Fish Fauna of the Nile

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Abstract The total number of fish species in the Nile drainage basin, which includes the River Nile, its affluent rivers and the connected Lakes, is currently estimated at more than 800. Of these, 128 species, belonging to 27 families, occur in the River Nile. The river comprises many different habitats (e.g. the swampy Sudd) each with a different species composition. The families Cichlidae, Cyprinidae, Mormyridae and Mochokidae comprise the majority of the fish species in the Nile drainage basin. The Mormyridae and Mochokidae have more representatives in the river than in the Lakes. The same holds for the Cyprinidae, with the exception of Lake Tana that harbours almost as many cyprinid species as the river. Cichlid species dominate the fish faunas of Lakes Edward, George, Victoria and Kyoga. Especially Lakes Victoria and Kyoga and their satellite Lakes are well known for their cichlid diversity. Prior to the human induced ecological changes, these Lakes contained about 600 haplochromine cichlid species in contrast to 46 native fish species belonging to 11 other families. The haplochromine cichlids comprise at least 15 trophic groups that are morphologically adapted to feed on specific food types. The boom of the introduced Nile perch in the 1980s as well as fishery and habitat deterioration had a strong impact on the haplochromine species and many other fish species, and about 200 endemic haplochromine species may have gone extinct. In Lake Tana, which is part of the head waters of the Blue Nile, the fish fauna is dominated by the cyprinid genera *Barbus* and *Labeobarbus*. The flock of 15 endemic *Labeobarbus* species in

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H.J. Dumont (ed.), *The Nile: Origin, Environments, Limnology and Human Use*,

this lake shows a trophic radiation similar to that of the haplochromine cichlids of Lake Victoria. Another notable inhabitant of Lake Tana is *Nemacheilus abyssinicus*, the only known representative of the Euro-Asiatic Balitoridae.

1 Introduction

In this chapter an overview is given of the fish fauna of the River Nile and its drainage basin, which includes among others the Lakes Victoria, Kyoga, Edward, George, Albert and Tana (Fig. 1). As the total number of fish species of the Nile drainage

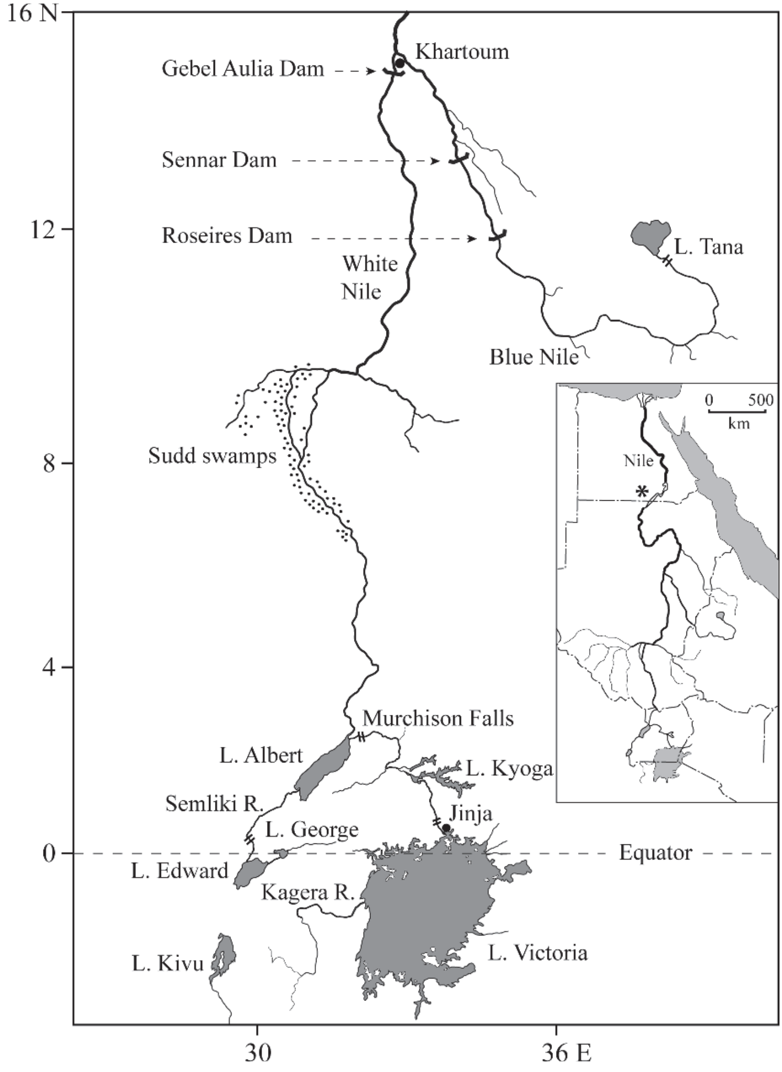

Fig. 1 Map of the River Nile and its tributaries. Asterisk in inset indicates the location of Lake Nasser/Nubia

basin amounts to over 800, it is impossible to discuss all of them. Therefore, we mainly deal with the fish families and genera that make up the Nile fauna, and give examples of representative species. A list of the fish species (+ authors) discussed in the present chapter and in the chapter Fisheries in the Nile System is given in the Appendix. Nomenclature of the higher fish taxa follows Nelson (2006). Nomenclature of the species follows the Check-List of the Freshwater Fishes of Africa (CLOFFA) parts I, II and IV (Daget et al., 1984, 1986, 1991), except for the Alestiidae (formerly African Characidae), the Schilbeidae and *Oreochromis*, for which respectively Paugy (1986), de Vos & Skelton (1990) and Trewavas (1983) are followed.

2 Ichthyofaunal Provinces

Boulenger (1907) was the first to divide Africa or the "Ethiopian region" into ichthyofaunal provinces, based on the distribution of freshwater fish. As more knowledge of the African freshwater fish became available, these provinces were modified (e.g. Poll, 1973; Roberts, 1975; Paugy et al., 1994; Hugueny & Lévêque, 1994). According to Roberts (1975), the Nile drainage basin, including the River Nile, its affluent rivers and the connected Lakes, covers several provinces. The major part of the River Nile, including Lakes Edward/George and Lake Albert (also called Lake Mobuto Sese Seko), is located in what has been defined as the Nilo-Sudan province (Fig. 2). Lake Tana and a large part of the Blue Nile have been included in the Abyssinian Highlands. The latter are considered a sub-province of the Nilo-Sudan province by Lévêque (1997). Lakes Victoria and Kyoga and the Victoria Nile were included in the East Coast province by Roberts (1975). Greenwood (1983), also included Lakes Edward and George in this province and later Snoeks et al. (1997) added Lake Kivu. However, according to Lévêque (1997) "it seems more correct to include Lake Victoria in the Nilo-Sudan province (as defined by Roberts, 1975), taking into account the affinities of the non-cichlid fauna with the Nile fauna". Recent molecular research suggests that the extensive endemic haplochromine cichlid fauna in Lakes Victoria and Kyoga also may have originated from Congolese-Nilotic ancestors rather than from East African riverine species (Seehausen et al., 2003), and that the haplochromine cichlids of Lakes Victoria, Edward, George and Albert form a monophyletic superflock (Verheyen et al., 2003). Therefore, we tentatively included the Lakes Victoria and Kyoga, and the Victoria Nile in the Nilo-Sudan province (Fig. 2). In the Nilo-Sudan province 15 endemic riverine genera (belonging to 11 families) were recognized (Table 1; Roberts, 1975). Ten of these genera occur in the Nile and its tributaries. In the Abyssinian Highlands no endemic riverine genera are present (Roberts, 1975).

