The ichthyogeography of Lake Kivu

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At present, Lake Kivu is considered to belong either to the Zaire ichthyofaunal province or, in case of a subdivision of the Great Lakes, to the Tanganyika region. In view of the geological history of the lake and its present ichthyofaunal composition, however, we recommend including Lake Kivu in the same ichthyofaunal province as lakes Victoria and Edward-George, namely, the East Coast Province.

In 1983, Greenwood[1] discussed the state of the inter- and intracontinental zoogeographical studies on the African freshwater fishes. In particular, he stressed the little progress made despite many decades of intensive research on the taxonomy of these fishes. This, to him, was due to the lack of phylogenetic information for many of the key taxa used in zoogeographical studies.

With regard to the intracontinental studies, Greenwood particularly discussed the value of the endemic cichlid taxa of the East African lakes for the study of ichthyogeography. He drew attention to the fact that some of the non-endemic species, especially the non-cichlids, which were used as indicators for the allocation of the various lakes to the ichthyofaunal provinces, could well be members of primitively widespread faunas. Based on his long experience with these cichlid taxa, and thereby challenging his earlier ideas[2] and those of Roberts,[3] he pointed out (p. 194) that lakes Edward, George and Victoria should be put in the same faunal region 'to be part of, or at least to have strong affinities with, the East Coast province' (sensu Roberts[3]).

Greenwood[1] further discussed the ichthyogeographical position of lakes Tanganyika and Malawi and briefly mentioned lakes Turkana and Albert. Nowhere, however, did he address the status of Lake Kivu. Because of its endemic haplochromine fauna, belonging to the Victoria super species flock (sensu Greenwood[4,5]) and taking into account the entire species composition of the lake basin, we believe that similar ichthyogeographical arguments may be advanced for Lake Kivu as was done by Greenwood for lakes Edward and George.

Geological history of the lake

Lake Kivu is one of the smaller lakes of the East African Lakes region, situated on the border between Rwanda and Zaire. Together with lakes Albert, Edward-George and Tanganyika, it forms the western loop of the East African rift valley system. At present, Lake Kivu is connected with Lake Tanganyika through its only outlet, the Rusizi River. Hence, Lake Kivu currently connects to the hydrographic system of the Zaire basin. There is some controversy as to the geological history of Lake Kivu (reviewed by Snoeks[6]). Before the Miocene uplifting in East Africa, the region of the present-day Lake Kivu was drained by a westward flowing river system to a central Zairean lake basin. In its present form, Lake Kivu is very recent. However, Snoeks[6] already stressed that the general idea that Lake Kivu originated only about 10 000 BP should be abandoned. According to Degens *et al.*,[7] a proto-Lake Kivu already existed before the present-day lake was formed. They concluded that a shallow lake must have existed in the present Lake Kivu area between 1 and 5 million years ago. According to Haberyan and Hecky,[8] the proto-Lake Kivu had a mid-Pleistocene origin. This proto-lake was connected with the ancient Lake Edward basin. In the Late Pleistocene (25 000–20 000 BP according to Beadle;[9] 14 000–11 000 BP according to Pouclet[10]), the northern valley of the ancient lake became blocked due to the eruptions of the Virunga volcanoes. Consequently, the closed-basin lake which had a low lake level around 14 000 BP filled up with water and the recent Lake Kivu was created. At about 9500–9200 years ago, a southwards outlet, the Rusizi, originated,[8] thus creating the present connection of Lake Kivu with Lake Tanganyika through regressive erosion. After this water flow reversal, the level of Lake Kivu kept fluctuating enormously, with Lake Kivu being either an open or a closed system.[6]

History of the ichthyofaunal status of Lake Kivu

Earlier workers on the ichthyogeography of Africa did not pay much attention to Lake Kivu as it was a relatively small lake of which little was known.

