



Review

The taxonomic diversity of the cichlid fish fauna of ancient Lake Tanganyika, East Africa

Fabrizia Ronco*, Heinz H. Büscher, Adrian Indermaur, Walter Salzburger

Zoological Institute, University of Basel, Vesalgasse 1, 4051 Basel, Switzerland

ARTICLE INFO

Article history:

Received 29 January 2019
 Received in revised form 10 April 2019
 Accepted 29 April 2019
 Available online 30 June 2019

Communicated by Björn Stelbrink

Keywords:

Biodiversity
 Ichthyodiversity
 Great Lakes
 Undescribed species

ABSTRACT

Ancient Lake Tanganyika in East Africa houses the world's ecologically and morphologically most diverse assemblage of cichlid fishes, and the third most species-rich after lakes Malawi and Victoria. Despite long-lasting scientific interest in the cichlid species flocks of the East African Great Lakes, for example in the context of adaptive radiation and explosive diversification, their taxonomy and systematics are only partially explored; and many cichlid species still await their formal description. Here, we provide a current inventory of the cichlid fish fauna of Lake Tanganyika, providing a complete list of all valid 208 Tanganyikan cichlid species, and discuss the taxonomic status of more than 50 undescribed taxa on the basis of the available literature as well as our own observations and collections around the lake. This leads us to conclude that there are at least 241 cichlid species present in Lake Tanganyika, all but two are endemic to the basin. We finally summarize some of the major taxonomic challenges regarding Lake Tanganyika's cichlid fauna. The taxonomic inventory of the cichlid fauna of Lake Tanganyika presented here will facilitate future research on the taxonomy and systematics and the ecology and evolution of the species flock, as well as its conservation.

© 2019 The Authors. Published by Elsevier B.V. on behalf of International Association for Great Lakes Research. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Contents

Introduction.....	1067
Cichlid taxonomy	1069
Described Tanganyikan cichlid species	1069
'Museum species'	1072
'Questionable species'	1073
Undescribed Tanganyikan cichlid species	1074
Taxonomic challenges in Lake Tanganyika cichlids	1074
Cases calling for revisions.....	1075
Conclusions	1075
Acknowledgements	1075

Introduction

Ancient lakes, defined here as lakes that have continuously existed for much of the Quaternary period or longer, are well known as biodiversity hot-spots. These long persisting freshwater bodies are typically very deep and rather isolated and usually

house extremely species-rich biological communities featuring exceptional levels of endemism (Brooks, 1950; Martens, 1997). The extraordinary species richness of these lakes is often the product of intralacustrine adaptive radiations, in the course of which a common ancestor diversifies rapidly into new, phenotypically distinct, species that occupy the available ecological niche space (Schluter, 2000; Salzburger et al., 2014). As a matter of fact, some of the most impressive cases of adaptive radiations are known from ancient lakes, as exemplified by the species flocks of cichlid

* Corresponding author.

E-mail address: fabrizia.ronco@unibas.ch (F. Ronco).

fishes in the East African Great Lakes (Fryer and Iles, 1972; Seehausen, 2015; Salzburger, 2018) or the amphipods in Lake Baikal (Macdonald et al., 2005). Besides being hot-spots of organismal diversity, ancient lakes may also serve as species reservoirs over time (Salzburger et al., 2002; Schelly and Stiassny, 2004; Wilson et al., 2004).

Scientific interest in ancient lakes and their faunas is manifold (e.g. Albrecht and Wilke, 2008; Larson and Schaeztl, 2001; Salzburger et al., 2014; Timoshkin et al., 2016; von Rintelen et al., 2014); yet, the different ancient lakes have received different levels of scientific attention. While Lake Baikal and the Laurentian Great Lakes are considered the best studied lakes in the world, the East African Great Lakes are under-studied in various aspects, for example with respect to their faunas and especially when it comes to taxa other than the cichlids (Salzburger et al., 2014). But even for the cichlid species flocks of the East African Great Lakes, which have been in the focus of taxonomic and speciation research for more than a century, the basic taxonomic structure is often poorly investigated. In Lake Malawi, for example, less than half of the estimated number of 800–1000 species are nominally described (Snoeks, 2000, 2004). Likewise, in Lake Victoria, only about 25% of the estimated amount of endemic species are described (Snoeks, 2000).

The situation is somewhat different for Lake Tanganyika, for which a much more comprehensive taxonomic record for cichlids is available (Snoeks et al., 1994). This is – at least to some extent – because the Tanganyikan cichlid species show greater differences to each other facilitating their classification (Snoeks, 2000), which can in turn be attributed to the relatively greater age of the lake's species flock compared to those of lakes Victoria (ca. 100–150 ka; Verheyen et al., 2003) and Malawi (ca. 700–800 ka; Malinsky et al., 2018; Meyer et al., 2017) and because of the polyphyletic nature of the Tanganyikan cichlid assemblage (Salzburger et al., 2002, 2005). Besides, there have been distinct periods of increased collection and classification activities with respect to the Tanganyikan cichlid fauna (see below).

Lake Tanganyika is the oldest (~9–12 Ma) of the East African Great Lakes and represents – by means of water volume – the largest body of freshwater in Africa (32,600 km² with a maximum depth of 1470 m) (Cohen et al., 1993; Salzburger et al., 2014). Lake Tanganyika's markedly diverse ichthyofauna is composed of 22 different fish families (Koblmüller et al., 2006; Fermon et al., 2017), including what is arguably the phenotypically most diverse cichlid assemblage in the world (Fryer and Iles, 1972; Salzburger et al., 2014). Apart from the cichlids, Lake Tanganyika is unique among the East African Great Lakes in having the by far highest proportion of endemic and morphologically diverse genera in groups of organisms other than cichlids (Salzburger et al., 2014). It is the Tanganyikan cichlids, however, that rank among the most noted model systems in evolutionary and speciation research (e.g. Irisarri et al., 2018; Muschick et al., 2012; Salzburger, 2018; Theis et al., 2017; Winkelmann et al., 2014), behavioural biology (e.g. Jungwirth et al., 2015; Theis et al., 2012; Young et al., 2019), and the study of the molecular mechanisms of trait evolution (e.g. Böhne et al., 2016; Santos et al., 2014). Despite the general interest in Tanganyikan cichlids, most previous studies have either focused on one particular species, on a sub-group of species (e.g. a genus or a tribe), or on a subset of taxa occurring in a particular area of the lake as a representative for the Tanganyikan cichlid radiation. As a consequence, some species and/or geographic regions are thoroughly investigated, whereas others remain under-studied. Overall, the scientific literature is vague when it comes to the actual number of cichlid species found in Lake Tanganyika, and even more so for other African Great Lakes. Well established online databases – such as FishBase (Froese and Pauly, 2019) or the Catalog of Fishes (Fricke et al., 2019) – are of moderate help in this con-

text as these are restricted to contain information about described species and their level of completeness depends on their curation, whereas undescribed species and varieties of existing species have mainly been discussed in extensive monographs (Konings, 2015) and/or hobbyists' journals.

Here we provide a concise overview of the currently described, valid cichlid species of Lake Tanganyika and list so far undescribed species as well as local varieties, taking into consideration the available literature including all first descriptions of cichlid species from the lake, as well as personal observations during many years of field collections (1980–2018) covering the majority of the shoreline of Lake Tanganyika (see Fig. 1). Note that we only considered species which we observed, and/or which have been reported to occur in the lake itself (i.e. lacustrine species), whereas purely riverine species are not discussed.

We do not aim to challenge or revise the taxonomic status of any of the described cichlid species from Lake Tanganyika. Instead, we (i) provide an up-to-date inventory of all Lake Tanganyika cichlid species considered valid in the light of the International Code of Zoological Nomenclature; (ii) report candidate taxa for future descriptions as new species based on personal observations and opinions; and (iii) identify the major areas of taxonomic uncertainty with regard to the cichlid species flock of Lake Tanganyika. The species inventory of Lake Tanganyika cichlids, compiled to

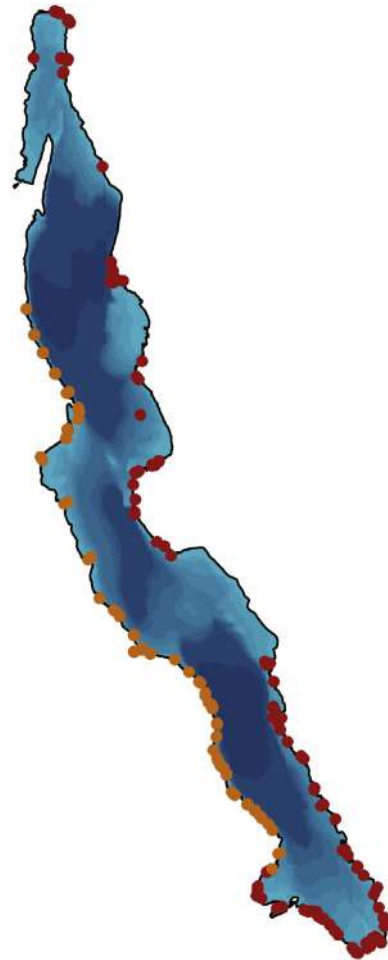


Fig. 1. Map of Lake Tanganyika with indicated localities visited for collection and diving activities. Orange circles represent sites visited before 1998 by only one author (HHB), red circles indicate locations sampled between 2007 and 2018 by all authors. Darker areas in the lake illustrate the three sub-basins of Lake Tanganyika. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the best of our knowledge, will serve as valuable resource for the scientific community interested in the Tanganyikan cichlid fish fauna.

Cichlid taxonomy

Before reviewing the current taxonomy of the cichlid fauna of Lake Tanganyika, we briefly discuss some of the general problems associated with the delineation of species in cichlids, in which, for various reasons, the classic species concepts are often not effective (reviewed in Salzburger, 2018). A first challenge emerges from the species-richness of the cichlid species flocks themselves, as it is often difficult for taxonomists to keep track of this diversity and to identify unambiguous characters on the basis of which species can be distinguished (Kornfield and Smith, 2000; Snoeks, 2000). The various cichlid species in the East African Great Lakes are very closely related, as a consequence of their origin via rapid adaptive radiation, which adds another level of complexity to taxonomic work (see e.g. Shaffer and Thomson, 2007; Van Steenberge et al., 2018). Furthermore, since the cichlid adaptive radiations are still ongoing, the boundaries between populations of the same species and two distinct species are often transitional (see e.g. Theis et al., 2014; Pauquet et al., 2018), making it difficult to draw a line between the alternatives that two sister-taxa are two species, rather than just one. Species delineation is further complicated by past introgressive hybridization events and ongoing gene flow between species, which appear to be rather common in cichlids (Anseeuw et al., 2012; Gante et al., 2016; Meier et al., 2017; Meyer et al., 2017; Irisarri et al., 2018). Finally, different approaches towards cichlid classification have been adopted over time, among taxonomists, and also among the radiations. What is considered a species thus differs among the cichlid species flocks of lakes Victoria, Malawi and Tanganyika. For example, whereas in lakes Victoria and Malawi, a difference in male nuptial colouration can be the sole diagnostic character distinguishing two species, different 'colour-morphs' are typically combined into the same species in Lake Tanganyika. This situation might partially reflect differences in the contribution of underlying evolutionary processes among the cichlid adaptive radiations in the East African Great Lakes (Van Steenberge et al., 2018). However, also within Lake Tanganyika, different criteria have been used in the delineation of cichlid species, and some valid species are separated by minor differences only. For example, *Neolamprologus longior* (Staeck, 1980) differs from its congener *N. leleupi* (Poll, 1956) by slight differences in body proportions and colouration only. Note that *N. longior*, among many other species, has initially been described as a sub-species. However, Poll (1986) refuted this concept for Lake Tanganyika cichlids and elevated all previously existing sub-species to the species level.

Species delineation in general, and in cichlids in particular is not an easy task and should incorporate the available suite of methods in an integrative framework (see Van Steenberge et al., 2015, 2018). Clearly, a uniform treatment in species delineation would be desirable; even if, at the end, each case has to be studied thoroughly and assessed individually. A re-evaluation of the Tanganyikan cichlid species and/or the revision of the taxonomic status of certain species is beyond the scope of this work. Instead, we aim to provide an overview of the current taxonomic status of the cichlid fish fauna of Lake Tanganyika. In the following, we subdivide the taxonomic diversity of Tanganyikan cichlids into the two categories 'described' and 'undescribed' species, whereby the former category includes what we classify as 'questionable species' and 'museum species'. This subdivision is to account for the situation that some Tanganyikan cichlids have been studied in much more detail than others, with many of them still awaiting formal

description, while again others have not been observed since their first description.

Described Tanganyikan cichlid species

It took a bit more than 30 years after Richard F. Burton (1821–1890) and John H. Speke (1827–1864) – in search of the source of the Nile – discovered Lake Tanganyika in 1858 (Burton, 1860) until the first lacustrine cichlids of Lake Tanganyika were described (Günther, 1894). Among them was *Astatotilapia burtoni* (Günther, 1894), a haplochromine species inhabiting the vegetated littoral zone of the lake as well as adjacent rivers and swamps. This widespread species has become one of the best studied cichlids and a common model species for behavioural, developmental and molecular studies (e.g. Böhne et al., 2016; Santos et al., 2014; Theis et al., 2012; Weitekamp and Hofmann, 2017).

After the first species descriptions by Albert K. L. G. Günther (1830–1914) in 1894, the number of formally described species increased rapidly around 1900 due to the comprehensive taxonomic work by George A. Boulenger (1858–1937) based on collections from expeditions to Lake Tanganyika conducted between 1894 and 1905 (see Fig. 2 and Table 1). A second major increase in species descriptions occurred between the 1940s and the 1980s through the extensive work of Max Poll (1908–1991) on the collections of the Belgian expedition to the lake between 1946 and 1947 (see Fig. 2 and Table 1). It was also Poll (Poll, 1986) who grouped the – at the time – 173 described Tanganyikan cichlid species into 12 tribes based on meristic and anatomical characters (note that in taxonomy a tribe is the rank between the genus and the family level). Subsequent taxonomic and molecular phylogenetic work erected additional tribes for some genera, while merging other tribes (Takahashi, 2003; Takahashi and Koblmüller, 2011; Dunz and Schlieven, 2013). According to our accounts, 208 cichlid species belonging to 57 genera and 16 tribes are described from Lake Tanganyika to date (including valid, lacustrine species only), while new taxa are added nearly every year (see Fig. 2 and Table 1). Our assignment of species into tribes largely follows the

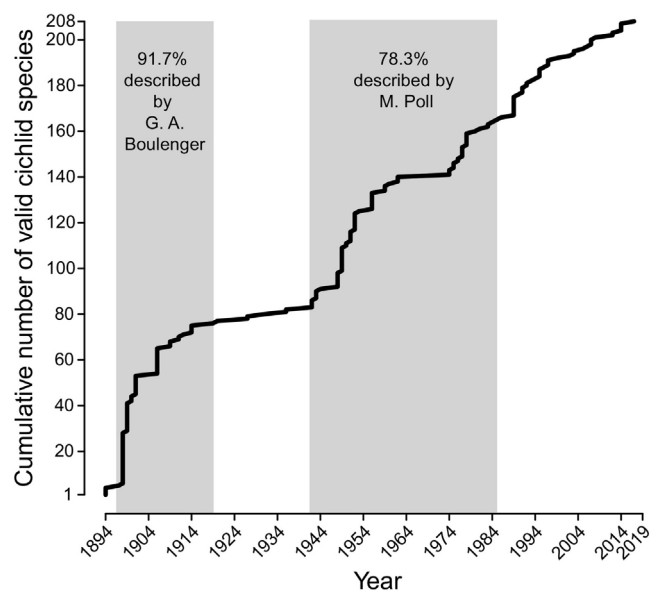


Fig. 2. Cumulative number of described cichlid species over time. The number of described species increased over the years steadily with a major increment around 1900, by the extensive work by George Boulenger, followed by a second steep ascent between the 1940's and the 1980's due to Max Poll's contributions. Note that only currently valid species are included, all later synonymized species are not considered in this study (see Table 1 for references).