An alternative map of freshwater ecoregions of the world, based on the distribution and composition of freshwater fish species, was published by Abell et al. (2008). According to this map, the Nile drainage basin covers six ecoregions: (1) the Lake Victoria basin, including Lakes Victoria, Kyoga, Edward/George and Kivu; (2) the Upper Nile, including the Semliki River and Lake Albert in the South and the Sudd in the North; (3) the Lower Nile, from Khartoum in the South to the Nile Delta and including the Blue Nile except its uppermost reaches; (4) the

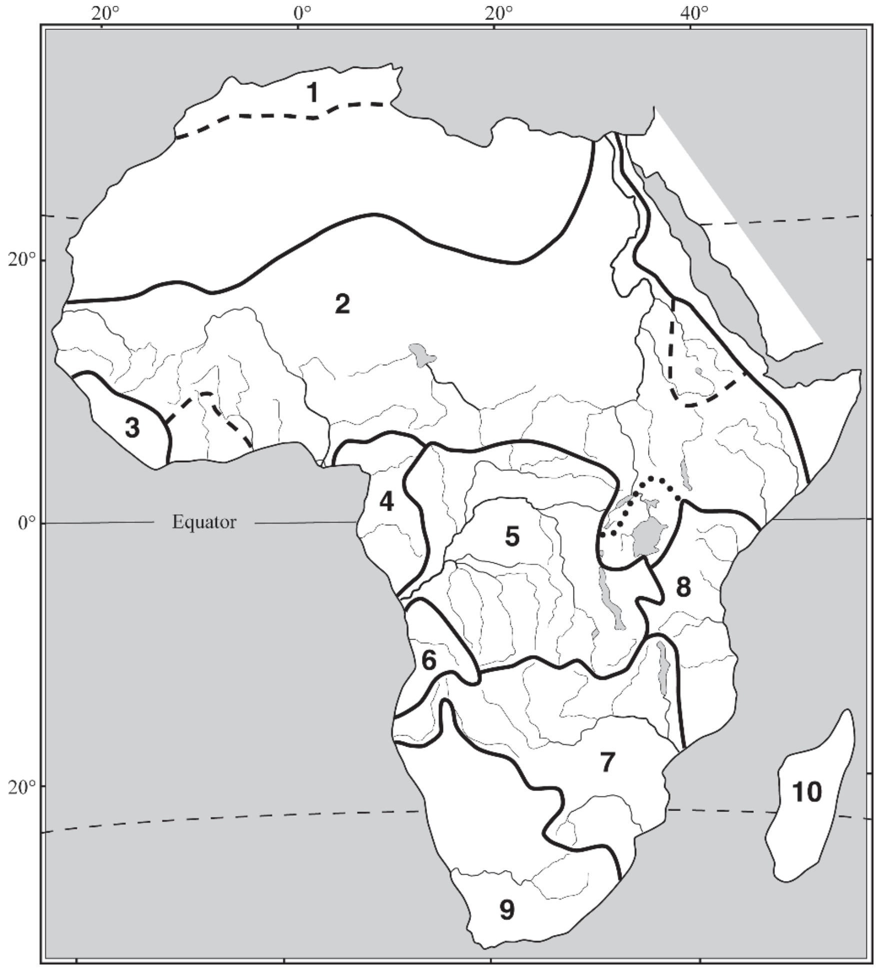

Fig. 2 Ichthyofaunal provinces in Africa, modified from Roberts (1975) and Lévêque (1997). Dashed lines indicate sub-provinces; dotted line indicates the border of the Nilo-Sudan province as suggested by Roberts (1975), which was tentatively modified based on suggestions in more recent literature (see text). 1 – Maghreb; 2 – Nilo-Sudan; 3 – Upper Guinea; 4 – Lower Guinea; 5 – Zaïre; 6 – Qaunza; 7 – Zambezi; 8 – East Coast; 9 – Southern; 10 – Malagasy province

Nile Delta; (5) the Ethiopian Highlands, defined by the two blocks of highland in Ethiopia, separated by the rift valley; and (6) Lake Tana.

3 Fish Species Composition in the Nile Drainage Basin

Greenwood (1976) referred to the fishes of the Nile drainage basin as the "extended Nile ichthyofauna" (Figs. 3 and 4). The knowledge of the fish fauna in the Nilotic Lakes is better than that in the rivers. According to Greenwood (1976), the diversity and

Table 1 Endemic riverine genera in the Nilo-Sudan province according to Roberts (1975), and their presence in the Nile drainage basin

Family	Endemic genus	Presence in Nile drainage basin
Osteoglossidae	*Heterotis*	+
Mormyridae	*Hyperopisus*	+
Gymnarchidae	*Gymnarchus*	+
Kneriidae	*Cromeria*	+
Distichodontidae	*Paradistichodus*	–
Citharinidae	*Citharidium*	–
Bagridae	*Clarotes*	+
	Pardiglanis	–
Schilbeidae	*Irvineia*	–
	Siluranodon	+
Amphiliidae	*Andersonia*	+
Mochokidae	*Brachysynodontis*	+
	Hemisynodontis	+
	Mochokus	+
Cichlidae	*Gobiocichla*	–

high level of endemicity of the fishes in some of the Lakes, the related evolutionary questions and the economic importance of many lake fishes have resulted in "rather more research being done on the fishes of the Nilotic Lakes than on the species inhabiting the Nile itself." During the past decades this discrepancy has only increased, as research on the Lakes, in particular Victoria and Tana, has expanded enormously. In the case of Lake Victoria, research was strongly stimulated by dramatic human-induced ecological perturbations (Witte et al., 2009).

Greenwood (1976) recorded some 320 species in 60 genera in the Nile drainage basin. However, in the past decades hundreds of new cichlid species were discovered in Lake Victoria and its satellite Lakes (van Oijen et al., 1981; Witte & van Oijen, 1995; Seehausen, 1996; Kaufman et al., 1997; Witte et al., 2007a), as well as some 20 new and resurrected cyprinid species in Lake Tana (Nagelkerke & Sibbing, 1997; Nagelkerke & Sibbing 2000; de Graaf et al., 2000; Dejen et al., 2002; Stiassny & Getahun, 2007). Therefore, we currently estimate the total number of fish species in the Nile drainage basin at 800+.

4 River Nile

In the 1970s the number of fish species recorded in the River Nile was 115, of which 26 were considered endemic and 74 species were shared with the River Niger (Greenwood, 1976). The species described by Bailey (1994) in a guide to the fishes of the River Nile in the Republic of the Sudan, also numbered 115. Lévêque (1997) listed 128 fish species belonging to 27 families for the total Nile (Table 2) of which 77 are shared with the Niger (Lévêque et al., 1991). This total number is modest, compared to that of the Niger, with 243 species (36 families), and the Congo with 787 species (31 families). The difference in species numbers between these river systems is partly explained by the size of the system. The number of

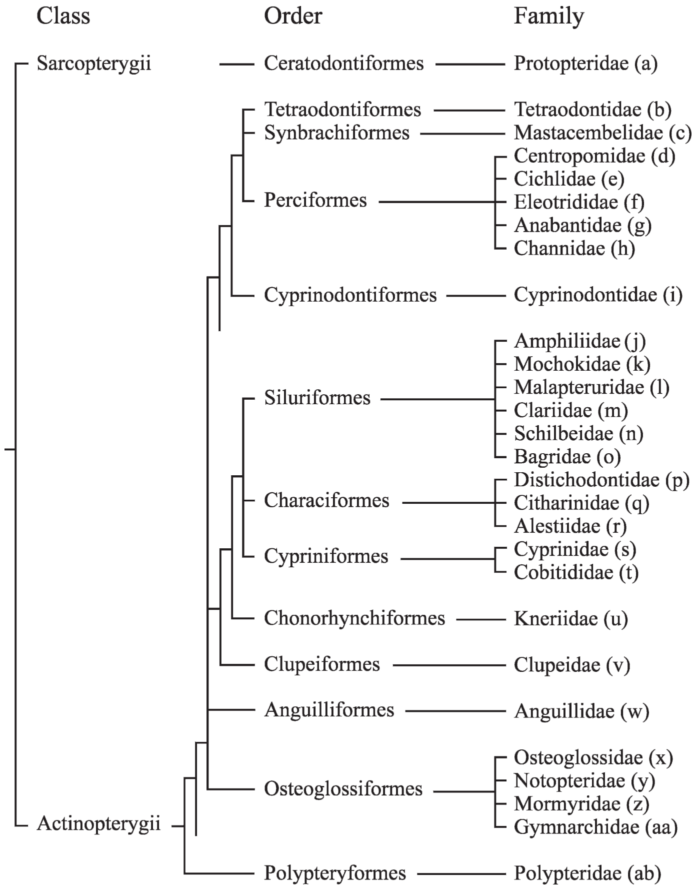

Fig. 3 Phylogenetic tree of the fish families occurring in the Nile drainage basin, based on Nelson 2006. Letters refer to representative species depicted in Fig. 4

fish species as a function of river basin area for 24 African rivers can be expressed as $Log_{10}\ N = 0.485\ Log_{10}\ B - 0.571$ ($r^2 = 0.876$; N = number of species; B = basin area in km^2; Welcomme, 2003).

