); 8 (f 6); 9 (f 1)		
Caudal peduncle scales (CPS)	16 (f 41)			16 (f 17)		
Cheek scales (ChS)	2/9 (f 1); 3/7 (f 2); 3/8 (f 6); 3/9 (f 11); 3/10 (f 7); 4/8 (f 1); 4/9 (f 11); 4/10 (f 1); 4/11 (f 1)			2/9 (f 3); 2/10 (f 1); 3/9 (f 5); 3/10 (f 4); 4/8 (f 3); 5/10 (f 1)		

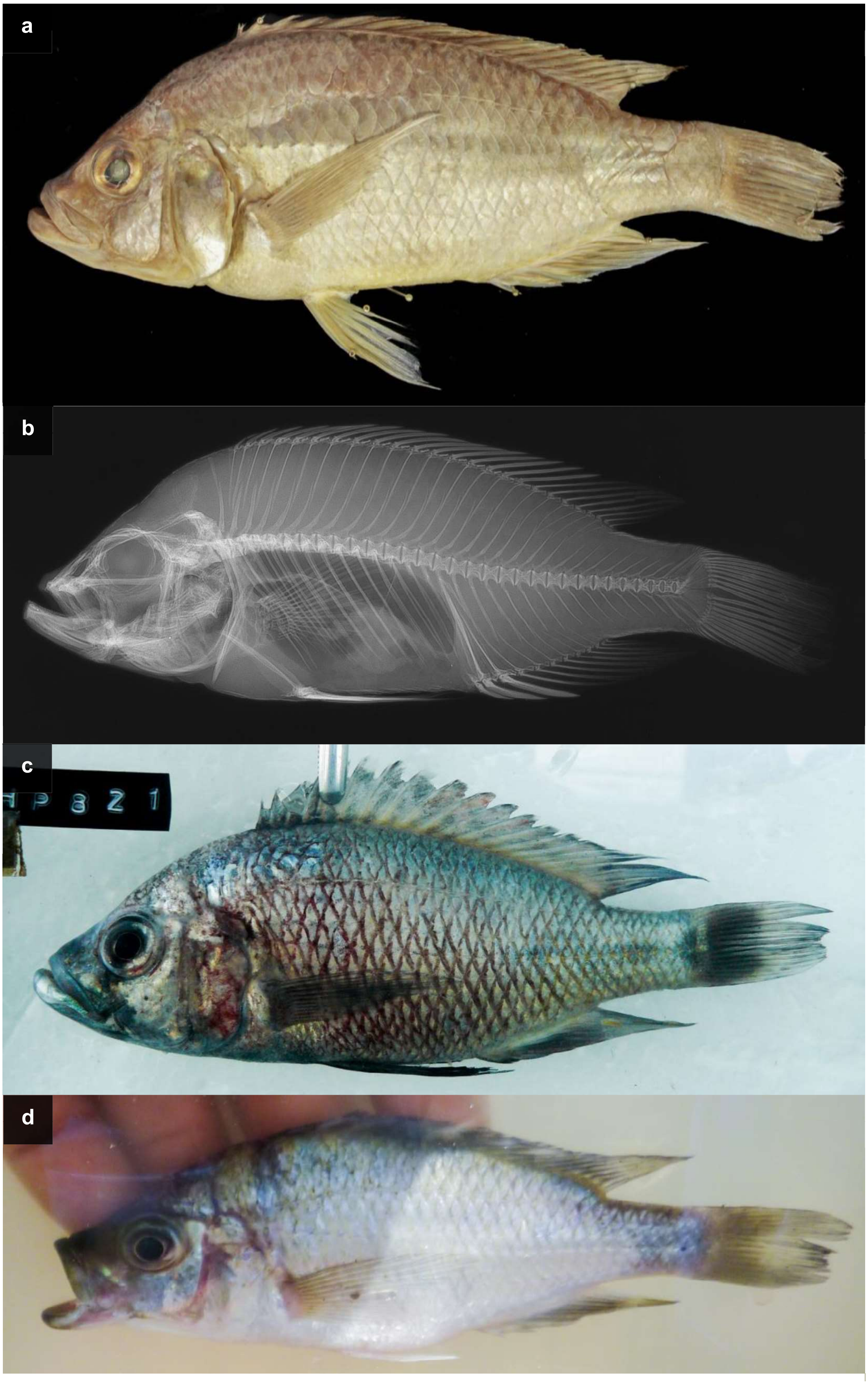

Figure 22 *Haplochromis taurinus*. (a, b) preserved picture and radiograph of the holotype, NHM 1933.2.23.406 [♀ SL 133.82 mm]. (c) Dominant male live colouration, RMCA HP821 [♂ SL 114.75 mm]. (d) Female live colouration, RMCA HP396 [♀ SL 101.08 mm]. Live pictures received from the RMCA ichtyology department.

