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Out of Lake Tanganyika: endemic lake fishes inhabit rapids of the Lukuga River

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The Lukuga River is a large permanent river intermittently serving as the only effluent of Lake Tanganyika. For at least the first one hundred km its water is almost pure lake water. Seventy-seven species of fish were collected from six localities along the Lukuga River. Species of cichlids, cyprinids, and clupeids otherwise known only from Lake Tanganyika were identified from rapids in the Lukuga River at Niemba, 100 km from the lake, whereas downstream localities represent a Congo River fish fauna. Cichlid species from Niemba include specialized algal browsers that also occur in the lake *(Simochromis babaulti*, *S. diagramma)* and one invertebrate picker representing a new species of a genus *(Tanganicodus)* otherwise only known from the lake. Other fish species from Niemba include an abundant species of clupeid, *Stolothrissa tanganicae*, otherwise only known from Lake Tanganyika that has a pelagic mode of life in the lake. These species demonstrate that their adaptations are not necessarily dependent upon the lake habitat. Other endemic taxa occurring at Niemba are known to frequent vegetated shore habitats or river mouths similar to the conditions at the entrance of the Lukuga, viz. *Chelaethiops minutus* (Cyprinidae), *Lates mariae* (Latidae), *Mastacembelus cunningtoni* (Mastacembelidae), *Astatotilapia burtoni*, *Ctenochromis horei*, *Telmatochromis dhonti*, and *Tylochromis polylepis* (Cichlidae). The Lukuga frequently did not serve as an effluent due to weed masses and sand bars building up at the exit, and low water levels of Lake Tanganyika. Since the Lukuga River does not have a permanent connection with Lake Tanganyika we hypothesize that its lake fishes are not temporary occurrences due to occasional spills from the lake. Apparently the Lukuga maintains a stable fish community that is independent of the lake, and may depend more on the flow of the major tributary, the left bank tributary Niemba River, than on outflow from Lake Tanganyika.

Introduction

Upwards of 470 fish species (described and undescribed), including about 300 cichlids (Cichlidae) and over 170 non-cichlids, are estimated to inhabit the East African Lake Tanganyika basin, including the lake and its affluent tributaries (De Vos & Snoeks, 1994; Snoeks, 2000). The lake harbours one of the most speciose assemblages of endemic cichlid fishes, with over 200 species described to date (Koblmüller et al., 2008; De Vos et al., 2001). This is less than the numbers in two other large lakes in Africa, Victoria and Malawi, despite Tanganyika being the oldest of these lakes. On the other hand, Tanganyika is the only one with species-rich lineages of both substrate-brooding and mouth-brooding cichlids (Coulter, 1991; Snoeks, 2000), whereas the others have only mouth-brooders. Tanganyika also is richer in several other fish groups than the other lakes,

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with two endemic genera and species of pellonuline clupeids (Clupeidae), four endemic species of *Lates* (Latidae), numerous endemic mastacembelids or spiny eels (Mastacembelidae) (Brown et al., 2010), a species flock of mochokid catfishes (Mochokidae) (Day & Wilkinson, 2006), and distinctive endemic genera of claroteid catfishes (Claroteidae) (Bailey & Stewart, 1984; Seegers, 2008).

Lake Tanganyika formed as a rift about 20 million years ago and the present lacustrine environment developed gradually, with the current ecological conditions achieved a little over 5 million years ago (Nishida, 1997; Cohen et al., 1997a). It is generally assumed that the fish fauna of Lake Tanganyika is derived from the Congo River basin, particularly because the major tributary, the Malagarasi River, has a fish fauna similar to that of the Congo River basin, and its east to west flow is suggestive of a former headwater of the Lualaba River, the major headstream of the Congo River. The origin of the Lake Tanganyika cichlid fauna is still a subject of discussion, but at least one major component, the Lamprologini, is otherwise known only from riverine conditions in the Congo basin (Schelly & Stiassny, 2004).

Lake Tanganyika has numerous tributaries, but most influx is from direct precipitation and 90–95 % of the water loss is from evaporation (1700 mm · a^{-1}) (Beauchamp, 1946). The only outlet is through the Lukuga River to the Lualaba River (Fig. 1). The Lukuga runs through a low, wide valley stretch along the mid-western shore of Lake Tanganyika, its entrance located within the lakeside town of Kalemie. It is estimated to account for up to 10 % of the water loss from the lake. Along its upper course it is a relatively narrow, shallow river with numerous rapids, and a high fall at Niemba (also known as Nyemba), about 100 km downstream from the lake. It is a relatively inaccessible river and difficult to navigate because of the rapids. Information on the fish fauna downstream of the entrance of the Lukuga is scarce, based on sporadic collections with relatively few specimens reported since Boulenger (1920).

The second author travelled in 1986 from Kalemie westward along the Lukuga to the Lualaba and was then able to collect in two locations near Niemba. Both stations were rapids, upstream from a major fall a little downstream from Niemba. The collections are of considerable significance because they contain species that are otherwise known only from Lake Tanganyika, and also species that are currently believed to be rock browsers and invertebrate pickers that evolved in the particular habitat and fish community in the lake.

The objective of this paper is to report on the composition of the Niemba collection, and to discuss the biogeographical significance of this highly unique fish community.

Material and methods

Specimens were sampled by the second author using rotenone at the following sites in the Lukuga River drainage, referenced by field numbers. The samples in focus are those from the vicinity of Niemba (Zaire 86-59–60); the remaining samples were sorted and identified in order to have a fuller overview of the Lukuga fish fauna. The Lukuga runs entirely within the Democratic Republic of the Congo.

Zaire 86-59: Lukuga River in the Kisimba-Kilia rapids 2 km downstream from the mouth of the Niemba River. 20–21 Aug 1986.

Zaire 86-60: Niemba River at its mouth into the Lukuga River. 21 Aug 1986.

Zaire 86-61: Luwoyeye River, about 10 km S of Nyunzu on road to Makimba. Shallow stream. Slow current, riffles, pools. Gravel yellow, orange, and black. Water almost black. Visibility to about 50–60 cm. 22 Aug 1986.

Zaire 86-62: Lubile River, about 50 km by road E of Kongolo (Kongolo-Nyunzu road). 22 Aug 1986.

Zaire 86-63: Luawe River, 6 km by road N of Nyunzu. Swampy, almost no current, to 1 m deep. Water clear, slightly blackish. Vegetated, some open water. 23 Aug 1986.

Zaire 86-64: Lufwango River, on road from Nyunzu to Kongolo, near Makundé. 23 Aug 1986.

The major part of the collection was kept in formalin and transferred to 70 % ethanol in 1988 and 2003. It was eventually sorted and identified in 2009 and catalogued in the Swedish Museum of Natural History, Stockholm (NRM). Specimens were identified by the first author, using comparative material in the NRM collection, supplemented by literature comparisons. Samples of two species were deposited in the California

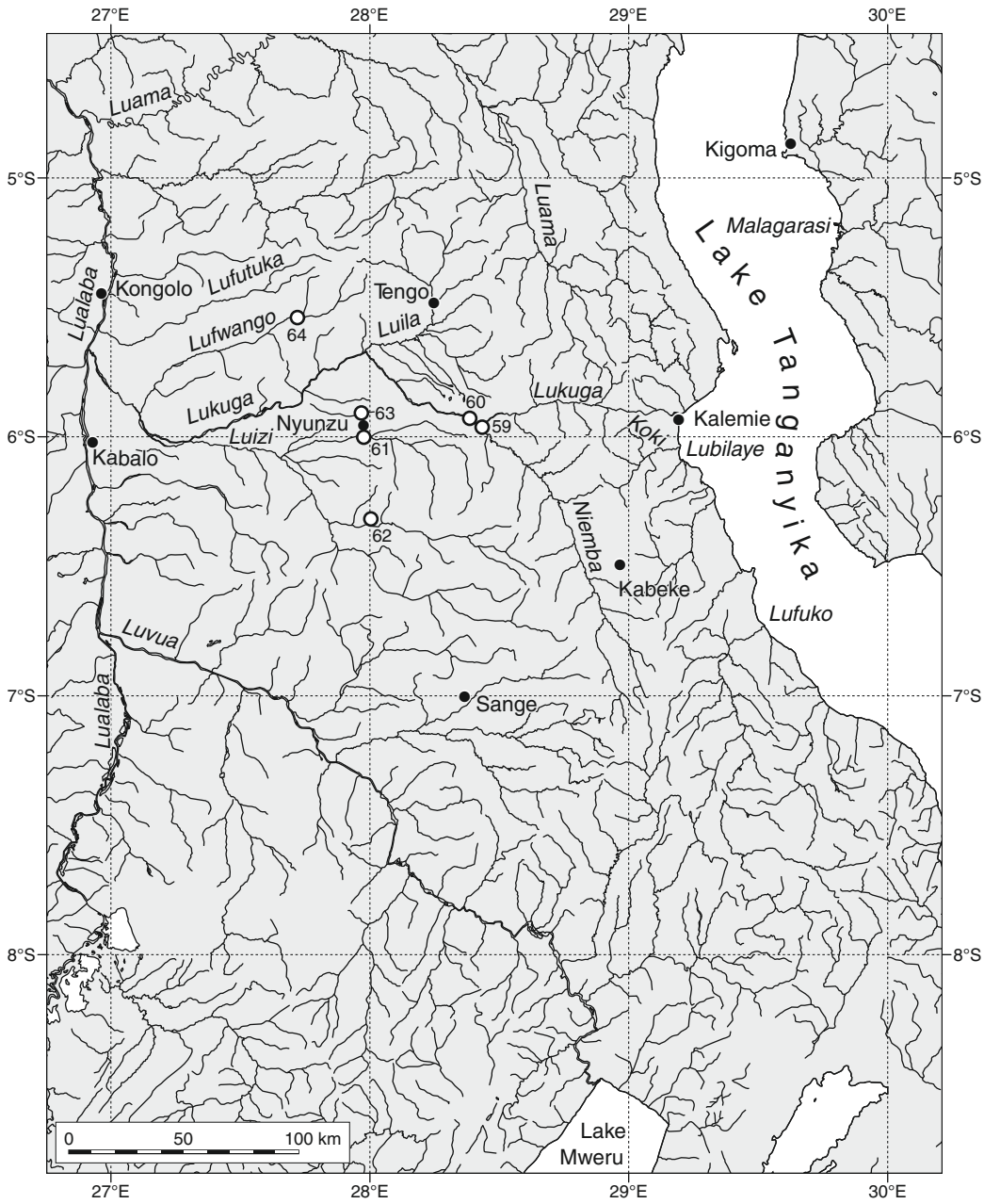

Fig. 1. Location of collecting sites at Niemba.

Academy of Sciences (CAS) and the Natural history Museum, London (BMNH).

A listing of species already reported from the Lukuga was made using available literature, and searching GBIF (http://data.gbif.org) and FishBase (http://www.fishbase.org) occurrence records. Some previous identifications of fishes from the Lukuga River were checked on specimens in the BMNH.