The Cyprinidae, Mormyridae, Mochokidae and Cichlidae together account for more than half the number of fish species in the River Nile (Table 2). The Mormyridae and Mochokidae have more representatives in the river than in the Lakes of the drainage basin (Table 3). The same holds for the Cyprinidae, with exception of Lake Tana that harbours almost as many cyprinid species as the river (Table 3). In contrast, the number of Cichlidae is considerably lower in the river than in the typical cichlid Lakes Edward, George, Victoria and Kyoga. The riverine cichlids comprise *Hemichromis fasciatus*, five haplochromine species (allocated to the genus *Thoracochromis*) and four tilapiine species, viz. *Tilapia zillii*, *Sarotherodon galilaeus, Oreochromis niloticus* and *O. aureus* (Lévêque et al., 1991).

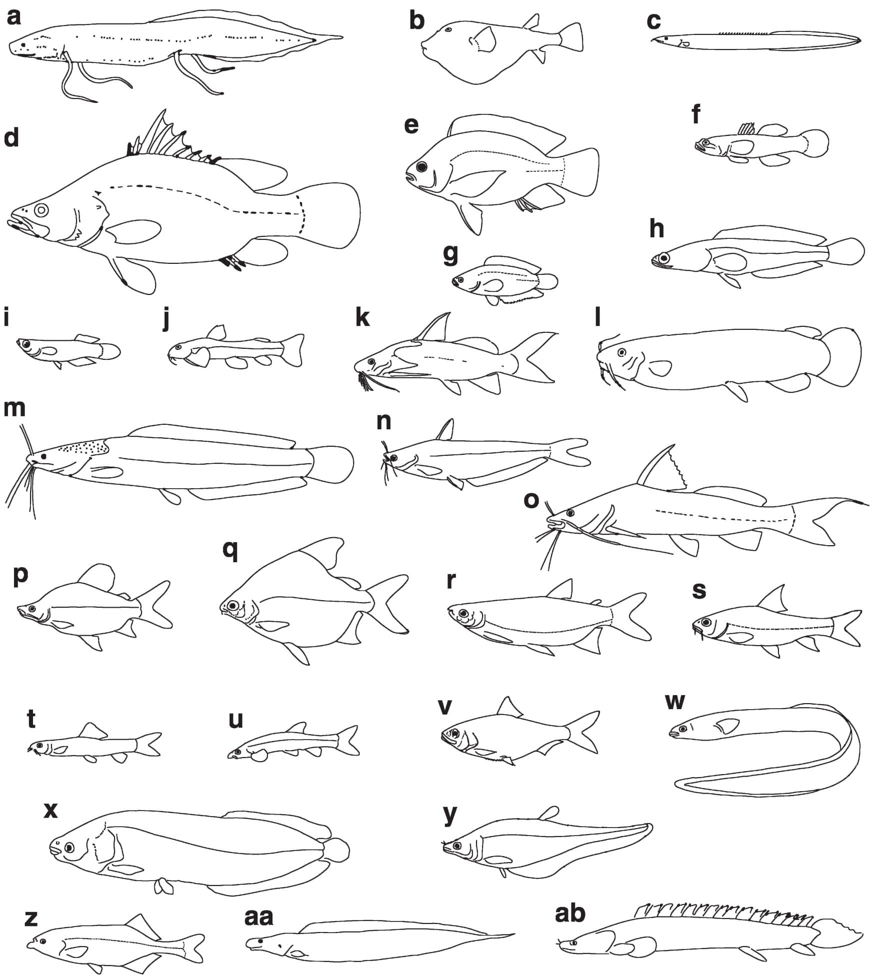

Fig. 4 Outline figures of representatives of the fish families in the Nile drainage basin. Letters refer to the families in Fig. 3. Redrawn from Nelson (1984) and van Oijen (1995)

Being the longest river in the world, the Nile comprises many different habitats, each with a different species composition. Well known is the Sudd, a swampy area of some 30,000–40,000 km^2 (Mohammed et al., 2006; Green & El-Moghraby, 2009), through which the Nile flows. Studies of the perennial wetland and the eastern seasonal-floodplain of the Sudd revealed 68 species, divided over 21 families (Table 2; Hickley & Bailey, 1986, 1987). Of these, 62 species were recorded in the permanent wetland of the Sudd (Hickley & Bailey, 1986) and only 23 species were caught in the seasonal floodplain (Hickley & Bailey, 1987). Several species from the latter habitat are known as obligatory or facultative air breathers e.g. *Protopterus aethiopicus*, *Polypterus senegalus*, *Heterotis niloticus*, *Xenomystis nigri*, *Clarias gariepinus*, *Ctenopoma muriei*, and *Parachanna obscura* (Hickley & Bailey, 1987). Concerning

Table 2 Total number of fish species in the River Nile (White and Blue) and some of its parts

Fish families	Nile	Sudd	L. Nubia
Protopteridae	2	1	–
Polypteridae	3	2	–
Anguilidae	1	–	–
Clupeidae	1	–	–
Osteoglossidae	1	1	–
Notopteridae	1	1	–
Mormyridae	15	8	4
Gymnarchidae	1	1	–
Kneriidae	1	–	–
Alestiidae	8	5	3
Distichodontidae	7	5	–
Citharinidae	2	3	2
Cyprinidae	25	9	4
Balitoridae	1	–	–
Bagridae	6	5	4
Schilbeidae	5	3	2
Amphiliidae	1	–	–
Clariidae	7	2	1
Malapteruridae	1	–	–
Mochokidae	15	5	2
Cyprinodontidae	7	4	–
Channidae	1	1	–
Centropomidae	2	1	1
Eleotridae	1	1	–
Cichlidae	10	7	2
Anabantidae	2	2	–
Mastacembelidae	–	–	–
Tetraodontidae	1	1	–
Total families	27	21	10
Total species	128	68	25

biomass, important species in Lakes and channels of the perennial wetland were the catfishes *Synodontis schall*, *S. frontosus* and *Auchenoglanis biscutatis*, the alestiid *Alestes dentex* and the osteoglossid *H. niloticus* (Hickley & Bailey, 1986). According to Hickley and Bailey (1986), “with exception of zooplanktivores all components of the trophic spectrum are well represented in lake communities” of the Sudd. In seasonal floodplains *Ctenopoma murei*, *Epiplatys spilargyreius*, *C. gariepinus*, *O. niloticus* and *P. obscura* were prominent (Hickley & Bailey, 1987).

A study of Lake Nubia (the part of man-made Lake Nasser within the Sudanese borders), using gill nets with stretched meshes ranging from 40 to 200 mm, revealed 25 fish species belonging to ten families (Table 2; Ali, 1984). Here the most important species were *Labeo niloticus*, *Lates niloticus*, *Hydrocynus forskalii* and *Alestes baremoze*.

Twelve freshwater fish species, including five cichlid species and the catfish *C. gariepinus*, are known from Lake Borullus of the Nile Delta (Dumont & El-Shabrawy, 2007).

Table 3 Number of fish species in the River Nile (White and Blue) and in lakes connected to it (Greenwood, 1966, 1974; Lévêque et al., 1991; Lévêque, 1997; Witte & van Oijen, 1995; Seehausen, 1996; Kaufman et al., 1997; Snoeks, 2000; Nagelkerke & Sibbing, 2000; de Graaf et al., 2002)

Fish families	R. Nile	L. Vict/Kyoga	L. Edw/G	L. Alb	L. Tana
Protopteridae	2	1	1	1	–
Polypteridae	3	–	–	1	–
Anguilidae	1	–	–	–	–
Clupeidae	1	–	–	–	–
Osteoglossidae	1	–	–	–	–
Notopteridae	1	–	–	–	–
Mormyridae	15	7	2	7	–
Gymnarchidae	1	–	–	–	–
Kneriidae	1	–	–	–	–
Alestiidae	8	2	–	5	–
Distichodontidae	7	–	–	–	–
Citharinidae	2	–	–	4	–
Cyprinidae	25	17	4	5	24
Balitoridae	1	–	–	–	1
Bagridae	6	1	1	3	–
Schilbeidae	5	1	–	2	–
Amphiliidae	1	–	–	–	–
Clariidae	7	6	4	2	1
Malapteruridae	1	–	–	1	–
Mochokidae	15	2	–	3	–
Cyprinodontidae	7	7	4	2	–
Channidae	1	–	–	–	–
Centropomidae	2	(1)	–	2	–
Eleotridae	1	–	–	–	–
Cichlidae	10	ca 600 (+4)	60	10	1
Anabantidae	2	1	2	–	–
Mastacembelidae	–	1	–	–	–
Tetraodontidae	1	–	–	–	–
Total families	27	12 (+1)	8	14	4
Total species	128	600–700	78	48	27

Numbers within brackets concern introduced taxa (see text).