Table 1

List of described, valid, lacustrine cichlid species of Lake Tanganyika. For each of the 208 species the tribe assignment, the initial name upon description, and the reported type locality are provided. If no holotype has been assigned, the sampling localities of the syntypes are listed. Note that for the two species *L. kungweensis* and *N. brichardi* the species name has changed and therefore both names and references are listed. Only native and still valid species have been considered. Superscript notation: ¹ Species we consider as 'museum species'; ² Species we consider as 'questionable species'; ³ Species with affinity to rivers, occurring in the lake and in the Lake Tanganyika basin; ⁴ Species not endemic to the Lake Tanganyika basin. LT = Lake Tanganyika; BUR = Burundi; DRC = Democratic Republic of Congo; TAN = Tanzania; ZAM = Zambia.

tribe	valid name	description	initial name upon description	type locality
Bathybatini	<i>Bathybates fasciatus</i>	Boulenger, 1901	<i>Bathybates fasciatus</i>	West Coast
	<i>Bathybates ferox</i>	Boulenger, 1898	<i>Bathybates ferox</i>	Kinyamkolo (= Mpulungu, ZAM)
	<i>Bathybates graueri</i>	Steindachner, 1911	<i>Bathybates graueri</i>	LT
	<i>Bathybates homii</i>	Steindachner, 1911	<i>Bathybates homii</i>	LT
	<i>Bathybates leo</i>	Poll, 1956	<i>Bathybates leo</i>	Nyanza Lac (BUR)
	<i>Bathybates minor</i>	Boulenger, 1906	<i>Bathybates minor</i>	Kituta (= Chituta Bay, ZAM), Lofu (= Lufubu, ZAM)
	<i>Bathybates vittatus</i>	Boulenger, 1914	<i>Bathybates vittatus</i>	Kilewa Bay (DRC)
	<i>Hemibates koningsi</i>	Schedel and Schlieven, 2017	<i>Hemibates koningsi</i>	Mpulungu (ZAM)
	<i>Hemibates stenosoma</i>	(Boulenger, 1901)	<i>Paratilapia stenosoma</i>	south end of LT (ZAM) and Maswa, south of Ujiji (TAN)
	Benthochromini	<i>Benthochromis horii</i>	Takahashi, 2008	<i>Benthochromis horii</i>
<i>Benthochromis melanoides</i>		(Poll, 1984)	<i>Haplotaxodon melanoides</i>	Albertville (= Kalemie, DRC)
Boulengerochromini	<i>Boulengerochromis tricoti</i>	(Poll, 1948)	<i>Haplotaxodon tricoti</i>	Karema (TAN), Moba Bay (DRC)
	<i>Boulengerochromis microlepis</i>	(Boulenger, 1899b)	<i>Tilapia microlepis</i>	Moliro (DRC)
Coptodini	<i>Coptodon rendalli</i> ^{3,4}	(Boulenger, 1897)	<i>Chromis rendalli</i>	Upper Shire River (Malawi)
Cyphotilapiini	<i>Ctenochromis benthicola</i>	(Matthes, 1962)	<i>Haplochromis benthicola</i>	Kalundu (DRC)
	<i>Cyphotilapia frontosa</i>	(Boulenger, 1906)	<i>Paratilapia frontosa</i>	Kigoma (TAN)
Cyprichromini	<i>Cyphotilapia gibberosa</i>	Takahashi and Nakaya, 2003	<i>Cyphotilapia gibberosa</i>	Kasenga (ZAM)
	<i>Cyprichromis coloratus</i>	Takahashi and Hori, 2006	<i>Cyprichromis coloratus</i>	Wonzye Point (ZAM)
	<i>Cyprichromis leptosoma</i>	(Boulenger, 1898)	<i>Paratilapia leptosoma</i>	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)
	<i>Cyprichromis microlepidotus</i>	(Poll, 1956)	<i>Limnochromis microlepidotus</i>	Ubwari (DRC)
	<i>Cyprichromis pavo</i>	Büscher, 1994	<i>Cyprichromis pavo</i>	Tembwe (DRC)
	<i>Cyprichromis zonatus</i>	Takahashi et al., 2002	<i>Cyprichromis zonatus</i>	Kasenga (ZAM)
	<i>Paracyprichromis brienii</i>	(Poll, 1981)	<i>Cyprichromis brienii</i>	Ubwari (DRC)
	<i>Paracyprichromis nigripinnis</i>	(Boulenger, 1901)	<i>Paratilapia nigripinnis</i>	Msambu (= Msamba, TAN)
	<i>Asprottilapia leptura</i>	Boulenger, 1901	<i>Asprottilapia leptura</i>	Msambu (= Msamba, TAN)
	<i>Aulonocranus dewindti</i>	(Boulenger, 1899b)	<i>Paratilapia dewindti</i>	Moliro (DRC)
Ectodini	<i>Callochromis macrops</i>	(Boulenger, 1898)	<i>Paratilapia macrops</i>	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)
	<i>Callochromis melanostigma</i>	(Boulenger, 1906)	<i>Pelmatochromis melanostigma</i>	Uvira (DRC), Kaboge (DRC), Niamkolo (= Mpulungu, ZAM), Lofu (= Lufubu, ZAM), Kituta (= Chituta Bay, ZAM)
	<i>Callochromis pleurospilus</i>	(Boulenger, 1906)	<i>Pelmatochromis pleurospilus</i>	Mpala (DRC), Tembwi (= Cap Tembwe, DRC)
	<i>Cardiopharynx schoutedeni</i>	Poll, 1942	<i>Cardiopharynx schoutedeni</i>	Usumbura (= Bujumbura, BUR)
	<i>Cunningtonia longiventralis</i>	Boulenger, 1906	<i>Cunningtonia longiventralis</i>	Niamkolo (= Mpulungu, ZAM)
	<i>Cyathopharynx foae</i>	(Vaillant, 1899)	<i>Ectodus foae</i>	LT, south
	<i>Cyathopharynx furcifer</i>	(Boulenger, 1898)	<i>Paratilapia furcifer</i>	Kinyamkolo (= Mpulungu, ZAM)
	<i>Ectodus descampsii</i>	Boulenger, 1898	<i>Ectodus descampsii</i>	LT
	<i>Enantiopus melanogenys</i>	(Boulenger, 1898)	<i>Ectodus melanogenys</i>	LT
	<i>Grammatotria lemairii</i>	Boulenger, 1899b	<i>Grammatotria lemairii</i>	Moliro (DRC)
	<i>Lestradea perspicax</i>	Poll, 1943	<i>Lestradea perspicax</i>	Rumonge (BUR)
	<i>Lestradea stappersii</i>	(Poll, 1943)	<i>Ophthalmotilapia stappersii</i>	Kilewa Bay (DRC)
	<i>Microdontochromis rotundiventralis</i>	Takahashi et al., 1997	<i>Microdontochromis rotundiventralis</i>	Nkumbula Island (ZAM)
	<i>Microdontochromis tenuidentata</i>	(Poll, 1951b)	<i>Xenotilapia tenuidentata</i>	Baie de Vua (= Livua, DRC)
	<i>Ophthalmotilapia boops</i>	(Boulenger, 1901)	<i>Tilapia boops</i>	Msambu (= Msamba, TAN)
	<i>Ophthalmotilapia heterodonta</i>	(Poll and Matthes, 1962)	<i>Oph. ventralis heterodontus</i>	Mboko Island (DRC)
	<i>Ophthalmotilapia nasuta</i>	(Poll and Matthes, 1962)	<i>Ophthalmochromis nasutus</i>	Kalungwe (DRC)
	<i>Ophthalmotilapia ventralis</i>	(Boulenger, 1898)	<i>Paratilapia ventralis</i>	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)
	<i>Xenotilapia bathyphilus</i>	(Poll, 1956)	<i>Xenotilapia ochrogenys bathyphilus</i>	Sumbu (ZAM)
	<i>Xenotilapia boulengeri</i>	(Poll, 1942)	<i>Enantiopus boulengeri</i>	Rumonge (BUR)
<i>Xenotilapia burtoni</i>	(Poll, 1951a)	<i>Xenotilapia longispinis burtoni</i>	Burton Bay (DRC)	
<i>Xenotilapia caudafasciata</i>	Poll, 1951b	<i>Xenotilapia caudafasciata</i>	Moba Bay (DRC)	
<i>Xenotilapia flavipinnis</i>	Poll, 1985	<i>Xenotilapia flavipinnis</i>	Bujumbura (BUR)	
<i>Xenotilapia longispinis</i>	Poll, 1951a	<i>Xenotilapia longispinis</i>	Ruzizi (BUR)	
<i>Xenotilapia nasus</i>	De Vos et al., 1995	<i>Xenotilapia nasus</i>	Gitaza, 29km south of Bujumbura (BUR)	
<i>Xenotilapia nigrolabiata</i>	Poll, 1951b	<i>Xenotilapia nigrolabiata</i>	M'Samba (= Msamba, TAN)	
<i>Xenotilapia ochrogenys</i>	(Boulenger, 1914)	<i>Enantiopus ochrogenys</i>	Kilewa Bay (DRC)	
<i>Xenotilapia ornatipinnis</i>	Boulenger, 1901	<i>Xenotilapia ornatipinnis</i>	Kibwesi (= Kibwesa/ Sibwesa, TAN)	
<i>Xenotilapia papilio</i>	Büscher, 1990	<i>Xenotilapia papilio</i>	Tembwe, (DRC)	
<i>Xenotilapia sima</i>	Boulenger, 1899b	<i>Xenotilapia sima</i>	Moliro (DRC)	
<i>Xenotilapia singularis</i>	(Boulenger, 1914)	<i>Stappersia singularis</i>	Kilewa Bay (DRC), Tulo (DRC)	
<i>Xenotilapia spilopterus</i>	Poll and Stewart, 1975	<i>Xenotilapia spilopterus</i>	Nkumbula Island (ZAM)	
<i>Eretmodus cyanostictus</i>	Boulenger, 1898	<i>Eretmodus cyanostictus</i>	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)	
<i>Eretmodus marksmithi</i>	Burgess, 2012	<i>Eretmodus marksmithi</i>	Makombe (BUR)	
<i>Spathodus erythrodon</i>	Boulenger, 1900	<i>Spathodus erythrodon</i>	Albertville (= Mtoa, DRC)	
<i>Spathodus marlieri</i>	Poll, 1950	<i>Spathodus marlieri</i>	Uvira (DRC)	
<i>Tanganicodus irsacae</i>	Poll, 1950	<i>Tanganicodus irsacae</i>	Uvira (DRC)	
<i>Astatotilapia burtoni</i> ³	(Günther, 1894)	<i>Chromis burtoni</i>	LT	
<i>Astatoreochromis straeleni</i> ³	(Poll, 1944)	<i>Haplochromis straeleni</i>	Lukuga river	
<i>Haplochromis stappersii</i> ³	Poll, 1943	<i>Haplochromis stappersii</i>	Lufuku river (= Mpala, DRC)	
<i>Ctenochromis horei</i>	Günther, 1894	<i>Chromis horei</i>	LT	
<i>Gnathochromis pfefferi</i>	(Boulenger, 1898)	<i>Paratilapia pfefferi</i>	Kinyamkolo (= Mpulungu, ZAM)	
<i>Interochromis loocki</i>	(Poll, 1949)	<i>Limnotilapia loocki</i>	Kigoma (TAN)	
<i>Limnotilapia dardennii</i>	(Boulenger, 1899b)	<i>Tilapia dardennii</i>	Moliro (DRC)	
<i>Lobochilotes labiatus</i>	(Boulenger, 1898)	<i>Tilapia labiata</i>	Kinyamkolo (= Mpulungu, ZAM)	
<i>Petrochromis ephippium</i>	(Brichard, 1989)	<i>Petrochromis trewavasae ephippium</i>	LT	
<i>Petrochromis famula</i>	Matthes and Trewavas, 1960	<i>Petrochromis famula</i>	LT	
<i>Petrochromis fasciolatus</i>	Boulenger, 1914	<i>Petrochromis fasciolatus</i>	Kapampa (DRC), Kilewa Bay (DRC)	
<i>Petrochromis horii</i>	Takahashi and Koblmüller, 2014	<i>Petrochromis horii</i>	Kasenga (ZAM)	
<i>Petrochromis macrognathus</i>	Yamaoka, 1983	<i>Petrochromis macrognathus</i>	Luhanga (DRC)	
<i>Petrochromis orthognathus</i>	Matthes, 1959a	<i>Petrochromis orthognathus</i>	Bemba (DRC)	
<i>Petrochromis polyodon</i>	Boulenger, 1898	<i>Petrochromis polyodon</i>	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)	
<i>Petrochromis trewavasae</i>	Poll, 1948	<i>Petrochromis trewavasae</i>	Moliro (DRC)	
<i>Pseudosimochromis babaulti</i>	(Pellegrin, 1927b)	<i>Simochromis babaulti</i>	Ouvira (= Uvira (DRC)	
<i>Pseudosimochromis curvifrons</i>	(Poll, 1942)	<i>Simochromis curvifrons</i>	Nyanza Lac (BUR)	
<i>Pseudosimochromis margaretae</i> ¹	(Axelrod and Harrison, 1978)	<i>Simochromis margaretae</i>	Kigoma (TAN)	
<i>Pseudosimochromis marginatus</i>	(Poll, 1956)	<i>Simochromis marginatus</i>	Manga (= Cape Banza area, DRC)	
<i>Simochromis diagramma</i>	(Günther, 1894)	<i>Chromis diagramma</i>	LT	
<i>Tropheus annectens</i>	Boulenger, 1900	<i>Tropheus annectens</i>	Albertville (= Mtoa, DRC)	
<i>Tropheus brichardi</i>	Nelissen and Thys van den Audenaerde, 1975	<i>Tropheus brichardi</i>	Nyanza Lac (BUR)	
<i>Tropheus duboisi</i>	Marlier, 1959	<i>Tropheus duboisi</i>	Bemba (DRC)	
<i>Tropheus kasabae</i> ²	(Nelissen, 1977)	<i>Tropheus moorii kasabae</i>	Kasaba Bay (= Kala Bay, ZAM)	
<i>Tropheus moorii</i>	Boulenger, 1898	<i>Tropheus moorii</i>	Kinyamkolo (= Mpulungu, ZAM)	
<i>Tropheus polli</i> ²	Axelrod, 1977	<i>Tropheus polli</i>	Bulu Island (= Karilani Island, TAN)	