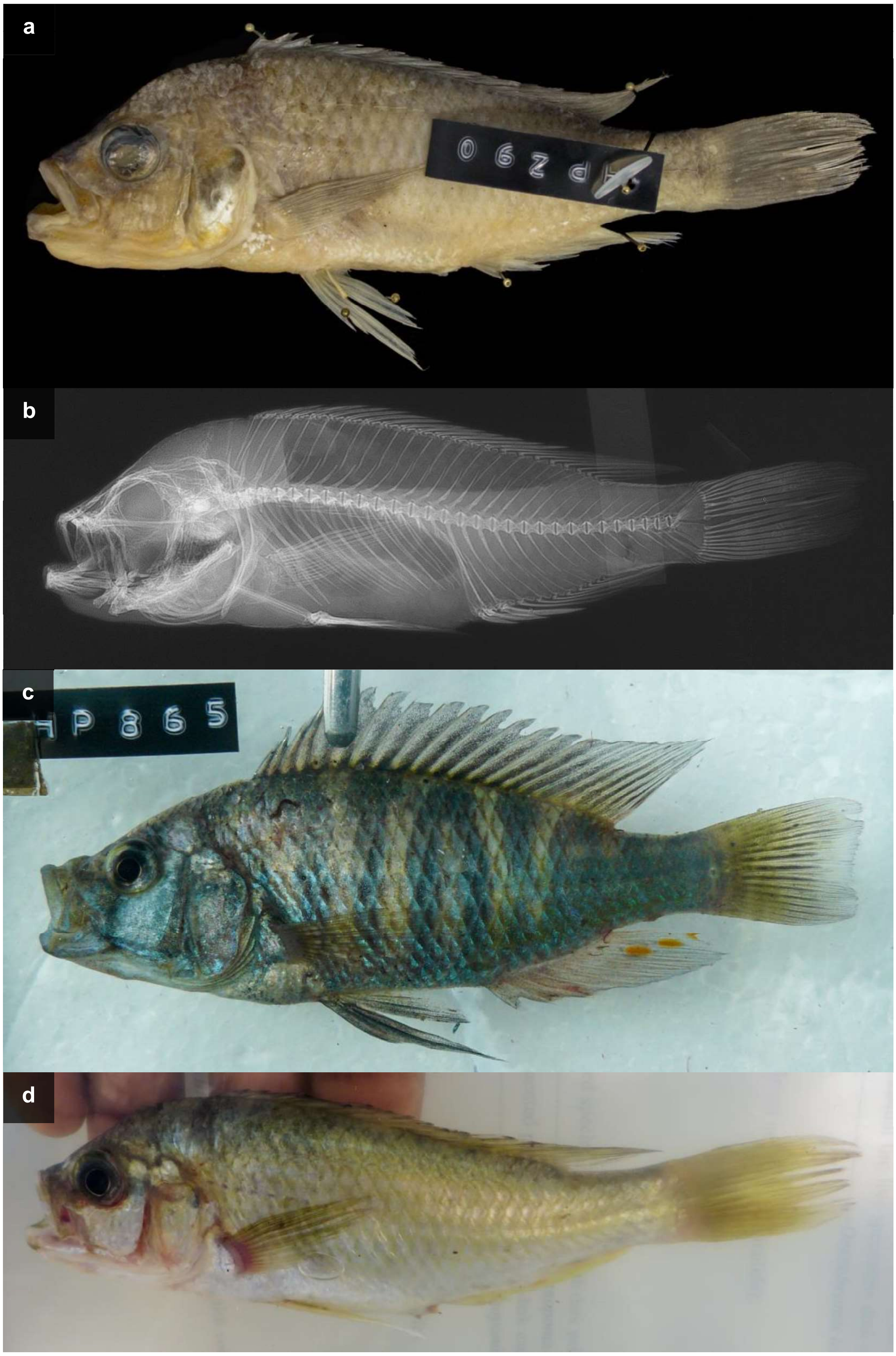

Figure 23 *Haplochromis* sp. ‘molossus’. (a-b, d) preserved and live pictures and radiograph of the holotype, a female, RMCA HP290 [♀ SL 104.17 mm]. (c) Dominant male live colouration, RMCA HP865 [♂ SL 93.52 mm]. Live pictures received from the RMCA ichtyology department.