5 Lake Albert

Lake Albert, with a surface of 6,800 km^2 and a maximum depth of 58 m, is the only major Nilotic lake that is not isolated by falls from the River Nile (Fig. 1). Consequently, many species in this lake also occur in the river. A total of 48 species belonging to 14 families has been reported for Lake Albert (Table 3; Greenwood 1966, 1974). The degree of endemism is relatively low (ca 13%); one endemic cyprinid, one centropomid and four haplochromine cichlid species (Greenwood, 1974, 1976). In contrast to the other Lakes, it shares the families Polypteridae, Citharinidae, Malapteruridae and the Centropomidae with the River

Nile (Table 3; note that the Nile perch – *Lates niloticus*, Centropomidae – was introduced into Lakes Victoria/Kyoga in the 1950s; see chapter on Fisheries in the Nile System). Further, compared to the other Lakes, Lake Albert has a relatively high number of species belonging to the families Alestiidae and Bagridae (Table 3). In contrast, the number of cichlid species is relatively low. Among the ten reported cichlid species from Lake Albert, four are tilapiines: viz. *Tilapia zillii*, *Sarotherodon galilaeus*, *Oreochromis niloticus* and *O. leucostictus* (Greenwood, 1966; Trewavas, 1983). The other six species are haplochromines (Greenwood, 1974).

Lake Turkana (formerly called Lake Rudolf), now completely isolated from the Nile (Johnson & Malala, 2009), has a fauna similar to that of Lake Albert. It includes many species that are shared by both Lakes and by the River Nile (Greenwood, 1976).

6 Lakes Edward and George

Lakes Edward and George are isolated from Lake Albert by falls in the Semliki River (Fig. 1), which are supposed to form a barrier to most fish species migrating upriver (Greenwood, 1976). The small and shallow Lake George (270 km^2, maximum depth 4 m) and the larger and deeper Lake Edward (2,325 km^2, maximum depth 117 m) are connected through the 36 km long, river-like Kazinga Channel (Green, 2009). At least 78 fish species, belonging to 8 families, are known from these Lakes (Table 3). The fish fauna is dominated by the family Cichlidae with 60+ species (Table 3; Snoeks, 2000). These include haplochromine cichlids, more than 90% of which are endemic, and two tilapiine species, *Oreochromis niloticus* and *O. leucostictus* (Greenwood, 1974; Snoeks, 2000).

7 Lakes Victoria and Kyoga before the 1980s

With a surface area of 68,800 km^2, Lake Victoria is the largest tropical lake in the world (Lehman, 2009). Compared to other large Lakes it is relatively shallow (maximum depth 70 m). On its way to Lake Albert, the water of Lake Victoria passes through Lake Kyoga (surface area 2,700 km^2, maximum depth 8 m). Lakes Victoria and Kyoga are cut off from Lake Albert and the Nile by the impassable Murchison Falls, which are some 40 m high. Further, Lake Victoria was isolated from the Victoria Nile and Lake Kyoga by the Ripon falls. Due to the Owen Falls dam, built downstream in the 1950s, the Ripon Falls were submerged (Fig. 1). However, the dam is probably an even more effective barrier than were the falls (Greenwood, 1974).

Though Greenwood (1967, 1974) found endemic haplochromine cichlids in Lake Kyoga, he suggested that the fishes of this lake are mostly conspecific with those of Lake Victoria and that it is very likely that the latter lake was the chief source of fish stocks for Lake Kyoga. Kaufman estimated the number of haplochromines endemic to Lake Kyoga at 100 species (Turner et al., 2001). Because relatively little information is available on the cichlid fauna of Lake Kyoga, we treat them together with those of Lake Victoria. When Lake Kyoga and the satellite Lakes of Victoria/Kyoga are included, the total number of haplochromine species in the area may rise to 600 or even more (Kaufman et al., 1997). This makes the fish fauna of Lakes Victoria/Kyoga extremely rich compared to that of all other parts of the Nile system (Table 3). However, Lakes Victoria/Kyoga harbour only 46 native non-cichlid species of which 16 are endemic and 10 are shared with the River Nile (Greenwood, 1974; Lévêque et al., 1991). These non-cichlid species belong to 11 families, so at the family level the diversity in Lakes Victoria/Kyoga is distinctly lower than in the River Nile (Table 3). Two indigenous tilapiines, *Oreochromis esculentus* and *O. variabilis*, are present in the Lakes, and four species (*O. niloticus*, *O. leucostictus*, *Tilapia zillii*, *T. rendalli*) were introduced in the 1950s (Welcomme, 1988). Apart from these cichlid species, the Nile perch (*Lates niloticus*), was also introduced (Welcomme, 1988; Witte et al., 2009).

More than 500 endemic haplochromine species, all female mouth brooders, are known from Lake Victoria alone (Greenwood, 1974; Kaufman & Ochumba, 1993; Witte & van Oijen, 1995; Seehausen, 1996; Witte et al., 2007a). They made up more than 80% of the demersal ichthyomass (Kudhongania & Cordone, 1974). Other prominent species in bottom trawl catches were *O. esculentus*, *Clarias gariepinus*, *Protopterus aethiopicus* and *Bagrus docmak* (Kudhongania & Cordone, 1974). Apart from these demersal fishes, the small pelagic cyprinid *Rastrineobola argentea* made an important contribution to the fish fauna in the lake (Okedi, 1974).

Several authors raised doubts about the taxonomic status of Lake Victoria haplochromines (Sage & Selander, 1975; Turner & Grosse, 1980; Crapon de Caprona & Fritzsch, 1984; Meyer, 1987). However, ecological research corroborated in many cases the biological soundness of species distinction originally based on male colouration and small morphological differences. That is, no indications of gene flow could be found between presumed species that live in sympatry (Hoogerhoud et al., 1983; Goldschmidt & Witte, 1990; Seehausen et al., 1998b).

Lake Victoria haplochromines have been classified into 15 trophic groups, each consisting of species sharing morphological characters related to the capture, uptake and processing of their dominant food source (Figs. 5 and 6; Greenwood, 1974; Witte & van Oijen, 1990, 1995). The morphological characters that were used by Greenwood (1979, 1980) for the revision of the genus *Haplochromis* and related taxa into more than 20 genera and several subgenera, show considerable overlap with those that characterize the trophic groups. During the past decades there have been extensive debates on the validity of the genera defined in this way by Greenwood (Hoogerhoud, 1984; Meyer et al., 1990; Lippitsch, 1993; Snoeks, 1994; Seehausen, 1996; van Oijen, 1996; Seehausen et al., 1998a). Because of the disagreements, and as a considerable number of the haplochromine species from Lake Victoria cannot be assigned to the "new" genera, we prefer to keep the species in the genus *Haplochromis* and add the new generic names in parenthesis, i. e. use them as subgenera.