tribe	valid name	description	initial name upon description	type locality
Lamprologini	<i>Altalamprologus calvus</i>	(Poll, 1978)	<i>Lamprologus calvus</i>	Chipimbi (ZAM)
	<i>Altalamprologus compressiceps</i>	(Boulenger, 1898)	<i>Lamprologus compressiceps</i>	Kinyamkolo (= Mpulungu, ZAM)
	<i>Chalinochromis brichardi</i>	Poll, 1974	<i>Chalinochromis brichardi</i>	south of Bujumbura (BUR)
	<i>Chalinochromis cyanophleps</i>	Kullander et al., 2014a	<i>Chalinochromis cyanophleps</i>	Namansi (TAN)
	<i>Chalinochromis popelini</i>	Richard, 1989	<i>Chalinochromis popelini</i>	Moba (DRC)
	<i>Julidochromis dickfeldi</i>	Staack, 1975	<i>Julidochromis dickfeldi</i>	between Cape Kachese and Cape Kamwankoko (ZAM)
	<i>Julidochromis marksmithi</i>	Burgess, 2014	<i>Julidochromis marksmithi</i>	Kerenge Island (TAN)
	<i>Julidochromis marlieri</i>	Poll, 1956	<i>Julidochromis marlieri</i>	Makobola (DRC)
	<i>Julidochromis ornatus</i>	Boulenger, 1898	<i>Julidochromis ornatus</i>	Mbity Rocks (= Mbita Rocks, ZAM)
	<i>Julidochromis regani</i>	Poll, 1942	<i>Julidochromis regani</i>	Nyanza Lac (BUR)
	<i>Julidochromis transcriptus</i>	Matthes, 1959b	<i>Julidochromis transcriptus</i>	Makobola (DRC)
	<i>Lamprologus callipterus</i>	Boulenger, 1906	<i>Lamprologus callipterus</i>	Mpala (DRC), Niamkolo (= Mpulungu, ZAM)
	<i>Lamprologus finalimus</i> ¹	Nichols and LaMonte, 1931	<i>Lamprologus finalimus</i>	Uvira (DRC)
	<i>Lamprologus kungweensis</i>	Poll, 1956	<i>Lam. ocellatus</i> (Poll, 1952) > <i>Lam. kungweensis</i> (Poll, 1956)	Kungwe Bay (TAN)
	<i>Lamprologus laparogramma</i>	Bills and Ribbink, 1997	<i>Lamprologus laparogramma</i>	Mpulungu (ZAM)
	<i>Lamprologus lemairi</i>	Boulenger, 1899b	<i>Lamprologus lemairi</i>	Moliro (DRC)
	<i>Lamprologus meleagris</i>	Büscher, 1991b	<i>Lamprologus meleagris</i>	Bwassa (DRC)
	<i>Lamprologus ocellatus</i>	(Steindachner, 1909b)	<i>Julidochromis ocellatus</i>	LT
	<i>Lamprologus ornatipinnis</i>	Poll, 1949	<i>Lamprologus ornatipinnis</i>	south of Mtoto, before Moba (DRC)
	<i>Lamprologus signatus</i>	Poll, 1952	<i>Lamprologus signatus</i>	Moba (DRC)
	<i>Lamprologus speciosus</i>	Büscher, 1991b	<i>Lamprologus speciosus</i>	Bwassa (DRC)
	<i>Lamprologus stappersi</i> ¹	Pellegrin, 1927a	<i>Lamprologus stappersi</i>	Sambala River (DRC)
	<i>Lepidolamprologus attenuatus</i>	(Steindachner, 1909b)	<i>Lamprologus attenuatus</i>	LT
	<i>Lepidolamprologus cunningtoni</i>	(Boulenger, 1906)	<i>Lamprologus cunningtoni</i>	Moliro (DRC)
	<i>Lepidolamprologus elongatus</i>	(Boulenger, 1898)	<i>Lamprologus elongatus</i>	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)
	<i>Lepidolamprologus kamambae</i>	Kullander et al., 2012	<i>Lepidolamprologus kamambae</i>	Kamamba Island (TAN)
	<i>Lepidolamprologus kendalli</i>	(Poll and Stewart, 1977)	<i>Lamprologus kendalli</i>	Mutondwe Island (ZAM)
	<i>Lepidolamprologus mimicus</i>	Schelly et al., 2007	<i>Lepidolamprologus mimicus</i>	Chituta Bay (ZAM)
	<i>Lepidolamprologus nkambae</i> ²	(Staack, 1978)	<i>Lamprologus nkambae</i>	Nkamba Bay (ZAM)
	<i>Lepidolamprologus profundicola</i>	(Poll, 1949)	<i>Lamprologus profundicola</i>	Cap Tembwe (DRC)
	<i>Neolamprologus bifasciatus</i>	Büscher, 1993	<i>Neolamprologus bifasciatus</i>	Lunangwa (DRC)
	<i>Neolamprologus boulengeri</i>	(Steindachner, 1909b)	<i>Julidochromis boulengeri</i>	LT
	<i>Neolamprologus brevis</i>	(Boulenger, 1899a)	<i>Lamprologus brevis</i>	Albertville (= Mtoa, DRC), in the mouth of a Catfish
	<i>Neolamprologus brichardi</i>	Poll, 1974	<i>Lam. savoryi elongatus</i> (Trewavas and Poll, 1952) > <i>N. brichardi</i> (Poll, 1974)	Kisoje (= Cape Kungwe area, TAN)
	<i>Neolamprologus buescheri</i>	(Staack, 1983)	<i>Lamprologus buescheri</i>	Cape Kachese (ZAM)
	<i>Neolamprologus calliurus</i>	(Boulenger, 1906)	<i>Lamprologus calliurus</i>	Tembwi (= Cap Tembwe, DRC)
	<i>Neolamprologus cancellatus</i> ²	Aibara et al., 2005	<i>Neolamprologus cancellatus</i>	Wonzy Point (ZAM)
	<i>Neolamprologus caudopunctatus</i>	(Poll, 1978)	<i>Lamprologus caudopunctatus</i>	Cape Kabeyeye (ZAM)
	<i>Neolamprologus chitamwebwai</i>	Verburg and Bills, 2007	<i>Neolamprologus chitamwebwai</i>	Cape Bangwe (TAN)
	<i>Neolamprologus christyi</i>	(Trewavas and Poll, 1952)	<i>Lamprologus christyi</i>	Mtosi (TAN)
	<i>Neolamprologus crassus</i>	(Brichard, 1989)	<i>Lamprologus crassus</i>	Luhanga Bay (DRC)
	<i>Neolamprologus cylindricus</i>	Staack and Seegers, 1986	<i>Neolamprologus cylindricus</i>	Chipwa (ZAM)
	<i>Neolamprologus falcicula</i>	Brichard, 1989	<i>Lamprologus falcicula</i>	Magara (BUR)
	<i>Neolamprologus fasciatus</i>	(Boulenger, 1898)	<i>Lamprologus fasciatus</i>	Kinyamkolo (= Mpulungu, ZAM)
	<i>Neolamprologus furcifer</i>	(Boulenger, 1898)	<i>Lamprologus furcifer</i>	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)
	<i>Neolamprologus gracilis</i>	(Brichard, 1989)	<i>Lamprologus gracilis</i>	Masanza (DRC)
	<i>Neolamprologus hecqui</i> ¹	(Boulenger, 1899a)	<i>Lamprologus hecqui</i>	Albertville (= Mtoa, DRC), in the mouth of a Catfish
	<i>Neolamprologus helianthus</i>	Büscher, 1997	<i>Neolamprologus helianthus</i>	Kamakonde (DRC)
	<i>Neolamprologus leleupi</i>	(Poll, 1956)	<i>Lamprologus leleupi</i>	Luhanga (DRC)
	<i>Neolamprologus leloupi</i>	(Poll, 1948)	<i>Lamprologus leloupi</i>	Mtoto (DRC)
	<i>Neolamprologus longicaudatus</i>	Nakaya and Gashagaza, 1995	<i>Neolamprologus longicaudatus</i>	Cape Banza, Ubwari Peninsula (DRC)
	<i>Neolamprologus longior</i>	(Staack, 1980)	<i>Neolamprologus leleupi longior</i>	between Kabogo point and Kibwe Bay (TAN)
	<i>Neolamprologus marunguensis</i>	Büscher, 1989	<i>Neolamprologus marunguensis</i>	Kapampa (DRC)
	<i>Neolamprologus meeli</i>	(Poll, 1948)	<i>Lamprologus meeli</i>	Katibili (DRC)
	<i>Neolamprologus modestus</i>	(Boulenger, 1898)	<i>Lamprologus modestus</i>	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)
	<i>Neolamprologus mondabu</i>	(Boulenger, 1906)	<i>Lamprologus mondabu</i>	Kaboge (= Kabogo, TAN)
	<i>Neolamprologus multifasciatus</i>	(Boulenger, 1906)	<i>Lamprologus multifasciatus</i>	Niamkolo Bay (= Mpulungu, ZAM)
	<i>Neolamprologus mustax</i>	(Poll, 1978)	<i>Lamprologus mustax</i>	Cape Nundo (ZAM)
	<i>Neolamprologus niger</i>	(Poll, 1956)	<i>Lamprologus niger</i>	Luhanga (DRC)
	<i>Neolamprologus nigriventris</i>	(Büscher, 1992b)	<i>Lamprologus nigriventris</i>	Lunangwa (DRC)
	<i>Neolamprologus obscurus</i>	(Poll, 1978)	<i>Lamprologus obscurus</i>	Cape Chipimbi (ZAM)
	<i>Neolamprologus olivaceus</i>	(Brichard, 1989)	<i>Lamprologus olivaceus</i>	Luhanga Bay (= Lunangwa Bay, DRC)
	<i>Neolamprologus pectoralis</i>	Büscher, 1991a	<i>Neolamprologus pectoralis</i>	Tembwe (DRC)
	<i>Neolamprologus petricola</i>	Poll, 1949	<i>Lamprologus petricola</i>	Mtoto Bay (DRC)
	<i>Neolamprologus pleuromaculatus</i>	(Trewavas and Poll, 1952)	<i>Lamprologus pleuromaculatus</i>	Usumbura (= Bujumbura, BUR)
	<i>Neolamprologus prochilus</i>	(Bailey and Stewart, 1977)	<i>Lamprologus prochilus</i>	Nyika Bay, Nkumbula Island, 2km north of Mpulungu (ZAM)
	<i>Neolamprologus pulcher</i>	(Trewavas and Poll, 1952)	<i>Lamprologus savoryi pulcher</i>	Kasanga (TAN)
	<i>Neolamprologus savoryi</i>	(Poll, 1949)	<i>Lamprologus savoryi</i>	Kigoma (TAN)
	<i>Neolamprologus schreyeni</i>	(Poll, 1974)	<i>Lamprologus schreyeni</i>	La chute (= 35 km south of Bujumbura, BUR)
	<i>Neolamprologus sexfasciatus</i>	(Trewavas and Poll, 1952)	<i>Lamprologus sexfasciatus</i>	Mtoto (DRC)
	<i>Neolamprologus similis</i>	Büscher, 1992a	<i>Neolamprologus similis</i>	Zongwe (DRC)
	<i>Neolamprologus splendens</i>	(Brichard, 1989)	<i>Lamprologus splendens</i>	Cape Zongwe (DRC)
	<i>Neolamprologus tetracanthus</i>	(Boulenger, 1899a)	<i>Lamprologus tetracanthus</i>	Albertville (= Mtoa, DRC)
	<i>Neolamprologus timidus</i>	Kullander et al., 2014b	<i>Neolamprologus timidus</i>	Ulwile Island (TAN)
	<i>Neolamprologus toae</i>	(Poll, 1949)	<i>Lamprologus toae</i>	Kavala Island, Braconé Bay (= Biila Island, DRC)
	<i>Neolamprologus tretocephalus</i>	(Boulenger, 1899a)	<i>Lamprologus tretocephalus</i>	Albertville (= Mtoa, DRC)
	<i>Neolamprologus variostigma</i>	Büscher, 1995b	<i>Neolamprologus variostigma</i>	Tembwe (DRC)
	<i>Neolamprologus ventralis</i>	Büscher, 1995a	<i>Neolamprologus ventralis</i>	Tembwe (DRC)
	<i>Neolamprologus walteri</i>	Verburg and Bills, 2007	<i>Neolamprologus walteri</i>	Tembo Rock (TAN)
	<i>Neolamprologus wauthioni</i> ¹	(Poll, 1949)	<i>Lamprologus wauthioni</i>	between Camp Jaques (Albertville = Kalemie, DRC) & Katibili (DRC)
	<i>Telmatochromis bifrenatus</i>	Myers, 1936	<i>Telmatochromis bifrenatus</i>	Kigoma (TAN)
	<i>Telmatochromis brachygnathus</i>	Hanssens and Snoeks, 2003	<i>Telmatochromis brachygnathus</i>	Cape Chaitika (ZAM)
	<i>Telmatochromis brichardi</i>	Louisy, 1989	<i>Telmatochromis brichardi</i>	Usumbura (= Bujumbura, BUR)
	<i>Telmatochromis dhonti</i>	(Boulenger, 1919)	<i>Lamprologus dhonti</i>	Albertville (= Kalemie, DRC)
	<i>Telmatochromis temporalis</i>	Boulenger, 1898	<i>Telmatochromis temporalis</i>	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)
	<i>Telmatochromis vittatus</i>	Boulenger, 1898	<i>Telmatochromis vittatus</i>	Mbity Rocks (= Mbita Rocks, ZAM)
	<i>Variabilichromis moorii</i>	(Boulenger, 1898)	<i>Lamprologus moorii</i>	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)

