Journal of Great Lakes Research 46 (2020) 1067–1078

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/ijglr

Review

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

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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.

Contents

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

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https://doi.org/10.1016/j.jglr.2019.05.009
0380-1330/

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 Schaetzl, 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 km^2 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 understudied. 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 context 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

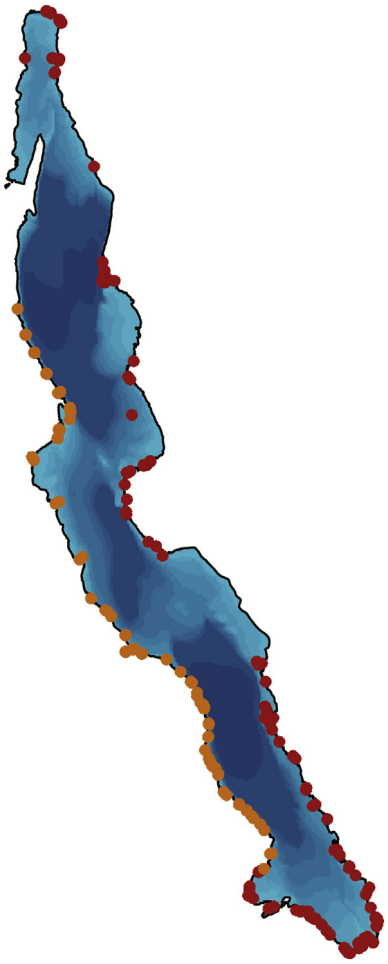

Fig. 1. Map of Lake Tanganyika with indicated localities visited for collection and diving activities. Orange circles represent sites visited before 1998 by only one author (HHB), red circles indicate locations sampled between 2007 and 2018 by all authors. Darker areas in the lake illustrate the three 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 Schliewen, 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

