Where ichthyofaunal provinces meet: the fish fauna of the Lake Edward system

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ABSTRACT

Based on literature, museum collections and three recent expeditions, an annotated species list of the Lake Edward drainage system is presented, excluding the endemic haplochromines. A total of 34 non-*Haplochromis* species belonging to 10 families and 21 genera are recorded from the system. Three of these are endemic and two others have been introduced in the region. Six species are new records for the Lake Edward system. A species accumulation curve indicates that we probably covered most of the non-*Haplochromis* species in the area sampled during the recent expeditions. However, undetected species might still be present in the Congolese part of the system, which is poorly sampled. A comparison of the species list with those of neighbouring basins confirmed the placement of the Lake Edward system within the East-Coast ichthyofaunal province.

Key words: biogeography, East-Coast Province, ichthyofaunal affinities, introduced species, Lake George

INTRODUCTION

The Lake Edward system (Figure 1) has a total catchment area of about 29 000 km². It comprises lakes Edward and George, the Kazinga Channel that connects these two lakes, several inflowing rivers, and some crater lakes (Beadle, 1974; Russel *et al.* 2003). Lake Edward has a surface area of 2 325 km² (Lehman, 2002), and is situated in the western arm of the East African Rift, on the border between the Democratic Republic of the Congo (DRC) and the Republic of Uganda. The deepest part of the lake (about 117 m) is a trench close to its western shoreline. From there, it rises gradually for over 30 km to the eastern shore in Uganda. The Kazinga Channel (ca. 40 km long) connects Lake Edward with the smaller Lake George, which has a surface area of 250 km² and lies completely within the borders of Uganda (Smith, 1995; Lehman, 2002). Lake George is very shallow, with an average depth of about 3 m across much of the lake. The water in this lake is less saline and contains a large amount of algae compared to Lake Edward (Beadle, 1974). The rivers of the system remain largely understudied in terms of physicochemical characteristics (Mbalassa *et al.*, 2014). They flow through a variety of habitats and provide spawning grounds for some lake fishes (Lowe-McConnell, 1987). Some of the main inflows of Lake Edward are the Nyamugasani and Lubilia rivers that drain the Ruwenzori Mountains in the north, the Ntungwe River, draining the Kigezi highlands in the southeast, and the Ishasha, Rutshuru, and Rwindi rivers that drain the Virunga Volcanoes in the south (Beadle, 1974; Russel *et al.*, 2003). The main inflowing rivers of Lake George are the Mubuku, Dura, and Mpanga rivers, which are generally small and of low stream order (Eggermont *et al.*, 2009). The sources of all these rivers are in the Ruwenzori Mountains (Beadle, 1974). The upper reaches of these rivers are characterised by steep gradients, rocky substrates and fast-flowing waters, whereas the lower reaches in the lowland plains and swamps of the rift valley floor are characterised by gentle gradient and slow-flowing waters (Eggermont *et al.*, 2009).

Given its complex hydrology, defining the boundaries of the system is not trivial. The drainage area (Figure 1) is delineated based on literature (Doornkamp & Temple, 1966; Greenwood, 1973; Odada & Olago, 2002; Russell & Johnson, 2006; Reardon & Chapman, 2009; Schraml & Tichy, 2010), and the topography of the region, examined on Google Earth. The system is bordered by the Congo basin in the west, and by the drainages of lakes Albert, Victoria and Kivu in the north, east and south respectively. It is an open system, as it drains into Lake Albert via the Semliki River, which has its origin near Ishango (DRC). Over its course, the Semliki drops about 300 m in altitude (Beadle, 1974). Most of this drop is over the Semliki rapids, located within a dense forest. These rapids (Figure 1) probably act as a geographic barrier, preventing fish from migrating from Lake Albert into Lake Edward (Worthington, 1954; Stewart, 2010). Therefore, they are considered to represent part of the drainage boundary of the latter system. Swampy areas straddle almost the whole eastern border of the Lake Edward system (Doornkamp & Temple, 1966; Greenwood, 1973). A complex connection exists with the Victoria drainage through the Katonga River. In the past, the entire Katonga once drained via the Mpanga into Lake George. After uplifting, most of this river now flows eastwards into Lake Victoria (Doornkamp & Temple, 1966; Reardon & Chapman, 2009). Currently, the eastern and western sections of the Katonga are connected by a large papyrus swamp that drains in both directions. A similar situation exists for the Ruizi River, located further south. Hence, the system's eastern border is defined as the western limit of these swampy watersheds (Figure 1).

Lake Edward is unique amongst the East African Great Lakes as its shoreline is completely surrounded by protected areas: the Virunga National Park (ViNP) on the Congolese side, and the Queen Elisabeth National Park (QENP) on the Ugandan side. The Virunga National Park is Africa's oldest national park, which was established in 1925 (Languy & de Merode, 2006). The entire western part of the shoreline of Lake George is also surrounded by the QENP. In the south, the system further includes the Bwindi Impenetrable National Park (BINP), whereas in the north, it contains the Ruwenzori Mountains National Park (RMNP) and the Kibale National Park (KNP) (Figure 1). Hence, in total, about 33% of the drainage system is located within national parks.