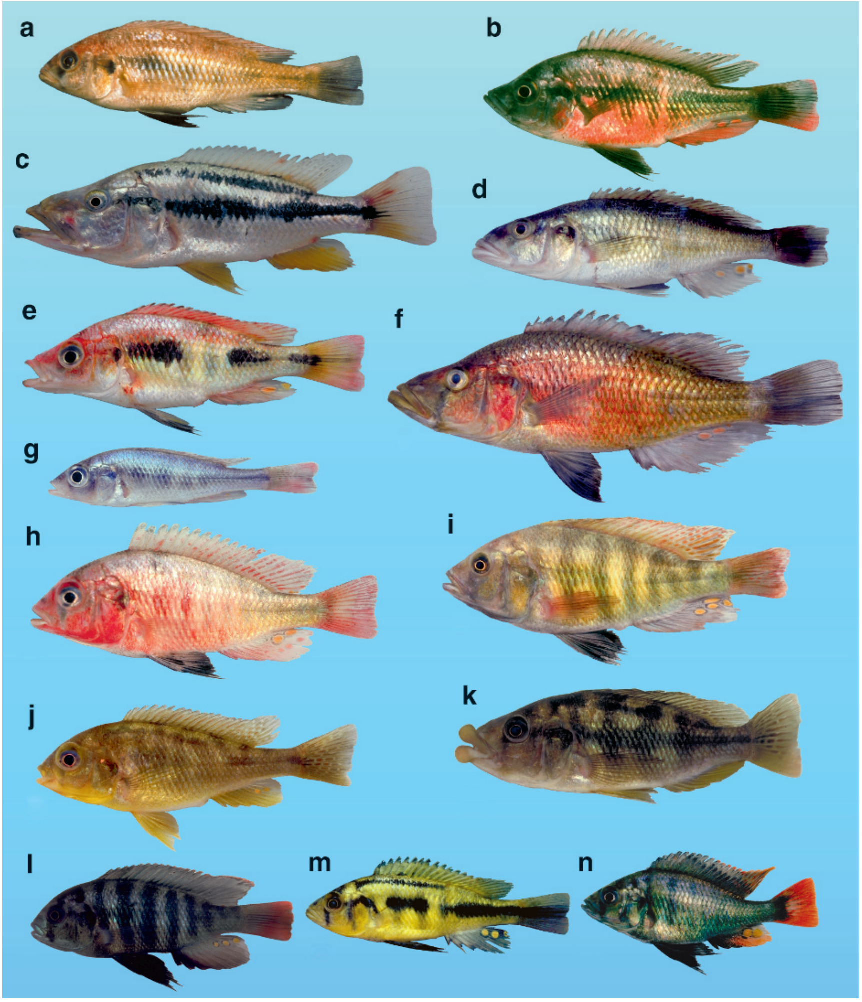

Fig. 5 Representatives of Lake Victoria haplochromine cichlids: (**a**) *H.* (*?*) *teunisrasi* (parasite eater); (**b**) *H.* (*Lipochromis*) *microdon* (paedophage); (**c**) *H.* (*Prognathochromis*) *macrognathus* (piscivore); (**d**) *H.* (*P.*) "dentex like" (piscivore); (**e**) *H.* (*P.*) "erythrocryptogramma" (prawn eater); (**f**) *H.* (*P.*) *argenteus* (piscivore); (**g**) *H.* (?) "argens" (zooplanktivore); (**h**) *H.* (*Labrochromis*) *teegelaari* (pharyngeal mollusc crusher); (**i**) *H.* (*Labrochromis*) *ishmaeli* (pharyngeal mollusc crusher); (**j**) *H.* (*Ptyochromis*) *sauvagei* (oral mollusc sheller); (**k**) *H.* (*Paralabidochromis*) *chilotes* (insectivore); (**l**) *H.* (*Neochromis*) *rufocaudalis* (algae grazer); (**m**) *H.* (*?*) "citrus" (phytoplanktivore); (**n**) *H.* (*Enterochromis*) "75" (detritivore/phytoplanktivore) (*see Color Plates*)

The trophic groups are not equally distributed over the lake. For instance, epilithic algae grazers are restricted to rocky shores and epiphytic algae grazers are mainly caught along shores with stands of rooted plants (e.g. Greenwood, 1974; Witte et al., 1992; Seehausen et al., 1997b). Insectivores and oral shelling molluscivores are mainly associated with hard substrates like sand and rocks, and

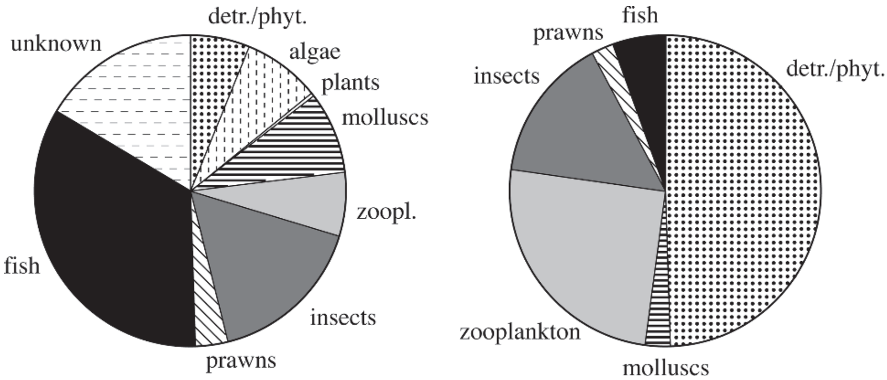

Fig. 6 Haplochromine trophic groups from Lake Victoria: (*left*) species composition in all habitats. Note that the paedophages and the scale scraper are included in the piscivores and that rare trophic types, like the parasite feeders and the crab eater, are not included; (*right*) biomass composition in sub-littoral waters (6–20 m deep)

detritivores with mud bottoms (e.g. Greenwood, 1974; Witte, 1981; Witte et al., 1992). With respect to the total number of species, the piscivores and insectivores were the most common groups (Fig. 6), however, concerning biomass the detritivores and zooplanktivores were most important, at least in the sub-littoral habitat (6–20 m deep; Fig. 6) and probably also in the open waters of the lake.

Molecular studies indicate that the 500+ haplochromine species of Lake Victoria evolved within the geologically short period of 100,000–400,000 years (Meyer et al., 1990; Nagl et al., 2000; Seehausen et al., 2003; Verheyen et al., 2003), and perhaps even in a much shorter time frame. Bottom core studies by Johnson et al. (1996) suggest that Lake Victoria fell dry completely 14,600 years ago. The reliability of the data has been questioned (Fryer, 2004), but see Stager & Johnson (2008). The origin, age and evolutionary history of the extraordinary speciose Lake Victoria haplochromines is still debated (Nagl et al., 2000; Seehausen et al., 2003; Verheyen et al., 2003; Seehausen, 2006). Nagl et al. (2000) suggested that the Lake Victoria haplochromines originated from trophic generalists, which lived in the East African river systems and in which mutations for morphological adaptations were already present as polymorphisms. Data of Seehausen et al. (2003) indicated that the Lakes Victoria/Edward flock is derived from the morphologically and ecologically diverse cichlid genus *Thoracochromis* from the Congo and Nile. Verheyen et al. (2003) explained the fast radiation of eco-morphological diversity in Lake Victoria haplochromines by their descent from the lacustrine, possibly already diversified, Lake Kivu ancestors. All four papers suggest that the Lake Victoria flock sensu stricto must be older than 14,600 years and that it is not strictly monophyletic. Rapid speciation has been suggested to be a typical feature of haplochromine cichlids (Seehausen, 2006) and is thought to be partly the result of sympatric speciation through disruptive sexual selection for conspicuous coloration (Maan et al., 2004) and strong assortative mating (Seehausen & van Alphen, 1998).

Learning in the form of sexual imprinting seems to facilitate assortative mating and reproductive isolation among closely related cichlid species (Verzijden & ten Cate, 2007).

Water clarity appears to be important for this mode of speciation and there is a significant correlation between the number of coexisting haplochromine species and transparency, among different East African Lakes and among localities within Lake Victoria (Seehausen et al., 1997a). The functional decoupling of the upper and lower pharyngeal jaws in cichlid fish may have contributed to the high degree trophic radiation of the haplochromines (Galis & Drucker, 1996).