tribe	valid name	description	initial name upon description	type locality
Limnochromini	<i>Baileychromis centropomoides</i>	(Bailey and Stewart, 1977)	<i>Leptochromis centropomoides</i>	3-4km west of Mpulungu (ZAM)
	<i>Gnathochromis permaxillaris</i>	(David, 1936)	<i>Limnochromis permaxillaris</i>	Rumonge (BUR)
	<i>Greenwoodochromis bellcrossi</i>	(Poll, 1976)	<i>Hemibates bellcrossi</i>	Mutondwe Island (ZAM)
	<i>Greenwoodochromis christyi</i>	(Trewavas, 1953)	<i>Limnochromis christyi</i>	LT
	<i>Limnochromis abeelei</i>	Poll, 1949	<i>Limnochromis abeelei</i>	between Cap Bwana Denge and Moni (DRC)
	<i>Limnochromis auritus</i>	(Boulenger, 1901)	<i>Paratilapia aurita</i>	Msambu (= Msamba, TAN)
	<i>Limnochromis staneri</i>	Poll, 1949	<i>Limnochromis staneri</i>	between Cap Bwana Denge and Moni (DRC)
	<i>Reganochromis calliurus</i>	(Boulenger, 1901)	<i>Paratilapia calliura</i>	Kalambo (TAN/ZAM)
	<i>Tangachromis dhanisi</i>	(Poll, 1949)	<i>Limnochromis dhanisi</i>	south of Mtoto, before Moba (DRC)
	<i>Triglachromis otostigma</i>	(Regan, 1920)	<i>Limnochromis otostigma</i>	Msambu (= Msamba, TAN), Mshale
Oreochromini	<i>Oreochromis niloticus eduardianus</i> ^{3,4}	(Boulenger, 1912)	<i>Tilapia eduardiana</i>	South-eastern slope of Mount Ruwenzoni (Uganda)
	<i>Oreochromis tanganicae</i>	(Günther, 1894)	<i>Chromis tanganicae</i>	LT
Perissodini	<i>Haplotaxodon microlepis</i>	Boulenger, 1906	<i>Haplotaxodon microlepis</i>	Niamkolo (= Mpulungu, ZAM), Kasawa (= Kasama, ZAM), Kasanga (TAN)
	<i>Haplotaxodon trifasciatus</i>	Takahashi and Nakaya, 1999	<i>Haplotaxodon trifasciatus</i>	Nkumbula Island (ZAM)
	<i>Perissodus eccentricus</i>	Liem and Stewart, 1976	<i>Perissodus eccentricus</i>	Chituta Bay (ZAM)
	<i>Perissodus microlepis</i>	Boulenger, 1898	<i>Perissodus microlepis</i>	Mbity Rocks (= Mbitya Rocks, ZAM)
	<i>Plecodus elaviae</i>	Poll, 1949	<i>Plecodus elaviae</i>	Usumbura (= Bujumbura, BUR)
	<i>Plecodus multidentatus</i>	Poll, 1952	<i>Plecodus multidentatus</i>	Moba (DRC)
	<i>Plecodus paradoxus</i>	Boulenger, 1898	<i>Plecodus paradoxus</i>	LT
	<i>Plecodus straeleni</i>	Poll, 1948	<i>Plecodus straeleni</i>	Cap Tembwe (DRC)
	<i>Xenochromis hecqui</i>	Boulenger, 1899a	<i>Xenochromis hecqui</i>	Albertville (= Mtoa, DRC)
	<i>Trematocara caparti</i>	Poll, 1948	<i>Trematocara caparti</i>	Karema (TAN)
Trematocarini	<i>Trematocara kufferathi</i>	Poll, 1948	<i>Trematocara kufferathi</i>	Karema (TAN)
	<i>Trematocara macrostoma</i>	Poll, 1952	<i>Trematocara macrostoma</i>	Moba (DRC)
	<i>Trematocara marginatum</i>	Boulenger, 1899b	<i>Trematocara marginatum</i>	Moliro (DRC)
	<i>Trematocara nigrifrons</i>	Boulenger, 1906	<i>Trematocara nigrifrons</i>	Sumbu (ZAM)
	<i>Trematocara stigmaticum</i>	Poll, 1943	<i>Trematocara stigmaticum</i>	LT
	<i>Trematocara unimaculatum</i>	Boulenger, 1901	<i>Trematocara unimaculatum</i>	Usumbura (= Bujumbura, BUR)
	<i>Trematocara variabile</i>	Poll, 1952	<i>Trematocara variabile</i>	Moba (DRC)
Tylochromini	<i>Trematocara zebra</i>	De Vos et al., 1996	<i>Trematocara zebra</i>	between Luhanga and Pemba (DRC)
	<i>Tylochromis polylepis</i>	(Boulenger, 1900)	<i>Pelmatochromis polylepis</i>	Albertville (= Mtoa, DRC), Kinyamkolo (= Mpulungu, ZAM)

molecular phylogenetics-based studies by Muschick et al. (2012) and Dunz and Schlieven (2013).

We would like to note that this compilation only contains those species, which are still valid; whereas, species that were synonymized subsequent to their description are not considered. Furthermore, we only report native species. Therefore, we did not include the Nile Tilapia, *Oreochromis niloticus* (Linnaeus, 1758). This species was introduced on several occasions in and around Lake Tanganyika but failed to successfully colonize the lacustrine zone of the lake and is mainly found in adjacent rivers. On the other hand, the subspecies *O. niloticus eduardianus* (Boulenger, 1912) was included in our list (see Table 1), as this taxon is considered native in the northern part of Lake Tanganyika.

'Museum species'

Most of the 208 described cichlid species of Lake Tanganyika can more or less readily be encountered while SCUBA diving or snorkelling, or bought on local fish markets. For example, in the last five years alone, we were able to collect specimens of 182 out of the 208 described Tanganyikan cichlid species during fieldwork campaigns in Burundi, the Democratic Republic of Congo (DRC), Tanzania and Zambia, and a similar number of species was photographically documented by a single biologist during ca. 750 h of underwater observations (Konings, 2015). On the other hand, there are five cichlid species that, following their initial description, have never been reported again from the wild (to the best of our knowledge). Here, we refer to these species as 'museum species', since they are only known from the type material in museum collections (see Table 1).

Three of these species, *L. stappersi* Pellegrin, 1927(a), *Neolamprologus hecqui* (Boulenger, 1899a), and *N. wauthioni* (Poll, 1949) have been collected from the western shoreline of Lake Tanganyika and only very little is known about the species' ecology, behaviour or distribution. The assessment of *L. stappersi* and *N. hecqui* is further complicated by the fact that for these species only the holotypes exist in museum collections. This makes it difficult to

compare them to other taxa, as no within-species variance can be determined. On top of this, the only available specimen of *N. hecqui* was collected from the mouth of a catfish (Poll, 1956) and is, hence, not in particularly good shape. Subsequent specimens collected as *N. hecqui* were all re-assigned as *L. meeli* and *L. boulengeri*, respectively (Van Wijngaarden, 1995; Konings, 2015). For *N. wauthioni*, a paratype series comprising 13 specimens collected between 1946 and 1947 has been deposited. Still, this species has never been collected again (except for some incorrectly identified specimens later assigned to *L. ocellatus* (Steindachner, 1909b) by Büscher (2007)). At this time and without new collections, it is difficult to judge whether these three species have unusually small distribution ranges restricted to under-explored sections of the shoreline or may, given their similarity to species described later, be senior synonyms of other taxa.

In contrast, there are two species supposedly occurring in well accessible areas of Lake Tanganyika, which have not been reported again after their descriptions and which we consequently list as additional 'museum species'. *Pseudosimochromis margaretae* (Axelrod and Harrison, 1978) was described on the basis of four specimens collected at a depth of three to six meters in the bay off Kigoma, Tanzania. While members of this genus are generally fairly easy to observe while snorkelling, we failed to collect or observe this species, despite intensive sampling, diving, and snorkelling activities at the reported type locality or elsewhere. The other species is *Lamprologus finalimus* Nichols and LaMonte, 1931 for which only the holotype exists. Intensive collection and research activities at and around the type locality in more recent years (see e.g. Van Steenberge et al., 2011; Mushagalusa et al., 2014; Fermon et al., 2017) did not reveal any further specimen of this species. In both cases the type material indicates a clear distinction from their congeners. This suggests that *P. margaretae* and *N. finalimus* are either extremely rare, have a very cryptic life style, or might have become extinct.

Additionally, we would like to mention here *Xenotilapia burtoni* (Poll, 1951a), although, according to our definition, this species does not entirely qualify as 'museum species'. A substantial type

series for this species was collected between 1946 and 1947 in the Burton Bay, DRC. However, to our knowledge this species was only reported again once after its initial description (Ferreira, 2007).

‘Questionable species’

Three out of the 208 formally described cichlid species of Lake Tanganyika are categorized as ‘questionable species’ here: *Tro-*

pheus kasabae (Nelissen, 1977), *T. polli* Axelrod, 1977, and *N. cancelatus* Aibara et al., 2005. The former two species were previously suggested, based on literature but not on morphological measurements, to be junior synonyms of *T. moori* Boulenger, 1898 and *T. annectens* Boulenger, 1900, respectively (Konings and Dieckhoff, 1992; Konings, 2013). We here agree that their species status is questionable, as in both cases the newly described species was never directly compared to the type material of *T. moori* and *T.*

Table 2

List of undescribed species and local varieties. The categorization is based on our personal opinions and observations from fieldwork and collection activities. The notation of the cheironyms follows the conventions explained in Snoeks (2000). LT = Lake Tanganyika; aff. = species affinis, suggesting that the taxon is similar, but distinct from the mentioned nominal species; cf. = conferre, suggesting the taxon to be comparable with the mentioned nominal species (Table 2).

tribe	cheironym	category	comment	distribution	references
Benthochromini	<i>Benthochromis</i> sp. "horii mahale"	variety	cf. <i>Benthochromis horii</i>	Mahale area	Konings, 2015
Cyphotilapia	<i>Cyphotilapia</i> sp. "5-bar frontosa"	variety	cf. <i>Cyphotilapia frontosa</i>	northern LT	Geneville, 2004; Konings, 2015; Takahashi et al., 2007 (referred to as: <i>Cyphotilapia</i> sp. "6-bar frontosa")
Cyprichromini	<i>Cyprichromis</i> sp. "dwarf jumbo"	potential species	aff. <i>Cyprichromis coloratus</i> : much smaller in body size and differs in colouration	northern LT	Konings, 2015; Tawil, 2008
	<i>Cyprichromis</i> sp. "jumbo"	potential species	aff. <i>Cyprichromis coloratus</i> : differs in colouration	southern LT	Konings, 2015
	<i>Cyprichromis</i> sp. "kibishi"	potential species	aff. <i>Cyprichromis zonatus</i> : differs in colouration and disjunct distribution	Kibishi area	Konings, 2015
	<i>Paracyprichromis</i> sp. "tembwe"	potential species	aff. <i>Paracyprichromis nigripinnis</i> : differs in caudal fin shape	Tembwe area (~40km south of Moba)	first report
Ectodini	<i>Paracyprichromis</i> sp. "brieni south"	variety	cf. <i>Paracyprichromis brieni</i>	southern LT	Konings, 2015
	<i>Ophthalmotilapia</i> sp. "paranasuta"	potential species	aff. <i>Ophthalmotilapia nasuta</i> : differs in head and fin shape, differs in behaviour	northern LT	Konings, 2015
	<i>Ophthalmotilapia</i> sp. "white cap"	potential species	aff. <i>O. ventralis</i> and aff. <i>O. heterodonta</i>	Tanzanian coast	Stæck, 2014
	<i>Xenotilapia</i> sp. "kileša"	potential species	aff. <i>Enantiopus melanogenys</i> : differs in melanin patterns	Kileša area	Konings, 2015 (referred to as <i>Enantiopus</i> sp. "kileša")
Haplochromini	<i>Xenotilapia</i> sp. "papilio sunflower"	potential species	aff. <i>Xenotilapia papilio</i> : differs in shape and colouration of the dorsal fin	southern LT	Koblmüller et al., 2004; Konings, 2015
	<i>Ectodus</i> sp. "north"	variety	cf. <i>Ectodus descampsi</i>	northern LT	Koblmüller et al., 2004; Konings, 2015
	<i>Xenotilapia</i> sp. "spilopterus north"	variety	cf. <i>Xenotilapia spilopterus</i>	northern LT	Konings, 2015
	<i>Haplochromis</i> sp. "chipwa"	potential species	aff. <i>Haplochromis stappersii</i> : genetic data shows strong divergence	southern tributaries and estuaries	Meyer and Indermaur et al., 2015
Tropheini	<i>Petrochromis</i> sp. "giant"	in preparation	description in preparation	Mahale to Kipili area	Mattsson, 2018, bioRxiv preprint
	<i>Petrochromis</i> sp. "kazumbae"	in preparation	description in preparation	Kigoma area	Mattsson, 2018, bioRxiv preprint
	<i>Petrochromis</i> sp. "macrognathus rainbow"	in preparation	description in preparation	Kipili area	Mattsson, 2018, bioRxiv preprint
	<i>Petrochromis</i> sp. "polyodon texas"	in preparation	description in preparation	Mahale to Kipili area	Mattsson, 2018, bioRxiv preprint
	<i>Petrochromis</i> sp. "red"	in preparation	description in preparation	Mahale area	Mattsson, 2018, bioRxiv preprint
	<i>Tropheus</i> sp. "black"	in preparation	description in preparation	northern LT	Van Steenberge, 2014
	<i>Tropheus</i> sp. "kirschfleck"	in preparation	description in preparation	northern LT	Van Steenberge, 2014
	<i>Tropheus</i> sp. "lunatus"	in preparation	description in preparation	Cape Kabogo, Maswa area	Van Steenberge, 2014; Van Steenberge et al., 2018
	<i>Tropheus</i> sp. "mpimbwe"	in preparation	description in preparation	Cape Mpimbwe	Konings, 2015; Van Steenberge, 2014
	<i>Tropheus</i> sp. "murago"	in preparation	description in preparation	Wapembwe area	Konings, 2015; Van Steenberge, 2014
	<i>Tropheus</i> sp. "red"	in preparation	description in preparation	south-western LT	Van Steenberge et al., 2011, 2018;
	<i>Petrochromis</i> sp. "kipili brown"	potential species	aff. <i>Petrochromis horii</i> : similar ecology, but has only 7 vertical bars in dorsal fin (versus 8 in <i>P. horii</i>)	Kipili area	Konings, 2015
<i>Petrochromis</i> sp. "moshi yellow"	variety	cf. <i>Petrochromis ephippium</i>	Mahale to Kipili area	Konings, 2015	
<i>Petrochromis</i> sp. "orthognathus ikola"	variety	cf. <i>Petrochromis orthognathus</i>	Ikola area	Koblmüller et al., 2010; Konings, 2015	
<i>Tropheus</i> sp. "brichardi kipili"	variety	cf. <i>Tropheus brichardi</i>	Kipili area	Karlsson and Karlsson, 2015; Van Steenberge et al., 2018	
<i>Tropheus</i> sp. "lukuga"	variety	cf. <i>Tropheus brichardi</i>	Lukuga area and central Tanzanian coast	Karlsson and Karlsson, 2015	
Lamprologini	<i>Altolamprologus</i> sp. "compressiceps shell"	potential species	aff. <i>Altolamprologus compressiceps</i> : distinct in body size and colouration	Lake wide on shell beds	Koblmüller et al., 2007, 2017; Konings, 2015; Konings and Dieckhoff 1992;
	<i>Chalinochromis</i> sp. "bifrenatus"	potential species	aff. <i>Chalinochromis brichardi</i> : distinct differences in colouration and caudal fin shape	southern Tanzanian coast	Konings, 2015; Van Steenberge et al., 2011
	<i>Julidochromis</i> sp. "kombe"	potential species	aff. <i>Julidochromis transcriptus</i> : differs in colouration and body shape and discontinuous distribution	Kombe area	Brichard, 1989; Konings, 2015
	<i>Julidochromis</i> sp. "unterfels"	potential species	aff. <i>Julidochromis</i> spp.: differs in behaviour from all known <i>Julidochromis</i> spp., mouth distinctly terminal, high body		first report
	<i>Lamprologus</i> sp. "ornatipinnis congo"	potential species	aff. <i>Lamprologus ornatipinnis</i> : more pronounced sexual size dimorphism, distinct dorsal fin shape	southern DRC coast	first report
	<i>Neolamprologus</i> sp. "caudopunctatus kipili"	potential species	aff. <i>Neolamprologus leloupi</i> : missing black margin on the caudal fin, larger body size; differs in body shape	Kipili area	Konings, 2015; Snoeks et al., 1994
	<i>Neolamprologus</i> sp. "cygnus"	potential species	aff. <i>Neolamprologus falcicula</i> : found in deeper waters, differs in behaviour and juvenile colouration	southern Tanzanian coast	Konings, 2015
	<i>Neolamprologus</i> sp. "eseki"	potential species	aff. <i>Neolamprologus mondabur</i> : differs in shape and colour of the caudal fin	Kipili area	Konings, 2015, 2005
	<i>Neolamprologus</i> sp. "falcicula mahale"	potential species	aff. <i>Neolamprologus falcicula</i> : differs in fin colouration and juvenile colouration, syntopic with <i>N. sp. "gracilis tanzania"</i>	Mahale area	first report
	<i>Neolamprologus</i> sp. "gracilis tanzania"	potential species	aff. <i>Neolamprologus gracilis</i> : differs in shape of the caudal fin, disjunct distribution, syntopic with <i>N. sp. "falcicula mahale"</i>	Mahale area	first report, see Konings, 2015 for distribution of <i>N. gracilis</i>
	<i>Neolamprologus</i> sp. "kombe"	potential species	aff. <i>N. savoryi</i> and aff. <i>N. brichardi</i> : shares traits of both species, potentially of hybrid origin	Kombe area	Büscher, 2018
	<i>Neolamprologus</i> sp. "ventralis stripe"	potential species	aff. <i>Neolamprologus ventralis</i> : differs in body colouration	western Zambia	first report
<i>Telmatochromis</i> sp. "longola"	potential species	aff. <i>Telmatochromis</i> spp.	Longola area	first report	
<i>Chalinochromis</i> sp. "ndobhoi"	variety	cf. <i>Chalinochromis brichardi</i>	Maswa and Kungwe Bay	Brichard, 1989; Konings, 2015	
<i>Julidochromis</i> sp. "marlieri south"	variety	cf. <i>Julidochromis marlieri</i>	southern LT	see Konings, 2015 for distribution of <i>J. marlieri</i>	
<i>Julidochromis</i> sp. "regani south"	variety	cf. <i>Julidochromis regani</i>	southern LT	see Konings, 2015 for distribution of <i>J. regani</i>	
<i>Lamprologus</i> sp. "ornatipinnis zambia"	variety	cf. <i>Lamprologus ornatipinnis</i>	southern LT	Gordon and Bills, 1999; Konings, 2015	
<i>Lepidolamprologus</i> sp. "meeli kipili"	variety	cf. <i>Lepidolamprologus attenuatus</i>	Kipili area	Konings, 2015	
<i>Neolamprologus</i> sp. "brevis magara"	variety	cf. <i>Neolamprologus brevis</i>	Magara area	Herrmann, 1987	
<i>Neolamprologus</i> sp. "daffodil"	variety	cf. <i>Neolamprologus pulcher</i>	Samazi / Kantalamba area	Konings, 2015	
<i>Neolamprologus</i> sp. "furfifer ulwile"	variety	cf. <i>Neolamprologus furcifer</i>	Ulwile area	Kullander et al., 2014	
<i>Neolamprologus</i> sp. "modabu mahale"	variety	cf. <i>Neolamprologus mondabu</i>	Mahale area	first report	
<i>Telmatochromis</i> sp. "dhonti north"	variety	cf. <i>Telmatochromis dhonti</i>	northern LT	Konings, 2015, cf. <i>T. caninus</i> (Poll, 1942), junior syn. of <i>T. dhonti</i> , (Poll, 1986)	
<i>Telmatochromis</i> sp. "dhonti twiyu"	variety	cf. <i>Telmatochromis dhonti</i>	southern Tanzanian coast	cf. <i>T. macrolepis</i> (Borodin, 1931), junior syn. of <i>T. dhonti</i> (Hanssens & Snoeks, 2001)	
<i>Telmatochromis</i> sp. "shell"	variety	cf. <i>Telmatochromis temporalis</i>	Lake wide on shell beds	Konings, 2015; Takahashi et al., 2012; Winkelmann et al., 2014	
Trematocarini	<i>Trematocara</i> sp. "north"	potential species	aff. <i>T. unimaculatum</i> , differs in fin colouration, head morphology and various mensic counts	Unknown, one specimen purchased on a fish market in Bujumbura.	first report