Continental Africa is divided into ten ichthyofaunal provinces that are based on ichthyofaunal similarities and reflect recent and historical connections between water bodies. The Lake Edward system is of high interest from a biogeographical point of view as it lies on the border of three ichthyofaunal provinces: the Nilo-Sudan, Congo and East-Coast provinces. The Lake Edward system is one of the few parts of the continent that was assigned to different provinces by different authors. Originally, it was placed in the Nilo-Sudan Province (Roberts, 1975), while the neighbouring Lake Victoria was included in the East-Coast Province, even though both drain into the Nile. This assignment has, however, been much debated over the years, with some studies placing the Lake Edward system in the Nilo-Sudan (Roberts, 1975; Skelton *et al.*, 1991; Witte *et al.*, 2009), and others in the East-Coast Province (Greenwood, 1983; Worthington & Lowe-McConnell, 1994; Snoeks *et al.*, 1997; Snoeks *et al.*, 2011). In the west, the Lake Edward system is situated close to the headwaters of some north-eastern tributaries of the Congo basin. Currently, both systems are separated by a series of mountain chains. However, during the Late Miocene/Pliocene, the paleo-lake Obweruka existed where now lakes Albert and Edward are situated, which was connected with the Aruwimi, one of these Congo tributaries (Van Damme & Pickford, 1999; Van Damme & Van Bocxlaer, 2009). This implies a past connection between the Congo and both lakes Albert and Edward.

The fossil record shows that the Pliocene fish fauna of Lake Edward was very different from the modern fauna and contained a rather Nilotic fauna that was, surprisingly, distinct from that of Lake Albert (Beadle, 1974; Stewart, 2010). During the Pleistocene, this fauna probably became extinct as a result of tectonic and/or climatic factors, including volcanic eruptions. The emitted ashes, perhaps containing toxic components, most likely exterminated the local fish fauna (Beadle, 1974; Stewart, 2010). The system was probably subsequently recolonised by an East-Coast fauna via extant hydrological connections with Lake Victoria (Beadle, 1974; Worthington & Lowe-McConnell, 1994; Stewart, 2010). Herein, we provide an annotated species list of the ichthyofauna of the Lake Edward system, and compare this with the faunas of the neighbouring basins, with the aim of providing a clear rationale for the position of the Lake Edward basin in one of the ichthyofaunal provinces.

Most of the former ichthyofaunal lists of the Lake Edward system were confined to either Uganda or the DRC, and often only reported the species collected during specific missions. Cunnington (1920) was the first to also present a table of fish species present in Lake Edward. Later, Worthington (1932) published a species list based on an expedition to the Ugandan lakes, which included the Ugandan part of Lake Edward. Faunistic studies on the Congolese side of the basin started with two large missions to the Virunga National Park, formerly named the Albert National Park, which were executed by de Witte (1933–1935) and Damas (1935–1936). Poll (1939a,b) published the species list that resulted from these missions. The next large exploration of the Congolese side of the basin was done by Hulot (1956), who evaluated the fisheries in lakes Kivu, Edward and Albert. In 1958, Greenwood published the '*Fishes of Uganda',* which summarised several older studies on the lakes and rivers of Uganda, with updated identifications. Although his study concerned Uganda, he also referred to Poll (1939a,b) and Hulot (1956) for species present in Lake Edward. Later, Greenwood (1973) executed a revision of the haplochromine cichlids of Lake George.

Lake Edward contains a large assemblage of endemic haplochromine cichlids, which are classified in the genus *Haplochromis* Hilgendorf 1888, following Hoogerhoud (1984), Snoeks (1994), van Oijen (1996), de Zeeuw *et al.* (2010), and Vranken *et al.* (2018). The taxonomy of the *Haplochromis* species from the Lake Edward system remains largely understudied and many of its species remain undescribed (Vranken *et al.* 2018). As this group is currently under revision and exhibits a much higher species richness than reported before, we did not include them in this study. Given their endemicity, excluding the species of *Haplochromis* from the study does not change any of the biogeographic comparisons. Two genera of more ancestral haplochromines, *Astatoreochromis* Pellegrin 1904 and *Pseudocrenilabrus* Fowler 1934, are included (Meier *et al*., 2017). These are much less species-rich, have broader distribution areas, and are mostly found in riverine habitats (Salzburger *et al*., 2005; Banyankimbona *et al*., 2013; but see Katongo *et al*., 2017).

The East African Great Lakes support one of the most important inland fisheries worldwide (Kaufman *et al*., 1996). Both lakes Edward and George are highly productive (Viner, 1969; Hecky & Degens, 1973), and sustain livelihoods for the large majority of the local communities (Orach-Meza *et al*., 1986; Dunn 1989). This especially holds for communities within the boundaries of the national parks, where fishing is one of the few allowed economic activities. However, over the last decade, the fishery appeared to have collapsed, especially in the Congolese part of the system, mainly due to the increasing pressure from the fast-growing human population (Mbalassa *et al*., 2015, Balole-Bwami *et al.,* 2017).

Given the incomplete and outdated species lists from the region, and the progress in taxonomic insights of several fish groups over the last decades, an updated species list of the Lake Edward system is necessary. Certainly, in view of the increasing pressures on the ecosystem, such a list is an indispensable tool for further management plans for sustainable fisheries and conservation measures.

MATERIAL & METHODS

Abbreviations: BINP: Bwindi Impenetrable National Park; BMNH: British Museum for Natural History (used for collection numbers of the NHM); EARS: East African Rift System; KNP: Kibale National Park; MRAC: Musée Royale de l'Afrique Centrale (used for collection numbers of the RMCA); NHM: Natural History Museum (London, UK); QENP: Queen Elisabeth National Park; RBINS: Royal Belgian Institute for Natural Sciences (Brussels, Belgium); RMCA: Royal Museum for Central Africa (Tervuren, Belgium); RMNP: Ruwenzori Mountains National Park; ViNP: Virunga National Park.