We follow the convention suggested by Berrebi et al. (1996), using *'Barbus'* (in single quotes) as generic name for African cyprinids tradition-

ally assigned to the catch-all genus *Barbus*, but not included in the monophyletic peri-Mediterranean genus *Barbus* sensu stricto (see Kottelat & Freyhof, 2007: 112, for current status of *Barbus*).

Results

Fish species previously reported from the Lukuga River. Altogether 57 species of fishes, four of them not identified to species, have been reported from the Lukuga and tributaries, representing 15 families (Table 1). Approximately 16 localities, some only designated by a river name, can be distinguished. Among those, Amisi, Albertville (presently known as Kalemie), Kalwe Lukwiba, and Greinerville (presently also known as Moluba) are upstream of Niemba, localities Tumbwe, Kabeke and Niemba River on the Niemba River, and the remaining pertaining to tributaries joining the Lukuga downstream of Niemba. Greinerville is on the water divide between the Lukuga and the Tanganyika tributary Lubilaye, the other upstream localities obviously close to or within Kalemie. Only 33 species have more specific localities, and it seems likely that those reported from Albertville or just Lukuga River by Boulenger (1919) are actually taken from the exit and nearby lake habitats. Those include characteristic lake cichlids such as *Aulonocranus dewindti*, *Plecodus paradoxus*, and *Limnotilapia dardenni*, and the endemic lake species *Stolothrissa tanganicae* (Clupeidae), *Lamprichthys tanganicanus* (Poeciliidae), and *Lates microlepis* (Latidae). Many more species are known from Kalemie, as reported by Poll (1953, 1956), but are excluded here as they represent the lake fauna, including species known to occur in vegetated areas along the lake. None of these excluded species have been reported from the Lukuga River itself.

Literature reports antedate important revisions and several identifications may be incorrect. It is also possible that the same species is recorded under different names. *Chiloglanis lukugae* and *C. pojeri* were described from the Lukuga drainage (Poll, 1944), but were actually collected in the Luvua drainage (Poll, 1953). Boulenger's (1920) sample of *Auchenoglanis occidentalis*, said to be from a ditch along the Lukuga River, consists of three juvenile specimens of *A. wittei* and one of *A. tanganicanus* (BMNH 1919.7.24:28–30). Nonetheless, 27 of the previously reported species were recovered in 1986, i. e. almost 50 %.

Three cichlid species were reported with confidence from the Lukuga drainage, viz. *Astatotilapia burtoni* from the Kalwe Lukwiba village some distance downstream from the entrance of the Lukuga (Poll, 1956), *Nanochromis squamiceps* from the tributary Luila River (David, 1936), and *Tylochromis polylepis* from Niemba (Stiassny, 1989). Other families reported included species known only from the Lukuga, from a wider area in the Congo basin excluding Lake Tanganyika, or species also known from Lake Tanganyika.

Fish species collected in tributaries of the Lukuga River in 1986. Thirty-nine species were identified from four collecting sites in Lukuga tributaries downstream of Niemba (Table 2). Juveniles of two species (*Labeo* sp., *Pseudocrenilabrus* sp.), probably represent species positively identified from adults in other samples. Two of the species *(Opsaridum ubangiense*, *Brycinus imberi)* are widespread species collected also at Niemba as well as in the Tanganyika basin. *Chiloglanis lukugae* is recorded only from the Luvua, Lukuga, and Tanganyika basin, and *Chiloglanis* sp. only from Niemba and downstream tributaries in the Lukuga drainage. Ten of the species collected in 1986 were reported previously from the Lukuga River. All of the positively identified tributary species (26) are known from elsewhere in the Congo basin, including the four that are also known from the Tanganyika basin *(Labeo dhonti*, *Brycinus imberi*, *Micralestes stormsi*, *Chiloglanis lukugae)*. Several species may be undescribed among those not positively identified, i. e., *Marcusenius* sp., *Pollimyrus* sp., *Parakneria* sp., five small species of *'Barbus'*, *Nannocharax* sp., *Amphilius* sp., *Chiloglanis* sp., *Aplocheilichthys* sp. and *Astatotilapia* sp. They represent genera widely distributed in the Congo basin, but also present in the Tanganyika basin. *Chiloglanis pojeri* is known only from the Luvua and Lukuga drainages.

Fish species collected at Niemba in 1986. Forty-three species of fishes were identified from the Lukuga and Niemba Rivers at Niemba (Table 3; the juvenile *Opsaridium* probably is *Opsaridium ubangiense*). Thirteen lake species are represented, of which 10 are endemic to Lake Tanganyika, and 12 occupying lacustrine habitats. Twenty-one species are known also from Kalemie. Ten are cichlid species, and six of these otherwise are known only from Lake Tanganyika, namely *As-*

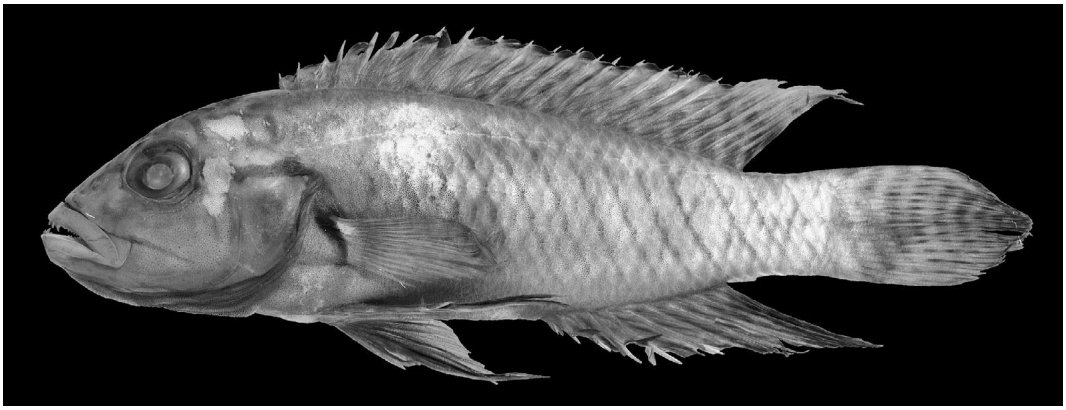

Fig. 2. *Telmatochromis dhonti*, NRM 13283, male, 45.2 mm SL; Democratic Republic of the Congo: Lukuga River at Niemba. Right side, reversed.

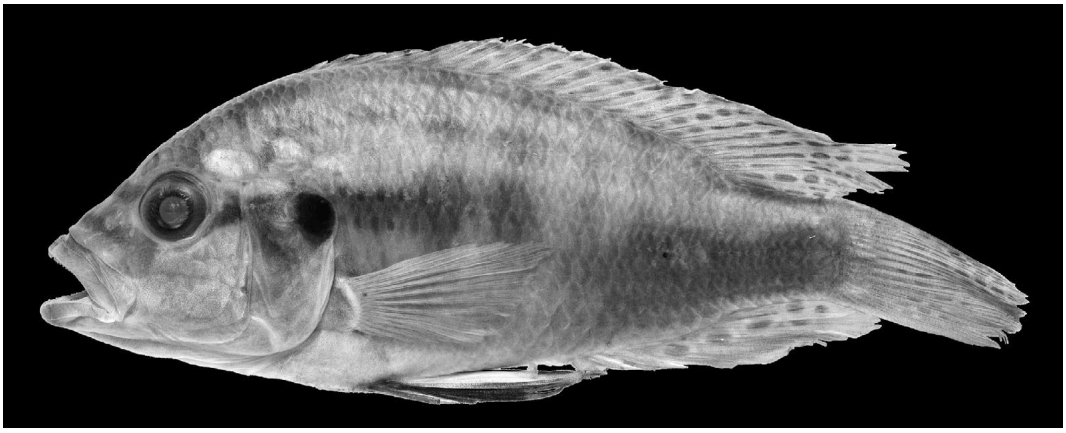

Fig. 3. *Astatotilapia burtoni*, NRM 51232, male, 68.7 mm SL; Democratic Republic of the Congo: Lukuga River at Niemba.

Fig. 4. *Simochromis diagramma*, NRM 13279, female, 67.5 mm SL; Democratic Republic of the Congo: Lukuga River at Niemba. Right side, reversed.

Table 1. Previous reports of fishes from the Lukuga River drainage, in systematic order. An asterisk (*) marks records based on specimens from the 1986 collections at Niemba. Records believed to be from the lake at Kalemie or in lake habitats at the very exit to the Lukuga are marked in the Lake column. Those marked in the River column are undoubtedly from river habitats. The Confirmed column shows species identified in the 1986 collections from the Lukuga River and tributaries. Locality stated lists localities as given in the source. *Chiloglanis lukugae* and *C. pojeri* were first described from near Kalemie, but the localities later corrected to the Luvua River (Poll, 1953).

family / current name	locality stated	river	confirmed	lake	reference
Clupeidae					
Stolothrissa tanganicae	Lukuga River		X	X	Boulenger, 1919
Kneriidae					
Kneria wittei	Makala; Sange, riv. Kankala; Mambwe; riv. Lukuga; Irtete; riv. Kilwe à Kahompwa	X			Poll, 1944, 1946, 1953
Cyprinidae					
'Barbus' neumayeri	Albertville; Luila	X		X	Boulenger, 1919 (as *B. serrifer*); David, 1936; Poll, 1946
'Barbus' taeniopleura	Albertville, Lukuga R.; riv. Lukuga, Village Amisi (Albertville); riv. Kilwe à Kahompwa			X	Boulenger, 1919; Poll, 1953
'Barbus' apleurogramma	riv. Lubile, affl. Luize, bassin Lukuga, km 45 route secondaire Nyunzu- Manono	X			De Vos, 1994, MRAC database (db)
'Barbus' holotaenia	Tumbwe, a village S.W. of the Kalemie River, on a small stream flowing into Niemba River, a tributary of Lukuga; Luila	X	X		Boulenger, 1920; David, 1936
'Barbus' humeralis	Luila; Lukuga drainage	X			David, 1936; Poll, 1946; Poll, 1953 (p. 13) (as *B. dolichosoma)*
'Barbus' lineomaculatus	Luila	X			David, 1936; Poll, 1946
'Barbus' lufukiensis	village Amisi, région d'Albertville, riv. Lukuga			X	Poll, 1953
'Barbus' miolepis	riv. Lubalaye à Tengo; riv. Kilwe à Kahompwa; riv. Lubile, affl. Luize, bassin Lukuga, km 45 route secondaire Nyunzu-Manono	X			Poll, 1953 (as *B. nicholsi*); De Vos 1994, MRAC db
'Barbus' oligogrammus	riv. Lukuga, à Niemba, bac, km 135 route Kalemie-Nyunzu, Shaba	X			De Vos 1994, MRAC db
'Barbus' tropidolepis	village Amisi, région d'Albertville, Lukuga			X	Poll, 1953
Chelaethiops congicus	Luila; Riv. Luila, afflt. de la Lovoi, tributaire de la Lukuga	X	X		David, 1936 (as *Engraulicypris moeruensis*); Poll, 1946 (as *E. congicus*)
Labeo dhonti	Tumbwe, a village S.W. of the Kalemie River, on a small stream flowing into the Niemba River, a tributary of the Lukuga	X	X		Boulenger, 1920; Poll 1946; Poll, 1953 (p. 13); Tshibwabwa, 1997
Labeobarbus caudovittatus	Tumbwe, a village S.W. of the Kalemie River, on a small stream flowing into the Niemba River, a tributary of the Lukuga	X	X		Boulenger, 1920 (as *Barbus euchilus* and *B. miochilus*)
Labeobarbus pojeri	riv. Lukuga	X	X		Poll, 1944, 1946 (as *Barbus pojeri*)
Opsaridium	ruisseau Munga, affl. Luwoyeye, affl. Luize, affl. Lukuga, km 156 route Kalemie-Nyunzu (entre Niemba et Nyunzu)	X			De Vos 1994, MRAC db
Opsaridium ubangiense	riv. Kilwe á Kahompwa; riv. Lubalaye à Tengo	X	X		Poll, 1953 (as *Barilius ubangensis*)