annectens, respectively, for which additionally the certainty of their type localities is under debate (see Konings, 2013; Konings and Dieckhoff, 1992 for details). At this stage, these two species should be considered valid until a solid revision of the genus *Tropheus* is available, which is currently in preparation (Van Steenberge, personal communication). The third species we consider a 'questionable species', *N. cancellatus*, is reported from a single location in Zambia only. It has previously been suggested based on morphological grounds that this species might represent a hybrid between members of the genus *Telmatochromis* and *Lamprologus* (sensu lato) (Konings, 2015). Recent genetic data (Ronco et al., unpublished) lend support to this hypothesis, so that we consider *N. cancellatus* an occasional, natural hybrid and thus list it as 'questionable species', needing further investigation.

Undescribed Tanganyikan cichlid species

In addition to the 208 formally described cichlid species (including 'museum species' and 'questionable species'), a substantial number of so far undescribed species have been identified, partly in the scientific literature, yet to a much larger extent in hobbyists' journals and in the ornamental fish trade (note that cichlids are very popular among aquarists). Lacking any proper scientific

description, these putative species (or local varieties) are usually referred to under cheironyms, such as trade names or the names of their location of origin. Quite a number of these undescribed species have been incorporated in scientific studies so that data on their morphology, ecology and/or behaviour as well as on their phylogenetic position and/or population structure exist (see e.g. Koblmüller et al., 2004, 2007; Egger et al., 2007; Meyer et al., 2015). However, their taxonomic status remains undefined. In Table 2, we list 55 undescribed cichlid species or local varieties reported from Lake Tanganyika in the scientific and/or popular literature, all of which we were able to observe and collect in the field and were subject to subsequent examinations. We have classified these taxa into the two categories 'local variety' or 'potential new species', based on personal observations and opinion (see Table 2). We do not claim here that this has any nomenclatural implications. Instead, our main intention is to emphasize the urgency of taxonomic revisions of many genera of Lake Tanganyika cichlids to clarify the status of the taxa mentioned in Table 2.

Taxonomic challenges in Lake Tanganyika cichlids

The taxonomy of cichlid fishes in general, and that of the cichlid species flocks in the East Africa Great Lakes in particular, is highly

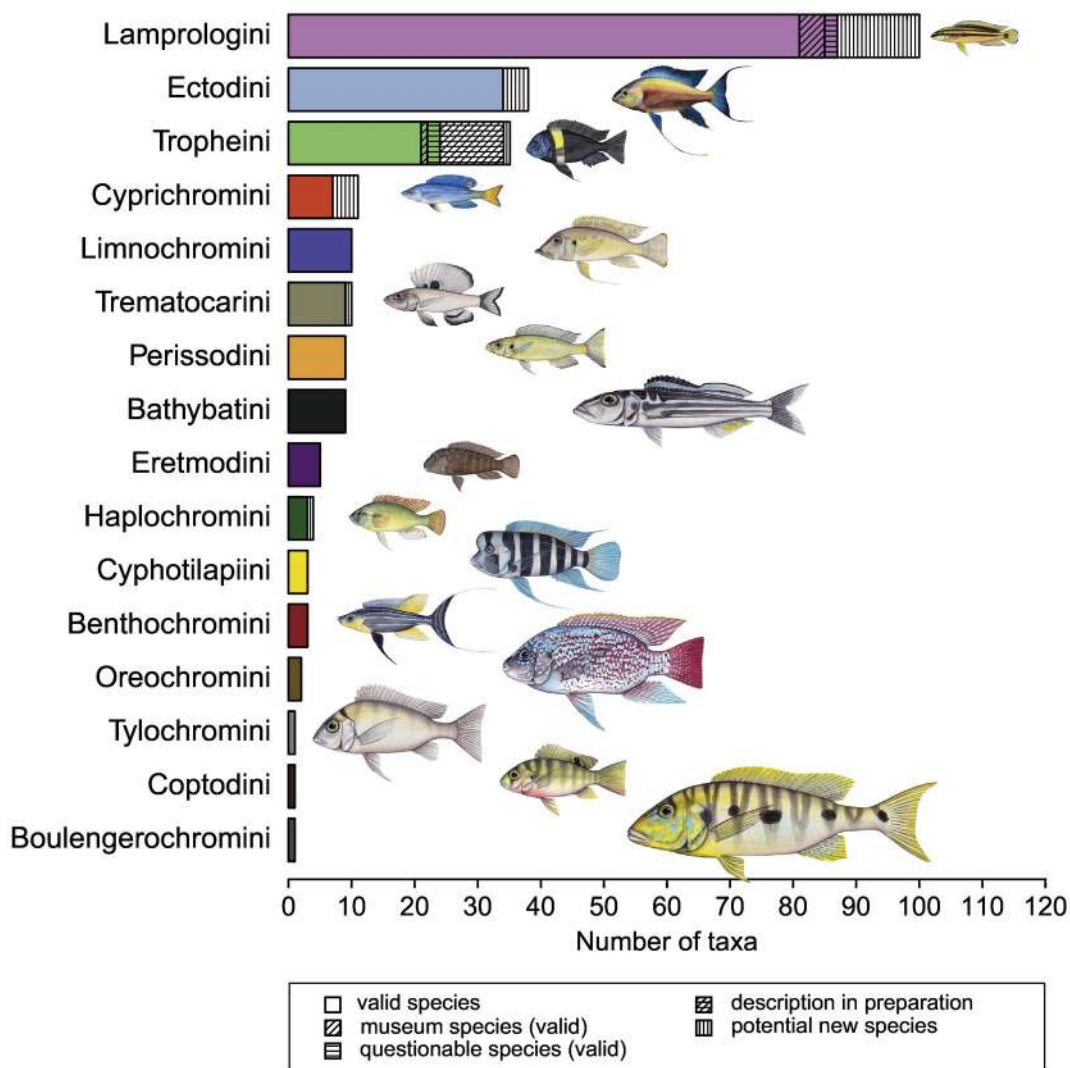


Fig. 3. Taxonomic diversity of Lake Tanganyika cichlids per tribe. Coloured partitions in the bar plot indicate the number of described species, different hatchings are used to highlight 'questionable species' and 'museum species'. White partitions refer to so far undescribed species of the two categories 'description in preparation' and what we classify as 'potential species'.

challenging (Snoeks et al., 1994; Snoeks, 2000), which is partly due to the sheer number of species present and their close relatedness. In Lake Tanganyika this is further complicated by cases of convergent evolution within the radiation (Muschick et al., 2012), which might have contributed to several generic misplacements. Additionally, many Tanganyikan cichlid species show complex distribution patterns, presumably shaped by the patchy distribution of habitats along the lake's shoreline in combination with major lake level fluctuations (among other reasons) (see e.g. Sturmbauer et al., 2001). During periods of the most extreme low water stands, the lake was subdivided into three sub-basins (Salzburger et al., 2014). This previous separation of the lake in sub-basins is reflected today by many sister-species pairs showing a north versus south distribution (probably reflecting allopatric diversification in the sub-basins) or an east versus west distribution (probably reflecting dispersal along the paleo shore lines). However, the current taxonomy of Lake Tanganyika cichlids does not treat such cases consistently. In some cases, vicariant species-pairs were nominally described as two species (e.g. *N. leleupi* (Poll, 1956) from the West and *N. longior* (Staack, 1980) from the East); in other cases, these were initially described as two species (e.g. *Telmatochromis dhonti* (Boulenger, 1919) from the South and *T. caninus* Poll, 1942 from the North) but later synonymized (Poll, 1986); while again in other cases only one species had been described (e.g. *N. gracilis* (Brichard, 1989) from the West with reports from a local variant at the eastern shore, *N. sp.* “gracilis tanzania”, see Table 2). Especially the East-West species pairs need revision, aiming at a more uniform taxonomic treatment of such sister-species pairs. Lake-wide sampling and phylogeographic studies (Rüber et al., 1999; Pauquet et al., 2018; Koblmüller et al., 2019) could serve as useful tool for future taxonomic revisions dealing with such difficult cases. Further, such studies can also contribute to the detection of yet unknown species. For example, a lake-wide genetic study of the tribe Eretmodini uncovered a distinct lineage within the genus *Eretmodus* (Rüber et al., 1999) which was later described as *Eretmodus marksmithi* Burgess, 2012.

Cases calling for revisions

Among Lake Tanganyika cichlids, several species are known to have been misplaced at the genus level. For example, Poll (1981) grouped two species, *Gnathochromis permaxillaris* (David, 1936) (type species of the genus *Gnathochromis*) and *G. pfefferi* (Boulenger, 1898) into the new genus *Gnathochromis*, based on morphological characteristics. Molecular work, however, placed *G. pfefferi* robustly within the Tropheini and *G. permaxillaris* within the Limnochromini (Salzburger et al., 2002; Takahashi, 2003). Yet, their generic name remains so far unchanged. The same applies to the genus *Ctenochromis* Pfeffer, 1893: Molecular data showed that *C. horei* (Günther, 1894) belongs to the Tropheini, while *C. benethicola* (Matthes, 1962) groups within the Cyphotilapiini (Muschick et al., 2012). In this case, none of the Tanganyikan species is the type species of the genus *Ctenochromis*. In both cases the generic misplacement affects only one or two species, respectively. However, within the Lamprologini the current genus assignment seems to disagree with the phylogenetic knowledge of the tribe for numerous taxa (see e.g. Colombo et al., 2016; Schelly et al., 2006). Those cases exemplify the need for a large-scale taxonomic revision of Lake Tanganyika cichlids.

Conclusions

We present a systematic overview of the taxonomic diversity of the lacustrine cichlid species flock from ancient Lake Tanganyika, East Africa. In particular, we provide an inventory of the valid cich-

lid fish species from Lake Tanganyika and list putatively undescribed species as well as local varieties. Based on this compilation, we estimate that Lake Tanganyika's cichlid species flock comprises at least 241 species, of which 208 (~86%) are nominally described and all but two (99.2%) are endemic to the basin (see Tables 1 and 2). To emphasize the demand for taxonomic revision, we highlighted some taxa at the species, genus and tribe level, needing further investigation.

Although Lake Tanganyika seems to be one of the most thoroughly examined aquatic ecosystems in tropical Africa, basic systematic work is pressing. Solid taxonomic knowledge is not only the basis for scientific study but also for nature conservation. As many other biodiversity hotspots, the unique ecosystem of Lake Tanganyika faces numerous anthropogenic threats. For example, the lake has become the focus of attention for future oil drilling projects (see Verheyen, 2016). A comprehensive understanding of the biological diversity of Lake Tanganyika is the basic prerequisite for any conservation measure, for example the delineation of small-scale protected areas (Sturmbauer, 2008). Although the IUCN Red List (International Union for Conservation of Nature's Red List of Threatened Species) accepts varieties and sub-population with reservations, valid species or subspecies are easier to assess in the system (IUCN Standards and Petitions Subcommittee, 2006).