A species list of the Lake Edward system was compiled based on literature (mainly Worthington, 1920; Poll, 1939a,b; Hulot, 1956; Greenwood, 1958), information in Fishbase (Froese & Pauly, 2018), museum collections (RMCA, RBINS, NHM), and the results of three recent field expeditions. Only non-*Haplochromis* species are included in the list. Museum records were checked and re-identified when necessary. Most of the museum records stem from the expeditions for which species lists have been published. However, records from the RMCA also included specimens from the Rutshuru and Ishasha systems in the Bwindi Impenetrable National Park (BINP) in Uganda, collected in 2005 by A. Kasangaki (BSU). As this expedition was the only significant contribution to the collections from this area since the fifties, the sampling sites are included in Figure 1 and Table 1, together with the sampling localities of our three recent expeditions. These expeditions were executed in the Ugandan part of the system, two during the wet season (October 2016, March 2017), and one during the dry season (January 2018). Sampling sites for these expeditions covered lakes Edward and George, the Kazinga Channel, several rivers and three crater lakes (Figure 1, Table 1). Because of security issues in the Congolese part of the system, we were unable to sample there. Specimens were either caught using gillnets with mesh sizes of 8, 10, 12, 15, 20, 25, 30 or 40 mm, scoop nets, a backpack electrofisher (Samus; 50–1200 V, 2–100 Hz), or bought at local landing sites. Fishes were euthanized with clove oil prior to preservation. All specimens were deposited at the RMCA, with collection numbers 2016–35, 2017–06 and 2018–08. Identifications were mainly based on revisions of families and genera, and on the original species descriptions. If necessary, specimens were compared to type specimens or other reference material from the RMCA collections. Taxonomic nomenclature follows Fricke *et al.* (2018). Some specimens could not be identified with certainty as they closely resembled valid species, but had consistent characters to differentiate them from already described species. These taxa, are indicated by 'cf.' in the species lists. Species authorities are listed in Table 1. Authorities who were cited at first mention of the species in the text are not included in Table 1.

To examine the ichthyogeographical affinity of the Lake Edward system, we evaluated the occurrence of the species found in the system in the Nilo-Sudan, East-Coast and Congo ichthyofaunal provinces (Table 2). The Congo Province includes also the Malagarazi and Lake Tanganyika systems, but not Lake Kivu. For the Nilo-Sudan and East-Coast provinces, the neighbouring basins of lakes Albert, Victoria and Kivu are listed separately. The downstream boundaries of these basins are defined respectively as: the outflow of Lake Albert into the Nile, the Murchison falls, and the outflow of the Rusizi, respectively. For the species with uncertain identities (indicated as 'cf.'), the distribution of the corresponding nominal species is given.

A species accumulation curve was plotted for the non-*Haplochromis* species collected during the three recent expeditions (2016-2018). For this, every sampling locality visited per day was considered to represent one sampling effort. Based on species incidences of all sampling efforts, species richness in the sampled area was estimated with the non-parametric, asymptotic Chao 2 estimator and 100 randomizations.

RESULTS

The identifications of the ca. 4,500 non-*Haplchromis* specimens from the three recent expeditions (2016–2018), combined with those from the museum collections and literature, resulted in a total of 34 non-*Haplochromis* species belonging to 10 families and 21 genera (Tables 2&3, Figure S1). This number includes all species that were recognized for the region, including one that still needs to be described. Fifteen of the species from the system were only found in rivers within the catchment area (Table 3). *Bagrus docmak, Clarias gariepinus, Labeobarbus altianalis, Oreochromis niloticus, Oreochromis leucostictus, Protopterus aethiopicus* and, to a lesser extent, *Mormyrus kannume,* are the commercially most important species of the system, being caught and sold at different landing sites around the lakes. Only two endemic non-*Haplochromis* species have been recorded, *Amphilius* sp. 'Bwindii' and *Laciris pelagica*. However, taxonomic revisions of specific groups could potentially reveal the presence of a greater amount of endemism (see below). Two species, *Coptodon zillii* and *Poecilia reticulata*, have been introduced into the system.

Twenty-seven of the 34 species were collected during the three recent expeditions. The species accumulation curve of those expeditions (Figure 2) illustrates that 25 out of these 27 species had already been collected after 48 out of the 125 sampling efforts, which was accomplished during the first expedition in 2016. One additional species, *Pseudocrenilabrus multicolour*, was collected during the second expedition, and another one, *Clarias alluaudi*, was collected during the third expedition. About one-third of the sampling sites were revisited over two or three expeditions. The estimated species richness for the area that was sampled during the three recent expeditions was 27.33, indicating that 99% of the estimated asymptotic richness was sampled.