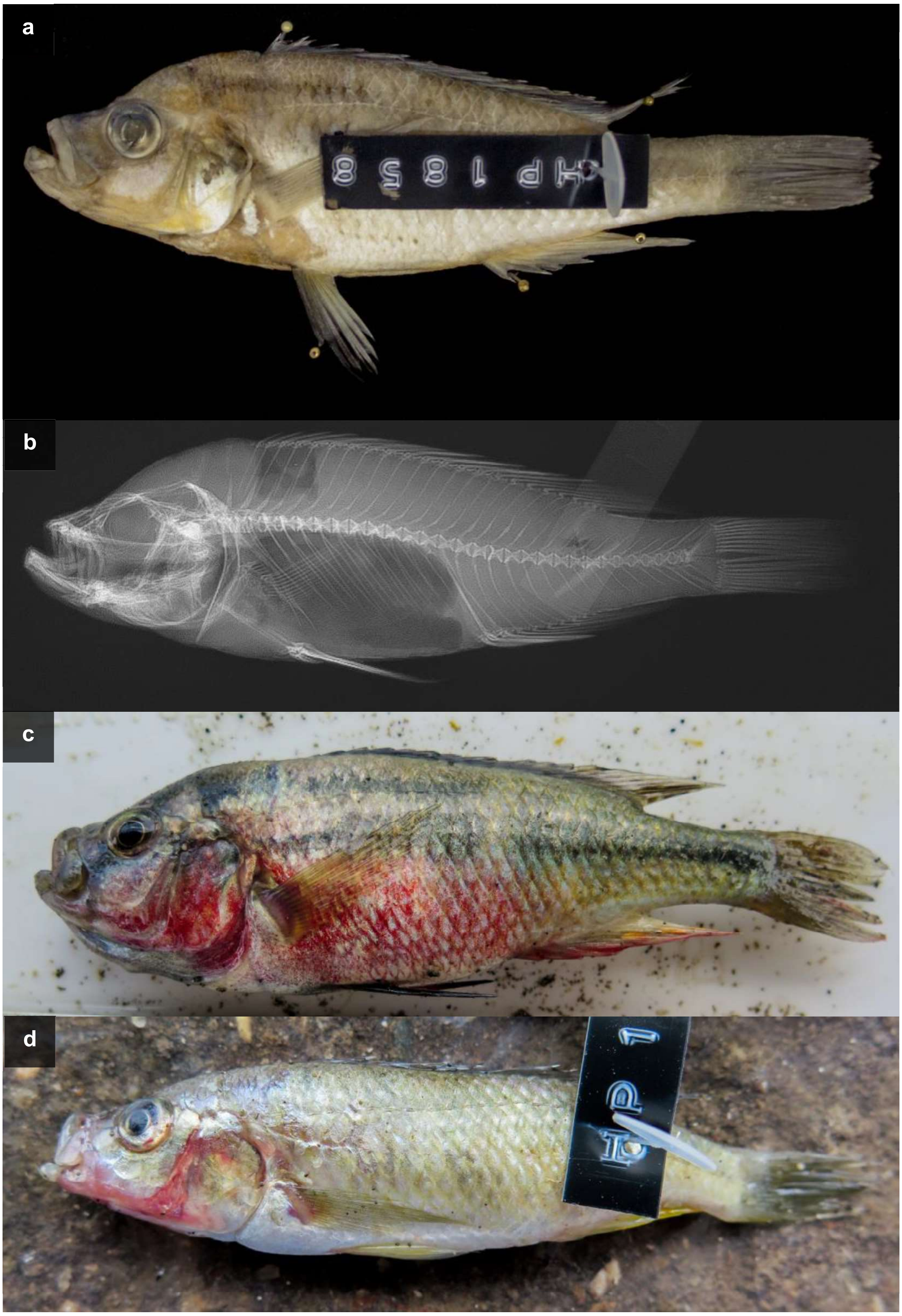

Figure 24 *Haplochromis* sp. ‘longicauda’. (a-b) preserved picture and radiograph of the holotype, RMCA HP1858 [♂ SL 85.67 mm]. (c) Dominant male live colouration, RMCA HIPE 2 (same jar as HP1797) [♂ SL 102.81 mm]. Juvenile live colouration, RMCA HP1797 [♂ SL 68.12 mm]. Live pictures received from the RMCA ichtyology department.