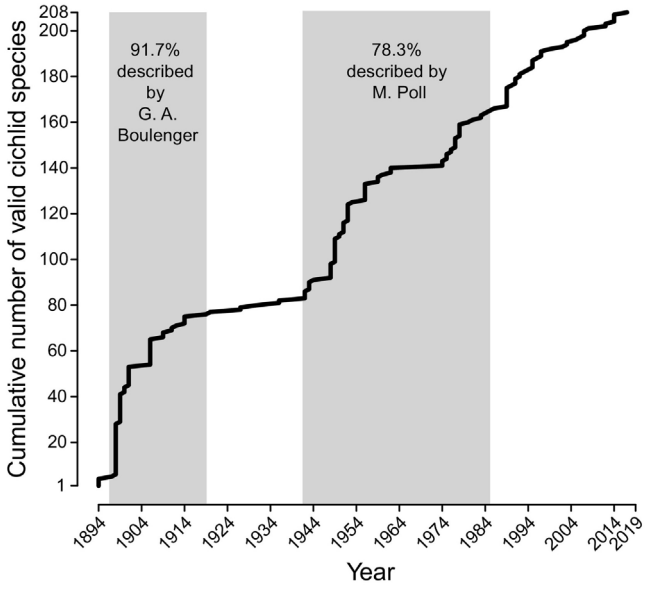

Fig. 2. Cumulative number of described cichlid species over time. The number of described species increased over the years steadily with a major increment around 1900, by the extensive work by George Boulenger, followed by a second steep ascent between the 1940's and the 1980's due to Max Poll's contributions. 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	*Bathybates fasciatus*	Boulenger, 1901	*Bathybates fasciatus*	West Coast
	Bathybates ferox	Boulenger, 1898	*Bathybates ferox*	Kinyamkolo (= Mpulungu, ZAM)
	Bathybates graueri	Steindachner, 1911	*Bathybates graueri*	LT
	Bathybates hornii	Steindachner, 1911	*Bathybates horni*	LT
	Bathybates leo	Poll, 1956	*Bathybates leo*	Nyanza Lac (BUR)
	Bathybates minor	Boulenger, 1906	*Bathybates minor*	Kituta (= Chituta Bay, ZAM), Lofu (= Lufubu, ZAM)
	Bathybates vittatus	Boulenger, 1914	*Bathybates vittatus*	Kilewa Bay (DRC)
	Hemibates koningsi	Schedel and Schliewen, 2017	*Hemibates koningsi*	Mpulungu (ZAM)
	Hemibates stenosoma	(Boulenger, 1901)	*Paratilapia stenosoma*	south end of LT (ZAM) and Maswa, south of Ujiji (TAN)
Benthochromini	*Benthochromis horii*	Takahashi, 2008	*Benthochromis horii*	Mtondwe Island (= Mutondwe Island, ZAM)
	Benthochromis melanoides	(Poll, 1984)	*Haplotaxodon melanoides*	Albertville (= Kalemie, DRC)
	Benthochromis tricoti	(Poll, 1948)	*Haplotaxodon tricoti*	Karema (TAN), Moba Bay (DRC)
Boulengerochromini	*Boulengerochromis microlepis*	(Boulenger, 1899b)	*Tilapia microlepis*	Moliro (DRC)
Coptodini	*Coptodon rendalli* [3,4]	(Boulenger, 1897)	*Chromis rendalli*	Upper Shire River (Malawi)
Cyphotilapiini	*Ctenochromis benthicola*	(Matthes, 1962)	*Haplochromis benthicola*	Kalundu (DRC)
	Cyphotilapia frontosa	(Boulenger, 1906)	*Paratilapia frontosa*	Kigoma (TAN)
	Cyphotilapia gibberosa	Takahashi and Nakaya, 2003	*Cyphotilapia gibberosa*	Kasenga (ZAM)
Cyprichromini	*Cyprichromis coloratus*	Takahashi and Hori, 2006	*Cyprichromis coloratus*	Wonzye Point (ZAM)
	Cyprichromis leptosoma	(Boulenger, 1898)	*Paratilapia leptosoma*	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)
	Cyprichromis microlepidotus	(Poll, 1956)	*Limnochromis microlepidotus*	Ubwari (DRC)
	Cyprichromis pavo	Büscher, 1994	*Cyprichromis pavo*	Tembwe (DRC)
	Cyprichromis zonatus	Takahashi et al., 2002	*Cyprichromis zonatus*	Kasenga (ZAM)
	Paracyprichromis brieni	(Poll, 1981)	*Cyprichromis brieni*	Ubwari (DRC)
	Paracyprichromis nigripinnis	(Boulenger, 1901)	*Paratilapia nigripinnis*	Msambu (= Msamba, TAN)
Ectodini	*Asprotilapia leptura*	Boulenger, 1901	*Asprotilapia leptura*	Msambu (= Msamba, TAN)
	Aulonocranus dewindti	(Boulenger, 1899b)	*Paratilapia dewindti*	Moliro (DRC)
	Callochromis macrops	(Boulenger, 1898)	*Paratilapia macrops*	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)