family / current name	locality stated	river	con-firmed	lake	reference
Raiamas salmolucius	Albertville, riv. Lukuga, village Amisi; riv. Lubalaye à Tengo; ruisseau Munga, affl. Luwoyeye, affl. Luize, affl. Lukuga, km 156 route Kalemie-Nyunzu (entre Niemba et Nyunzu)	X	X		Poll, 1953 (as *Barilius salmolucius*); De Vos 1994, MRAC db
Alestidae					
Brycinus kingsleyae	Lukuga à Tengo	X	X		Poll, 1953 (p. 13) (as *Alestes kingsleyae)*
Bryconaethiops boulengeri	riv. Lubalaye à Tengo	X	X		Poll, 1953
Micralestes acutidens	riv. Kilwe à Kakompwa	X	X		Poll, 1953 (p. 13)
Micralestes humilis	Lukuga drainage			X	Poll, 1953 (p. 13)
Micralestes stormsi	Greinerville, Lukuga; riv. Lubalaye à Tengo	X	X		Poll, 1953
Micralestes vittatus	Albertville			X	Boulenger, 1919 (as *Alestes vittatus*)
Amphiliidae					
Amphilius uranoscopus	Kabeke, a village 30 miles south of Tumbwe, on the Niemba River	X			Boulenger, 1920 (As *S. platychir)*, redet. by Skelton & Teugels, 1981)
Phractura lindica	Lukuga drainage; Kabeke, a village 30 miles south of Tumbwe, on the Niemba River	X	X		Boulenger, 1920 (as *P. lukugae*); Poll, 1953 (p. 13)
Zaireichthys heterurus	Niemba	X	X		Roberts, 2003*
Zaireichthys rotundiceps	Kitwe; riv. Kilwe, affluent de la Lukuga à Kahompwa	X	X		Roberts, 2003; Poll, 1953 (as *Leptoglanis brevis*)
Mochokidae					
Chiloglanis	riv. Luwoyeye, bassin Lukuga, au pont route Nyunzu-Muhuya (± 10km S. Nyunzu)	X			De Vos 1994, MRAC db
Chiloglanis lukugae	riv. Lubalaye à Tengo; riv. Luwoyeye, bassin Lukuga, au pont route Nyunzu-Muhuya (± 10km S. Nyunzu)	X	X		Poll, 1953; De Vos 1994, MRAC db
Chiloglanis pojeri	riv. Luwoyeye, bassin Lukuga, au pont sur route Nyunzu-Mukuya (± 10km S. Nyunzu), ss-région Kalemie; riv. Munga, affl. Luwoyeye, bassin Lukuga, ± 185 km de Kalemie, près de Nyunzu	X	X		De Vos 1994, MRAC db
Clariidae					
Clarias	riv. Uma, affl. Mwishe, affl. Luama, km 75 route Kalemie-Niemba	X			De Vos 1994, MRAC db
Clarias	ruisseau Kala (marais), associé au Luwoyeye, ss-affl. Lukuga, près de Mukenza km 183 route Kalemie-Nyunzu	X			De Vos 1994, MRAC db
Clarias alluaudi	A ditch (marigot) along the Lukuga River	X			Boulenger, 1920 (as *C. hilgendorfi)*
Clarias dhonti	Kabeke, a village 30 miles south of Tumbwe, on the Niemba River	X			Boulenger, 1920 (as *Allabenchelys dhonti*)
Claroteidae					
Auchenoglanis wittei	A ditch (marigot) along the Lukuga River; Albertville, riv. Lukuga, près du bac; village Amisi, région d'Albertville, riv. Lukuga	X	X		Boulenger, 1920; Poll, 1953 (both as *A. occidentalis)*
Auchenoglanis tanganicanus	A ditch (marigot) along the Lukuga River	X			Boulenger, 1920

family / current name	locality stated	river	con-firmed	lake	reference
Schilbeidae					
Pareutropis debauwi	Riv. Lubalaye à Tengo	X	X		De Vos, 1995
Schilbe marmoratus	Luila; Riv. Luila, affluent de la riv. Lovoi, tributaire de la Lukuga; Lukuga drainage	X	X		David, 1936; Poll, 1946, 1953 (p. 13), De Vos, 1995
Poeciliidae					
Lacustricola pumilus	Lukuga R.; Albertville, Kalimié R., Lukuga R.; village Amisi, région d'Albertville, Lukuga; riv. Lubalaye; Greinerville, riv. Lukuga	X	X	X	Boulenger, 1919 (as *Haplochilus dhonti* and *Haplochilus pumilus*); Poll, 1953 (as *Aplocheilichthys pumilus*)
Lamprichthys tanganicanus	Lukuga R.			X	Boulenger, 1919
Mastacembelidae					
Mastacembelus congicus	Amisi, riv. Lukuga, près d'Albertville			X	Poll, 1953 (p. 13)
Mastacembelus frenatus	A ditch (marigot) along the Lukuga River; riv. Lukuga, à Niemba, bac, km 135 route Kalemie-Nyunzu, Shaba	X	X		Boulenger, 1920 (as *M. mellandi*); De Vos, 1994, MRAC db
Latidae					
Lates microlepis	village Amisi, région d'Albertville, Lukuga			X	Poll, 1953
Cichlidae					
Astatoreochromis straeleni	riv. Lukuga, région d'Albertville; rivière Lukuga, près du bac d'Albertville			X	Poll, 1944, 1956 (both as *Haplochromis straeleni*)
Astatotilapia burtoni	Albertville, Kalimié R., Lukuga R.; riv. Lukuga, région d'Albertville; rivière Lukuga, près du village Kalwe Lukwiba		X	X	Boulenger, 1919 (as *Tilapia burtoni*); Poll, 1944; Poll, 1956 (as *Haplochromis burtoni*)
Aulonocranus dewindti	Lukuga R.			X	Boulenger, 1919 (as *Paratilapia lukugae*)
Ctenochromis horei	Lukuga R.		X	X	Boulenger, 1919 (as *Tilapia horii*)
Limnotilapia dardennii	Lukuga R.			X	Boulenger, 1919 (as *Tilapia dardennii*)
Lobochilotes labiatus	Albertville			X	Boulenger, 1919
Nanochromis squamiceps	Luila	X			David, 1936
Oreochromis tanganicae	Albertville			X	Boulenger, 1919 (as *Petrochromis tanganicae)*
Plecodus paradoxus	Albertville			X	Boulenger, 1919
Simochromis diagramma	Albertville		X	X	Boulenger, 1919
Telmatochromis dhonti	Albertville		X	X	Boulenger, 1919 (as *Lamprologus dhonti*)
Tilapia zillii	Lukuga R.			X	Boulenger, 1919 (as *Tilapia melanopleura*)
Tylochromis polylepis	Niemba	X	X		Stiassny, 1989*
Anabantidae					
Ctenopoma muriei	A ditch (marigot) along the Lukuga River	X			Boulenger, 1920 (as *Anabas ctenotis*)
Lepidosirenidae					
Protopterus aethiopicus	Albertville; a ditch (marigot) along the Lukuga River; Riv. Luisi, à Nyunzu			X	Boulenger, 1919; Boulenger, 1920; Poll, 1946

tatotilapia burtoni, *Ctenochromis horei*, *Simochromis babaulti*, *S. diagramma*, *Telmatochromis dhonti*, and *Tylochromis polylepis*. One of the cichlid species, *Astatotilapia* sp., is not recognizable as any of the known species of that genus, but potentially represents a species from the Tanganyika basin.

Another one of the cichlid species, here referred to as *Tanganicodus* sp., is new to science

Fig. 5. *Simochromis babaulti*, NRM 13278, male, 73.3 mm SL; Democratic Republic of the Congo: Lukuga River at Niemba.

Fig. 6. *Ctenochromis horei*, NRM 60177, male, 88.2 mm SL; Democratic Republic of the Congo: Lukuga River at Niemba.

and is being formally described elsewhere. It is closely related to *Tanganicodus irsacae*, which inhabits rocky shores of Lake Tanganyika. It differs in colour pattern and details of the dentition. *Oreochromis niloticus* is known from Lake Tanganyika, but not otherwise from the Congo River basin. It is an aquaculture species with feral populations well outside its natural range, and Trewavas (1983: 141) reported specimens from the lower Congo near Kinshasa. There is no indication that the specimens of *O. niloticus* from Niemba would result from aquaculture. *Oreochromis upembae*, however, is only known from the Luapula River drainage, and is, with reservation for the unidentified species of *Astatotilapia*, the only cichlid species collected at Niemba that does not occur also in Lake Tanganyika or does not belong to an endemic Tanganyika genus.

Among non-cichlids identified, five species are known otherwise only from Lake Tanganyika, viz., *Chelaethiops minutus*, *Stolothrissa tanganicae*, *Lates mariae*, *Mastacembelus cunningtoni*, and *Lacustricola pumilus*. Eight species are known from other localities in the Congo basin, but are absent from Lake Tanganyika. Thirteen species are widespread and found both in Lake Tanganyika and the Congo basin. *Raiamas moorii* is not found elsewhere in the Congo basin, except the Lukuga River, and occurs also in the Malagarasi River, and in Lakes Rukwa and Kivu. *Labeobarbus pojeri* probably occurs elsewhere. It was synonymized with the sympatric *L. caudovittatus* by Poll (1953). Two species of *Mastacembelus* and two small species of *'Barbus'* appear to be undescribed.

Discussion

The Lukuga River. The Lukuga River is about 350 km long, and receives at least seven small tributaries upstream of Niemba. When the second author passed the upper course of the Lukuga in 1986, the exit was very narrow, less than 100 m wide, widening to about 200 m 1–2 km downstream. The water was clear, greenish blue. The tributary Niemba River itself is a major river certain to maintain a flow even when the outflow from Lake Tanganyika is blocked. The mean annual discharge of the Lukuga River is 271 $m^3 \cdot s^{-1}$ from a catchment area of 270 900 km^2 (Shahin, 2002) and 75 $m^3 \cdot s^{-1}$ at the outflow (Langenberg, 2008).