Boulenger[11] did not discuss Lake Kivu and apparently included it, as he did for all rift-valley lakes, in the Megapotamian sub-region. This region corresponds more or less to the present Nilo-Sudan, Upper and Lower Guinea and Quanza provinces (sensu Roberts[3] and Greenwood[1]), a large part of the Zambezi Province and part of the East Coast Province, namely, the Lake Victoria basin.

Pellegrin[12] also did not mention Lake Kivu, but in contrast to Boulenger[11] created a separate subregion, '*Mégalimnique équatoriale*', in which he grouped lakes Victoria, Tanganyika and Malawi and which, according to his map,[13] included Lake Kivu as well as lakes Edward and George, but not Lake Albert.

Nichols and Griscom[14] (p. 741) stated that lakes Victoria and Albert Edward (= Edward) are 'undoubtedly homologue in their ichthyofauna with the Nile basin'. However, on the map, Lake Edward is included in West Tropical Africa, as well as lakes Kivu and Tanganyika, the latter representing 'a great problem'.

Poll[15] was the first to discuss Lake Kivu: '*le Kivu pouvant être rapproché du Tanganyika*' (p. 51) and '*le lac Kivu dont la faune, quoique insignifiante, offre quelques éléments tanganiciens*' (p. 55). Both lakes were classified into a separate Tanganyika region. Poll furthermore created a separate region for lakes Victoria and Edward and included Lake Albert in the Nile Province.

Matthes[16] mentioned Lake Kivu as part of his Congo region, while lakes Victoria, Edward and Albert were considered to belong to the Nile region as a separate division called '*Le Nil victorien*', which, especially with respect to Lake Victoria, had clear affinities with the Eastern region.

Roberts[3] produced the first detailed document on the geographical distribution of African freshwater fishes. He placed Lake Kivu in the Zaire Province, indicating weak faunistic relationships both with the Nile and with Lake Tanganyika (Table 7, p. 311). Lakes Albert, Edward and George were placed in the Nilo-Sudan Province, while the Lake Victoria basin was ranged

within the East Coast Province.

Greenwood[1] more or less agreed upon the division of Roberts,[3] but found evidence in the phylogeny of the haplochromine cichlids to include lakes Edward and George in the same region as Lake Victoria.

Skelton *et al.*[17] slightly modified the provinces of Roberts, delimiting three additional provinces corresponding with the three major lake systems, Victoria, Malawi and Tanganyika, the last including Lake Kivu (Fig. 7.1, p. 212). They did not follow the suggestion of Greenwood[1] regarding lakes Edward and George, which were included in the Nilo-Sudanian region.

Skelton[18] reviewed the diversity and the distribution of the freshwater fishes of East and southern Africa, but did not include the major lakes in his discussion.

Worthington and Lowe-McConnell[19] adopted Greenwood's suggestion and included lakes Edward and George in their Victorian fish fauna zone. According to these authors, the former nilotic fauna of Lake Edward disappeared during a period of drought, after which repopulation followed via contact with the Lake Victoria system. On their map, Lake Kivu is included in the Zairean zone, although they included the discussion on this lake in the chapter on the Victorian Fish Region and stated that the fish fauna of lake Kivu 'remains akin to that of Lake Victoria' (p. 207).

The ichthyofauna of Lake Kivu with comments on species distributions

Currently, 28 fish species are known from Lake Kivu and its affluents, of which 19 are cichlids and 9 non-cichlids (Table 1). It is clear that, apart from the 15 endemic haplochromines currently distinguished, Lake Kivu has a very poor fish fauna. As for Lake Edward, a surprising absence of several taxa, elsewhere in Africa very common, is noteworthy. Interestingly, and as already noted by Greenwood,[2] the 'absentee families' from Lake Edward are also absent from Lake Kivu, but the fauna of Kivu is even poorer. Among the possible causes for this poor fauna are the recent origin of the present-day lake, combined with the high tectonic activity in the area (e.g. the upwelling of poisonous gases, and lava flows entering the lake) which might have destroyed part of the fauna already present in the proto-Lake Kivu. Lake Kivu has a relatively high salinity and is isolated without any major river system allowing for the invasion of fishes[6] (Fig. 1). In addition, periods of drought combined with a higher salinity might have played a role in the restriction or reduction of the number of taxa.