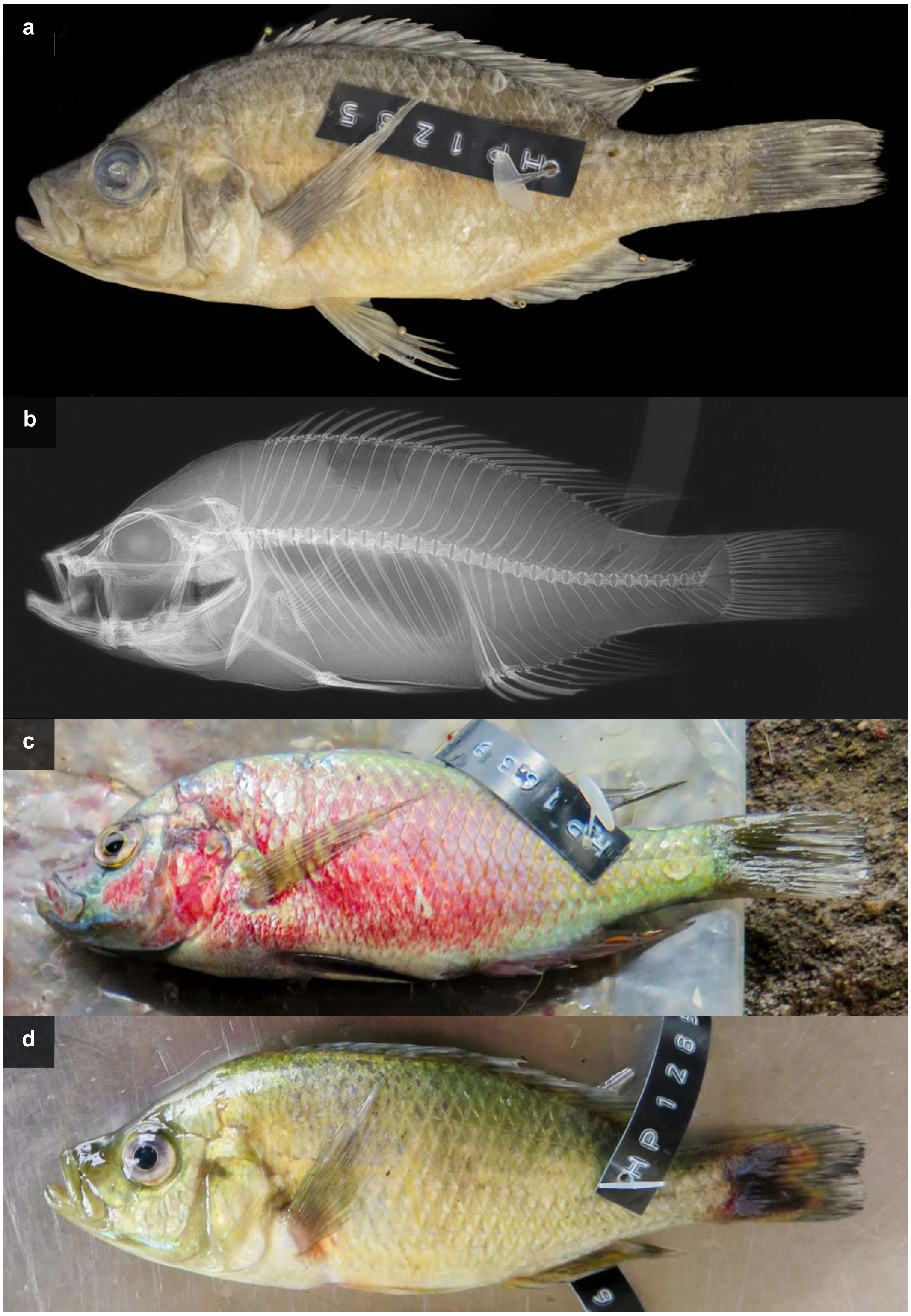

Figure 25 *Haplochromis* sp. ‘relictidens’. (a-b, d) preserved and live pictures and radiograph of the holotype, a female, RMCA HP1285 [♀ SL 112.93 mm]. (c) Dominant male live colouration, RMCA HP1689 [♂ SL 105.90 mm]. Live pictures received from the RMCA ichtyology department.