The Lukuga River was discovered by Cameron (Cameron & Markham, 1875: 223–224) to be the outlet of Lake Tanganyika, but at that time, in 1874, the upper portion was apparently clogged with reed and almost blocked by a sand bank, and Cameron, although confirming the flow, did descend the river only for 4–5 miles. Stanley (1878: 397) visited the upper Lukuga in 1876, travelling some distance downriver. He categorized it as a clear river, but reported the entrance as more or less swampy and overgrown with papyrus. Stanley concluded that the river must have been almost dry in 1874, but reported a significant rise in the water level of Lake Tanganyika between 1871 and 1878 and projected that the Lukuga would soon become an important river draining the rising lake. Information on rising lake level also was transmitted to Hore (1882) who visited the lake in 1879–1880. Hore set up a gauge and found the lake level slowly falling. This was explained by informants as a consequence of the barrier across the Lukuga having broken away. Hore visited the Lukuga outlet in 1880 and mapped the uppermost course, representing a day's travel which was made on foot because the rapids were considered too difficult to pass with a canoe (Hore, 1882: 11–13).

The Lukuga River has a prominent position in explanations of the history of the fish fauna of Lake Tanganyika. Because of its entrance opposite the Malagarasi River, it has been suggested that a continuous Malagarasi-Lukuga was disrupted by the rift that led to the formation of Lake Tanganyika (Beadle, 1981). A former connection between the Malagarasi and Congo, but not necessarily the Lukuga, is supposed to explain very similar or identical species occurring in both the Malagarasi and the Lualaba (upper Congo) Rivers. The most prominent example, *Oreochromis malagarasi* and *O. upembae*, were at first thought to be a single species, but are now regarded as two barely distinguishable species (Trewavas, 1983). It remains difficult to explain why these species would not have become more different in the 20 million years of separation, and it is unlikely that such old connections would be expressed by identical or near-identical species on both sides of the lake. De Vos et al. (2001) suggested that a deep canyon, contestably interpreted as former river bed at hypothesized lower lake levels (Beadle, 1981: 285) in direction of the Lugumba River is better aligned with the Malagarasi River. It is also hypothesized that the Lukuga would have been a very recent or Pleistocene passageway for several large Congo species into Lake Tanganyika (Beadle, 1981: 284, listing *Hydrocynus goliath*, *Distichodus fasciatus*, *Labeo lineatus*), but these species have not been found in the Lukuga River. It seems likely that the rapids and water chemistry in the upper Lukuga are efficient barriers for upstream dispersal of many species from the Lualaba.

Lake Tanganyika has experienced considerable oscillation in water stands throughout its existence, as summarized by Cohen et al. (2007b). The water level was 350 m below the present 390 000–360 000 years ago, and has since been both well above and below the present level. When lower than present, the Lukuga River would have ceased to be a lake outlet. The present lake level seems to have developed after a low stand 40 000–35 000 years ago, and has been about the same over the last 18 000 years. Minor fluctuations of lake levels of as much as –40 m during the Holocene may have affected the outflow several times judging from ostracod data from the last 2500 years (Alin & Cohen, 2003), and stromatolite data from the last 2800 years (Cohen et al., 1997b). The latter authors consider alluvial masses at the exit into the Lukuga River to be the main factor to regulate lake stands in more recent years. Devroey (1938) summarized observations on the Lukuga River between 1846 and 1938. The lake was 10 m higher in the late 1870s, but has been at about the same level as today from the 1890s (Devroey, 1938: fig. 1). Water flow in the Lukuga was somewhat low in the period 1945 to 1960, in part due to the construction of a barrage in Kalemie in the late 1950s, but after that increased considerably, to between about 0.5 and 1 $m^3 \cdot s^{-1}$

in monthly average, both because of increased precipitation in the region and self-cleaning of the river bed, but then dropped back to 1960s flows again in the 1990s (Bergonzini et al., 2002).

Although the Lukuga has repeatedly been blocked at the exit in recent times, and the present fast flowing upper part of the river may not be more than a little over 100 years in existence, the several tributaries, including the Niemba River, must certainly have fed the Lukuga when it was not open to Lake Tanganyika.

Fishes cannot ascend the river from below the falls at Niemba, but there are no collections of fishes from between Niemba and the Lualaba to clearly demonstrate a faunal shift; collections downstream of Niemba were all made in tributaries. It remains a possibility that the Tanganyika fauna continues downriver. Lualaba species are found at Niemba, and some Niemba species like *Hydrocynus vittatus* are found both in the Congo basin and Lake Tanganyika, although not necessarily following a trajectory through the Lukuga. Although collections are sparse, no Tanganyika endemics are found downstream of the falls at Niemba and certainly none in the Lualaba, which is reasonably well investigated, although there may be no physical barrier to downstream dispersal of fishes from Lake Tanganyika.

One important aspect of possible dispersal of Lake Tanganyika cichlids is the water chemistry. The water in Lake Tanganyika is characterized by alkalinity (pH 8–9) and high concentrations particularly of Cl^- (28.0 ppm), Na^+ (64.2 ppm), K^+ (33.5 ppm), and Mg^{2+} (43.7 ppm), contributing to a high salinity (0.530 psu) (Beauchamp, 1946; Beadle, 1981: 6). It is likely that the alkalinity remains so for most of the course of the Lukuga, being gradually reduced by tributaries. Banister & Bailey (1979: 209) and Bailey (1986: 204) reported Lukuga water at the mouth as highly mineralized (pH 8.7, 21 ppm Ca^{2+}, 38 ppm Mg^{2+}) and grey-green, contrasting with Lualaba water which slightly upstream had pH 8, 14 ppm Ca, no magnesium and grey-brown turbid water. The Lualaba has pH readings between 6.4 and 8.2 in the tabular report of Bailey (1986), and relatively high mineral content, but the magnesium content of the Lukuga River is outstanding. The Congo River at Kinshasa has pH 6.5 and negligible calcium and magnesium (Bailey, 1986).

We are unaware of information on the chemistry of the water of the Lukuga tributaries, but Congo basin waters are generally soft, with a low pH. Alone differences between the Tanganyika like waters of the Lukuga and those of the Lualaba, i.e., high magnesium levels, high pH and hardness, may prevent or impede upstream dispersal of fish species from the Lualaba as well as prevent or impede downstream dispersal of Tanganyika species.

Previous reports on the Lukuga ichthyofauna. Early reports on fishes collected from the Lukuga do not give precies localities. Boulenger (1919, 1920) reported on collections made by Dhont-De Bie from the Niemba and Lukuga rivers (Table 1). We believe that the first collection as a whole probably came from close to the lake exit and not from far downstream into the Lukuga, because of the composition of the sample and the difficulty of accessing the river. In the second collection, specifically from the Niemba and Lukuga rivers, (Table 1) it is uncertain whether specimens from Tumbwe came from the Lukuga drainage, as stated by Boulenger, or from the Lubilaye drainage into Lake Tanganyika, because Tumbwe is located within the Lubilaye drainage. The "ditch [marigot] along the Lukuga R." may have been close to the lake. The presence of both *Auchenoglanis wittei* (a Congo River species) and *A. tanganicanus* (a lake endemic) from that locality supports that view. *Clarias dhonti*, reported by Boulenger (1920) from Kabeke, is only recorded from the Lukuga and Koki rivers, the latter draining to Lake Tanganyika (Ferraris, 2007).

Poll (1944) reported on a collection from rivers in the region of Albertville (= Kalemie), describing *Kneria wittei*, *Barbus pojeri*, *Chiloglanis lukugae*, *C. pojeri*, and *Haplochromis straeleni* (currently *Astatoreochromis straeleni*) as new species from the Lukuga River. The single specimen of *A. straeleni* is said to be taken from a sample of 193 specimens of *Haplochromis burtoni* (currently *Astatotilapia burtoni*) from "Riv. Lukuga", but the more precise localities of the other species are doubtful. Poll (1953: 165) explained that the type series of *Chiloglanis lukugae* did not come from near Albertville or even the Lukuga as reported by Poll (1944), but from Sange and Mambwe on the road from Kalemie to Kiambi, in the Luvua drainage, which flows into the Lualaba south of the Lukuga. However, Poll (1952b) also identified as *C. lukugae* specimens from the Lukuga (Tengo, Lubalaye River, downstream from Niemba), Ruzizi, and Lubilaye drainages, the latter two

Table 2. Species recorded from the Lukuga River tributaries downstream from Niemba collected in 1986. N(61-64) = number of specimens from Luwoyeye River (field number ZAIRE86-61), Lubile River (field number ZAIRE86-62), Luawe River (field number ZAIRE86-63, and Lufwango River (field Number ZAIRE86-64). Niemba = occurs at Niemba. Previous = previously reported from the Lukuga River. Tanganyika basin = occurs in Tanganyika basin. Congo = occurs in the Congo River basin. None of these species are known to be endemic to Lake Tanganyika.

family / species	N (61)	N (62)	N (63)	N (64)	Niemba	previous	Tanganyika basin	Congo	distribution
Mormyridae									
Gnathonemus petersii	3							X	West Africa to Congo basin (Gosse, 1984)
Marcusenius sp.			2					?	
Petrocephalus grandoculis	2							X	Congo basin (Gosse, 1984)
Pollimyrus sp.	13			1				?	
Kneriidae									
Parakneria sp.	20	3		2				?	
Cyprinidae									
'Barbus' holotaenia	3					X		X	Congo and Ogowe basins, Mayumbe and Chiloango Rivers (Lévêque & Daget, 1984)
'Barbus' sp. (Lukuga 2)	21			17				?	
'Barbus' sp. (Lukuga 9)	4							?	
'Barbus' sp. (Lukuga 11)			8					?	
'Barbus' sp. (Lukuga 6)			2	1				?	
'Barbus' sp. (Lukuga 7)			1					?	
Clypeobarbus pleuropholis	5			1				X	Congo basin and Lake Chad (Lévêque & Daget, 1984)
Labeo dhonti	1					X	X	X	Tanganyika tributaries, southern Congo basin (Tshibwabwa, 1997)
Labeo sp. (juvenile)	2							N/A	
Opsaridium ubangiense	4	1			X	X		X	Northern Congo basin (Skelton, 1996)
Raiamas sp. (juvenile)	1							N/A	
Citharinidae									
Nannocharax luapulae				2				X	Luapula, Luvua and Lualaba Rivers (Daget & Gosse, 1984)
Nannocharax sp.	1							?	
Neolebias trilineatus	2							X	Middle and Lower Congo basin (Daget & Gosse, 1984)
Alestidae									
Brycinus imberi				3	X		X	X	Widespread in Central and East Africa, including Lakes Tanganyika and Rukwa, Malagarasi River, Congo River basin, Zambezi River basin (Seegers, 1996)
Brachypetersius pseudonummifer	12			1				X	Congo basin (Paugy, 1984)
Brycinus kingsleyae	6					X		X	Widespread in West Africa and Congo basin (Paugy & Schaefer, 2007)
Bryconaethiops boulengeri	4					X		X	Congo basin (Paugy, 1984)
Micralestes lualabae	17							X	Lualaba River (Paugy, 1984)
Micralestes stormsi	9				X	X	X	X	Ruzizi, Lukuga, Lubalaye, Malagarasi Rivers, Congo, Chad and Iiuri basins (Poll, 1953, De Vos et al., 2001, Paugy, 1984)