8 Lakes Victoria and Kyoga after the 1980s

During past few decades the composition of the fish fauna in Lakes Victoria and Kyoga changed dramatically due to anthropogenic perturbations in the ecosystem. The boom of the introduced Nile perch in the 1980s as well as fishery and habitat deterioration (Witte et al., 2009) had a strong impact on the haplochromine cichlids and many other fish species (Ogutu-Ohwayo, 1990; Witte et al., 1992; Goudswaard & Witte, 1997; Goudswaard et al., 2002a,b, 2008). It was estimated that some 200 of the endemic haplochromine species may have gone extinct (Witte et al., 1992). The highly structured rocky shores and papyrus fringes, where Nile perch densities are low, were less affected by Nile perch than the sub-littoral and offshore waters (Witte et al., 1992, 2007a; Seehausen, 1996). However, the decrease in water transparency due to eutrophication may have caused hybridization among several haplochromine species, including those living along rocky shores (Seehausen et al., 1997a; Seehausen, 2006). Lake Victoria haplochromines are rather tolerant to low oxygen concentrations (Verheyen et al., 1986; Chapman et al., 1995; Rutjes et al., 2007), therefore the impact of the increased hypoxic conditions due to eutrophication (Hecky et al., 1994) may have been less severe than suggested (Witte et al., 2005).

Some satellite Lakes of Lakes Victoria and Kyoga were not invaded by Nile perch or affected by eutrophication. These Lakes, each with their own endemic haplochromines, still have a relatively pristine fish fauna, including some types of haplochromines that seem to have vanished from the main Lakes (Ogutu-Ohwayo, 1993; Mwanja et al., 2001; Aloo, 2003; Mbabazi et al., 2004).

In the course of the 1990s, after a decline in Nile perch in Lake Victoria due to intensive fishing, a slow resurgence of some haplochromine species was observed, mainly zooplanktivores and detritivores (Witte et al., 1995, 2000, 2007b; Seehausen et al., 1997b; Balirwa et al., 2003). Of each group only about 30% of the species recovered and the ratio between detritivores and zooplanktivores reversed (Witte et al., 2007a, b). Before the 1980s detritivores made up about 50% of the haplochromine biomass in the sublittoral waters and zooplanktivores about 25% (Fig. 6; Goldschmidt et al., 1993), whereas by 2001 detritivores constituted only 15% and zooplanktivores more than 80%. However, the majority of the species did not recover. Many of the highly specialized trophic types like scale eaters, parasite eaters and prawn eaters have not been caught since the 1980s, whereas piscivores and paedophages are extremely rare now, both with respect to numbers of individuals and species. Balirwa et al. (2003) suggested that conservation of biodiversity and fishery sustainability may not have to be antitheses in the management of Lake Victoria. A modelling study suggested that Nile perch prefer and grow fastest on a haplochromine prey base (Kaufman & Schwarz, 2002). If the model is realistic, it would suggest that it is worth thinking of management strategies that allow enough fishing on Nile perch to ensure an abundance of their haplochromine prey, but not so much pressure as to threaten the Nile perch stock itself (Balirwa et al., 2003). However, to allow maintenance and restoration of haplochromine diversity, the urgent measures must include serious attempts to reverse the eutrophication of Lake Victoria (Seehausen et al., 1997a; Balirwa et al., 2003; Witte et al., 2005).

Responses to the environmental changes were observed in several fish species in Lake Victoria. Reproductive strategies changed in the tilapiine cichlid *Oreochromis niloticus* (Ojuok et al., 2007) and in haplochromine cichlids and the cyprinid *Rastrineobola argentea* (Wanink & Witte 2000a; Manyala & Ojuok, 2007). Dietary shifts were observed in zooplanktivorous and detritivorous haplochromines (van Oijen &Witte, 1996; Katunzi et al., 2003; Kishe-Machumu et al., 2008), in *Rastrineobola argentea* (Wanink, 1998), in *Oreochromis niloticus* (Gophen et al., 1993; Bwanika et al., 2006; Njiru et al., 2007), in the catfishes *Bagrus docmak* and *Schilbe intermedius* (Olowo & Chapman, 1999), and the alestiid *Brycinus sadleri* (Wanink & Joordens, 2007). In all these cases the amount of macro-invertebrates in the diets increased strongly. Morphological adaptations to the increased hypoxic conditions, the decreased water transparency and the changes in diet were observed in the cyprinid *R. argentea* and in the haplochromines (Wanink & Witte, 2000b; Chapman et al., 2008; Kishe-Machama et al., 2008; Witte et al., 2008).

9 Lake Tana

Lake Tana is part of the headwaters of the Blue Nile; it has a surface area of 3,100 km^2 and a maximum depth of only 14 m (Vijverberg et al., 2009). The shallow lake is not stratified and extremely turbid; Secchi depths range from 0.3 m in the wet season to 1.8 m in some sheltered areas during the dry season (Sibbing & Nagelkerke, 2001). The ca 40 m high Blue Nile falls at Tissisat, 30 km downstream from the lake, form an effective barrier to the migration of fish from the lower Blue Nile basin into Lake Tana. Until the 1990s the fish fauna of Lake Tana had been poorly studied (Greenwood, 1976; Lévêque, 1997). Greenwood (1976) wrote that "Lake Tana, as far as can be told from its poorly studied fauna, should be considered merely as part of the Blue Nile". However, he also noted that the occurrence in Lake Tana of *Nemacheilus abyssinicus*, the only known representative in Africa of the Euro-Asiatic family Balitoridae (then placed in the family Cobitidae), "reemphasises the need for further detailed studies" on Lake Tana fishes (Greenwood, 1976). Such studies were started in the 1990s (Nagelkerke et al., 1994, 1995a, b; Sibbing et al., 1994, 1998; Dixon et al., 1996; Mina et al., 1996; Nagelkerke & Sibbing, 1996, 1997, 2000; Wudneh, 1998; Dgebuadze et al., 1999). The presence of *N. abyssinicus*, until then based on a single specimen, was confirmed in small streams close to Lake Tana and in large parts of the Ethiopian plateau (Dgebuadze et al., 1994). A single specimen was found in the deep part of the lake (Nagelkerke, 1997). The only cichlid in this highly turbid lake is the tilapiine *Oreochromis niloticus tana* and the only catfish *Clarias gariepinus*. The latter was originally described as *C. tsanensis* by Boulenger (1902) but later synonymised with *C. gariepinus* (Teugels, 1986).

In contrast to the headwater Lakes of the White Nile where haplochromine cichlids dominate, the fish fauna of Lake Tana is dominated by the cyprinid genera *Barbus* and *Labeobarbus*. Of the 93 species of freshwater fishes reported for Ethiopia (Getahun & Stiassny, 1998; Froese & Pauly, 2001; Stiassny & Getahun, 2007), 44 species are cyprinids, and in Lake Tana alone 24 cyprinid species are found (Table 3), of which 18 are endemic to the lake. The large barbs of Lake Tana (up to 100 cm) were first described by Rüppell (1836) as five *Barbus* and one *Labeobarbus* species. Later, Bini (1940) identified 10 species, including 23 subspecies, and considered them as a separate subgenus *Labeobarbus*. Inadequate descriptions and keys forced Banister (1973) to a revision of the large barbs of East-Africa. He lumped all 50 nominal species and subspecies into a single highly variable species *Barbus intermedius*, composed of two subspecies: *Barbus intermedius intermedius*, including all Lake Tana barbs, and *Barbus intermedius australis*. Following detailed morphological and ecological characters (Nagelkerke et al., 1994; Nagelkerke & Sibbing, 1997), immuno-genetics (Dixon et al., 1996), reproductive segregation (Nagelkerke & Sibbing, 1996) and ontogenetic development (Nagelkerke et al., 1995b) the large barbs of Lake Tana were upgraded from distinct morphotypes (Nagelkerke et al., 1994) into 15 endemic species in addition to the non-endemic *B. intermedius* (Nagelkerke & Sibbing, 1997, 2000). Although Mina et al. (1996) and Dgebuadze et al. (1999) only partly agreed on the specific status of the large barbs and favoured the description of the barb diversity by plastic phenotypes of *Barbus intermedius*, several follow-up studies confirmed morphological, ecological, reproductive and genetic segregation (Kruiswijk et al., 2005; de Graaf et al., 2003a,b; Palstra et al., 2004; de Graaf et al., 2005, 2008). Palstra et al. (2004) assigned all large hexaploid barbs of Lake Tana to the genus *Labeobarbus* following suggestions by Bini (1940), Berrebi (1995), Skelton (2002) and Berrebi & Tsigenopoulos (2003). This better reflects the phylogenetic distance between the hexaploid large barbs (Golubtsov & Krysanov, 1993) and the small diploid barbs of Lake Tana, also supported by molecular data (de Graaf et al., 2003b; de Graaf et al., 2007).