Three of the four tilapias present in the lake are introduced. *Oreochromis macrochir* (Boulenger 1912) and *Tilapia rendalli* (Boulenger 1896) (at that time still named *T. melanopleura* Duméril, 1858) were introduced from 1948 on into fish ponds in the Kivu drainage, originating from ponds near Lubumbashi (formerly Elisabethville). At least two strains of *O. macrochir* were introduced: the Luapula-Moero strain with the star-shaped nest and the Kafue strain [at that time erroneously named *T. andersonii* (Castelnau 1861)] with the volcano-shaped nest.[20,21] The presence in the lake of *T. rendalli* and *O. macrochir*, which evidently escaped from fish ponds, was first noted by the Murakoze-I expedition in 1979.[21] A third introduced species, *O. leucostictus* (Trewavas 1933), was reported for the first time in 1986, when two specimens were collected at Gisenyi in the northern part of the lake. Despite an intensive sampling programme from 1979 to 1988,[6] it had never been caught before nor again afterwards. Therefore, and although we found no written report of transports of *O. leucostictus* in the area, it is obvious that the presence of *O. leucostictus* in Lake Kivu is also the result of an artificial introduction. According to Trewavas,[22] the natural distribution of this species is restricted to the lakes Edward and Albert systems.

The only autochthonous tilapia is *Oreochromis niloticus* (Linnaeus 1758). This species is present in the Abyssinian Highlands, in nearly the whole Nilo-Sudan Province and in the lakes Kivu

Table 1. Ichthyofaunal composition of Lake Kivu. For autochthonous species, the currently known natural distribution is indicated.

Clupeidae	
Limnothrissa miodon Boulenger, 1906	Introduced[26]
Cyprinidae	
Raiamas moorii (Boulenger, 1900)	Lake Tanganyika, Lake Kivu, Malagarasi, Lake Rukwa[21,31]
Barbus kerstenii Peters, 1868	Distribution still under discussion. Currently cited from lakes Victoria, Edward-George and Kivu basins, coastal rivers in Kenya and Tanzania, Okavango, Cunene, Zambezi system, Save, possibly Aswa River in Upper Nile[35,37]
Barbus pellegrini Poll, 1939	Lakes Edward–George, Kivu, Tanganyika & Rukwa basins[31,35]
Barbus apleurogramma Boulenger, 1911	Lakes Victoria, Edward-George, Kivu, Tanganyika and Rukwa basins, possibly Lukuga system, coastal rivers in Kenya and Tanzania, possibly Aswa river in Upper Nile system and Aou, in Chad[31,35,37,42]
Barbus altianalis Boulenger, 1900	Lakes Victoria, Kyoga, Edward–George and Kivu basins, Rusizi and northern part of Lake Tanganyika[43]
Amphiliidae	
Amphilius cf. uranoscopus (Pfeffer, 1889)	Distribution still under discussion; coastal rivers in east and south-east Africa, Okavango, Zambezi system, lakes Victoria, Kivu, Tanganyika and Victoria systems, Upper Zaire system[46,57]
Clariidae	
Clarias liocephalus Boulenger, 1898	Lakes Victoria, Edward–George, Kivu, Tanganyika basin, Malagarasi, Bangweulu–Mweru system, Lake Rukwa, Cunene, Okavango, Zambezi system and possibly in Lake Malawi catchment[18,58]
Clarias gariepinus (Burchell, 1822)	Almost pan-African[45]
Cichlidae	
Oreochromis niloticus (Linnaeus, 1758)	Senegal, Gambia, Niger, Benue, Volta, Chad system, Jebel Marra, Nile, Yarkon River (Israel), Lake Turkana system, lakes Albert, Edward–George, Kivu and Tanganyika basins, Lake Tana, Lake Baringo, Suguta River, Ethiopian rift valley lakes from Lake Zwai to Lake Stefani, Omo system, Awash system[20,22] [populations from the latter three regarded as *O. cancellatus* (Nichols, 1923) by Seyoum and Kornfield[59]].
Oreochromis macrochir (Boulenger, 1912)	Introduced (escaped from fish ponds)[20,21]
Oreochromis leucostictus (Trewavas, 1933)	Introduced (escaped from fish ponds?)
Tilapia rendalli (Boulenger, 1896)	Introduced (escaped from fish ponds)[20,21]
Haplochromis spp. (15 species)	All endemic[6]