family / species	N (61)	N (62)	N (63)	N (64)	Niemba	previous	Tanganyika basin	Congo	distribution
Schilbeidae									
Pareutropius debauwi	7			1		X		X	Widespread in Congo basin (De Vos, 1995)
Pareutropius mandevillei	13							X	Congo basin (De Vos, 1995)
Schilbe marmoratus	3					X		X	Widespread in Congo basin (De Vos, 1995)
Amphiliidae									
Amphilius sp.	9							?	
Phractura lindica	11			1	X			X	Lualaba and Lindi Rivers (Seegers, 2008), including P. lukugae
Zaireichthys rotundiceps	3							X	Widespread in Congo basin and East Africa (Roberts, 2003) CAS 92623
Mochokidae									
Chiloglanis lukugae	29	11			X	X	X	X	Luvua and Lubilaye Rivers, Tanganyika tributaries (Poll, 1953)
Chiloglanis pojeri	9					X		X	Luvua River drainage (Poll, 1953)
Chiloglanis sp.		16			X			?	
Poeciliidae									
Aplocheilichthys sp.			58					?	
Cichlidae									
Astatotilapia sp.	3			1				?	
Orthochromis stormsi	1							X	Along Luapula and Congo Rivers (Greenwood & Kullander, 1994)
Pseudocrenilabrus nicholsi			53					X	East central Congo Basin (Skelton, 1991)
Pseudocrenilabrus sp. (juvenile)		1						N/A	
Thoracochromis sp. (juvenile)	1							N/A	
Eleotrididae									
Kribia nana				1				X	West Africa, Congo, Chad and Nile basins (Pezold et al., 2007)
Anabantidae									
Microctenopoma nanum	2							X	Lower Guinea and Congo basin (Norris, 2007)
Microctenopoma ocellifer			15					X	Upper Lualaba River (Norris, 1995)
Sum species 39	28	4	7	12	5	10	4	26	

tributaries to Lake Tanganyika. As pointed out by Seegers (2008: 317) the figure used by Poll (1953) to illustrate *C. lukugae* shows *C. asymetricaudalis*, described by De Vos (1993). Revision of Poll's *Chiloglanis* material would be worthwhile to clarify species identities. Mambwe (in the Luvua drainage) is also the type locality for *C. pojeri*, but it was not commented on by Poll (1953: 167), who added a specimen from the Koki River, which drains to Lake Tanganyika south of Kalemie. It thus seems that *C. pojeri* was never before collected in the Lukuga. Ng & Bailey (2006), on the basis of Poll's (1944) descriptions alone, synonymised *C. pojeri* with *C. lukugae*, and as first revisers selected the latter name to have priority. We identified three species of *Chiloglanis* in our Lukuga collection (Tables 2–3). In accordance with the information in Poll (1944) we use the name *C. pojeri* for a species with a single row of well separated teeth in the lower jaw, and *C. lukugae* for a species with the teeth of the lower jaw collected in a dense group. The third species, for which we have no species name, is similar to *C. lukugae* in the dentition of the lower jaw, but the oral disk is only weakly papillate and the margin is almost round, with only shallow notches in comparison to *C. lukugae* in which the disk is extensively papillated and several long

Table 3. Species recorded from the Lukuga and Niemba rivers at Niemba in 1986. N(59) = number of specimens from mouth of Niemba River (field station ZAIRE86-59). N(60) = number of specimens from Kisimba Kilia rapids in the Lukuga River (field station ZAIRE86-60). Lake = occurs in Lake Tanganyika; Lacustrine = occurs in lake proper (not restricted to marshes, river mouths, or similar peripheral habitats); Kalemie = recorded from the Kalemie area.

family / species	N (59)	N (60)	lake	lacus-trine	Kale-mie	distribution
Mormyridae						
Hippopotamyrus discorhynchus	1	6	X		X	Widespread in East Africa, including Lakes Tanganyika, Malawi, Upper Congo and Zambezi Rivers (Poll, 1953)
Marcusenius macrolepidotus		3				Upper Congo basin, Cunene, Okavango, Zambezi River systems, coastal South East Africa (Skelton, 2001)
Clupeidae						
Microthrissa cf. *minuta*	2					*M. minuta* in Congo basin (Gourène & Teugels, 1989)
Stolothrissa tanganicae		414	Endemic	X	X	Lake Tanganyika (Poll, 1956)
Cyprinidae						
'Barbus' eutaenia		3	X			Congo, Cuanza, Cunene, Okavango, and Zambezi River basins, affluents of Lake Tanganyika, SE African drainages (Lévêque & Daget, 1984; Skelton, 2001)
'Barbus' sp. 'serrated'		4	N/A	N/A	N/A	
'Barbus' sp. 'striped'	13	18	N/A	N/A	N/A	
Chelaethiops congicus	2		X			Widely distributed in Congo River basin, also Lake Tanganyika (Lévêque & Daget, 1984)
Chelaethiops minutus	1		Endemic	X	X	Lake Tanganyika (Poll, 1953)
Labeobarbus caudovittatus		2	X			Widely distributed in Congo River basin, also Lake Tanganyika tributaries (Lévêque & Daget, 1984)
Labeobarbus pojeri	12	15		N/A		Lukuga River (Poll, 1944)
Opsaridium sp. (juvenile)		1	N/A	N/A	N/A	
Opsaridium ubangiense	3	3		N/A		Lubalaye River (Poll, 1953), northern Congo River basin (Skelton, 1996)
Raiamas moorii		5	X	X	X	Lakes Tanganyika, Rukwa, Kivu, Malagarasi River basin (Seegers, 1996)
Raiamas salmolucius	3	2	X		X	Ruzizi, Lubalaye, Lukuga, Malagarasi Rivers, Congo River basin (Poll, 1953; Lévêque & Daget, 1984)
Alestidae						
Alestes macropthalmus	7		X		X	Widespread in central Africa, including most of Congo River basin, and Lake Tanganyika (Paugy, 1986)
Brycinus imberi		3	X		X	Widespread in Central and East Africa, including Lakes Tanganyika and Rukwa, Malagarasi River, Congo River basin, Zambezi River basin (Seegers, 1996)
Hydrocynus vittatus		1	X		X	Widespread in tropical Africa, including Congo River basin and Lake Tanganyika (Seegers, 1991)
Micralestes acutidens	1	2		N/A		Widespread in Congo River basin, also Cunene, Okavango and Zambezi River basins (Skelton, 2001)
Micralestes stormsi	23	42		N/A	X	Ruzizi, upper Lukuga, and Lubalaye Rivers (Poll. 1953), Malagarasi River (De Vos et al., 2001), Conoa, Chad, Ituri basins (Paugy, 1984)
Amphiliidae						
Doumea alula	5			N/A		Congo basin including Lualaba (Seegers, 2008)
Phractura lindica		2		N/A		Lukuga and Lindi Rivers (Seegers, 2008)
Zaireichthys heterurus	1			N/A		Congo basin (Roberts, 2003) CAS 92618

family / species	N (59)	N (60)	lake	lacus-trine	Kale-mie	distribution
Mochokidae						
Chiloglanis lukugae	10	99		N/A		Also from Luvua River drainage (Poll, 1953)
Chiloglanis sp.	14	47	N/A	N/A		
Synodontis decorus	1			N/A		Congo River basin (Seegers, 2008)
Claroteidae						
Auchenoglanis wittei	3	5		N/A	X	Congo and Lualaba Rivers (Retzer, 2010)
Bagridae						
Bagrus docmak	2		X		X	Nile basin, including lakes; Niger, Senegal, Volta, Lake Chad basins (Risch, 1986)
Latidae						
Lates mariae		1	Endemic	X		Lake Tanganyika (Poll, 1953)
Mastacembelidae						
Mastacembelus cunningtoni	1	4	Endemic	X	X	Lake Tanganyika (Coulter, 1991)
Mastacembelus frenatus		1	X	X	X	Lakes Victoria, Tanganyika, and Rukwa, upper Nile River basin, Rufiji River, Zambezi River, upper Congo River basin (Seegers, 1996),
Mastacembelus sp. 'B'	1	2	N/A	N/A	N/A	
Mastacembelus sp. 'C'	17		N/A	N/A	N/A	
Poeciliidae						
Lacustricola pumilus	3	14	X		X	Lake Tanganyika, Lukuga River (Poll, 1953; Seegers et al., 2003)
Cichlidae						
Astatotilapia burtoni	4	27	Endemic	X	X	Lake Tanganyika and tributaries (Poll, 1956)
Astatotilapia sp.		1	N/A	N/A	N/A	
Ctenochromis horei	16	14	Endemic	X	X	Lake Tanganyika (Poll, 1956)
Oreochromis niloticus		20	X		X	Widespread in West Africa, Lake Tanganyika and Nile system (Trewavas, 1983)
Oreochromis upembae		1		N/A		Lualaba and Luvua Rivers, Congo River at Isange (Trewavas, 1983)
Simochromis babaulti	48	1	Endemic	X	X	Lake Tanganyika (Poll, 1956)
Simochromis diagramma	49		Endemic	X	X	Lake Tanganyika (Poll, 1956)
Tanganicodus sp.	36		?	N/A		
Telmatochromis dhonti	4		Endemic	X	X	Lake Tanganyika (Hanssens & Snoeks, 2001)
Tylochromis polylepis		1	Endemic	X	X	Lake Tanganyika (Stiassny, 1989)

projections extend from the posterior margin.

Poll (1946) reviewed literature records and specimens from the Lukuga River, adding only *Protopterus aethiopicus* from Nyunzu. Poll (1953: 12–13), summarizing previous reports and collections made by the Tanganyika Hydrobiological Investigation 1946–1947 (Poll, 1952a), listed six species known exclusively from the Lukuga drainage, but not from other rivers in the Tanganyika watershed, viz. *Micralestes humilis*, *'Barbus' humeralis*, *Labeo dhonti*, *Engraulicypris congicus*, *Phractura lindica*, and *Schilbe marmoratus*. The collections of 1946–1947, comprising 14 non-cichlid species (Poll, 1953) were made in the Lubalaye and Kilwe Rivers, tributaries to the Luila River, and at Greinerville a little downstream from the entrance of the Lukuga River (Poll, 1952*a*: 116). Only *Lacustricola pumilus* and *Micralestes stormsi* were recorded from Greinerville. Poll (1953) also listed specimens from "village Amisi", near Kalemie. Poll's (1956) report on the cichlids collected by the 1946–1947 investigation, lists species according to occurrence (Poll, 1956: 6–9), with one species from the upper course of rivers (*Orthochromis malagaraziensis*, from the Malagarasi River), three from both upper and lower courses of rivers *(Astatotilapia burtoni*, *Astatoreochromis stappersii*, and *A. vanderhorsti)*, and 15 species from lower courses of rivers. The only species with localities in the Lukuga River, however, is *A. burtoni* from near the Kalwe Lukwiba village, apparently on the upper Lukuga. A specimen of *Astatoreochromis straeleni* is reported from the Lukuga River near the Albertville ferry. The 1946–1947

investigation collected extensively at Kalemie, from where a very large number of species are reported. Among those found at Niemba (Table 1), 21 species are also reported from Kalemie (Poll, 1953, 1956).