Amphiliidae. Four amphiliid species were recorded, all from the system's rivers. Amphiliidae are known to be mainly found in riverine habitats. *Amphilius jacksonii* was described from the Hima River, a tributary of Lake George, and has subsequently been reported throughout a large part of Eastern Africa. A revision (Thomson *et al.*, 2015), however, revealed *A. jacksonii* to be a species complex, reducing the distribution of *A. jacksonii* to the Lake Edward drainage, the Kagera basin (Lake Victoria system), and the Rufiji and Rufugu rivers (coastal rivers in the East-Coast Province). Collections from the Ivi River in the BINP revealed existence of specimens that closely resemble *A. jacksonii*, but clearly differ in several morphological features. These specimens were therefore considered to represent a new species, *A.* sp. 'Bwindii', which is currently being formally described (Kasangaki & Snoeks, in prep.). Other amphiliid specimens, initially identified as *A. uranoscopus,* but subsequently as *A. kivuensis* (re-identified by Thomson in 2010) was found in the Ishasha River and its tributaries Munyaga, and Ihihizo. A re-examination of the specimens, however, revealed them to differ from both *A. uranoscopus* and *A. kivuensis* mainly in having a smaller body depth and interorbital distance, and a longer and more slender caudal peduncle. These specimens are listed as *A.* cf. *kivuensis* pending a detailed genetic and morphological study to evaluate their taxonomic status.

The fourth amphiliid species found in the drainage system is *Zaireichthys rotundiceps*. This species was previously reported to be very widespread, occurring in the Lake Victoria, Rufiji and Lake Rukwa systems (Seegers, 2008), and several river systems in Southern Africa (Skelton, 1993). In the revision of Eccles *et al.* (2011), several new species from southern Africa were described that used to be lumped under *Z. rotundiceps,* and the latter was considered to be restricted to Tanzania. *Zaireichthys rotundiceps* was not listed in previous species lists of the system, but specimens were collected from the Rwimi River (by R. Wildekamp) and the Munyaga River (BINP collection) and recorded as *Z. rotundiceps* in the RMCA collections (2004-23-P-001–003; 2005-19-P-066–067). These specimens were not included in the revision of Eccles *et al.* (2011), and could not be allocated to any of the newly described species of that study, but do fit the diagnosis of *Z. rotundiceps*.

Anabantidae. Two anabantids occur in the Lake Edward system. *Ctenopoma muriei* is a species with a remarkable distribution (Norris *et al.,* 1988), known from the Nile, tributaries of lakes Victoria, Tanganyika and Albert, the Rusizi and Malagarazi, and the upper Congo. *Microctenopoma damasi* on the other hand is only known from the Lake Edward drainage and the Semliki River and its affluents. In the Semliki River, it has been found downstream as well as upstream of the Semliki rapids. This means this species is present in both the Edward and Albert drainage system. During our recent expeditions, we only collected two specimens of *M. damasi* and ten of *C. muriei.*

Bagridae. This family is represented by a single species: *Bagrus docmak*. It is one of the most important fisheries target species from the lakes, and is, in some seasons, the most abundant fish found on the markets. It is most often caught over hard substrates (Lock, 1982). We noticed the presence of two colour forms, with most specimens having a grey colour, while others have a golden-yellow colouration (Figure S1a,b). According to local fishermen, this colour variation is linked to the different habitats where the specimens were caught, with the yellow specimens being captured in inshore, vegetation-rich habitats, and the grey specimens more offshore, over rocky substrates. As there does not seem to be any other morphological difference (but without having executed a morphometric study), these differences in colour probably represent intraspecific variation. A remarkable finding was that in almost all specimens, a parasitic nematode was found in the cavity anteriorly of the eye, dorsally of the autopalatine, either on one, or on both sides.

Cichlidae. Two commercially important species of the system are the tilapias *Oreochromis niloticus* and the smaller-sized *O. leucostictus*. Although *O. niloticus* used to be the dominant species on landing sites around the lakes, its numbers have declined over the last decades (Balole-Bwami *et al.*, 2017). We also found four specimens of *Coptodon zillii,* a species native to Northern and Central Africa, which has been widely introduced for aquaculture and weed control (Welcomme, 1988). In Western Uganda, the species was introduced into a large number of crater lakes in the 1940's and subsequent years (Efitre *et al.*, 2007, 2016). Since its presence in the Edward system had not been reported until the recent surveys, it may have reached the system relatively recently. However, given its resemblance with *O. leucostictus,* its presence might also have been unnoticed until now.

Three haplochromine genera, *Astatoreochromis*, *Pseudocrenilabrus* and *Haplochromis*, are found in the Lake Edward system. The first two genera are represented by a single species each, *A. alluaudi* and *P. multicolor*. Both species mainly occur in the system's rivers (Greenwood, 1973). These species are also known from the Lake Victoria drainage, and *P. multicolor* also occurs in the drainage of Lake Albert and the downstream stretches of the Nile. All other species belong to the genus *Haplochromis* sensu Hoogerhoud (1984) and van Oijen (1996), and form an assemblage of 60–100 lacrustine species (Greenwood, 1991; Vranken *et al.*, 2018). Of these, 31 have so far been formally described (Vranken *et al.,* 2018).