and Tanganyika systems (Table 1). It is absent from the East Coast Province as defined by Roberts.[3] According to Thys van den Audenaerde,[20] the subspecies present in Lake Kivu, currently named *O. niloticus eduardianus* (Boulenger 1912), is also present in the lakes Edward–George basins and in Lake Tanganyika and the Rusizi River. Probably it also inhabits several other Tanganyika affluents, including the Malagarasi and Lufubu river systems. Trewavas[22] considered the same subspecies to be present in the Lake Albert system as well, but noted that the population of Lake Albert and the Albert Nile differed somewhat from those of lakes Edward, George and Kivu. A morphological difference between these two populations was already noted by Thys van den Audenaerde,[20] who classified the Lake Albert population within the Nile subspecies, separate from the Edward–Kivu–Tanganyika.

The remaining cichlids are all haplochromines that are endemic to the lake. At present they are considered to belong to the large Victoria–Edward–Kivu super-flock,[4,6] although Greenwood[4,23] was unable to find a uniquely derived character for this flock. It is assumed that the majority of the species of this flock share a common ancestry not shared with the haplochromines of lakes Albert and Turkana.[1] The species from these lakes which Greenwood[23] classified within *Thoracochromis* probably derived from a common ancestor shared with the Nile haplochromines and some species of the Zaire River. In 1983,[1] he mentioned one exception from Lake George (*Haplochromis petronius* Greenwood 1973) but apparently overlooked another species from Lake Edward, *Haplochromis pharyngalis* Poll, 1939, which he previously included also in the Albert–Turkana group.[23]

The molecular studies currently available on taxa of the Victoria–Edward–Kivu super species flock and of other lakes and river systems appear to support the monophyly of this flock.[24] However, these studies did not include representatives of Lake Kivu since, at present, no DNA has been sequenced from these taxa.

Snoeks[6] discussed the relationships of the haplochromines from Lake Kivu. He pointed out that as far as could be inferred from morphological data, the closest relatives of many of the Lake Kivu species are not necessarily found within the lake, but rather within the other lakes of the super-flock. Other data based on enzyme analysis[25] and the morphology of scales (Lippitsch, pers. comm.) indicate, however, that all or nearly all of the Lake Kivu haplochromines may form a monophyletic assemblage. While it certainly cannot be excluded that some of the Kivu haplochromines, the relationships of which could not be defined until now,[6] indeed might be closely related, the assumption of a monophyletic origin of the Lake Kivu haplochromines is in conflict with the prevailing hypothesis that this super-flock comprises several lineages whose members cut across the boundaries imposed by the present-day shores.[4] It is clear that, to resolve this problem, more information is needed from other, molecular techniques. Such a study would be even more relevant if not only Lake Kivu haplochromines, but also taxa from lakes Edward and George were involved.

As far as currently can be assumed, the outcome of this debate is of minor importance for the discussion on the ichthyogeographical position of Lake Kivu. Indeed, even if all of the Lake Kivu haplochromines prove to represent a monophyletic assemblage, then, most probably, this assemblage would still be part of the large Victoria–Edward–Kivu super-flock, eventually at a higher level of universality. Hence, the direct ancestral species evidently would have had an East Coast Province origin rather than a Zairean one.