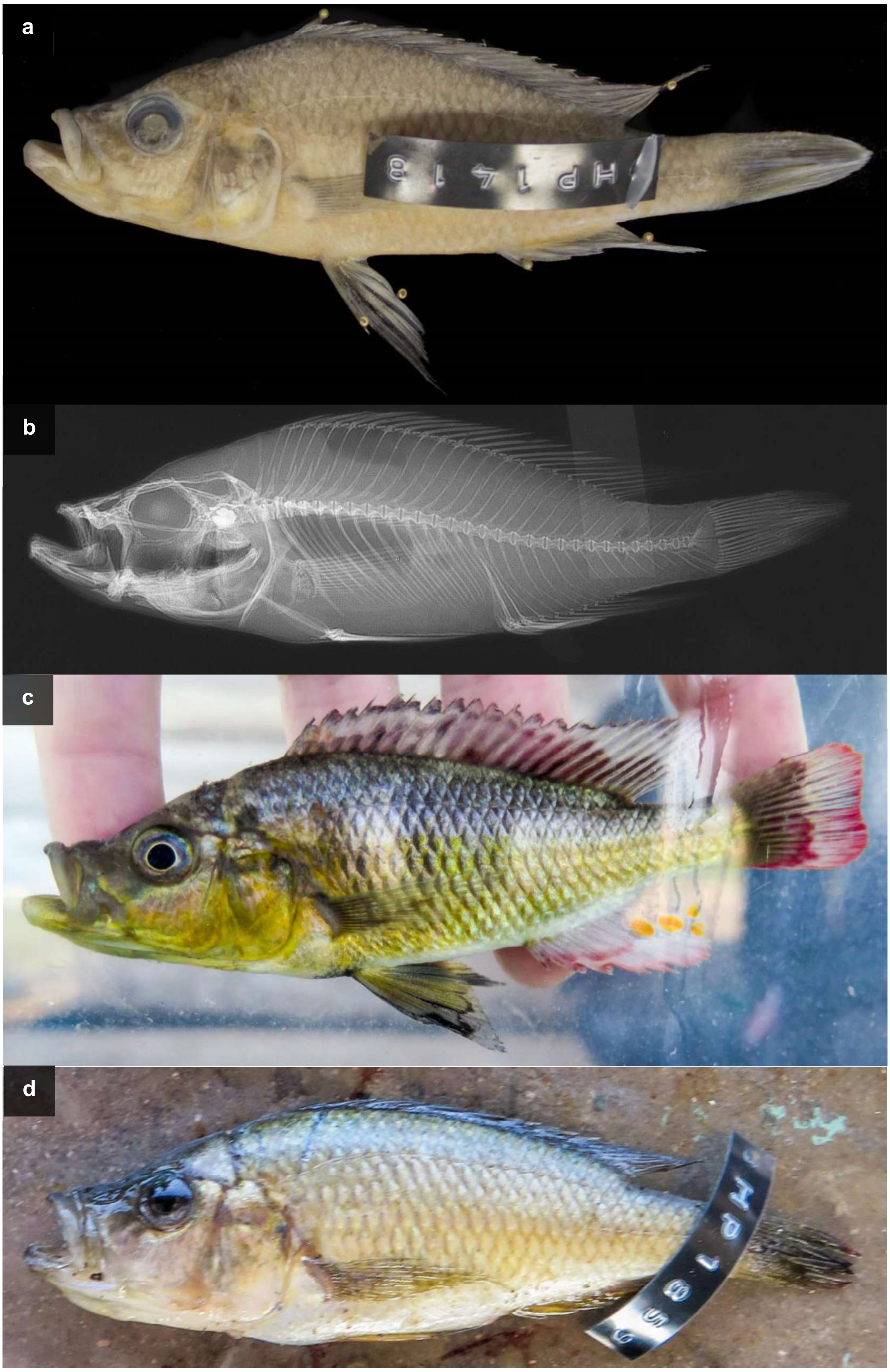

Figure 26 *Haplochromis* sp. ‘curvidens’. (a-c) preserved and live pictures and radiograph of the holotype, a dominant male, RMCA HP1858 [♂ SL 91.13 mm]. Female live colouration, RMCA HP1859 [♀ SL 94.84 mm].Live pictures received from the RMCA ichtyology department.