Clariidae. One of the commercially most important fishes of the system is *Clarias gariepinus,* which is the most-widespread African freshwater fish. Other species of *Clarias* from the drainage are *C. alluaudi, C. liocephalus* and *C. werneri.* Distinguishing *C. liocephalus* from some other species of the genus can be difficult. The main diagnostic character of the species is the degree of development of lateral head bones. This development is, however, size-dependent in many species of *Clarias* (Teugels, 1986), and, in addition, exceptions occur in several species. Additionally, *C. liocephalus* is often confused with some species of *Clariallabes* Boulenger 1900. However, the identification of the Lake Edward specimens of *C. liocephalus* was confirmed by an ongoing study of this species (Kasongo, pers. comm.). *Clarias alluaudi* and *C. werneri* are morphologically very similar, and their synonymy has been suggested (Poll, 1939a; Greenwood, 1958). Teugels (1986) confirmed the morphological similarity between *C. alluaudi* and *C. werneri,* but identified some clear differences, mainly in the numbers of dorsal (65-79 vs 79-92) and anal fin rays (57–64 vs. 64–79), vertebrae (52–55 vs. 58–62) and gill rakers (12–16 vs. 17–21). The reports of *C. werneri* (Poll, 1939a,b) and *C. alluaudi* (Greenwood,1958) from the Lake Edward system are based on the same three specimens, housed at the RMCA (MRAC P-64768–64770). These three specimens were re-identified as *C. alluaudi* by Teugels (1986), which was checked and confirmed during this study. These three specimens are currently the only reported specimens of *C. alluaudi* from the system. Only one additional small specimen of *C. alluaudi,* was collected in the Nyamweru River during the recent expeditions. In addition, one specimen was caught that we identified as *C. werneri* based on the diagnostic characters mentioned by Teugels (1986). This specimen was caught in a pool at the Katunguru landing site. Hence, for now, the presence of *C. werneri* in the Lake Edward drainage is solely based on this specimen. The presence of *Heterobranchus longifilis* in Lake Edward is only based on a single specimen collected by Hulot (1956) on the Congolese side of Lake Edward. We examined this specimen (ISNB 13537), and confirmed its identification.

Cyprinidae. Apart from the Cichlidae, which contains the diverse assemblage of *Haplochromis*, the Cyprinidae is the most species-rich family in the Lake Edward system (Tables 2&3). In Africa, this is one of the most common freshwater fish families, often predominant in 'high Africa' sensu Roberts (1975). The genus *Enteromius* is the second largest genus (after *Haplochromis*) of African fishes, and species distinction can be very difficult. According to the various species list published, six species of *Enteromius* occur in the system: *E. apleurogramma, E. kerstenii, E. neumayeri* (Fisher 1884)*, E. pellegrini, E. perince* and *E. stigmatopygus*. In addition, one museum record of *E. cercops* (Whitehead 1960) is known from the system (BMNH 1966.9.1.5–7), but we re-identified these specimens as *E. perince*. However, taxonomic problems exist among the species of *Enteromius* from the system. *Enteromius neumayeri* and *E. pellegrini* are morphologically very similar and display a high intraspecific variability (Greenwood, 1962), rendering correct species identification problematic and highlighting the need for a revision. As we currently could not delineate two distinct morphological groups within the *E. pellegrini/neumayeri*-like specimens from the system, we opted to list them as a single species. As they seem to correspond more with *E. pellegrini,* with their long barbels and pelvic fin inserted anteriorly of the dorsal fin insertion, they are listed as *E. pellegrini.* Difficulties were also encountered in distinguishing between *E. perince* and *E. stigmatopygus*, which was already mentioned by Banister (1987) in his study on the Nilotic small barbs..

All species of *Enteromius* from the Lake Edward system are widely distributed and none of them is described from the system. *Enteromius apleurogramma, E. kerstenii* and *E. pellegrini* were described from localities in the East-Coast Province, respectively Lake Victoria, a coastal river in Tanzania, and Lake Kivu, while *E. perince* and *E. stigmatopygus* were described from and widely distributed in the Nile system (Table 2). Genetic studies already revealed that widespread species of *Enteromius* often represent complexes of species that are actually confined to smaller distribution areas (Van Ginneken *et al.*, 2017; Schmidt *et al.*, 2017). It is therefore likely that some of these species may not correspond to the species that they are currently attributed to. Hence, a revision, including a comparison with type specimens and topotypic specimens, is needed.

Labeobarbus altianalis is one of the widespread and commercially important species in the system. It occurs in the shallower parts of lakes Edward and George (Greenwood, 1966), and migrates into the upper reaches of the rivers to spawn (Copley, 1958). We observed variation in the development of the mental lobe on the lower lip, with some specimens having a well-developed mental lobe, while this lobe was less to only slightly developed in others. Variation in mouth shape was already mentioned by Poll (1939b) and is a generally-known phenomenon in species of *Labeobarbus* (Vreven *et al.*, 2016). We also observed variation in body depth and colouration, with some specimens having a deeper body and a more whitish colour, while most specimens had a shallower body and a more yellowish colour (Figure S1c,d). This, however, seemed to be intraspecific variation, as preliminary DNA barcoding results revealed specimens with different colour patterns to share the same mtDNA haplotype. Both *Labeobarbus ruwenzorii* and *L. somereni* are described from the Ruwenzori area, from the Rwimi and Sebwe Rivers respectively. While *L. ruwenzorii* is endemic to the area, found in the Rwimi, Mubuku and Sebwe rivers (Lévêque & Daget, 1984), *L. somereni* is also found in other higher altitude rivers outside the Lake Edward system (Banister, 1973). Banister (1973) suggested that these two species hybridize. No museum records of either of these two species are present at the RMCA, nor were they captured during the recent expeditions, probably because the upper parts of these higher altitude rivers have not been sampled intensively. Three specimens of the Ihihizu River (affluent of the Ishasha River) in the BINP were identified as *L. ruwenzorii.* This record would constitute a substantial expansion of the known distribution area of the species. However, these specimens seem to differ from *L. ruwenzorii* in having longer caudal fin rays and slightly fewer lateral line scales. Further study is needed to assess the taxonomic status of these specimens.