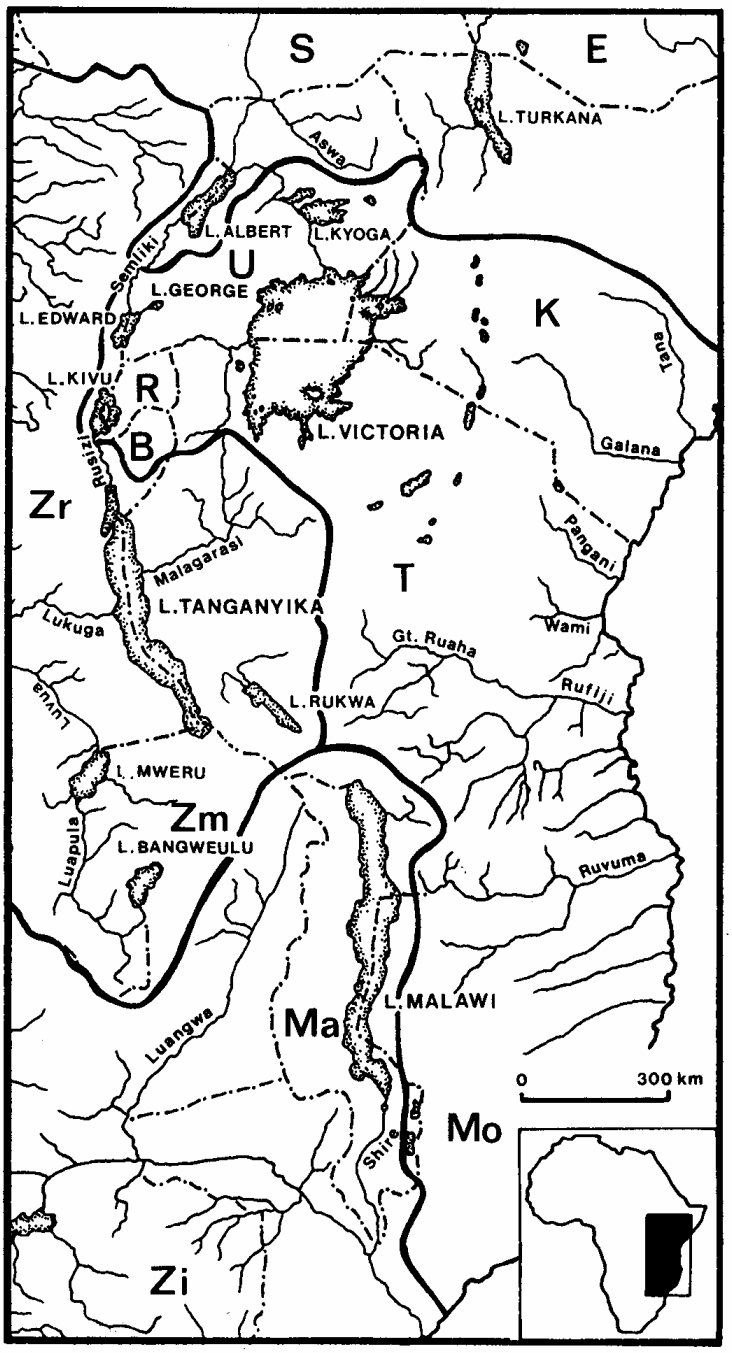

Fig. 1. Map showing the East Coast ichthyofaunal province with the inclusion of lakes Edward–George and Kivu. East Coast boundaries are based on Roberts[3] and Greenwood,[1] but have been slightly modified according to various detailed maps present in the Vertebrate Section of the Africa Museum, Tervuren. Following Seegers,[31] the Rukwa system has been included in the same region as the Malagarasi system. B, Burundi; E, Ethiopia; K, Kenya; Ma, Malawi; Mo, Mozambique; R, Rwanda; S, Sudan; T, Tanzania; Zm, Zambia; Zi, Zimbabwe; Zr, Zaire.