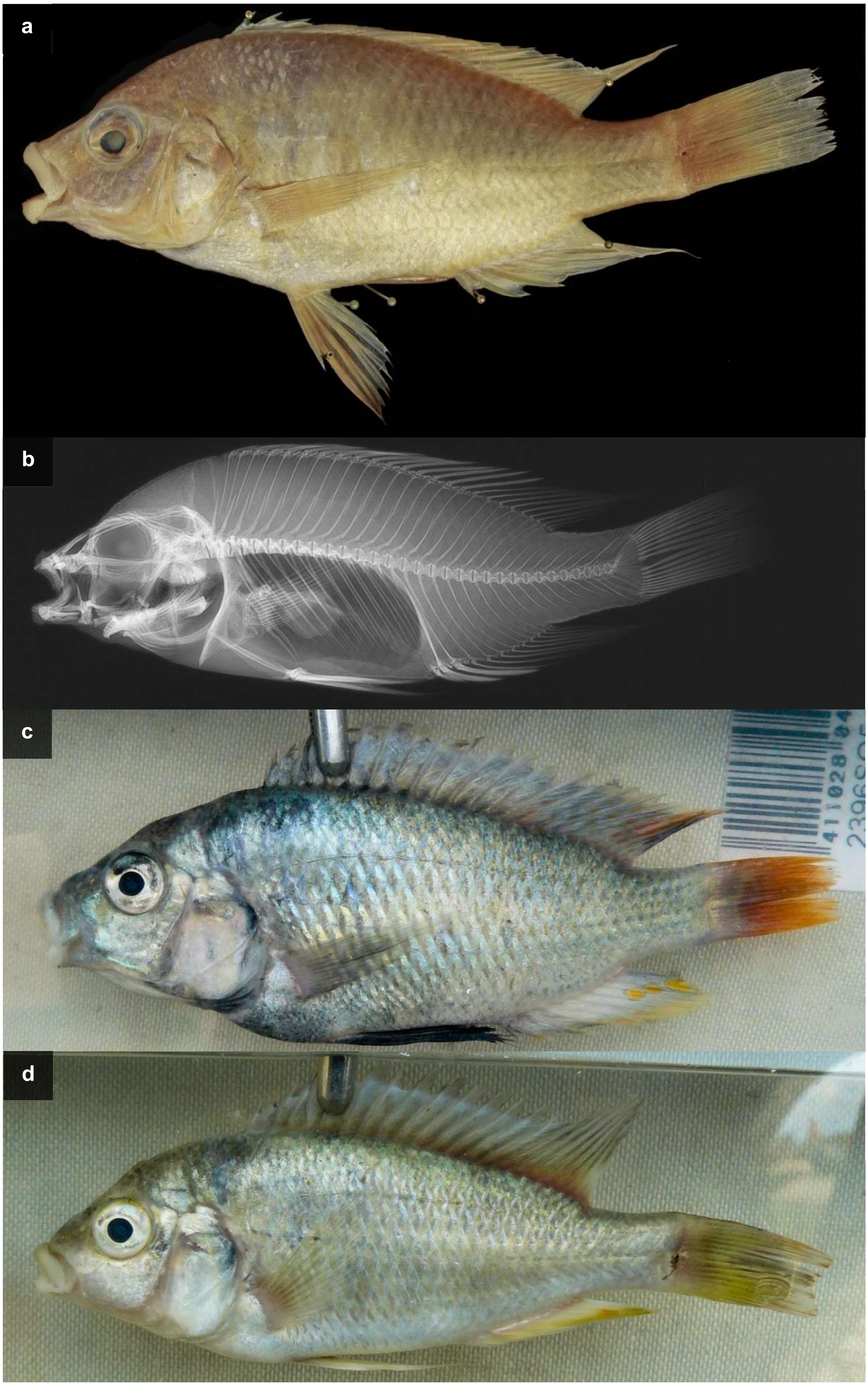

Figure 27 *Haplochromis labiatus*. (a-b) preserved picture and radiograph of the holotype, NHM 1933.2.23.403 [♂ SL 104.33 mm]. (c) dominant male colouration, RMCA HIPE 2 [♂ SL *unknown*]. (d) female live colouration, RMCA HIPE 2 [♀ SL *unknown*]. Live pictures received from the RMCA ichtyology department.