Mormyridae. The only two elephantfish species from the system are *Mormyrus kannume,* which was only found in the lakes, and *Pollimyrus nigricans,* only found in the rivers. Hulot (1959) mentioned the presence of *Mormyrus caschive* Linnaeus 1758 in Lake Edward. However, these specimens, housed at the RBINS, have been re-identified as *M. kannume* by Reizer (1964). Two additional specimens (BMNH 1932.6.13.310 & 331) had also been identified as *M. caschive*. For these specimens, the dorsal fin ray counts (71 and 74) fall within the range of *M. kannume* (57–75) instead of *M. caschive* (76–90) (Reizer, 1964). Notes (possibly from the collector Worthington) on these specimens refer to *M.* sp. 'near longirostris', suggesting that these specimens were then considered not to belong to *M.*

caschive. One of the two specimens could easily be identified as *M. kannume.* The other, however, was in a very poor state, but is also likely to belong to *M. kannume.*

Poeciliidae. This family, which used to include the oviparous African lampeyes, has recently been restricted to the American live bearers, while the oviparous African lampeyes are classified as Procatopodidae (Bragança *et al.* 2018). In the Lake Edward system, *Poecilia reticulata* was found in many of the smaller streams and tributaries flowing into the lakes and the channel, and in the Nkuguté and Nyambikere crater lakes.

This species is native to Northeast South America, to the Caribbean Islands, Venezuela, Guyana and northern Brazil (Lucinda, 2003), and has been introduced in warm tropical and subtropical waters all over the world. Although some introductions may have resulted from escapes or releases from aquaria, the species has mostly been introduced for mosquito control, which was also the reason for their introduction in Uganda (Deacon *et al.*, 2011). Worldwide, however, mosquito control generally failed, while these introductions did have negative effects on native fish species (Global Invasive Species Database, 2018). The present study provides the first report of *P. reticulata* in the Lake Edward system.

Procatopodidae. Four species of African lampeyes have been recorded from the system. Of these, only *Lacustricola vitschumbaensis* and *Platypanchax modestus* have been collected during the recent expeditions. *Lacustricola vitschumbaensis* was found in swampy areas near the shores of lakes Edward and George. Outside the Lake Edward system, this species occurs in the Kyoga system and in the northern part of Lake Victoria (Wildekamp, 1995). The deep-bodied *Platypanchax modestus* was sampled in several streams flowing into lakes Edward and George and in crater lakes. It has a peculiar distribution pattern as it also occurs in the upper reaches of the Ituri/Aruwimi, a tributary of the Congo River basin, a distribution pattern shared with freshwater molluscs (Poll & Lambert, 1965; Schultheiß *et al.*, 2014). Species delimitation and biogeographical studies on *P. modestus* populations from the Ituri/Aruwimi and the Lake Edward system are currently being carried out to examine whether the populations of both systems constitute two different species. The pelagic, clupeomorph-like *Laciris pelagica*, is a slender species, endemic to the deep and open waters of Lake Edward. It has not been collected from the system since the 1950's, though, in that period, Hulot collected over a thousand specimens (present in RBINS). These specimens were collected at 10–20 meters depth, with the use of dynamite. Given their small size and habitat at greater depths, it is not surprising that we collected no specimens with the fishing methods used during our recent expeditions. *Lacustricola bukobanus* is widespread over the African great lakes region, including the Lake Edward system (Wildekamp, 1995). During the recent expeditions, it was not collected. In some species lists (e.g. Poll, 1939a,b; Hulot, 1956; Greenwood, 1958) *Aplocheilichthys pumilus* (Boulenger 1906) was listed, based on specimens from the Molindi and Rutshuru rivers (DRC). These were, however, re-identified as *L. bukobanus* (Seegers *et al.*, 2003).

Protopteridae. The only species of lungfish found in the Lake Edward system is *Protopterus aethiopicus.* This large-sized species is of great importance for the local fisheries. Similar to *B. docmak* and *L. altianalis,* variation in colour pattern was also observed in this species. Most specimens had a grey-greenish colour dorsally and beige ventrally. A leopard pattern was variably visible on the dorsal side, and much less often also on the ventral side. Sometimes, a reddish hue was visible ventrally, which in rare cases expanded dorsally. We found some specimens with a strongly deviating colour pattern. These were bright yellow, but still had a red hue. On these specimens, the leopard-pattern was less pronounced, except on the caudal part (Figure S1e,f). According to local fishermen, this colour variation is linked to the habitat, with the yellowish forms caught closer to the shore.

DISCUSSION

This study provides the first annotated checklist of the ichthyofauna of the Lake Edward system.

Five species are documented for the first time from the system: *Amphilius* cf. *kivuensis, A.* sp. 'Bwindii', *Zaireichthys rotundiceps, Coptodon zillii* and *Poecilia reticulata.* The first three were already collected before our recent expeditions but were never documented in literature. The latter two are introduced species that were not yet documented from the region, nor present in existing collections. Additionally, *Clarias werneri* should be considered to represent a new record. Although Poll (1939a) mentioned this species, the specimens on which this record was based, were re-identified as *C. alluaudi.* The single specimen identified as *C. werneri* collected during our recent expeditions is thus the first and only record of that species from the system.

Some specimens from historical collections were re-identified, resulting in the removal of four species that were present in former lists. This is the case for *Enteromius neumayeri, E. cercops, Mormyrus caschive*, and *Aplocheilichthys pumilus*.