	Callochromis melanostigma	(Boulenger, 1906)	*Pelmatochromis melanostigma*	Uvira (DRC), Kaboge (DRC), Niamkolo (= Mpulungu, ZAM), Lofu (= Lufubu, ZAM), Kituta (= Chituta Bay, ZAM)
	Callochromis pleurospilus	(Boulenger, 1906)	*Pelmatochromis pleurospilus*	Mpala (DRC), Tembwi (= Cap Tembwe, DRC)
	Cardiopharynx schoutedeni	Poll, 1942	*Cardiopharynx schoutedeni*	Usumbura (= Bujumbura, BUR)
	Cunningtonia longiventralis	Boulenger, 1906	*Cunningtonia longiventralis*	Niamkolo (= Mpulungu, ZAM)
	Cyathopharynx foae	(Vaillant, 1899)	*Ectodus foae*	LT, south
	Cyathopharynx furcifer	(Boulenger, 1898)	*Paratilapia furcifer*	Kinyamkolo (= Mpulungu, ZAM)
	Ectodus descampsii	Boulenger, 1898	*Ectodus descampsii*	LT
	Enantiopus melanogenys	(Boulenger, 1898)	*Ectodus melanogenys*	LT
	Grammatotria lemairii	Boulenger, 1899b	*Grammatotria lemairii*	Moliro (DRC)
	Lestradea perspicax	Poll, 1943	*Lestradea perspicax*	Rumonge (BUR)
	Lestradea stappersii	(Poll, 1943)	*Ophthalmotilapia stappersii*	Kilewa Bay (DRC)
	Microdontochromis rotundiventralis	Takahashi et al., 1997	*Microdontochromis rotundiventralis*	Nkumbula Island (ZAM)
	Microdontochromis tenuidentata	(Poll, 1951b)	*Xenotilapia tenuidentata*	Baie de Vua (= Livua, DRC)
	Ophthalmotilapia boops	(Boulenger, 1901)	*Tilapia boops*	Msambu (= Msamba, TAN)
	Ophthalmotilapia heterodonta	(Poll and Matthes, 1962)	*Oph. ventralis heterodontus*	Mboko Island (DRC)
	Ophthalmotilapia nasuta	(Poll and Matthes, 1962)	*Ophthalmochromis nasutus*	Kalungwe (DRC)
	Ophthalmotilapia ventralis	(Boulenger, 1898)	*Paratilapia ventralis*	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)
	Xenotilapia bathyphilus	(Poll, 1956)	*Xenotilapia ochrogenys bathyphilus*	Sumbu (ZAM)
	Xenotilapia boulengeri	(Poll, 1942)	*Enantiopus boulengeri*	Rumonge (BUR)
	Xenotilapia burtoni	(Poll, 1951a)	*Xenotilapia longispinis burtoni*	Burton Bay (DRC)
	Xenotilapia caudafasciata	Poll, 1951b	*Xenotilapia caudafasciata*	Moba Bay (DRC)
	Xenotilapia flavipinnis	Poll, 1985	*Xenotilapia flavipinnis*	Bujumbura (BUR)
	Xenotilapia longispinis	Poll, 1951a	*Xenotilapia longispinis*	Ruzizi (BUR)
	Xenotilapia nasus	De Vos et al., 1995	*Xenotilapia nasus*	Gitaza, 29km south of Bujumbura (BUR)
	Xenotilapia nigrolabiata	Poll, 1951b	*Xenotilapia nigrolabiata*	M'Samba (= Msamba, TAN)
	Xenotilapia ochrogenys	(Boulenger, 1914)	*Enantiopus ochrogenys*	Kilewa Bay (DRC)
	Xenotilapia ornatipinnis	Boulenger, 1901	*Xenotilapia ornatipinnis*	Kibwesi (= Kibwesa/ Sibwesa, TAN)
	Xenotilapia papilio	Büscher, 1990	*Xenotilapia papilio*	Tembwe, (DRC)
	Xenotilapia sima	Boulenger, 1899b	*Xenotilapia sima*	Moliro (DRC)
	Xenotilapia singularis	(Boulenger, 1914)	*Stappersia singularis*	Kilewa Bay (DRC), Tulo (DRC)