The last desiccation of Lake Tana was estimated in the same period (between 18,700 and 16,700 BP; Lamb et al. 2007) as that in Lake Victoria (Johnson et al., 1996; Stager & Johnson, 2008). The *Labeobarbus* species flock probably evolved from a highly polymorph *Labeobarbus intermedius* complex, still present along the shore of Lake Tana (Nagelkerke & Sibbing, 2000), by sympatric speciation following disruptive selection on trophic structures (Sibbing et al., 1998).

Varicorhinus beso is another large (up to 40 cm) cyprinid in Lake Tana. It is closely related to *Labeobarbus*, which is also apparent from some hybrids found (Nagelkerke & Sibbing, 2000). The small barb species are considered to belong to '*Barbus* sensu lato' by Howes (1987); they are diploid, have diverging instead of parallel striae on the exposed part of their scales, and smaller dorsal spines than *Labeobarbus*. Three species of small (<10 cm) barbs (*Barbus*, subgenus *Enteromius*) are known from Lake Tana: *Barbus humilis*, *Barbus pleurogramma* and the recently described pelagic *Barbus tanapelagius*. The species *Barbus trispilopleura* that was also reported from the lake (Boulenger, 1902) formed a continuous range in appearance with *Barbus humilis* and has been synonymized as a shallow water ecotype of *Barbus humilis* (Dejen et al., 2002). Molecular analyses show the genetic similarity between the benthivorous *Barbus humilis* and the zooplanktivorous *Barbus tanapelagius*, which probably evolved from the first mentioned species after production of zooplankton increased in the incipient Lake Tana (de Graaf et al., 2007).

According to Boulenger (1911), the genus *Garra* has two species in Lake Tana, *G. dembeensis* and *G. quadrimaculatus*. In a recent revision by Stiassny & Getahun (2007) the latter species was re-identified and described as *G. dembecha*, a new species that also occurs outside the lake in Eritrea, Kenya and Tanzania. Stiassny & Getahun (2007) also described two new endemic species for Lake Tana, viz. *G. regressus* (formerly *G. microstoma*, Getahun 2000) and *G. tana*.

All Lake Tana barbs and labeobarbs evolved from benthic riverine species; many adapted to new spatial and trophic niches after the origin of Lake Tana (Fig. 7 and 8; Nagelkerke & Sibbing, 1996; Sibbing et al., 1998; Sibbing & Nagelkerke, 2001; Palstra et al., 2004, de Graaf et al., 2008). The most conspicuous group, and the most deviating from the ancestral benthivore design, are the piscivores with four obligatory (prey > 80% fish) and four predominantly (prey > 60% fish) piscivorous species (Sibbing et al., 1998; Sibbing & Nagelkerke, 2001). Although limited in prey size (to ca 15% of their fork length, de Graaf et al., 2003c) labeobarbs are successful piscivores in Lake Tana, probably due to the absence of specialized and competing piscivores belonging to other fish families and the abundance of small *Barbus* and *Garra* in the proper size range of their processing capacity. Much like the polymorph *Labeobarbus intermedius* shore complex of Lake Tana, other labeobarb species feed on varied benthos (mixtures of insect larvae and detritus) and are segregated by habitat (mainly littoral rocks, littoral mud, sub-littoral or offshore benthopelagic; de Graaf et al., 2008). Whereas two species additionally take molluscs, only a single labeobarb feeds substantially on macrophytes (Sibbing & Nagelkerke, 2001; Vijverberg et al., 2009, Fig. 8). Zooplankton is partitioned among all juvenile *Labeobarbus*, adults of *L. brevicephalus* and the obligatory zooplanktivorous *B. tanapelagius* (Dejen et al., 2006). Phytoplankton seems to be a vacant food niche; it is, however, exploited by the abundant littoral *Oreochromis niloticus*. The small *Garra* species utilize the benthic algae, just like *Varicorhinus beso* which may feed more on the periphyton on littoral weeds and reed beds.

In contrast to Lake Victoria, the ichthyofauna of Lake Tana lacks fishes with extreme specialisations as found in paedophages, prawn eaters, crab eaters, parasite feeders and scale eaters. The cyprinid design, lacking oral jaw teeth, a stomach and

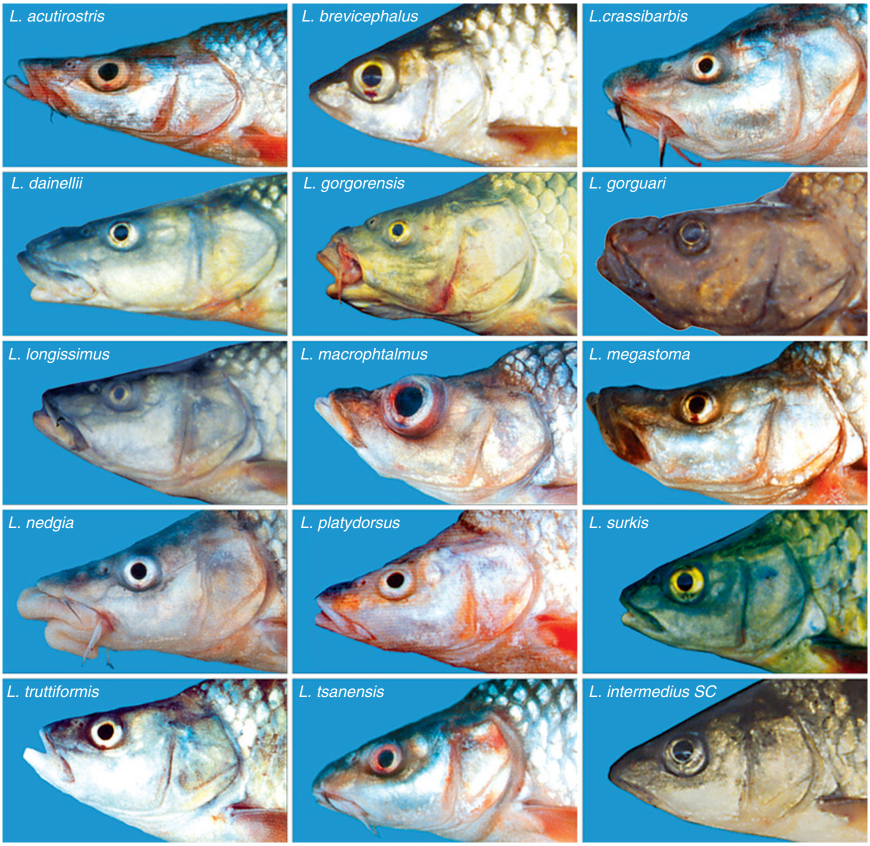

Fig. 7 Representatives of *Labeobarbus* species from Lake Tana. Obligatory piscivores (>80% fish): *L. acutirostris*, *L. truttiformis*, *L. longissimus*, *L. dainellii*, *L. megastoma*; facultative piscivores (>60% fish): *L. gorguari*, *L. platydorsus*; herbivores/molluscivores/detritivores: *L. surkis*, *L. gorgorensis*; polyphagous barbs: *L. brevicephalus*, *L. macrophthalmus*; benthivores: *L. nedgia*, *L. tsanensis*, *L. crassibarbis*, *L. intermedius* shore complex (*see Color Plates)*

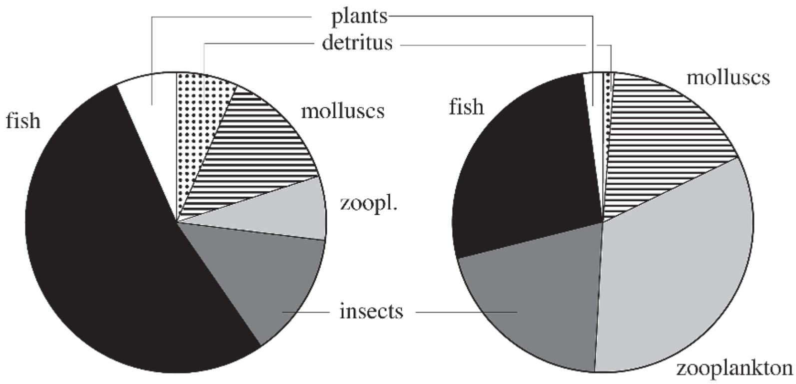

Fig. 8 Labeobarb trophic groups from Lake Tana: (*left*) species composition; (*right*) biomass composition

cellulases, may impose serious phylogenetic constraints on some trophic specializations. However, cyprinids possess highly developed and diversified pharyngeal jaws. This pharyngeal jaw system enables cyprinid fish to break down otherwise inaccessible tough and strong food types (Sibbing & Nagelkerke, 2001). Another speciality of the cyprinids is the sensory and highly muscular palatal organ required for sorting food from the non-food benthos (Sibbing et al., 1986). Equipped with these features the cyprinids found their niches mainly in the benthic zone. Their flexibility and opportunistic strength is demonstrated by the natural evolutionary experiment in Lake Tana, where they even expand into the piscivorous level due to the lack of competitors.