De Vos et al. (2001), referring to personal communication with K. E. Banister, reported that one could find numerous Tanganyikan lacustrine species in the Lukuga down to the confluence with the Lualaba, and also referred to personal observations of species of *Lates*, *Simochromis*, *Ctenochromis*, and *Telmatochromis* in the Lukuga. It is possible that the collections reported here at least to some extent were included in the above report, for which voucher specimens were not listed.

Non-cichlid species collected at Niemba in 1986. No clupeid species has previously been reported from the Lukuga River. Of the two clupeid species collected from Niemba, *Stolothrissa tanganicae* is otherwise endemic to the lake where it is one of the major pelagic fishery species (Abe, 1997). The *Stolothrissa* were sampled just inside of the mouth of the Niemba River and thus from more lentic conditions. The two small specimens of *Microthrissa* are similar to *M. minuta* from the northern Congo basin, also a small species (Gourene & Teugels, 1989), and may represent an undescribed species. Species of *Microthrissa* are found over a large part of the Congo basin (Gourene & Teugels, 1989). The second clupeid species in Lake Tanganyika, *Limnothrissa miodon*, is not present in the collection from Niemba. The two species of clupeids in Lake Tanganyika are sister species and form the sister group of remaining central and West African pellonuline clupeids. Their separation from other Congo species dates to at least 2 million years ago (Wilson et al., 2008). There is a rich fauna of pellonuline clupeids in the Congo basin, but clupeids are notably absent from the Malagarasi River.

Poll (1953: 86) synonymized *Barbus euchilus*, *B. miochilus*, and *B. pojeri* with the widely distributed *B. caudovittatus*, and was followed by Banister (1953). These species are now placed in *Labeobarbus*. We recognize two species of *Labeobarbus* among our specimens from Niemba. One of them apparently is *L. caudovittatus* and agrees with the descriptions of *B. miochilus* and *B. euchilus*. The second species agrees with the description of *B. pojeri*. It differs from *L. caudovittatus* in absence of dark bands on the caudal fin and in the well ossified last unbranched dorsal-fin ray.

We cannot recognize species of *Barbus* previously reported from the Lukuga River drainage (Table 1) – *'Barbus' humeralis*, *'B.' lufukiensis*, *'B.' taeniopleura*, *'B.' miolepis*, *'B.' tropidolepis*, *'B.' oligogrammus*, and *'B.' apleurogramma* – among cyprinid specimens from Niemba. The collection includes a species similar to the description of *'B.' taeniopleura*, but with a much shorter caudal peduncle, and one more small-sized species which we cannot identify. We notice that the taxonomy of small African barbels is in a state of confusion, and precise identifications are probably not possible at this time.

Phractura lukugae was synonymized with *P. lindica* from the Lindi River near Kisangani by Poll (1946), followed by Skelton & Teugels (1986). We compared our specimens of *Phractura* with the holotype of *P. lukugae* (BMNH 1919.7.24:32) and a syntype of *P. lindica* (BMNH 1902.4.14:25). Although Boulenger (1902) reported and figured *P. lindica* with a gap between the supraoccipital process and the predorsal shield, in the examined syntype the process abuts the predorsal shield. In the holotype of *P. lukugae* and our Lukuga specimens there is a gap between the process and the shield. Specimens of *Phractura* from Lukuga tributaries downstream of Niemba differ from those from Niemba in the colour pattern with distinct dark blotches on body and fins and numerous small dark spots on the side vs. uniform brownish with fewer dark spots in specimens from Niemba. We identify all as *P. lindica*, but note that there may be reason to revise the species taxonomy of *P. lindica* and *P. lukugae*.

Species of *Chiloglanis*, *Doumea*, *Phractura*, and *Zaireichthys* are rheophilic, representing genera only found in rivers. Especially the genus *Chiloglanis* is rich in species with limited distribution, some occurring in rivers tributaries to Lake Tanganyika (Seegers, 2008). The *Chiloglanis* captured at Niemba were mostly from gravelly areas in the Lukuga River close to the mouth of the Niemba River. *Phractura*, *Doumea* and *Zaireichthys* are absent from the Lake Tanganyika basin.

Until the revision of Retzer (2010) *Auchenoglanis occidentalis* was considered as a widespread species occurring over much of tropical Africa, including both the Congo basin and Lake Tanganyika (Risch, 1986; Teugels et al., 1991). Retzer (2010) revalidated *A. tanganicanus*, which is endemic to Lake Tanganyika, and *A. wittei* from the Congo and Lualaba rivers. The specimens of

Auchenoglanis from Niemba constitute the first record of *A. wittei* from the Lukuga.

Four species of *Mastacembelus* were identified. One adult specimen represents *M. frenatus*, widely distributed in East Africa and the Congo basin, including Lake Tanganyika. Five small specimens probably represent *M. cunningtoni*, otherwise only known from the lake. Remaining specimens represent two highly characteristic species, but available literature does not permit identification. Most mastacembelid species in Lake Tanganyika are littoral species associated with rocky substrate, but *M. cunningtoni* is a deepwater species found over sandy and muddy bottoms (Abe, 1997).

Lates mariae is one of four endemic species of *Lates* in Lake Tanganyika. It is predominantly a deep-water pelagic species, but young specimens may forage in the littoral weed beds (Abe, 1997).

Cichlid species collected at Niemba. *Simochromis diagramma* and *S. babaulti*, are two species associated with the rocky shores in Lake Tanganyika. Categorized by Yamaoka (1997) as browsers, they have specialized dentition for biting and tearing off pieces of epilithic multicellular benthic algae.

The species of *Tanganicodus* found at Niemba has the same morphology and almost identical dentition, and is expected to have the same feeding ecology as *T. irsacae*, which is endemic to Lake Tanganyika. *Tanganicodus irsacae* is an invertebrate picker, with only a few slender teeth anteriorly in the jaws gradated in length from short posteriorly to very long anteriorly. The main food is chironomid larvae taken in debris from the epilithic growth of rocks in the surf region. *Tanganicodus irsacae* stays on the bottom, and can stabilize itself in position in the surf using the pelvic fins as anchors (Yamaoka, 1997). It is thus similar to many rheophilic riverine cichlids, which are also bottom-living, e. g., *Teleocichla* in South America, *Gobiocichla*, *Teleogramma*, riverine *Lamprologus*, *Orthochromis*, and *Steatocranus* in Africa (Kullander, 1988; Roberts & Stewart, 1976).

Two species of *Oreochromis* are present in the Niemba collection, but represented by juveniles only. *Oreochromis niloticus* is otherwise widespread in Northeast and West Africa, but absent from the Congo basin except for Lake Tanganyika (Trewavas, 1983: fig. 51). The specimens from Niemba are thus clearly of lake origin. Trewavas (1983) identified *O. niloticus* from Lake Tanganyika as subspecies *O. n. eduardianus*, shared with northern lakes Edward, George, and Kivu, and obviously having dispersed into Lake Tanganyika from Lake Kivu. Trewavas (1983: 143) presented only one trenchant character from the nominotypical form in the Nile basin and West Africa, viz. male breeding colour, and Thys van den Audenaerde (1964: 82, as *T. n. regani*) listed only slightly shallower body and shorter fin spines in large specimens. One juvenile specimen of *Oreochromis* with 17 gill-rakers, 15 dorsal-fin spines, and three dark blotches on the side, agrees with *O. upembae* which occurs in the Lualaba north to the Kisangani area, and has been collected at the mouth of the Lukuga River (Trewavas, 1983: fig. 147; Thys van den Audenaerde, 1964: fig. 14). This species is most similar to *O. malagarasi* in the Malagarasi River, and Trewavas (1983: 424) apparently considered them as sister taxa, separated by Lake Tanganyika. Because only a juvenile specimen is available, the identification remains tentative. It is at least not identical with *O. tanganicae*, which is endemic to Lake Tanganyika, and no additional species of *Oreochromis* have been reported from the lake. *Oreochromis karomo* is restricted to the Malagarasi River.

Astatotilapia burtoni is a very common species in vegetated parts of Lake Tanganyika, including river mouths, and was already reported as abundant in the Kalemie region (Poll, 1956). *Telmatochromis dhonti* was originally described from Kalemie, and has since been reported from several locations in the lake (Hanssens & Snoeks, 2001). *Ctenochromis horei* is a small piscivore occurring over sandy bottoms in Lake Tanganyika (Brichard, 1989). A specimen was reported from the Ruzizi River at Bugarama by Poll (1952a).

Tylochromis polylepis is a relatively large species, reaching 276 mm SL (Stiassny, 1989), occurring along the shores of Lake Tanganyika, particularly near and into river mouths and lagoons. It was originally described from Kalemie by Boulenger (1900). It is a bottom feeder, feeding on ostracods, gastropods, and insect larvae (Stiassny, 1989). The genus is widespread in rivers of West Africa and the Congo basin. Koch et al. (2007) ruled out the option that *T. polylepis* in Lake Tanganyika would descend from dispersal from the Congo basin through the Lukuga, and suggested instead a southern lake tributary, the Lufubu River captured from the upper Congo River, and in the period 375 000–510 000 years ago. The species is present in the lower Lufubu

River (NRM 24125) but not in the Lualaba. Besides four specimens reported by Stiassny (1989), a single juvenile specimen, 21.9 mm SL, is available from Niemba.

In summary, four cichlid species from Niemba represent three genera known only from Lake Tanganyika *(Telmatochromis, Simochromis, Tanganicodus)*, and one of these species (*Tanganicodus* sp.) is known only from the Lukuga and Niemba Rivers at Niemba. One species is known elsewhere only from the Lualaba and Luvua Rivers *(Oreochromis upembae)*. One species, *O. niloticus*, represents a widespread species in West Africa, the Nile River system and Lake Tanganyika, but absent from the riverine Congo River drainage. Three species are endemic to Lake Tanganyika, but represent genera also occurring outside the lake, both in eastern Africa and the Congo basin *(Astatotilapia burtoni*, *Ctenochromis horei*, *Tylochromis polylepis)*. One species of *Astatotilapia*, finally, cannot presently be identified, but we believe it may represent a species from Lake Tanganyika.

Tributary species downstream of Niemba. The species composition of samples from Lukuga tributaries (Table 2) downstream of Niemba overlap with previous reports (Table 1), but is distinct from the Niemba localities (Table 3) and reports marked as Lake occurrences in Table 1. Five of the 42 species from Niemba occur in downstream tributaries. These samples may not be exhaustively representative, however, as 14 of the more widespread Congo River basin species at Niemba are not present in the samples from downstream tributaries. Five species from downstream tributaries are also recorded from Lake Tanganyika, none of them endemic, and all of them present over a wider area. No lacustrine Tanganyika species are present in the downstream samples. This is interpreted as indication of a faunal shift most likely referable to the falls at Niemba, with Congo species below the falls, and a mixed fauna of Congo species and Tanganyika species in and above the falls. Samples from the Lukuga River itself below the falls are absent, however.