	Xenotilapia spilopterus	Poll and Stewart, 1975	*Xenotilapia spilopterus*	Nkumbula Island (ZAM)
Eretmodi	*Eretmodus cyanostictus*	Boulenger, 1898	*Eretmodus cyanostictus*	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)
	Eretmodus marksmithi	Burgess, 2012	*Eretmodus marksmithi*	Makombe (BUR)
	Spathodus erythrodon	Boulenger, 1900	*Spathodus erythrodon*	Albertville (= Mtoa, DRC)
	Spathodus marlieri	Poll, 1950	*Spathodus marlieri*	Uvira (DRC)
	Tanganicodus irsacae	Poll, 1950	*Tanganicodus irsacae*	Uvira (DRC)
Haplochromini	*Astatotilapia burtoni* [3]	(Günther, 1894)	*Chromis burtoni*	LT
	Astatoreochromis straeleni [3]	(Poll, 1944)	*Haplochromis straeleni*	Lukuga river
	Haplochromis stappersii [3]	Poll, 1943	*Haplochromis stappersii*	Lufuku river (= Mpala, DRC)
Tropheini	*Ctenochromis horei*	Günther, 1894	*Chromis horei*	LT
	Gnathochromis pfefferi	(Boulenger, 1898)	*Paratilapia pfefferi*	Kinyamkolo (= Mpulungu, ZAM)
	Interochromis loocki	(Poll, 1949)	*Limnotilapia loocki*	Kigoma (TAN)
	Limnotilapia dardennii	(Boulenger, 1899b)	*Tilapia dardennii*	Moliro (DRC)
	Lobochilotes labiatus	(Boulenger, 1898)	*Tilapia labiata*	Kinyamkolo (= Mpulungu, ZAM)
	Petrochromis ephippium	(Brichard, 1989)	*Petrochromis trewavasae ephippium*	LT
	Petrochromis famula	Matthes and Trewavas, 1960	*Petrochromis famula*	LT
	Petrochromis fasciolatus	Boulenger, 1914	*Petrochromis fasciolatus*	Kapampa (DRC), Kilewa Bay (DRC)
	Petrochromis horii	Takahashi and Koblmüller, 2014	*Petrochromis horii*	Kasenga (ZAM)
	Petrochromis macrognathus	Yamaoka, 1983	*Petrochromis macrognathus*	Luhanga (DRC)
	Petrochromis orthognathus	Matthes, 1959a	*Petrochromis orthognathus*	Bemba (DRC)
	Petrochromis polyodon	Boulenger, 1898	*Petrochromis polyodon*	Mbity Rocks (= Mbita Rocks, ZAM), Kinyamkolo (= Mpulungu, ZAM)
	Petrochromis trewavasae	Poll, 1948	*Petrochromis trewavasae*	Moliro (DRC)
	Pseudosimochromis babaulti	(Pellegrin, 1927b)	*Simochromis babaulti*	Ouvira (= Uvira (DRC)
	Pseudosimochromis curvifrons	(Poll, 1942)	*Simochromis curvifrons*	Nyanza Lac (BUR)
	Pseudosimochromis margaretae [1]	(Axelrod and Harrison, 1978)	*Simochromis margaretae*	Kigoma (TAN)
	Pseudosimochromis marginatus	(Poll, 1956)	*Simochromis marginatus*	Manga (= Cape Banza area, DRC)
	Simochromis diagramma	(Günther, 1894)	*Chromis diagramma*	LT
	Tropheus annectens	Boulenger, 1900	*Tropheus annectens*	Albertville (= Mtoa, DRC)
	Tropheus brichardi	Nelissen and Thys van den Audenaerde, 1975	*Tropheus brichardi*	Nyanza Lac (BUR)
	Tropheus duboisi	Marlier, 1959	*Tropheus duboisi*	Bemba (DRC)
	Tropheus kasabae [2]	(Nelissen, 1977)	*Tropheus moorii kasabae*	Kasaba Bay (= Kala Bay, ZAM)
	Tropheus moorii	Boulenger, 1898	*Tropheus moorii*	Kinyamkolo (= Mpulungu, ZAM)
	Tropheus polli [2]	Axelrod, 1977	*Tropheus polli*	Bulu Island (= Karilani Island, TAN)