Acknowledgements We thank our colleagues from the Haplochromis Ecology Survey Team (HEST), the Tanzania Fisheries Research Institute (TAFIRI), the Amhara Region Agricultural Research Institute (ARARI) and the Lake Tana Fisheries and other Aquatic Resources Research Centre for their co-operation. We wish to thank Martin Brittijn for making the figures. Figures 3b, f, j, l, p, q, t-y, aa, ab, were redrawn with permission of John Wiley & Sons from Fishes of the World 2nd edition by J.S. Nelson, Copyright ©1984 John Wiley & Sons, Inc. The research on Lake Victoria was financially supported by The Netherlands Foundation for the Advancement of Tropical Research (WOTRO), the Section for Research and Technology of The Netherlands Minister of Development Co-operation, Leiden University, the Schure-Beijerinck-Popping Fonds, the van Tienhoven Stichting and Yellow Springs Instruments. The research on Lake Tana was financially supported by WOTRO, Wageningen University, the Schure Beijerinck-Popping Fonds and the Interchurch Foundation Ethiopia-Eritrea (Urk).

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Appendix

Species mentioned in the text of the chapters *Fish fauna of the Nile* and *Fisheries in the Nile system*, with authors and families to which the species belong

Species	Author	Family	Notes
Alestes baremoze	(De Joannis, 1835)	Alestiidae	Formerly *baremose*, Characidae
A. dentex	(Linnaeus, 1758)	Alestiidae	Formerly Characidae
Auchenoglanis biscutatis	(Geoffroy Saint-Hilaire, 1809)	Bagridae	
Bagrus bajad	Forsskål, 1775	Bagridae	Formerly *bayad*
B. docmak	Forsskål, 1775	Bagridae	
Barbus altianalis	Boulenger, 1903	Cyprinidae	
B. bynni	Forsskål, 1775	Cyprinidae	
B. humilis	Boulenger, 1902	Cyprinidae	
B. intermedius australis	Banister, 1973	Cyprinidae	Now *Labeobarbus*
B. intermedius intermedius	Rüppell, 1836	Cyprinidae	Now *Labeobarbus*
B. pleurogramma	Boulenger, 1902	Cyprinidae	
B. tanapelagius	de Graaf et al., 2000	Cyprinidae	
B. trispilopleura	Boulenger, 1902	Cyprinidae	In L. Tana synonym with *humilis*
Brycinus jacksonii	(Boulenger, 1912)	Alestiidae	Formerly Characidae
B. nurse	(Myers, 1929)	Alestiidae	Formerly Characidae
Clarias gariepinus	(Burchell, 1822)	Clariidae	Formerly *lazera*;
Ctenopoma murei	(Boulenger, 1906)	Anabantidae	
Epiplatys spilargyreius	(Duméril, 1861)	Cyprinodontidae	Formerly *E. marnoi*
Garra dembeensis	(Rüppell, 1836)	Cyprinidae	
G. dembecha	Stiassny & Getahun, 2007	Cyprinidae	Formerly *quadrimaculatus* (non-Rüppell)
G. regressus	Stiassny & Getahun, 2007	Cyprinidae	Formerly *microstoma*
G. tana	Stiassny & Getahun, 2007	Cyprinidae	
Haplochromis (*?*) “argens”	Cheironym	Cichlidae	
H. (*Prognathochromis*) *argenteus*	Regan, 1922	Cichlidae	
H. (*Paralabidochromis*) *chilotes*	(Boulenger, 1911)	Cichlidae	
H. (*?*) “citrus”	Cheironym	Cichlidae	
H. (*Prognathochromis*) *dentex*	Regan, 1922	Cichlidae	
H. (*Prognathochromis*) “erythrocryptogramma”	Cheironym	Cichlidae	
H. (*Labrochromis*) *ishmaeli*	Boulenger, 1906	Cichlidae	

(continued)

(continued)

Species	Author	Family	Notes
H. (*Lipochromis*) *microdon*	(Boulenger, 1906)	Cichlidae	
H. (*Neochromis*) *rufocaudalis*	Seehausen & Bouton, 1998	Cichlidae	
H. (*Ptyochromis*) *sauvagei*	Pfeffer, 1896	Cichlidae	
H. (*Labrochromis*) *teegelaari*	Greenwood & Barel, 1978	Cichlidae	
H. (*?*) *teunisrasi*	Witte & Witte-Maas, 1981	Cichlidae	
H. (*Enterochromis*) "75"	Cheironym	Cichlidae	
Hemichromis fasciatus	Peters, 1858	Cichlidae	
Heterotis niloticus	Rüppell, 1829	Osteoglossidae	
Hydrocynus forskalii	(Cuvier, 1819)	Alestiidae	Formerly *forskahlii*, Characidae
Labeo altivelis	Peters, 1852	Cyprinidae	
L. niloticus	(Forsskål, 1775)	Cyprinidae	
L. mesops	Günther, 1868	Cyprinidae	
L. victorianus	Boulenger, 1901	Cyprinidae	
Labeobarbus acutirostris	(Bini, 1940)	Cyprinidae	
L. brevicephalus	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
L. crassibarbis	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
L. dainellii	(Bini, 1940)	Cyprinidae	
L. gorgorensis	(Bini, 1940)	Cyprinidae	
L. gorguari	(Rüppel, 1836)	Cyprinidae	
L. intermedius	(Rüppell, 1836)	Cyprinidae	
L. longissimus	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
L. macrophtalmus	(Bini, 1940)	Cyprinidae	
L. megastoma	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
L. nedgia	Rüppel, 1836	Cyprinidae	
L. platydorsus	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
L. surkis	(Rüppel, 1836)	Cyprinidae	
L. truttiformis	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
L. tsanensis	(Nagelkerke & Sibbing, 1997)	Cyprinidae	
Lates niloticus	(Linnaeus, 1758)	Centropomidae	
Nemacheilus abyssinicus	Boulenger, 1902	Balitoridae	Formerly Cobitidae
Neobola bredoi	(Poll, 1945)	Cyprinidae	

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Species	Author	Family	Notes
Oreochromis aureus	(Steindachner, 1864)	Cichlidae	
O. esculentus	(Graham, 1929)	Cichlidae	
O. leucostictus	(Trewavas, 1933)	Cichlidae	
O. niloticus	(Linnaeus, 1758)	Cichlidae	
O. niloticus tana	Seyoum and Kornfield, 1992	Cichlidae	
O. variabilis,	(Boulenger, 1906)	Cichlidae	
Parachanna obscura	(Günther, 1861)	Channidae	Formerly *Channa*, Ophicephalidae
Polypterus senegalus	Cuvier, 1829	Polypteridae	
Protopterus aethiopicus	Heckel, 1851	Protopteridae	
Rastrineobola argentea	(Pellegrin, 1904)	Cyprinidae	
Sarotherodon galilaeus	(Linnaeus, 1758)	Cichlidae	
Synodontis frontosus	Vaillant, 1895	Mochokidae	
S. schall	(Bloch & Schneider, 1801)	Mochokidae	
Synodontis victoria	Boulenger, 1906	Mochokidae	
Tilapia rendalli	Boulenger, 1896	Cichlidae	
T. zillii	(Gervais, 1848)	Cichlidae	
Varicorhinus beso	Rüppell, 1836	Cyprinidae	
Xenoclarias eupogon	(Norman, 1928)	Clariidae	
Xenomystis nigri	(Günther, 1868)	Notopteridae	