Acknowledgements

We would like to thank Adolfe Irakoze, Gerald Katai, George Kazumbe, Dinny Mwanakulya, Jimmy Sichilima, and Humphry D. Sichilima Jr., for their help and support during field work; Victoria Huwiler, Mireille Schreyen-Brichard, Humphry D. Sichilima, and Craig Zytkow for providing infrastructure on site; Julie Himes for fish illustrations in Fig. 3; Gaspard Banyankimbona (University of Burundi), Nshombo Muderhwa and Pascal Masilya (Centre de Recherche en Hydrobiologie, Uvira, DR Congo), Ishmael Kimirei (TAFIRI, Kigoma, Tanzania), and Taylor Banda and Lawrence Makasa (Department of Fisheries, Mpulungu, Zambia) for assistance with research permits; Yves Fermon for his help in the field and valuable discussions on cichlid taxonomy; and Lukas Rüber and an anonymous reviewer for valuable comments to improve this manuscript. The authors would further like to acknowledge funding through the University of Basel, the Swiss National Science Foundation and the European Research Council (ERC).

References

- Aibara, M., Takahashi, T., Nakaya, K., 2005. Neolamprologus cancellatus, a new cichlid fish from Lake Tanganyika, Africa. *Ichthyol. Res.* 52, 354–359. <https://doi.org/10.1007/s10228-005-0296-0>.
- Albrecht, C., Wilke, T., 2008. Ancient Lake Ohrid: biodiversity and evolution. *Hydrobiologia* 615, 103–140. <https://doi.org/10.1007/s10750-008-9558-y>.
- Anseeuw, D., Nevado, B., Busselen, P., Snoeks, J., Verheyen, E., 2012. Extensive introgression among ancestral mtDNA lineages: phylogenetic relationships of the Utaka within the Lake Malawi cichlid flock. *Int. J. Evol. Biol.* 2012, 1–9. <https://doi.org/10.1155/2012/865603>.
- Axelrod, G.S., 1977. A new species of *Tropheus* (Pisces: Cichlidae) from Lake Tanganyika. *The J.L.B. Smith Institute of Ichthyology* 17, 1–12.
- Axelrod, G.S., Harrison, J.A., 1978. *Simochromis margaretae*, a new species of cichlid fish from Lake Tanganyika. *The J.L.B. Smith Institute of Ichthyology* 19, 1–16.
- Bailey, R.M., Stewart, D.J., 1977. Cichlid fishes from Lake Tanganyika: additions to the Zambian fauna including two new species. *Occasional Papers of the Museum of Zoology University of Michigan* 679, 1–30.
- Bills, R.I., Ribbink, A.J., 1997. Description of *Lamprologus laparogramma* sp. nov., and rediagnosis of *Lamprologus signatus* Poll 1956 and *Lamprologus kungweensis* Poll 1952, with notes on their ecology and behaviour (Teleostei: Cichlidae). *S. Afr. J. Sci.* 93, 555–564.
- Böhne, A., Wilson, C.A., Postlethwait, J.H., Salzburger, W., 2016. Variations on a theme: genomics of sex determination in the cichlid fish *Astatotilapia burtoni*. *BMC Genomics* 17, 1–12. <https://doi.org/10.1186/s12864-016-3178-0>.
- Borodin, N.A., 1931. Some new cichlid fishes from lakes Nyasa, Tanganyika and Viktoria in Central Africa. *Proceedings of the New England Zoological Club* 12, 49–54.

- Boulenger, G.A., 1897. Descriptions of new fishes from the Upper Shiré River, British Central Africa, collected by Dr. Percy Rendall, and presented to the British Museum by Sir Harry H. Johnston, K.C.B. *Proceedings of the Zoological Society of London*, 915–920.
- Boulenger, G.A., 1898. Report on the collection of fishes made by Mr. J. E. S. Moore in Lake Tanganyika during his expedition, 1895–96. *Transactions of the Zoological Society of London* 15, 1–30.
- Boulenger, G.A., 1899a. Poissons nouveaux du Congo. Cinquième Partie. Cyprins, Silures, Cyprinodontes, Acanthoptérygiens. *Annales du Musée du Congo Belge* 1, 15–127.
- Boulenger, G.A., 1899b. Second contribution to the ichthyology of Lake Tanganyika. On the fishes obtained by the Congo Free State Expedition under Lieut. Lemaire in 1898. *Transactions of the Zoological Society of London* 15, 87–96.
- Boulenger, G.A., 1900. Matériaux pour la faune du Congo. Poissons nouveaux du Congo. Sixième Partie. Mormyres, Characins, Cyprins, Silures, Acanthoptérygiens, Dipneustes. *Annales du Musée du Congo Belge, Zoologie, Série 1*, 129–164.
- Boulenger, G.A., 1901. Diagnoses of new fishes discovered by Mr. J. E. S. Moore in lakes Tanganyika and Kivu. *Ann. Mag. Nat. Hist.* 7, 1–6.
- Boulenger, G.A., 1906. Fourth contribution to the ichthyology of Lake Tanganyika. Report on the collection of fishes made by Dr. W. A. Cunningham during the Third Tanganyika Expedition, 1904–1905. *Transactions of the Zoological Society of London* 17, 537–601.
- Boulenger, G.A., 1912. Descriptions of three new African cichlid fishes of the genus *Tilapia*, preserved in the British Museum. *Ann. Mag. Nat. Hist.* 10, 138–140.
- Boulenger, G.A., 1914. Mission Stappers au Tanganyika-Moero. Diagnoses de poissons nouveaux. I. Acanthoptérygiens, Opisthomes, Cyprinodontes, *Revue de Zoologie Africaine* 3, 442–447.
- Boulenger, G.A., 1919. On a collection of fishes from Lake Tanganyika, with descriptions of three new species. *Proceedings of the Zoological Society of London*, 17–20.
- Brichard, P., 1989. Cichlids and all the other fishes of Lake Tanganyika. T.F.H. Publications, Neptune City, NJ.
- Brooks, J.L., 1950. Speciation in ancient lakes. *Q. Rev. Biol.* 25, 131–176.
- Burgess, W.E., 2012. A new species of goby cichlid of the genus *Eretmodus*, *E. marksmithi*, (Pisces: Cichlidae) from the Northern part of Lake Tanganyika, *Tanganika Magazyn* 12, 23–31.
- Burgess, W.E., 2014. *Juidochromis marksmithi*, A New Species of Julidochromis from the Tanzanian Coast of Lake Tanganyika. *Tanganika Magazyn* 15, 40–49.
- Burton, R.F., 1860. The lake Regions of Central Africa. Longman, Green, Longman, and Roberts, London 2, 1–468.
- Büscher, H.H., 1989. Ein neuer Tanganjika-Cichlide aus Zaire: *Neolamprologus marunguensis* n. sp. (Cichlidae, Lamprologini). *Die Aquarien- und Terrarienzeitschrift (DATZ)* 42, 739–743.
- Büscher, H.H., 1990. *Xenotilapia papilio* n. sp., ein neuer Cichlide aus dem Tanganjikasee (Cichlidae, Ectodini). *Die Aquarien- und Terrarienzeitschrift (DATZ)* 43, 289–293.
- Büscher, H.H., 1991a. Ein neuer Tanganjikasee-Cichlide aus Zaire: *Neolamprologus pectoralis* n. sp. (Cichlidae, Lamprologini). *Die Aquarien- und Terrarienzeitschrift (DATZ)* 44, 784–789.
- Büscher, H.H., 1991b. Neue Schneckencichliden aus dem Tanganjikasee: *Lamprologus meleagris* n. sp. und *L. speciosus* n. sp. (Cichlidae, Lamprologini). *Die Aquarien- und Terrarienzeitschrift (DATZ)* 44, 374–382.
- Büscher, H.H., 1992a. Ein neuer Cichlide aus dem Tanganjikasee: *Neolamprologus similis* n. sp. *Die Aquarien- und Terrarienzeitschrift (DATZ)* 45, 520–525.
- Büscher, H.H., 1992b. *Neolamprologus nigriventris* n. sp.: Ein neuer Tanganjikasee-Cichlide (Cichlidae, Lamprologini). *Die Aquarien- und Terrarienzeitschrift (DATZ)* 45, 778–783.
- Büscher, H.H., 1993. *Neolamprologus bifasciatus* n. sp.: Ein neuer Tanganjikasee-Cichlide (Cichlidae, Lamprologini). *Die Aquarien- und Terrarienzeitschrift (DATZ)* 46, 385–389.
- Büscher, H.H., 1994. *Cyprichromis pavo* n. sp.: Ein neuer Cichlide aus dem Tanganjikasee. *Die Aquarien- und Terrarienzeitschrift (DATZ)* 46, 257–264.
- Büscher, H.H., 1995a. Ein neuer Cichlide aus dem Tanganjikasee: *Neolamprologus ventralis* n. sp. (Cichlidae, Lamprologini). *Die Aquarien- und Terrarienzeitschrift (DATZ)* 48, 379–382.
- Büscher, H.H., 1995b. Ein neuer Cichlide von der zairischen Küste des Tanganjikasees: *Neolamprologus variostigma* n.sp. (Cichlidae, Lamprologini). *Die Aquarien- und Terrarienzeitschrift (DATZ)* 48, 794–797.
- Büscher, H.H., 1997. Ein neuer Cichlide aus dem Tanganjikasee: *Neolamprologus helianthus* (Cichlidae, Lamprologini). *Die Aquarien- und Terrarienzeitschrift (DATZ)* 50, 701–706.
- Büscher, H.H., 2007. Ein verschollener Buntbarsch, *Die Aquarien- und Terrarienzeitschrift (DATZ)* 6, 58–61.
- Büscher, H.H., 2018. Eine mysteriöse *Neolamprologus*-Art aus Sambia. *DCG-Informationen* 49, 254–259.
- Cohen, A.S., Soreghan, M.J., Scholz, C.A., 1993. Estimating the age of formation of lakes: an example from Lake Tanganyika, East African Rift system. *Geology* 21, 511–514.
- Colombo, M., Indermaur, A., Meyer, B.S., Salzburger, W., 2016. Habitat use and its implications to functional morphology: niche partitioning and the evolution of locomotory morphology in Lake Tanganyikan cichlids (Perciformes: Cichlidae). *Biol. J. Linn. Soc.* 118, 536–550. <https://doi.org/10.1111/bj.12754>.
- David, L., 1936. Contribution à l'étude de la faune ichthyologique du lac Tanganyika. *Revue de Zoologie et de Botanique Africaines* 28, 149–160.
- De Vos, L., Risch, L., Thys van den Audenaerde, D., 1995. *Xenotilapia nasus*, nouvelle espèce de poisson des zones sous-littorale et benthique du Nord du lac Tanganyika (Perciformes: Cichlidae). *Ichthyological Exploration of Freshwaters* 6, 377–384.
- De Vos, L., Nshombo, M., Thys van den Audenaerde, D., 1996. *Trematocara zebra* (Perciformes; Cichlidae), nouvelle espèce du nord-ouest du Lac Tanganyika (Zaire). *Belgian Journal Of Zoology* 126, 3–20.
- Dunz, A.R., Schliwien, U.K., 2013. Molecular phylogeny and revised classification of the haplotilapiine cichlid fishes formerly referred to as “*Tilapia*”. *Mol. Phylogenet. Evol.* 68, 64–80. <https://doi.org/10.1016/j.ympev.2013.03.015>.
- Egger, B., Koblmüller, S., Sturmbauer, C., Sefc, K.M., 2007. Nuclear and mitochondrial data reveal different evolutionary processes in the Lake Tanganyika cichlid genus *Tropheus*. *BMC Evol. Biol.* 7, 1–14. <https://doi.org/10.1186/1471-2148-7-137>.
- Fermon, Y., 2007. Étude de l'État des lieux de la partie nord du lac Tanganyika dans le cadre du Programme Pêche d'Action Contre la Faim en République Démocratique du Congo. Action Against Hunger, USA.
- Fermon, Y., Nshombo, M., Muzumani, R., Benoît, J., 2017. Guide de la faune des poissons de la côte congolaise d'Ubwari à la Ruzizi. Lac Tanganyika. Editions de l'Association France Cichlid, F-31540 Fontoubrière Saint Julia.
- Fricke, R., Eschmeyer, W.N., van der Laan, R., 2019. Eschmeyer's Catalog of Fishes: Genera, Species, References <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>.
- Froese, R., Pauly, D., 2019. FishBase: www.fishbase.org.
- Fryer, G., Iles, T.D., 1972. The cichlid fishes of the Great Lakes of Africa. T.F.H. Publications, Neptune City, NJ.
- Gante, H.F., Matschiner, M., Malmstrøm, M., Jakobsen, K.S., Jentoft, S., Salzburger, W., 2016. Genomics of speciation and introgression in Princess cichlid fishes from Lake Tanganyika. *Mol. Ecol.* 25, 6143–6161. <https://doi.org/10.1111/mec.13767>.
- Genevieve, E., 2004. Distribution écologie et collecte du genre *Cyphotilapia* Regan, 1920. *L'an Cichlidé* 4, 53–66.
- Gordon, A.K., Bills, I.R., 1999. Aspects of the feeding and reproductive biology of the Lake Tanganyikan cichlid, *Lamprologus ornatipinnis* (Pisces, Cichlidae). *Environ. Biol. Fish* 55, 431–441. <https://doi.org/10.1023/A:1007540121262>.
- Günther, A.C.L.G., 1894. Descriptions of reptiles and fishes collected by Mr. E. Coode-Hore on Lake Tanganyika. *Proceedings of the Zoological Society of London* 1893, 628–632.
- Hanssens, M., Snoeks, J., 2001. A revised synonymy of *Telmatochromis temporalis* (Teleostei, Cichlidae) from Lake Tanganyika (East Africa). *J. Fish Biol.* 58, 639–655. <https://doi.org/10.1006/jfbi.2000.1475>.
- Hanssens, M., Snoeks, J., 2003. A new species and geographical variation in the *Telmatochromis temporalis* complex (Teleostei, Cichlidae) from Lake Tanganyika. *J. Fish Biol.* 63, 593–616. <https://doi.org/10.1046/j.1095-8649.2003.00173.x>.
- Herrmann, H.J., 1987. *Die Buntbarsche der Alten Welt -Tanganjikasee*. Kernen, Germany.
- Irisarri, I., Singh, P., Koblmüller, S., Torres-Dowdall, J., Henning, F., Franchini, P., Fischer, C., Lemmon, A.R., Lemmon, E.M., Thallinger, G.G., Sturmbauer, C., Meyer, A., 2018. Phylogenomics uncovers early hybridization and adaptive loci shaping the radiation of Lake Tanganyika cichlid fishes. *Nat. Commun.* 9, 1–12. <https://doi.org/10.1038/s41467-018-05479-9>.
- IUCN Standards and Petitions Subcommittee, 2006. Guidelines for Using the IUCN Red List - Categories and Criteria.
- Jungwirth, A., Brena, P.F., Keller, I., Taborisky, M., 2015. Polygyny affects paternal care, but not survival, pair stability, and group tenure in a cooperative cichlid. *Behav. Ecol.* 0, 1–9. <https://doi.org/10.1093/beheco/aru194>.
- Karlsson, M., Karlsson, M., 2015. Anmerkungen zu *Richards Tropheus: Tropheus brichardi*, *Tropheus* sp. “*Crescentic*”, *Tropheus* sp. “*Lukuga*” und “*Kushangaza*”. *DCG-Informationen* 46, 146–161.
- Koblmüller, S., Salzburger, W., Sturmbauer, C., 2004. Evolutionary relationships in the sand-dwelling cichlid lineage of Lake Tanganyika suggest multiple colonization of rocky habitats and convergent origin of biparental mouthbrooding. *J. Mol. Evol.* 58, 79–96. <https://doi.org/10.1007/s00239-003-2527-1>.
- Koblmüller, S., Sturmbauer, C., Verheyen, E., Meyer, A., Salzburger, W., 2006. Mitochondrial phylogeny and phylogeography of East African squeaker catfishes (Siluriformes: Synodontis). *BMC Evol. Biol.* 6, 1–16. <https://doi.org/10.1186/1471-2148-6-49>.
- Koblmüller, S., Duftner, N., Sefc, K.M., Aibara, M., Stipacek, M., Blanc, M., Egger, B., Sturmbauer, C., 2007. Reticulate phylogeny of gastropod-shell-breeding cichlids from Lake Tanganyika - the result of repeated introgressive hybridization. *BMC Evol. Biol.* 7, 1–13. <https://doi.org/10.1186/1471-2148-7-7>.
- Koblmüller, S., Egger, B., Sturmbauer, C., Sefc, K.M., 2010. Rapid radiation, ancient incomplete lineage sorting and ancient hybridization in the endemic Lake Tanganyika cichlid tribe *Tropheini*. *Mol. Phylogenet. Evol.* 55, 318–334. <https://doi.org/10.1016/j.ympev.2009.09.032>.
- Koblmüller, S., Nevado, B., Makasa, L., Van Steenberghe, M., Vanhove, M.P.M., Verheyen, E., Sturmbauer, C., Sefc, K.M., 2017. Phylogeny and phylogeography of *Altalamprologus*: ancient introgression and recent divergence in a rock-dwelling Lake Tanganyika cichlid genus. *Hydrobiologia* 791, 35–50. <https://doi.org/10.1007/s10750-016-2896-2>.
- Koblmüller, S., Zangl, L., Börger, C., Dail, D., Vanhove, M.P.M., Sturmbauer, C., Sefc, K.M., 2019. Only true pelagics mix: comparative phylogeography of deepwater bathybatine cichlids from Lake Tanganyika. *Hydrobiologia* 832, 93–103. <https://doi.org/10.1007/s10750-018-3752-3>.