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

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

molecular phylogenetics-based studies by Muschick et al. (2012) and Dunz and Schliewen (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 (Fermon, 2007).

'Questionable species'

Three out of the 208 formally described cichlid species of Lake Tanganyika are categorized as 'questionable species' here: *Tropheus kasabae* (Nelissen, 1977), *T. polli* Axelrod, 1977, and *N. cancellatus* 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	*Benthochromis* sp. "horii mahale"	variety	*cf. Benthochromis horii*	Mahale area	Konings, 2015
Cyphotilapiini	*Cyphotilapia* sp. "5-bar frontosa"	variety	*cf. Cyphotilapia frontosa*	northern LT	Genevelle, 2004; Konings, 2015; Takahashi et al., 2007 (referred to as: *Cyphotilapia* sp. "6-bar frontosa")
Cyprichromini	*Cyprichromis* sp. "dwarf jumbo"	potential species	*aff. Cyprichromis coloratus*: much smaller in body size and differs in colouration	northern LT	Konings, 2015; Tawil, 2008
	Cyprichromis sp. "jumbo"	potential species	*aff. Cyprichromis coloratus*: differs in colouration	southern LT	Konings, 2015
	Cyprichromis sp. "kibishi"	potential species	*aff. Cyprichromis zonatus*: differs in colouration and disconjunct distribution	Kibishi area	Konings, 2015
	Paracyprichromis sp. "tembwe"	potential species	aff. *Paracyprichromis nigripinnis*: differs in caudal fin shape	Tembwe area (~40km south of Moba)	first report
	Paracyprichromis sp. "brieni south"	variety	*cf. Paracyprichromis brieni*	southern LT	Konings, 2015
Ectodini	*Ophthalmotilapia* sp. "paranasuta"	potential species	*aff. Ophthalmotilapia nasuta*: differs in head and fin shape, differs in behaviour	northern LT	Konings, 2015
	Ophthalmotilapia sp. "white cap"	potential species	*aff. O. ventralis* and *aff. O. heterodonta*	Tanzanian coast	Staeck, 2014
	Xenotilapia sp. "kilesa"	potential species	aff. *Enantiopus melanogenys*: differs in melanin patterns	Kilesa area	Konings, 2015 (referred to as *Enantiopus* sp. "kilesa")
	Xenotilapia sp. "papilio sunflower"	potential species	*aff. Xenotilapia papilio:* differs in shape and colouration of the dorsal fin	southern LT	Koblmüller et al., 2004; Konings, 2015
	Ectodus sp. "north"	variety	*cf. Ectodus descampsi*	northern LT	Koblmüller et al., 2004; Konings, 2015
	Xenotilapia sp. "spilopterus north"	variety	*cf. Xenotilapia spilopterus*	northern LT	Konings, 2015
Haplochromini	*Haplochromis* sp. "chipwa"	potential species	*aff. Haplochromis stappersii*: genetic data shows strong divergence	southern tributaries and estuaries	Meyer and Indermaur et al., 2015
Tropheini	*Petrochromis* sp. "giant"	in preparation	description in preparation	Mahale to Kipili area	Mattsson, 2018, bioRxiv preprint
	Petrochromis sp. "kazumbae"	in preparation	description in preparation	Kigoma area	Mattsson, 2018, bioRxiv preprint
	Petrochromis sp. "macrognathus rainbow"	in preparation	description in preparation	Kipili area	Mattsson, 2018, bioRxiv preprint
	Petrochromis sp. "polyodon texas"	in preparation	description in preparation	Mahale to Kipili area	Mattsson, 2018, bioRxiv preprint
	Petrochromis sp. "red"	in preparation	description in preparation	Mahale area	Mattsson, 2018, bioRxiv preprint
	Tropheus sp. "black", *Tropheus* sp. "kirschfleck"	in preparation	description in preparation	northern LT	Van Steenberge, 2014
	Tropheus sp. "lunatus"	in preparation	description in preparation	Cape Kabogo, Maswa area	Van Steenberge, 2014
	Tropheus sp. "mpimbwe"	in preparation	description in preparation	Cape Mpimbwe	Van Steenberge, 2014; Van Steenberge et al., 2018
	Tropheus sp. "murago"	in preparation	description in preparation	Wapembwe area	Konings, 2015; Van Steenberge, 2014
	Tropheus sp. "red"	in preparation	description in preparation	south-western LT	Konings, 2015; Van Steenberge, 2014; Van Steenberge et al., 2011, 2018;
	Petrochromis sp. "kipili brown"	potential species	*aff. Petrochromis horii*: similar ecology, but has only 7 vertical bars in dorsal fin (versus 8 in *P. horii*)	Kipili area	Konings, 2015
	Petrochromis sp. "moshi yellow"	variety	*cf. Petrochromis ephippium*	Mahale to Kipili area	Konings, 2015
	Petrochromis sp. "orthognathus ikola"	variety	*cf. Petrochromis orthognathus*	Ikola area	Koblmüller et al., 2010; Konings, 2015
	Tropheus sp. "brichardi kipili"	variety	*cf. Tropheus brichardi*	Kipili area	Karlsson and Karlsson, 2015; Van Steenberge et al., 2018