We examined the ichthyofaunal affinities of the Lake Edward system with the Nilo-Sudan, East-Coast, and Congo ichthyofaunal provinces (Table 2). Hydrologically, the Lake Edward system is connected with the Nile basin (Nilo-Sudan Province) via the Semliki, but at the same time it is not fully separated from the Lake Victoria system (East-Coast Province) by marshy areas on the Katonga and Ruizi rivers. Of the non-*Haplochromis* species, only three are endemic to the system: *Amphilius* sp. 'Bwindii', *Labeobarbus ruwenzorii* and *Laciris* *pelagica*. For the remaining native non-*Haplochromis* species, a larger number of species is shared with the rest of the East-Coast than with the Nilo-Sudan Province, respectively 25 vs. 16. Eighteen species also occur in the Congo ichthyofaunal province, though many of them are only found in the Lake Tanganyika basin. Most of the species shared with the Nile also occur in the East-Coast Province. The exceptions are *Microctenopoma damasi, Oreochromis leucosticus, Enteromius perince, E. stimatopygus* and *Labeo forskalii.* The other three species of *Enteromius* are only shared with the East-Coast and not with the Nilo-Sudan Province. The species of *Enteromius* are, however, currently under revision and their taxonomic assignments might change. Hence, distribution patterns of nominal species of *Enteromius* might not be well-suited for biogeographic comparisons. In addition, the taxonomy of the genus *Labeo* is very confusing (Van Steenberge *et al.*, 2016, 2017) and many of the East-African species in the genus have an uncertain taxonomic status (Seegers *et al*., 2003). *Labeo forskalii* was described from the Nile River system, suggesting that the population in the Lake Edward system could possibly represent a different species, but this needs to be confirmed with further taxonomic studies.

The cichlid *O. leucostictus* is a sister species to *O. esculentus* (Graham 1928), a species from the Lake Victoria drainage system (Klett & Meyer, 2002), and is thus part of an East-Coast genetic line. *Oreochromis leucostictus* was probably able to migrate from Lake Edward into Lake Albert via the Semliki. Although the Semliki rapids, and the Katonga and Ruizi swamps are considered as geographic barriers to the Lake Edward system, it remains possible that, occasionally, species have overcome them. *Microctenopoma damasi* as well, probably managed to spread downstream via the Semliki rapids, whereas the swamp-dwelling *Pseudocrenilabrus multicolor* probably managed to disperse through the Katonga and Ruizi swamps. The only species that is shared with the Congo Province and not with the East-Coast or Nilo-Sudan provinces is *Platypanchax modestus*. The population from the Congo basin, however, might constitute a different species. In a comparison of the ichthyofauna of the north-eastern tributaries of the Congo basin and the Lake Edward system, no evidence was found of recent exchange of other fish taxa (Decru *et al*., 2017). Most species of the Edward system that also occur in the Nile are large species such as *B. docmak, O. niloticus, C. gariepinus* and *M. kannume*. Possibly, these species could have survived the climatic and tectonic hazards leading to the extermination of part of the historical Nilotic ichthyofauna of Lake Edward (Beadle, 1974; Worthington & Lowe-McConnell, 1994). However, as these species also occur natively in Lake Victoria, except for *O. niloticus*, which has been introduced there, the most plausible hypothesis would be that these species entered Lake Edward from the east. Yet, this scenario was contradicted by a population-genetic study on *Bagrus docmak*, which revealed a larger similarity between populations from the Lake Edward system with those of Lake Albert, than with those of Lake Victoria (Basiita *et al.*, 2017). Similar population-genetic studies could also provide more information on the origin of the other species from the Lake Edward system.

The ichthyofauna of the Lake Edward system is much poorer in numbers of families and orders than that of the Nile system. It lacks 21 families that are present in the Nile basin, eight of which occur in Lake Albert: Alestidae, Malapteruridae, Mochokidae, Schilbeidae, Polypteridae, Citharinidae and Latidae. It also lacks the endemic riverine genera of the Nile and the Nilo-Sudan Province as defined by Roberts (1975). The Lake Edward system lacks seven families that are present in Lake Victoria, of which only four are native to that lake: Alestidae, Mastacembelidae, Mochokidae and Schilbeidae. On the other hand, all families occurring in the basin also occur in Lake Victoria. The modern fish fauna of the Lake Edward system is thus very different from that of the Nile and Lake Albert, and resembles more that of Lake Victoria (see also Greenwood, 1966; Stewart, 2010). It also shares some species with Lake Kivu, which is included in the East-Coast Province (Snoeks *et al*., 1997). In addition, the endemic haplochromines of lakes Edward and George belong to a species flock that originated from Lake Kivu and spread to Lake Victoria (Verheyen *et al.*, 2003; Elmer *et al*., 2009). As lakes Kivu and Victoria are included in the East-Coast Province, this provides an additional reason to include the Lake Edward system into this province as well. Although representatives of this flock have also colonised Lake Albert, haplochromines are much less dominant and abundant there. To conclude, our results support the inclusion of the Lake Edward system in the East-Coast Province (Greenwood, 1983; Snoeks *et al*., 1997; Snoeks and Getahun, 2013).