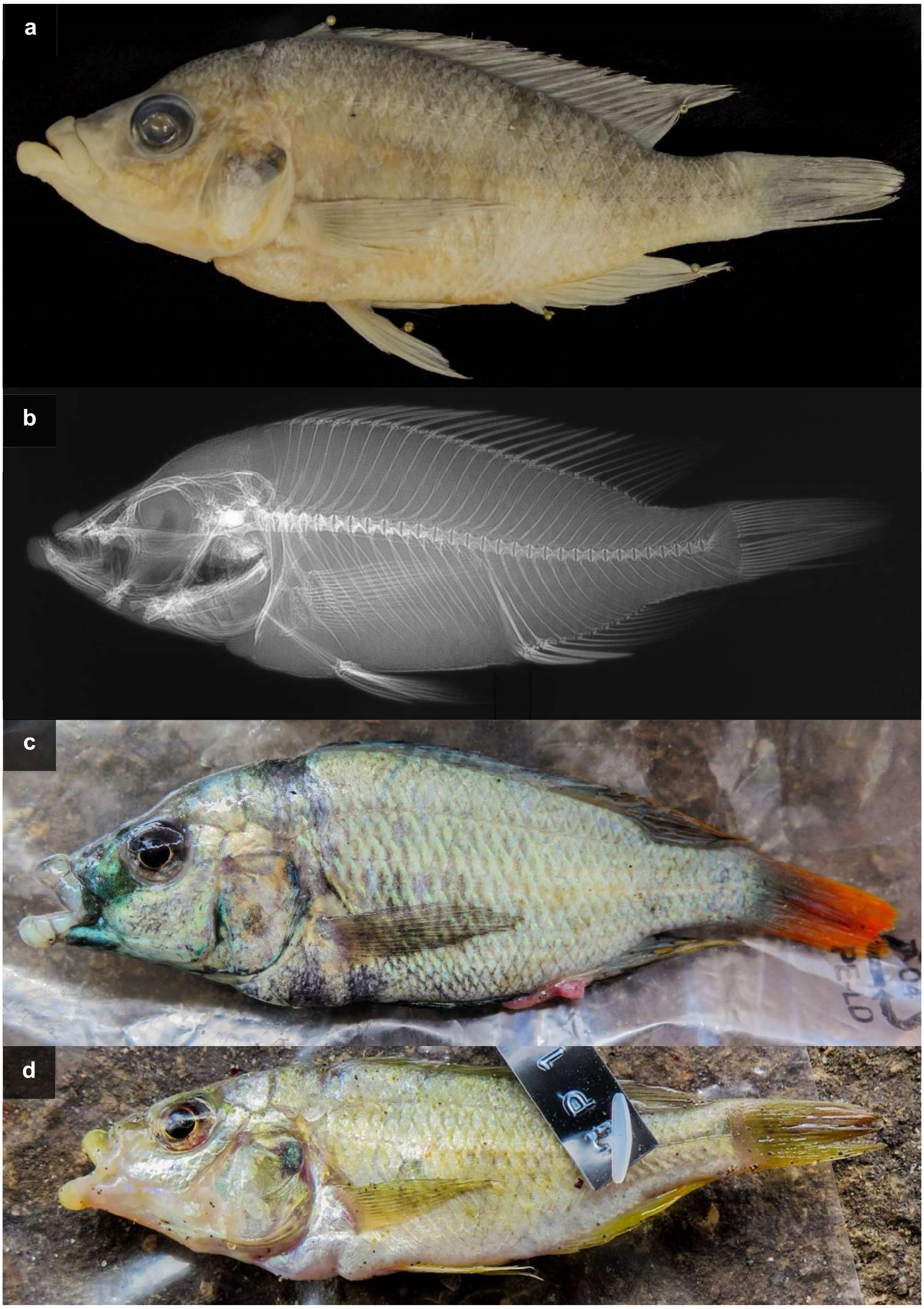

Figure 28 *Haplochromis* sp. 'lobatus'. (a-b) preserved pictures and radiograph of the holotype, RMCA [♀ 104.56 SL mm]. Male live colouration, RMCA HP1859 [♀ SL *unknown*]. Female live colouration, RMCA HP1859 [♀ SL *unkown*].Live pictures received from the RMCA ichtyology department.

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