Significance of Lake Tanganyika endemics in the Lukuga River. Although Lake Tanganyika has close to 100 affluent tributaries, and fish collections have been made in many of them, not least in the Malagarasi River, few if any populations of specialized endemic lake cichlids have been found in rivers. Poll (1952b) reported *Aulonocranus dewindti*, *Callochromis pleurospilus* and *Ectodus descampsii* from the Kamvivira River at the northern extreme of the lake, but it was not stated how far upstream. A specimen of *Ctenochromis horei* was reported from the Ruzizi River at Bugarama by Poll (1952b), which if correct, would be a spectacular exception.

Our material from the Niemba demonstrates that lake cichlids and other fish species believed to be endemic to the lake are capable of forming viable populations outside of the lake, but also that the actual dispersal barrier must be the Lukuga rapids in addition to differences in water chemistry between the lake and the Congo basin rivers. A number of interesting issues arise when taking into consideration the water level fluctuations in the lake and the recurrent observations that the outlet is regularly blocked.

The Congo basin includes numerous rapids and low falls, and specialized rheophilic fishes. The rapids habitat at Niemba is not uncommon in the Congo basin. It may still be significant for the acclimatization of Tanganyika cichlids. The cichlid species observed at Niemba are either species that are reported from vegetated parts and river mouths around the lake, or species predominantly found on rocky coasts. The shore waters of Lake Tanganyika experience considerable, strong and rapid wave movement. Fishes observed along the shores are constantly affected by the water mass moving in and out. Those species may consequently be expected to be able to manage water velocities characterizing rapids. The rocky substrate is comparable, and because the river is rather shallow, with clear water, there should be abundant aufwuchs to feed from just like in the lake. The two species of *Simochromis* which normally are found in shallow waters along rocky shores in the lake are thus in a similar environment in Niemba. The invertebrate picker, *Tanganicodus* sp., is very similar to the lake endemic *T. irsacae*, which lives in the surf along the shoreline (Brichard, 1989: 411).

The Niemba cichlids show clearly that lake conditions are not sufficient to explain the presence of specialized cichlid species, since apparently these species can survive in lotic conditions, and for that matter many are kept in aquarium under captive conditions that may differ considerably from lake conditions (Brichard, 1989). Lake cichlids do not ascend the major tributary, the

Malagarasi very far (De Vos et al., 2001). Instead the Malagarasi has its own specialized rheophilic cichlids, six species of the genus *Orthochromis* (De Vos et al., 2001), which is also represented in the Congo River basin and Lake Mweru basin (Greenwood & Kullander, 1994; as *Schwetzochromis*). One sample of *Orthochromis stormsi* (NRM 45081) was obtained from near Nyunzu far downstream of the mouth of the Niemba River, and this species is widespread in the Congo River basin (Greenwood & Kullander, 1994). The Malagarasi River also has a species, *Neolamprologus devosi*, which belongs to the lake species flock, but has not been found outside the lower Malagarasi River (Schelly et al., 2003). It then would be a case of speciation outside the lake like the *Tanganicodus* species at Niemba

The near-absence of species of the Lamprologini (*Lamprologus* in the Congo River basin; *Chalinochromis*, *Julidochromis*, *Lepidiolamprologus*, *Neolamprologus*, *Telmatochromis*, *Lamprologus*, *Variabilichromis*, and *Altolamprologus* in Lake Tanganyika) at Niemba is noteworthy. This is the only lake group with numerous endemic species, and some endemic genera in the lake that has been hypothesized to have been derived from a specific Congolese ancestor (Schelly, 2007). There are several species of *Lamprologus* reported from rapids in the Congo basin (Schelly & Stiassny, 2004), but none of these are present in collections from the Lukuga River drainage.

Conclusions. The Niemba collection shows clearly that some species until now believed to be stenotypic and adapted to lacustrine littoral and pelagic conditions in Lake Tanganyika are able to live and reproduce in lotic conditions in a river where the fish community includes several species from the lake. The presence of a putative endemic species of cichlid (*Tanganicodus* sp.), so far only found near Niemba, suggest a possibility that the flow of the Niemba if not that of the Lukuga, has been permanent for sufficient time for speciation within a genus otherwise confined to the lake; one must be careful here, that the taxonomy of several groups of lake cichlids, including *Tanganicodus* is not well known. The circumstance that all other cichlid species at Niemba are the same as in the lake may suggest that they arrived there recently, or that there has been sufficient gene flow from the lake to maintain their species identity. With the exception of *Tanganicodus* sp., all of them are fairly widespread species in the lake environment, and some of the species are known to enter swamps and river mouths along the lake. If there were a constant outflow of cichlids from Lake Tanganyika down to Niemba, perhaps we should expect many more species. We should also expect many more characids, cyprinids, catfish, and other non-cichlids. The Niemba fauna may thus be relatively established, constituting a true local fish community instead of depending on spill-over from Lake Tanganyika, and upheld by a constant water flow from the Niemba River, with rare fish invasions from the lake.

Further collecting along the Lukuga, and particularly along the Niemba, will certainly be instrumental in the further analyzing the role of the Lukuga as a historical and ecological component of the Lake Tanganyika fish fauna.

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Literature cited

Abe, N. 1997. Ecology of non-cichlids in the littoral zone of Lake Tanganyika. Pp. 243–273 in H. Kawanabe, M. Hori & M. Nagoshi (eds.), Fish communities in Lake Tanganyika. Kyoto University Press, Kyoto.

Alin, S. R. & A. S. Cohen. 2003. Lake-level history of Lake Tanganyika, East Africa, for the past 2500 years based on ostracode-inferred water-depth reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology, 199: 31–49.

Bailey, R. G. 1986. The Zaïre River system. Pp. 201–214 in B. R. Davies & K. F. Walker (eds.), The ecology of river systems. Junk, Dordrecht.

Bailey, R. M. & J. D. Stewart. 1984. Bagrid catfishes from Lake Tanganyika, with a key and descriptions of new taxa. Miscellaneous Publications, Museum of Zoology, University of Michigan, 168: 1–41.

Banister, K. E. 1973. A revision of the large *Barbus* (Pisces, Cyprinidae) of East and Central Africa. Studies on African Cyprinidae Part II. Bulletin of the British Museum (Natural History), Zoology, 26: 1–148.

Banister, K. E. & R. G. Bailey. 1979. Fishes collected by the Zaïre River Expedition, 1974–1975. Zoological Journal of the Linnean Society, 66: 205–249.

Beadle, L. C. 1981. The inland waters of tropical Africa. An introduction to tropical limnology. Second edition. Longman, London & New York, 475 pp.

Beauchamp, R. S. A. 1946. Lake Tanganyika. Nature, 3981: 183–184.

Bergonzini, L., Y. Richard & P. Camberlin. 2002. Variation interannuelle du bilan hydrique du lac Tanganyika (1932–1995): changement dans la relation précipitation-excédent lacustre. Hydrological Sciences Journal, 47: 781–796.

Berrebi, P., M. Kottelat, P. Skelton & P. Ráb. 1996. Systematics of *Barbus*: state of the art and heuristic comments. Folia Zoologica, 45, Supplement 1: 5–12.

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, Zoologie, 1 (5): 129–164.

— 1919. On a collection of fishes from Lake Tanganyika, with descriptions of three new species. Proceedings of the Zoological Society of London, 1919: 17–20.

— 1920. On some new fishes from near the west coast of Lake Tanganyika. Proceedings of the Zoological Society of London, 1919: 399–404.

Brewster, B. 1986. A review of the genus *Hydrocynus* Cuvier 1819 (Teleostei: Characiformes). Bulletin of the British Museum (Natural History), Zoology, 50: 163–206.

Brichard, P. 1989. Pierre Brichard's book of cichlids and all the other fishes of Lake Tanganyika. T.F.H. Publications, Neptune City, 544 pp.

Brown, K. J., L. Rüber, R. Bills & J. J. Day. 2010. Mastacembelid eels support Lake Tanganyika as an evolutionary hotspot of diversification. BMC Evolutionary Biology, 10 (188): 1–11.

Cameron, V. L. & C. R. Markham. 1875. Examination of the southern half of Lake Tanganyika. Journal of the Royal Geographical Society of London, 45: 184–228.

Cohen, A. S., K.-E. Lezzar, J.-J. Tiercelin & M. Soreghan. 1997a. New palaeogeographic and lake-level reconstructions of Lake Tanganyika: implications for tectonic, climatic and biological evolution in a rift lake. Basin Research, 9: 107–132.

Cohen A. S., M.-R. Talbot, S. M. Awramik, D. L. Dettman & P. Abell. 1997b. Lake level and paleoenvironmental history of Lake Tanganyika, Africa, as inferred from late Holocene and modern stromatolites. Geological Society of America Bulletin, 109: 444–460.

Coulter, G. W. (ed.). 1991. Lake Tanganyika and its life. Natural History Museum Publications, London, 354 pp.

David, L. 1936. Contribution á l'étude de la faune ichthyologique du lac Tanganyka. Revue de Zoologie et de Botanique Africaines, 28: 149–160.

Day, J. J. & M. Wilkinson. 2006. On the origin of the *Synodontis* catfish species flock from Lake Tanganyika. Biology Letters, 2: 548–552.

De Vos, L. 1993. Le genre *Chiloglanis* (Siluriformes, Mochokidae) dans le bassin de la Ruzizi: description de deux nouvelles espèces. Journal of African Zoology, 107: 153–168.

— 1995. A systematic revision of the African Schilbeidae (Teleostei, Siluriformes). Musée Royal de l'Afrique Centrale, Annales, Sciences Zoologiques, 271: 1–450.

De Vos, L., L. Seegers, L. Taverne & D. Thys van den Audenaerde. 2001. L'ichtyofaune du basin de la Malagarasi (Système du Lac Tanganyika): une synthèse de la connaissance actuelle. Annales, Musée Royal de l'Afrique Centrale, Sciences Zoologiques, 285: 117–152.

De Vos, L. & J. Snoeks. 1994. The non-cichlid fishes of Lake Tanganyika. Archiv für Hydrobiologie, 44: 39–405.

Devroey, E. 1938. Le problème de la Lukuga exutoire du lac Tanganika. Mémoires, Institut Royal Colonial Belge, Section des Sciences Techniques, Collection in-8°, 1 (3): 1–127.

Ferraris, C. J. 2007. Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes), and catalogue of siluriform primary types. Zootaxa, 1418: 1–628.

Gourène, G. & G. G. Teugels. 1989. Révision systématique du genre *Microthrissa* Boulenger, 1902 des eaux douces africaines (Pisces, Clupeidae). Revue d'Hydrobiologie Tropicale, 22: 129–156.

Greenwood, P. & S. O. Kullander. 1994. A taxonomic review and redescription of *Tilapia polyacanthus* and *T. stormsi* (Teleostei: Cichlidae), with descriptions of two new *Schwetzochromis* species from the Upper Zaïre River drainage. Ichthyological Exploration of Freshwaters, 5: 161–180.

Hanssens, M. & J. Snoeks. 2001. A revised synonymy of *Telmatochromis temporalis* (Teleostei, Cichlidae) from Lake Tanganyika (East Africa). Journal of Fish Biology, 58: 639–655.

Hore, E. C. 1882. Lake Tanganyika. Proceedings of the Royal Geographical Society and Monthly Record of Geography, 4: 1–28.