	Tropheus sp. "lukuga"	variety	*cf. Tropheus brichardi*	Lukuga area and central Tanzanian coast	Karlsson and Karlsson, 2015
Lamprologini	*Altolamprologus* sp. "compressiceps shell"	potential species	*aff. Altolamprologus compressiceps*: distinct in body size and colouration	Lake wide on shell beds	Koblmüller et al., 2007, 2017; Konings, 2015; Konings and Dieckhoff 1992;
	Chalinochromis sp. "bifrenatus"	potential species	*aff. Chalinochromis brichardi*: distinct differences in colouration and caudal fin shape	southern Tanzanian coast	Konings, 2015; Van Steenberge et al., 2011
	Julidochromis sp. "kombe"	potential species	*aff. Julidochromis transcriptus*: differs in colouration and body shape and discontinuous distribution	Kombe area	Brichard, 1989; Konings, 2015
	Julidochromis sp. "unterfels"	potential species	*aff. Julidochromis spp.*: differs in behaviour from all known *Julidchromis* spp., mouth distinctly terminal, high body		first report
	Lamprologus sp. "ornatipinnis congo"	potential species	aff. *Lamprologus ornatipinnis:* more pronounced sexual size dimorphism, distinct dorsal fin shape	southern DRC coast	first report
	Neolamprologus sp. "caudopunctatus kipili"	potential species	*aff. Neolamprologus leloupi*: missing black margin on the caudal fin, larger body size; differs in body shape	Kipili area	Konings, 2015; Snoeks et al., 1994
	Neolamprologus sp. "cygnus"	potential species	*aff. Neolamprologus falcicula*: found in deeper waters, differs in behaviour and juvenile colouration	southern Tanzanian coast	Konings, 2015
	Neolamprologus sp. "eseki"	potential species	*aff. Neolamprologus mondabu*: differs in shape and colour of the caudal fin	Kipili area	Konings, 2015, 2005
	Neolamprologus sp. "falcicula mahale"	potential species	*aff. Neolamprologus falcicula:* differs in fin colouration and juvenile colouration, syntopic with *N.* sp. "gracilis tanzania"	Mahale area	first report
	Neolamprologus sp. "gracilis tanzania"	potential species	aff. *Neolamprologus gracilis*: differs in shape of the caudal fin, disconjunct distribution, syntopic with *N.* sp. "falcicula mahale"	Mahale area	first report, see Konings, 2015 for distribution of *N. gracilis*
	Neolamprologus sp. "kombe"	potential species	*aff. N. savoryi and aff. N. brichardi:* shares traits of both species, potentially of hybrid origin	Kombe area	Büscher, 2018
	Neolamprologus sp. "ventralis stripe"	potential species	*aff. Neolamprologus ventralis*: differs in body colouration	western Zambia	first report
	Telmatochromis sp. "longola"	potential species	*aff. Telmatochromis spp.*	Longola area	first report
	Chalinochromis sp. "ndobhoi"	variety	*cf. Chalinochromis brichardi*	Maswa and Kungwe Bay	Brichard, 1989; Konings, 2015
	Julidochromis sp. "marlieri south"	variety	*cf. Julidochromis marlieri*	southern LT	see Konings, 2015 for distribution of *J. marlieri*
	Julidochromis sp. "regani south"	variety	*cf. Julidochromis regain*	southern LT	see Konings, 2015 for distribution of *J. regani*
	Lamprologus sp. "ornatipinnis zambia"	variety	*cf. Lamprologus ornatipinnis*	southern LT	Gordon and Bills, 1999; Konings, 2015
	Lepidiolamprologus sp. "meeli kipili"	variety	*cf. Lepidiolamprologus attenuatus*	Kipili area	Konings, 2015
	Neolamprologus sp. "brevis magara"	variety	*cf. Neolamprologus brevis*	Magara area	Herrmann, 1987
	Neolamprologus sp. "daffodil"	variety	*cf. Neolamprologus pulcher*	Samazi / Kantalamba area	Konings, 2015
	Neolamprologus sp. "furcifer ulwile"	variety	*cf. Neolamprologus furcifer*	Ulwile area	Kullander et al., 2014
	Neolamprologus sp. "modabu mahale"	variety	*cf. Neolamprologus mondabu*	Mahale area	first report
	Telmatochromis sp. "dhonti north"	variety	*cf. Telmatochromis dhonti*	northern LT	Konings, 2015, *cf. T. caninus* (Poll, 1942), junior. syn. of *T. dhonti,* (Poll, 1986)
	Telmatochromis sp. "dhonti twiyu"	variety	*cf. Telmatochromis dhonti*	southern Tanzanian coast	*cf. T. macrolepis* (Borodin,1931), junior syn. of *T. dhonti* (Hanssens & Snoeks, 2001)
	Telmatochromis sp. "shell"	variety	*cf. Telmatochromis temporalis*	Lake wide on shell beds	Konings, 2015; Takahashi et al., 2012; Winkelmann et al., 2014
Trematocarini	*Trematocara* sp. "north"	potential species	*aff. T. unimaculatum,* differs in fin colouration, head morphology and various meristic 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