Two introduced fish species have been discovered: *Coptodon zillii* and *Poecilia reticulata*. In addition, in the Nkuguté Crater Lake, many Louisiana red swamp crayfish, *Procambaris clarkii* Girard 1852, were recorded. This species, native to the southern and south eastern parts of the United States of America and northern Mexico, has been introduced for human consumption in Africa, where its range is expanding in Kenya, Uganda and Zambia (Smart *et al*., 2002; Nunes *et al.*, 2016). Freshwater crayfish can alter ecosystem functioning due to destruction of aquatic macrophytes, disruption of macro-invertebrate communities, competition with native invertebrates, predation on fish and amphibian eggs, and disturbance of fish breeding habitats (de Moor, 2010; Nunes *et al.*, 2016). As they are also known to feast on fishes caught in nets, they cause an additional economic loss by reducing the value and making it difficult to sell the fish catches. For now, *P. clarkii* has only been reported from one crater lake of the Lake Edward system. A full-scale eradication program of the species in that crater lake would probably be the best option to prevent further spread and mitigate negative impacts on the entire ecosystem.

Brown trout, *Salmo trutta* Linnaeus 1758, and rainbow trout, *Oncorhynchus mykiss* (Walbaum 1792), were introduced into the rivers of the Rwenzori Mountains in the 1930's (Eggermont *et al.*, 2009). Some of these, the Nyamugasani, Nyamwamba and Mubuku rivers and their tributaries, belong to the Lake Edward system. According to Eggermont *et al.* (2009), very few or no specimens are still present today. However, a report from the Uganda Wildlife Authority (Makombo, 2015) still mentions their presence in the Mubuku River. Although no specimens were recorded during our recent surveys, local communities indicated that trout is present in these rivers. Because there are no specimens of trout in any of the museum collections, it is not possible to confirm the identities of the species that were introduced in these rivers. As a result, trout was not included in the species list for the present study.

During our recent sampling efforts (2016–2018) 79% of the non-*Haplochromis* species currently known from the system were collected. The species accumulation curve indicates that almost all non-*Haplochromis* species were covered. However, this curve and the estimated species coverage of 99% is only based on results from the areas of where recent expeditions were undertaken. Three of the seven species that were not recorded from the present study were only previously recorded from rivers that were not sampled during the recent expeditions: *Amphilius* cf. *kivuensis* and *A.* sp. 'Bwindii' were collected in the BINP, which was not accessible for sampling; and for *Lacustricola bukobanus,* there are, for the Lake Edward system, currently only museum records from the Molindi and Rutshuru rivers in the DRC. Further studies are needed to determine potential other causes for the failure of sampling these species again. *Labeobarbus ruwenzorii* and *L. somereni* are known from the higher altitude rivers in the Ruwenzori area, which were not sampled intensively during the recent expeditions. Museum records of *Laciris pelagica* and *Heterobranchus longifilis* all stem from the Lake Edward itself. *Laciris pelagica* was probably not collected during the recent expeditions because of our fishing methods. The status of *H. longifilis* in the system is uncertain, as it was never collected since Hulot (1956). However, *H. longifilis* in generally known to be an uncommon species (Eccles, 1992).

Undetected diversity might still be present in the Congolese part of the system. The Congolese portion of Lake Edward contains some habitats, such as rocky shorelines and deep-water habitats that are scarce or absent on the Ugandan portion of the lake. Additionally, as a substantial part of the non-*Haplochromis* fish diversity is found in rivers, and as some species are only found in very confined riverine parts of the system (e.g., *Amphilius* cf. *kivuensis, A.* sp. 'Bwindii', *Clarias werneri, C. alluaudi*), it is possible that the poorly sampled rivers in the western portion of the Lake Edward system may contain undocumented diversity.

Given the increasing pressure on the aquatic environment and the observed decline in fish catches in the Lake Edward system (Languy & Kujirakwinja, 2006; Bassa *et al.*, 2015; Lubala *et al.*, 2017), the development of management plans for sustainable fisheries will be indispensable. The present checklist forms a much-needed baseline to develop such conservation measures. Knowledge on the species diversity is also necessary to conduct ecological and population-genetic studies to get further insight into the ecosystem. Given that the observed decline in fisheries seems to be more severe on the Congolese part of Lake Edward (Vakily, 1989; Languy & de Merode, 2006), additional sampling efforts in that region are certainly necessary.

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SUPPORTING INFORMATION

Figure S1. Photographs of all non-*Haplochromis* fish species from the Lake Edward system, caught during the three most recent expeditions (2016-2018). (a-b) *Bagrus docmak*, (c-d) *Labeobarbus altianalis*, (e-f) *Protopterus aethiopicus*, (g) *Amphilius jacksonii*, (h) *Zaireichthys rotundiceps*, (i) *Ctenopoma muriei*, (j) *Microctenopoma damasi*, (k) *Astatoreochromis alluaudi*, (l) *Coptodon zillii*, (m) *Oreochormis niloticus*, (n) *Oreochormis leucostictus*, (o) *Pseudocrenilabrus multicolor*, (p) *Clarias alluaudi*, (q) *Clarias gariepinus*, (r) *Clarias liocephalus*, (s) *Clarias werneri*, (t) *Enteromius cf. apleurogramma*, (u) *Enteromius kerstenii*, (v) *Enteromius cf. pellegrini*, (w) *Enteromius perince*, (x) *Enteromius stigmatopygus*, (y) *Labeo forskalii*, (z) *Mormyrus kannume*, (aa) *Pollimyrus nigricans*, (ab) *Poecilia reticulata*, (ac) *Lacustricola vitschumbaensis*, (ad) *Platypanchax modestus*.

CONTRIBUTIONS

E.D., M.V., J.S. and N.V. executed sampling; E.D. identified the specimens, except for the killifish, which were identified by P.B., and the haplochromines which were identified by N.V.; distribution map is created by N.V.; all authors contributed to the final manuscript.

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