- Konings, A., 2005. Back to Nature Guide to Tanganyika cichlids (2nd Editio. ed. Fohrmann Aquaristik).
- Konings, A., 2013. *Tropheus* in their natural habitat. Cichlid press, El Paso.
- Konings, A., 2015. Tanganyika Cichlids in their natural habitat, 3th Editio. ed. Cichlid Press, El Paso.
- Konings, A., Dieckhoff, H.W., 1992. Tanganyika Secrets. Cichlid press, El Paso.
- Kornfield, I., Smith, P.F., 2000. African cichlid fishes: model systems for evolutionary biology. *Annu. Rev. Ecol. Evol. Syst.* 31, 163–196.
- Kullander, S.O., Karlsson, M., Karlsson, M., 2012. *Lepidiolamprologus kamambae*, a new species of cichlid fish (Teleostei: Cichlidae) from Lake Tanganyika. *Zootaxa* 3492, 30–48.
- Kullander, S.O., Karlsson, M., Karlsson, M., Norén, M., 2014a. *Chalinochromis cyanophleps*, a new species of cichlid fish (Teleostei: Cichlidae) from Lake Tanganyika. *Zootaxa* 3790, 425–438. <https://doi.org/10.11646/zootaxa.3790.3.2>.
- Kullander, S.O., Norén, M., Karlsson, M., Karlsson, M., 2014b. Description of *Neolamprologus timidus*, new species, and review of *N. Furcifer* from Lake Tanganyika (Teleostei: Cichlidae). *Ichthyological Exploration of Freshwaters* 24, 301–328.
- Larson, G., Schaetzl, R., 2001. Origin and evolution of the Great Lakes. *J. Great Lakes Res.* 27, 518–546. [https://doi.org/10.1016/S0380-1330\(01\)70665-X](https://doi.org/10.1016/S0380-1330(01)70665-X).
- Liem, K.F., Stewart, D.J., 1976. Evolution of the scale-eating cichlid fishes of Lake Tanganyika: a generic revision with a description of a new species. *Bulletin of the Museum of Comparative Zoology* 147, 319–350.
- Louisy, P., 1989. Description de *Telmatochromis brichardi* (Pisces, Cichlidae, Lamprologini), espèce nouvelle du lac Tanganyika. *Revue française d'aquariologie* 15, 79–85.
- Macdonald, K.S., Yampolsky, L., Duffy, J.E., 2005. Molecular and morphological evolution of the amphipod radiation of Lake Baikal. *Mol. Phylogenet. Evol.* 35, 323–343. <https://doi.org/10.1016/j.ympev.2005.01.013>.
- Malinsky, M., Svardal, H., Tyers, A.M., Miska, E.A., Genner, M.J., Turner, G.F., Durbin, R., 2018. Whole-genome sequences of Malawi cichlids reveal multiple radiations interconnected by gene flow. *Nature Ecology & Evolution* 2, 1940–1955. <https://doi.org/10.1038/s41559-018-0717-x>.
- Marlier, G., 1959. Observations sur la biologie littorale du Lac Tanganyika. *Revue de Zoologie et de Botanique Africaines* 59, 164–183.
- Martens, K., 1997. Speciation in ancient lakes. *Trends Ecol. Evol.* 12, 177–182.
- Matthes, H., 1959a. Un cichlide nouveau du Lac Tanganyika: *Petrochromis orthognathus* n. sp. *Revue de Zoologie et de Botanique Africaines* 60, 335–341.
- Matthes, H., 1959b. Un cichlide nouveau du lac Tanganyika *Julidochromis transcriptus* n. sp. *Revue de Zoologie et de Botanique Africaines* 60, 126–130.
- Matthes, H., 1962. Poissons nouveaux ou intéressants du lac Tanganyika et du Ruanda. *Annales, Musée Royal de l'Afrique Centrale, Tervuren, Belgique. Série in* 80. *Sciences Zoologique* 111, 27–88.
- Matthes, H., Trewavas, E., 1960. *Petrochromis famula* n. sp., a cichlid fish of Lake Tanganyika. *Revue de Zoologie et de Botanique Africaines* 61, 349–357.
- Mattsson, C., 2018. A Morphological and Molecular Analysis of the Species Diversity of the Cichlid Genus *Petrochromis* from Lake Tanganyika (Teleostei: Cichlidae). *bioRxiv Preprint*. <https://doi.org/10.1101/280263>.
- Meier, J.I., Marques, D.A., Mwaiko, S., Wagner, C.E., Excoffier, L., Seehausen, O., 2017. Ancient hybridization fuels rapid cichlid fish adaptive radiations. *Nat. Commun.* 8, 1–11. <https://doi.org/10.1038/ncomms14363>.
- Meyer, B.S., Indermaur, A., Ehrensperger, X., Egger, B., Banyankimbona, G., Snoeks, J., Salzburger, W., 2015. Back to Tanganyika: a case of recent trans-species-flock dispersal in East African haplochromine cichlid fishes. *R. Soc. Open Sci.* 2, 1–5. <https://doi.org/10.1098/rsos.140498>.
- Meyer, B.S., Matschiner, M., Salzburger, W., 2017. Disentangling incomplete lineage sorting and introgression to refine species-tree estimates for Lake Tanganyika cichlid fishes. *Syst. Biol.* 66, 531–550. <https://doi.org/10.1093/sysbio/syw069>.
- Muschick, M., Indermaur, A., Salzburger, W., 2012. Convergent evolution within an adaptive radiation of cichlid fishes. *Curr. Biol.* 22, 2362–2368. <https://doi.org/10.1016/j.cub.2012.10.048>.
- Mushagalusa, C.D., Nshombo, M., Lushombo, M., 2014. Littoral fisheries on Cichlidae (Pisces) from the northwestern part of Lake Tanganyika, East Africa. *Aquat. Ecosyst. Health Manag.* 17, 41–51.
- Myers, G.S., 1936. Report on the fishes collected by H. C. Raven in Lake Tanganyika in 1920. *Proceedings of the United States National Museum* 84, 1–15.
- Nakaya, K., Gashagaza, M.M., 1995. *Neolamprologus longicaudatus*, a New Cichlid Fish from the Zairean Coast of Lake Tanganyika. *Japanese Journal of Ichthyology* 42, 39–43.
- Nelissen, M.H.J., 1977. Description of *Tropheus moorii kasabae* n. spec. (Pisces, Cichlidae) from the south of Lake Tanganyika. *Revue de Zoologie Africaine* 91, 237–242.
- Nelissen, M.H.J., Thys van den Audenaerde, D., 1975. Description of *Tropheus brichardi* sp. nov. from Lake Tanganyika (Pisces, Cichlidae). *Revue de Zoologie Africaine* 89, 974–980.
- Nichols, J.T., LaMonte, F.R., 1931. A new *Lamprologus* from Lake Tanganyika. *Am. Mus. Novit.* 478, 1–2.
- Pauquet, G., Salzburger, W., Egger, B., 2018. The puzzling phylogeography of the haplochromine cichlid fish *Astatotilapia burtoni*. *Ecology and Evolution* 8, 5637–5648. <https://doi.org/10.1002/ece3.4092>.
- Pellegrin, J., 1927a. Description de Cichlidés et d'un Mugilidé nouveaux du Congo belge. *Revue de Zoologie Africaine* 15, 52–57.
- Pellegrin, J., 1927b. Mission Guy Babault, poissons du lac Tanganyika. *Bulletin du Muséum National d'Histoire Naturelle* 33, 499–501.
- Pfeffer, G., 1893. Ostafrikanische Fische gesammelt von Herrn Dr. F. Stuhlmann im Jahre 1888 and 1889. In: *Jahrbuch Der Hamburgischen Wissenschaftlichen Anstalten*, pp. 127–177.
- Poll, M., 1942. Cichlidae nouveaux du lac Tanganyika appartenant aux collections du Musée du Congo. *Revue de Zoologie et de Botanique Africaines* 36, 343–360.
- Poll, M., 1943. Descriptions de poissons nouveaux du Lac Tanganyika, appartenant aux familles des Clariidae et Cichlidae. *Revue de Zoologie et de Botanique Africaines* 37, 305–318.
- Poll, M., 1944. Descriptions de poissons nouveaux recueillis dans la région d'Albertville (Congo belge) par le Dr. G. Pojer, *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 20, 1–12.
- Poll, M., 1948. Descriptions de Cichlidae nouveaux recueillis par la mission hydrobiologique belge au Lac Tanganyika (1946–1947). *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 24, 1–31.
- Poll, M., 1949. Deuxième série de Cichlidae nouveaux recueillis par la mission hydrobiologique belge en Lac Tanganyika (1946–1947). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 25, 1–55.
- Poll, M., 1950. Description de deux Cichlidae pétricoles du lac Tanganyika. *Revue de Zoologie et de Botanique Africaines* 43, 292–302.
- Poll, M., 1951a. Troisième série de Cichlidae nouveaux recueillis par la mission hydrobiologique belge au lac Tanganyika (1946–1947). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 27, 1–11.
- Poll, M., 1951b. Troisième série de Cichlidae nouveaux recueillis par la mission hydrobiologique belge au lac Tanganyika (1946–1947) (suite 1+2). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 27, 1–7.
- Poll, M., 1952. Quatrième série de Cichlidae nouveaux recueillis par la mission hydrobiologique belge au lac Tanganyika (1946–1947). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 28, 1–20.
- Poll, M., 1956. Poissons Cichlidae. In: *Exploration Hydrobiologique Du Lac Tanganyika*, pp. 1946–1947 (Résultats Scientifiques).
- Poll, M., 1974. Contribution à la faune ichthyologique du lac Tanganyika, d'après les récoltes de P. Brichard. *Revue de Zoologie Africaine* 88, 99–110.
- Poll, M., 1976. *Hemibates bellcrossi* sp. n. du lac Tanganyika. *Revue de Zoologie Africaine* 90, 1017–1020.
- Poll, M., 1978. Contribution à la connaissance du genre *Lamprologus* Schth. Description de quatre espèces nouvelles, réhabilitation de *Lamprologus mondabu* et synopsis remanié des espèces du lac Tanganyika. *Bulletin de la classe des sciences Académie Royale de Belgique (série 5) (64)*, 725–758.
- Poll, M., 1981. Contribution à la faune ichthyologique du lac Tanganyika. Révision du genre *Limnochromis* Regan, 1920. Description de trois genres nouveaux et d'une espèce nouvelle: *Cyprichromis brieni*. *Annales de la Société royale zoologique de Belgique* 111, 163–179.
- Poll, M., 1984. *Haplotaxodon melanoides* sp. n. du lac Tanganyika (Pisces, Cichlidae). *Revue de Zoologie Africaine* 98, 677–681.
- Poll, M., 1985. Description de *Xenotilapia flavipinnis* sp.n. du lac Tanganyika (Pisces, Cichlidae) *Revue de Zoologie Africaine* 99, pp. 105–109.
- Poll, M., 1986. Classification des Cichlidae du lac Tanganyika, Tribus, genres et espèces (Brussels).
- Poll, M., Matthes, H., 1962. Trois poissons remarquables du Lac Tanganyika. *Annales, Musée Royal de l'Afrique Centrale, Tervuren, Belgique. Série in* 80. *Sciences Zoologique* 111.
- Poll, M., Stewart, D.J., 1975. A new cichlid fish of the genus *Xenotilapia* from Lake Tanganyika, Zambia (Pisces, Cichlidae). *RevZoolAfr* 89, 919–924.
- Poll, M., Stewart, D., 1977. Un nouveau *Lamprologus* du sud du Lac Tanganyika (Zambia) (Pisces, Cichlidae). *Revue de Zoologie Africaine* 91, 1047–1056.
- Regan, C.T., 1920. On a new cichlid fish from Lake Tanganyika. *Ann. Mag. Nat. Hist.* 9, 152.
- Renn, S.C.P., Machado, H.E., Duftner, N., Sessa, A.K., Harris, R.M., Hofmann, H.A., 2018. Gene expression signatures of mating system evolution. *Genome* 61, 287–297. <https://doi.org/10.1139/gen-2017-0075>.
- Rüber, L., Verheyen, E., Meyer, A., 1999. Replicated evolution of trophic specializations in an endemic cichlid fish lineage from Lake Tanganyika. *Proc. Natl. Acad. Sci.* 96, 10230–10235. <https://doi.org/10.1073/pnas.96.18.10230>.
- Salzburger, W., 2018. Understanding explosive diversification through cichlid fish genomics. *Nat. Rev. Genet.* 19, 705–717. <https://doi.org/10.1038/s41576-018-0043-9>.
- Salzburger, W., Meyer, A., Baric, S., Verheyen, E., Sturmbauer, C., 2002. Phylogeny of the Lake Tanganyika cichlid species flock and its relationship to the Central and East African haplochromine cichlid fish faunas. *Syst. Biol.* 51, 113–135. <https://doi.org/10.1080/106351502753475907>.
- Salzburger, W., Mack, T., Verheyen, E., Meyer, A., 2005. Out of Tanganyika: genesis, explosive speciation, key-innovations and phylogeography of the haplochromine cichlid fishes. *BMC Evol. Biol.* 5, 1–15. <https://doi.org/10.1186/1471-2148-5-17>.
- Salzburger, W., Van Boclaere, B., Cohen, A.S., 2014. Ecology and evolution of the African Great Lakes and their faunas. *Annu. Rev. Ecol. Evol. Syst.* 45, 519–545. <https://doi.org/10.1146/annurev-ecolsys-120213-091804>.
- Santos, M.E., Braasch, I., Boileau, N., Meyer, B.S., Sautour, L., Böhne, A., Belting, H.G., Affolter, M., Salzburger, W., 2014. The evolution of cichlid fish egg-spots is linked with a cis-regulatory change. *Nat. Commun.* 5. <https://doi.org/10.1038/ncomms6149>.
- Schedel, F.D.B., Schliwien, U.K., 2017. *Hemibates koningsi* spec. nov: a new deep-water cichlid (Teleostei: Cichlidae) from Lake Tanganyika. *Zootaxa* 4312, 92–112. <https://doi.org/10.11646/zootaxa.4312.1.4>.