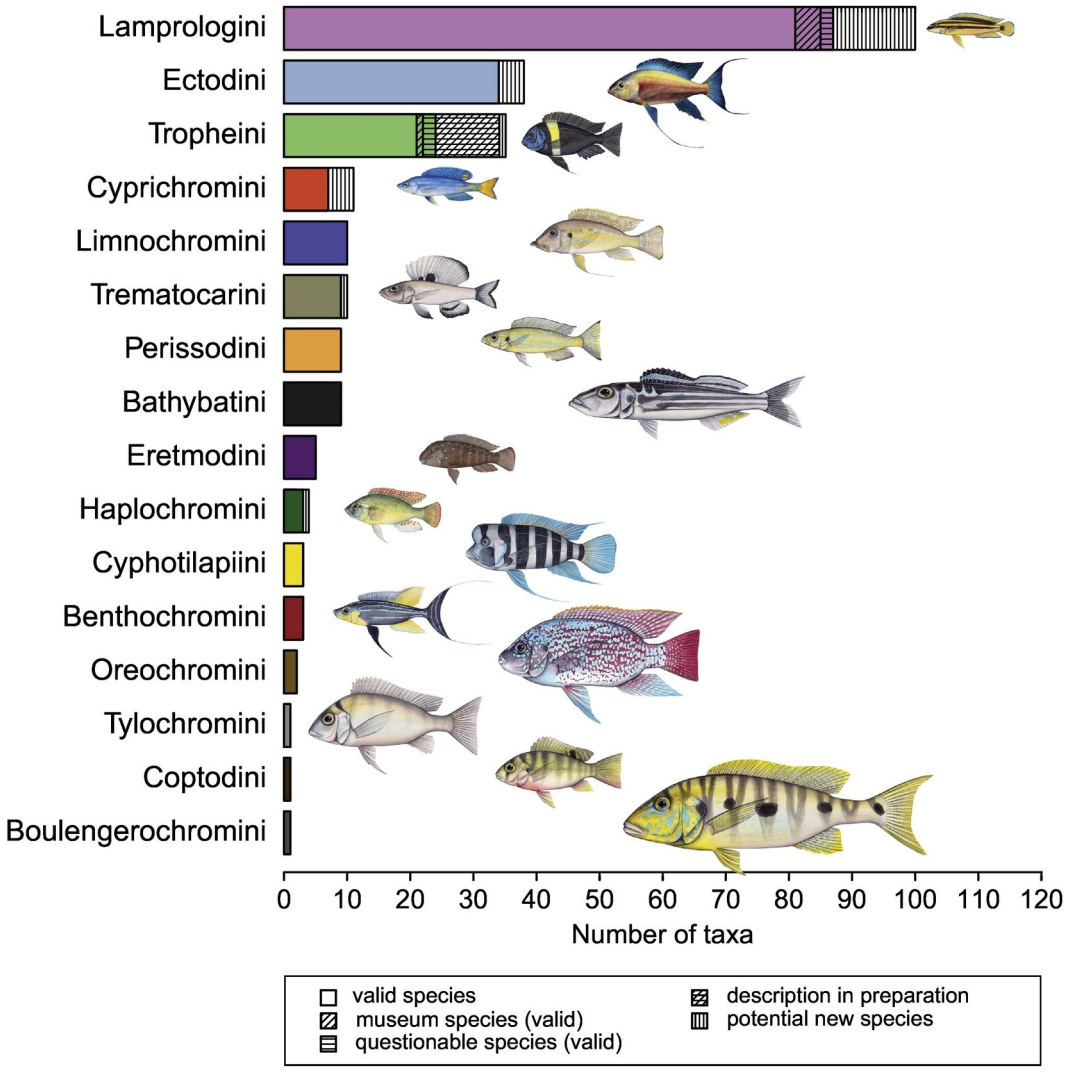

Fig. 3. Taxonomic diversity of Lake Tanganyika cichlids per tribe. Coloured partitions in the bar plot indicate the number of described species, different hatchings are used to highlight 'questionable species' and 'museum species'. White partitions refer to so far undescribed species of the two categories '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* (Staeck, 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. benthicola* (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 cichlid 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).

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