Howes, G. J. 1984. A review of the anatomy, taxonomy, phylogeny and biogeography of the African neoboline cyprinid fishes. Bulletin of the British Museum (Natural History), Zoology, 47: 155–185.

Koblmüller, S., K. M. Sefc & C. Sturmbauer. 2008. The Lake Tanganyika cichlid species assemblage: recent advances in molecular phylogenetics. Hydrobiologia, 615: 5–20.

Koch, M., S. Koblmüller, K. M. Sefc, N. Duftner, C. Katongo & C. Sturmbauer. 2007. Evolutionary history of the endemic Lake Tanganyika cichlid fish *Tylochromis polylepis*: a recent intruder to a mature adaptive radiation. Journal of Zoological Systematics and Evolutionary Research, 45: 64–71.

Kottelat, M. & J. Freyhof. 2007. Handbook of European freshwater fishes. Kottelat, Cornol & Freyhof, Berlin, 646 pp.

Kullander, S. O. 1988. *Teleocichla*, a new genus of South American rheophilic cichlid fishes with six new species. Copeia, 1988: 196–230.

Langenberg, V. T. 2008. On the limnology of Lake Tanganyika. PhD Dissertation, University of Wageningen.

Lévêque, C. & J. Daget. 1984. Cyprinidae. Pp. 217–342 in J. Daget, J.-P. Gosse & D. F. E. Thys van den Audenaerde (eds.), Check-list of the freshwater fishes of Africa, Volume 1. Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Musée Royal de l'Afrique Centrale, Tervuren and Office de la Recherche Scientifique et Technique Outre-Mer, Paris.

Nishida, M. 1997. Phylogenetic relationships and evolution of Tanganyikan cichlids: a molecular perspective. Pp. 3–23 in H. Kawanabe, M. Hori & M. Nagoshi (eds.), Fish Communities in Lake Tanganyika. Kyoto University Press, Kyoto.

Ng, H. H. & R. M. Bailey. 2006. *Chiloglanis productus*, a new species of suckermouth catfish (Siluriformes: Mochokidae) from Zambia. Occasional Papers of the Museum of Zoology, University of Michigan, 378: 1–13.

Norris, S. M. 1995. *Microctenopoma uelense* and *M. nigricans*, a new genus and two new species of anabantid fishes from Africa. Ichthyological Exploration of Freshwaters, 6: 357–376.

— 2007. Anabantidae. Pp. 251–268 in M. L. J. Stiassny, G. G. Teugels & C. D. Hopkins (eds.), Poissons d'eaux douces et saumâtres de basse Guinée, ouest de l'Afrique centrale, Volume 2, IRD, MNHN, MRAC, Paris.

Paugy, D. 1984. Characidae. Pp. 140–183 in J. Daget, J.-P. Gosse & D. F. E. Thys van den Audenaerde (eds.), Check-list of the freshwater fishes of Africa, Volume 1. Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Musée Royal de l'Afrique Centrale, Tervuren and Office de la Recherche Scientifique et Technique Outre-Mer, Paris.

— 1986. Révision systématique des *Alestes* et *Brycinus* africains (Pisces, Characidae). ORSTOM, Paris, 295 pp.

Paugy, D. & S. A. Schaefer. 2007. Alestidae. Pp. 348–411 in M. L. J. Stiassny, G. G. Teugels & C. D. Hopkins (eds.), Poissons d'eaux douces et saumâtres de basse Guinée, oest de l'Afrique centrale, Volume 1, IRD, MNHN, MRAC, Paris.

Pezold, F., I. J. Harrison & P. J. Miller. 2007. Eleotridae. Pp. 472–490 M. L. J. Stiassny, G. G. Teugels & C. D. Hopkins (eds.), Poissons d'eaux douces et saumâtres de basse Guinée, ouest de l'Afrique centrale, Volume 2, IRD, MNHN, MRAC, Paris.

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 (3): 1–12.

— 1946. Révision de la faune ichthyologique du lac Tanganika. Annales du Musée du Congo Belge, (I), 4: 141–364.

— 1952a. Les Vertébrés. Exploration Hydrobiologique du Lac Tanganika (1946–1947). Résultats Scientifiques, 1: 102–165.

— 1952b. Poissons de rivières de la region des lacs Tanganika et Kivu recueillis par G. Marlier. Revue de Zoologie et de Botanique Africaines, 46: 221–236.

— 1953. Poissons Non Cichlidae. Exploration Hydrobiologique du Lac Tanganika (1946–1947). Résultats Scientifiques, 3 (5B): 1–619.

— 1956. Poissons Cichlidae. Exploration Hydrobiologique du Lac Tanganika (1946–1947). Résultats Scientifiques, 3 (5A): 1–251.

— 1974. Synopsis et distribution géographique des Clupeidae d'eau douce africans, descriptions de trois espèces novelles. Académie Royale de Belgique, Bulletin de la Classe des Sciences, 5e Série, 40: 141–161.

Retzer, M. E. 2010. Taxonomy of *Auchenoglanis* Günther 1865 (Siluriformes: Auchenoglanididae). Zootaxa, 2655: 25–51.

Risch, L. 1986. Bagridae. Pp. 2–35 in J. Daget, J.-P. Gosse & D. F. E. Thys van den Audenaerde (eds.), Check-list of the freshwater fishes of Africa, Volume 2. Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Musée Royal de l'Afrique Centrale, Tervuren and Office de la Recherche Scientifique et Technique Outre-Mer, Paris.

Roberts, T. R. 2003. Systematics and osteology of Leptoglaninae, a new subfamily of the African catfish family Amphiliidae, with descriptions of three new genera and six new species. Proceedings of the California Academy of Sciences, 54: 81–132.

Roberts, T. R. & D. J. Stewart. 1976. An ecological and systematic survey of fishes in the rapids of the lower Zaïre or Congo River. Bulletin of the Museum of Comparative Zoology, 147: 239–317.

Schelly, R. 2007. Lamprologine phylogenetics: insights from morphology. Pp. 171–179 in J. Snoeks, J. P. Laleye & P. Vandewalle (eds.), Proceedings of the Third International Conference of African Fish and Fisheries, Cotonou, Benin, 10–14 November 2003. Journal of Afrotropical Zoology, Special issue.

Schelly, R. & M. L. J. Stiassny. 2004. Revision of the Congo River *Lamprologus* Schilthuis, 1891 (Teleostei: Cichlidae), with descriptions of two new species. American Museum Novitates, 3451: 1–40.

Schelly, R., M. L. J. Stiassny & L. Seegers. 2003. *Neolamprologus devosi* sp. n., a new riverine lamprologine cichlid (Teleostei, Cichlidae) from the lower Malagarasi River, Tanzania. Zootaxa, 373: 1–11.

Seegers, L. 1996. The fishes of the Lake Rukwa drainage. Annales, Musée Royal de l'Afrique Centrale, Sciences Zoologiques, 278: 1–407.

— 2008. The catfishes of Africa. Aqualog Verlag, Rodgau, 604 pp.

Seegers, L., L. De Vos & D. O. Okeyo. 2003. Annotated checklist of the freshwater fishes of Kenya (excluding the lacustrine haplochromines from Lake Victoria). Journal of East African Natural History, 92: 11–47.

Shahin, M. 2002. Hydrology and water resources of Africa. Kluwer, Dordrecht, 688 pp.

Skelton, P. H. 1991. *Pseudocrenilabrus*. Pp. 394–398 in J. Daget, J.-P. Gosse & D. F. E. Thys van den Audenaerde (eds.), Check-list of the freshwater fishes of Africa. Volume 4. Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Musée Royal de l'Afrique Centrale, Tervuren and Office de la Recherche Scientifique et Technique Outre-Mer, Paris.

— 1996. A review of *Opsaridium zambezense* (Pisces: Cyprinidae) from southern Africa with description of a new species from Malawi. Ichthyological Exploration of Freshwaters, 7: 59–84.

— 2001. A complete guide to the freshwater fishes of southern Africa. Struik, Cape Town, 395 pp.

Skelton, P. H. & G. G.Teugels. 1986. Amphiliidae. Pp. 54–65 in J. Daget, J.-P. Gosse & D. F. E. Thys van den Audenaerde (eds.), Check-list of the freshwater fishes of Africa, Volume 2. Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Musée Royal de l'Afrique Centrale, Tervuren and Office de la Recherche Scientifique et Technique Outre-Mer, Paris.

Snoeks, J. 2000. How well known is the ichthyodiversity of the ancient African lakes? In A. Rossiter & H. Kawanabe (eds), Ancient lakes: biodiversity, ecology and evolution. Advances in Ecological Research, 31: 17–38.

Stanley, H. M. 1878. A geographical sketch of the Nile and Livingstone (Congo) basins. Proceedings of the Royal Geographical Society of London, 22: 382–410.

Stiassny, M. L. J. 1989. A taxonomic revision of the African genus *Tylochromis* (Labroidei, Cichlidae); with notes on the anatomy and relationships of the group. Annales, Musée Royal de l'Afrique Centrale, Sciences Zoologiques, 258: 1–161.

Stiassny, M. L. J., G. Teugels & C. D. Hopkins (eds.). 2007. Poisons d'eaux douces et saumâtres de basse Guinée, ouest de l'Afrique centrale. Volume 2. Institut de Recherche pour le Développement, Paris, Muséum National d'Histoire Naturelle, Paris & Musée Royal de l'Afrique Centrale, Tervuren, 603 pp.

Taverne, L. & L. De Vos. 1997. Ostéologie et morphologie d'un bariliiné nouveau du bassin de La Malagarasi (système du lac Tanganyika): *Opsaridium splendens* sp. n. (Teleostei: Cyprinidae). Journal of African Zoology, 111: 281–300.

Teugels, G. G., L. Risch, L. de Vos & D. F. E. Thys van den Audenaerde. 1991. Generic review of the African bagrid genera *Auchenoglanis* and *Parauchenoglanis*, with description of a new genus. Journal of Natural History, 25: 499–517.

Thys van den Audenaerde, D. F. E. 1964. Révision systématique des espèces congolaises du genre *Tilapia* (Pisces, Cichlidae). Annales, Musée Royal de l'Afrique Centrale, Série in-8°, Sciences Zoologiques, 124: 1–155.

Trewavas, E. 1983. Tilapiine fishes of the genera *Sarotherodon*, *Oreochromis* and *Danakilia*. British Museum (Natural History), London, 583 pp.

Tshibwabwa, S. M. 1997. Systématique des espèces africaines du genre *Labeo* (Teleostei, Cyprinidae) dans les regions ichtyogéographiques de Basse-Guinée et du Congo. Presses Universitaires de Namur, Namur, 530 pp.

Wilson, A. B., G. G. Teugels & A. Meyer. 2008. Marine incursion: the freshwater herring of Lake Tanganyika are the product of a marine invasion into West Africa. PLoS ONE, 3(4), e1979.

Yamaoka, K. 1997. Trophic ecomorphology of Tanganyikan cichlids. Pp. 27–56 in H. Kawanabe, M. Hori & M. Nagishi (eds), Fish communities in Lake Tanganyika. Kyoto University Press, Kyoto.

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