- Schelly, R.C., Stiassny, M.L.J., 2004. Revision of the Congo river *Lamprologus* Schilthuis, 1891 (Teleostei: Cichlidae), with descriptions of two new species. *Am. Mus. Novit.* 3451, 1–40. doi:[https://doi.org/10.1206/0003-0082\(2004\)451](https://doi.org/10.1206/0003-0082(2004)451).
- Schelly, R., Salzburger, W., Koblmüller, S., Duftner, N., Sturmbauer, C., 2006. Phylogenetic relationships of the lamprologine cichlid genus *Lepidiolamprologus* (Teleostei: Perciformes) based on mitochondrial and nuclear sequences, suggesting introgressive hybridization. *Mol. Phylogenet. Evol.* 38, 426–438. doi:<https://doi.org/10.1016/j.ympev.2005.04.023>.
- Schelly, R., Takahashi, T., Bills, R., Hori, M., 2007. The first case of aggressive mimicry among lamprologines in a new species of *Lepidiolamprologus* (Perciformes: Cichlidae) from Lake Tanganyika. *Zootaxa* 1638, 39–49.
- Schluter, D., 2000. *The Ecology of Adaptive Radiation*. Oxford University Press, New York.
- Seehausen, O., 2015. Process and pattern in cichlid radiations - inferences for understanding unusually high rates of evolutionary diversification. *New Phytol.* 207, 304–312. doi:<https://doi.org/10.1111/nph.13450>.
- Shaffer, H.B., Thomson, R.C., 2007. Delimiting species in recent radiations. *Syst. Biol.* 56, 896–906.
- Snoeks, J., 2000. How well known is the Ichthyodiversity of the Large East African Lakes? *Adv. Ecol. Res.* 31, 17–38.
- Snoeks, J., 2004. The cichlid diversity of Lake Malawi/Nyasa/Niassa: identification, distribution and taxonomy. Cichlid Press, El Paso, TX, U.S.A.
- Snoeks, J., Rüber, L., Verheyen, E., 1994. The Tanganyika problem: comments on the taxonomy and distribution patterns of its cichlid fauna. *Archiv für Hydrobiologie–Beiheft Ergebnisse der Limnologie* 44, 355–372.
- Staeck, W., 1975. A New Cichlid Fish From Lake Tanganyika: *Julidochromis Dickfeldi* sp. n. (Pisces, Cichlidae) *Revue de Zoologie Africaine*, 89, pp. 981–986.
- Staeck, W., 1978. Ein neuer Cichlide aus dem südlichen Tanganikasee: *Lamprologus nkambae* n. sp. *Revue de Zoologie Africaine* 92, 436–441.
- Staeck, W., 1980. Ein neuer Cichlide vom Ostufer des Tanganikasees: *Lamprologus Ieleupi longior* n. ssp. (Pisces, Cichlidae). *Revue de Zoologie Africaine* 94, 11–14.
- Staeck, W., 1983. *Lamprologus buescheri* n. sp. from the Zambian part of Lake Tanganyika (Pisces: Cichlidae). *Senckenberg. Biol.* 63, 325–328.
- Staeck, W., 2014. Eine neue geografische Farbvariante von *Ophthalmitilapia* sp. “Whitecap”, 46. *DCG-Informationen*, pp. 136–138.
- Staeck, W., Seegers, L., 1986. *Neolamprologus cylindricus* spec. nov. Beschreibung eines neuen Tanganjikacichliden aus dem südlichen Tansania und dem östlichen Sambia. *Die Aquariens- und Terrarienzeitschrift (DATZ)* 39, 448–451.
- Steindachner, F., 1909a. Über eine neue Tilapia- und Lamprologus-Art aus dem Tanganikasee und über *Brachyplatystoma (Taenionema) platynema* Blgr. aus der Umgebung von Pará. *Anzeiger der Akademie für Wissenschaftlichen, Wien. Mathematisch-Naturwissenschaftlichen Klasse* 46, 443–447.
- Steindachner, F., 1909b. Über einige neue Fischarten aus dem Tanganikasee. *Anzeiger der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftlichen Klasse* 46, 399–404.
- Steindachner, F., 1911. Beiträge zur Kenntnis der Fischfauna des Tanganikasees und des Kongogebietes. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftlichen Klasse* 120, 1171–1186.
- Sturmbauer, C., 2008. The Great Lakes in East Africa: biological conservation considerations for species flocks. *Hydrobiologia* 615, 95–101. doi:<https://doi.org/10.1007/s10750-008-9554-2>.
- Sturmbauer, C., Baric, S., Salzburger, W., Rüber, L., Verheyen, E., 2001. Lake level fluctuations synchronize genetic divergences of cichlid fishes in African Lakes. *Mol. Biol. Evol.* 18, 144–154. doi:<https://doi.org/10.1093/oxfordjournals.molbev.a003788>.
- Takahashi, T., 2003. Systematics of Tanganyikan cichlid fishes (Teleostei: Perciformes). *Ichthyol. Res.* 50, 367–382. doi:<https://doi.org/10.1007/s10228-003-0181-7>.
- Takahashi, T., 2008. Description of a new cichlid fish species of the genus *Benthochromis* (Perciformes: Cichlidae) from Lake Tanganyika. *J. Fish Biol.* 72, 603–613. doi:<https://doi.org/10.1111/j.1095-8649.2007.01727.x>.
- Takahashi, T., Hori, M., 2006. Description of a new Lake Tanganyikan cichlid fish of the genus *Cyprichromis* (Perciformes: Cichlidae) with a note on sexual dimorphism. *J. Fish Biol.* 68, 174–192. doi:<https://doi.org/10.1111/j.0022-1112.2006.001055.x>.
- Takahashi, T., Koblmüller, S., 2011. The adaptive radiation of cichlid fish in Lake Tanganyika: a morphological perspective. *Int. J. Evol. Biol.*, 1–14 doi:<https://doi.org/10.4061/2011/620754>.
- Takahashi, T., Koblmüller, S., 2014. A new species of *Petrochromis* (Perciformes: Cichlidae) from Lake Tanganyika. *Ichthyol. Res.* 61, 252–264. doi:<https://doi.org/10.1007/s10228-014-0396-9>.
- Takahashi, T., Nakaya, K., 1999. New species of *Haplotaxodon* (Perciformes: Cichlidae) from Lake Tanganyika, Africa. *Copeia*, 101–106.
- Takahashi, T., Nakaya, K., 2003. New species of *Cyphotilapia* (Perciformes: Cichlidae) from Lake Tanganyika, Africa. *American Society of Ichthyologists and Herpetologists* 2003, 824–832.
- Takahashi, T., Yanagisawa, Y., Nakaya, K., 1997. *Microdontochromis rotundiventralis*, a new cichlid fish (Perciformes: Cichlidae) from Lake Tanganyika. *Ichthyol. Res.* 44, 109–117. doi:<https://doi.org/10.1007/BF02678689>.
- Takahashi, T., Hori, M., Nakaya, K., 2002. New species of *Cyprichromis* (Perciformes: Cichlidae) from Lake Tanganyika, Africa. *Copeia*, 1029–1036.
- Takahashi, T., Ngatunga, B., Snoeks, J., 2007. Taxonomic status of the six-band morph of *Cyphotilapia frontosa* (Perciformes: Cichlidae) from Lake Tanganyika, Africa. *Ichthyol. Res.* 54, 55–60. doi:<https://doi.org/10.1007/s10228-006-0374-y>.
- Takahashi, T., Ota, K., Kohda, M., Hori, M., 2012. Some evidence for different ecological pressures that constrain male and female body size. *Hydrobiologia* 684, 35–44.
- Tawil, P., 2008. The Exquisite *Cyprichromis* from Kigoma, a “dwarf jumbo”. *Cichlid News Magazine* 17, 6–16.
- Theis, A., Salzburger, W., Egger, B., 2012. The function of anal fin egg-spots in the cichlid fish *Astatotilapia burtoni*. *PLoS One* 7, doi:<https://doi.org/10.1371/journal.pone.0029878> e29878.
- Theis, A., Ronco, F., Indermaur, A., Salzburger, W., Egger, B., 2014. Adaptive divergence between lake and stream populations of an East African cichlid fish. *Mol. Ecol.* 23, 5304–5322. doi:<https://doi.org/10.1111/mec.12939>.
- Theis, A., Roth, O., Cortesi, F., Ronco, F., Salzburger, W., Egger, B., 2017. Variation of anal fin egg-spots along an environmental gradient in a haplochromine cichlid fish. *Evolution* 71, 766–777. doi:<https://doi.org/10.1111/evo.13166>.
- Timoshkin, O.A., Samsonov, D.P., Yamamuro, M., Moore, M.V., Belykh, O.I., Malnik, V. V., Sakirko, M.V., Shirokaya, A.A., Bondarenko, N.A., Domyshcheva, V.M., Fedorova, G.A., Kochetkov, A.I., Kuzmin, A.V., Likhnev, A.G., Medvezhonkova, O.V., Nepokrytkh, A.V., Pasyukova, E.M., Poberezhnaya, A.E., Potapskaya, N.V., Rozhkova, N.A., Sheveleva, N.G., Tikhonova, I.V., Timoshkina, E.M., Tomberg, I. V., Volkova, E.A., Zaitseva, E.P., Zvereva, Y.M., Kupchinsky, A.B., Bukshuk, N.A., 2016. Rapid ecological change in the coastal zone of Lake Baikal (East Siberia): is the site of the world’s greatest freshwater biodiversity in danger? *J. Great Lakes Res.* 42, 487–497. doi:<https://doi.org/10.1016/j.jglr.2016.02.011>.
- Trewavas, E., 1953. A new species of the cichlid genus *Limnochromis* of Lake Tanganyika. *Bulletin du Musée Royal d’Histoire Naturelle de Belgique* 29, 1–3.
- Trewavas, E., Poll, M., 1952. Three new species and two new subspecies of the genus *Lamprologus*, Cichlid fishes of Lake Tanganyika. *Bulletin de l’Institut Royal des Sciences Naturelles de Belgique* 28, 1–16.
- Vaillant, L.L., 1899. *Protopterus retropinnis* et *Ectodus foae*. *Bulletin du Muséum National d’Histoire Naturelle* 5, 219–222.
- Van Steenberge, M., Vanhove, M.P.M., Muzumani Risasi, D., Mulimbwa N’Sibula, T., Muterezi Bukinga, F., Pariselle, A., Gillardin, C., Vreven, E., Raeymaekers, J.A.M., Huysse, T., Volckaert, F.A.M., Nshombo Muderhwa, V., Snoeks, J., 2011. A recent inventory of the fishes of the north-western and central western coast of Lake Tanganyika (Democratic Republic Congo). *Acta Ichthyol. Piscat.* 41, 201–214.
- Van Steenberge, M., Pariselle, A., Huysse, T., Volckaert, F.A.M., Snoeks, J., Vanhove, M. P.M., 2015. Morphology, molecules, and monogenean parasites: an example of an integrative approach to cichlid biodiversity. *PLoS One* 10, 1–42. doi:<https://doi.org/10.1371/journal.pone.0124474>.
- Van Steenberge, M., Raeymaekers, J.A.M., Hablützel, P.I., Vanhove, M.P.M., Koblmüller, S., Snoeks, J., 2018. Delineating species along shifting shorelines: *Tropheus* (Teleostei, Cichlidae) from the southern subbasin of Lake Tanganyika. *Front. Zool.* 15, 1–18. doi:<https://doi.org/10.1186/s12983-018-0287-4>.
- Van Steenberge, M., 2014. *Species and Speciation in Tropheus, Simochromis and Pseudosimochromis: A Multidisciplinary Approach to a Cichlid Radiation from Lake Tanganyika*. KU Leuven.
- Van Wijngaarden, C., 1995. *Distributiepatronen van de Lamprologinen*. KU Leuven, Belgium.
- Verborg, P., Bills, R., 2007. Two new sympatric species of *Neolamprologus* (Teleostei: Cichlidae) from Lake Tanganyika, East Africa. *Zootaxa* 1612, 25–44.
- Verheyen, E., 2016. Oil extraction imperils Africa’s Great Lakes. *Science* 354, 561–562. doi:<https://doi.org/10.1126/science.aal1722>.
- Verheyen, E., Salzburger, W., Snoeks, J., Meyer, A., 2003. Origin of the superflock of cichlid fishes from Lake Victoria, East Africa. *Science* 300, 325–329. doi:<https://doi.org/10.1126/science.1080699>.
- von Rintelen, T., Marwoto, R.M., Haffner, G.D., Herder, F., 2014. Preface: speciation research in ancient lakes – classic concepts and new approaches. *Hydrobiologia* 739, 1–6. doi:<https://doi.org/10.1007/s10750-014-2028-9>.
- Weitekamp, C.A., Hofmann, H.A., 2017. Neuromolecular correlates of cooperation and conflict during territory defense in a cichlid fish. *Horm. Behav.* 89, 145–156. doi:<https://doi.org/10.1016/j.yhbeh.2017.01.001>.
- Wilson, A.B., Glaubrecht, M., Meyer, A., 2004. Ancient lakes as evolutionary reservoirs: evidence from the thalassoid gastropods of Lake Tanganyika. *Proc. R. Soc. B* 271, 529–536. doi:<https://doi.org/10.1098/rspb.2003.2624>.
- Winkelmann, K., Genner, M.J., Takahashi, T., Rüber, L., 2014. Competition-driven speciation in cichlid fish. *Nat. Commun.* 5, doi:<https://doi.org/10.1038/ncomms4412>.
- Yamaoka, K., 1983. A revision of the cichlid fish genus *petrochromis* from Lake Tanganyika, with description of a new species. *Japanese Journal of Ichthyology* 30, 129–141.
- Young, R.L., Ferkin, M.H., Ockendon-Powell, N.F., Orr, V.N., Phelps, S.M., Pogány, Á., Richards-Zawacki, C.L., Summers, K., Székely, T., Trainor, B.C., Urrutia, A.O., Zachar, G., O’Connell, L.A., Hofmann, H.A., 2019. Conserved transcriptomic profiles underpin monogamy across vertebrates. *PNAS* 116, 1331–1336. doi:<https://doi.org/10.1073/PNAS.1813775116>.