In contrast to the Lake Kivu cichlids, none of the autochthonous non-cichlid species is endemic to the lake.

The freshwater clupeids *Limnothrissa miodon* Boulenger, 1906 and *Stolothrissa tanganicae* Regan, 1917 were introduced in 1959 from Lake Tanganyika.[26] The former species became a well-established consumption fish in the lake, with present fishery production of a few thousand tons annually. *Stolothrissa tanganicae*, on the other hand, obviously did not thrive well in the lake and has not been recorded since.

The bariliine genus *Raiamas* Jordan, 1919 is distributed in the Nilo-Sudan, Guinean and Zairean provinces.[27] The sole representative of this group in Lake Kivu, *R. moorii* (Boulenger 1900), was considered to be endemic to lakes Tanganyika and

Kivu.[28] This species lives also in most affluent rivers of Lake Tanganyika and has been recorded from the Lake Rukwa system.[29–31] According to Boulenger,[32] the Rukwa population perhaps belongs to a distinct species. Indeed, slight morphological differences have been noted with the Tanganyika population[31,32] but Taverne (in litt.) is of the opinion that those differences merely result from a sufficiently long geographic isolation and do not justify the erection of a new taxon for this population. Marlier[33] suggested that the Kivu population represents a different race from the Tanganyika population, but no evidence or further details were given. *Raiamas moorii* is thought to be the only species able to have invaded Lake Kivu from Lake Tanganyika through the Rusizi.[33,34]

The taxonomic status of the three small *Barbus* species from the Kivu system was reviewed by De Vos and Thys van den Audenaerde,[35] who also corrected some of the earlier distribution data. Since a similar review for other regions is lacking, however, some uncertainties on their distribution remain and, indeed, the nomenclature and status of many small *Barbus* is still under discussion.

Currently, *Barbus kerstenii* Peters, 1868 is believed to have a large distribution throughout the East Coast and the Zambezi provinces (Table 1). This 'species' probably represents a complex of several closely related species and/or races. The Lake Kivu population of '*B. kerstenii*' represents a form characterized by a striking orange or reddish spot on the gill covers, bright orange fins, and 24 to 27 scales along a complete lateral line. In many affluents both in the north and the south of Lake Tanganyika, a possibly distinct but very closely related species exists which is currently identified as *B. oligogrammus* David, 1936. This latter fish often presents a duller colour pattern and frequently shows a reduced lateral line system. It is probable that '*B. kerstenii*' from Lake Kivu issued from a Lake Edward system stock and, most likely, is conspecific with '*B. kerstenii*' found in the Lake Victoria system. Nevertheless, we observed slightly shorter barbels in a series of individuals originating from the Akagera system (Upper Victoria basin) compared with individuals from Lake Kivu. Despite Greenwood's interesting work on certain small *Barbus* from East, Central and South Africa,[36] it is still necessary to confirm through study whether this Victoria–Edward–Kivu fish indeed represents the same species as the type material of *B. kerstenii*. *Barbus kerstenii* has been mentioned once from the Aswa River (Uganda, Upper Nile) by Greenwood.[37] However, it was not cited again in his account on the fishes of Uganda,[38] nor by Lévêque *et al.*[39] in their check-list of Nilo-Sudanian freshwater fishes. If the species is indeed present in this area, then this represents the only record in the Nilo-Sudan Province (but see also *B. apleurogramma*).

Barbus pellegrini Poll, 1939 is widely distributed in the lakes Kivu, Edward and Tanganyika systems, particularly in the affluent rivers,[35] and occurs also in the Lake Rukwa basin[31] probably as the result of an old link between the Rukwa basin and the Malagarasi system.

Barbus apleurogramma Boulenger, 1911 has a mainly East Coast distribution (Table 1), but the species is also present in the Lake Tanganyika system. In addition, there are two records from the Nilo-Sudan region, which were both overlooked by Lévêque *et al.*[39] in their check-list of Nilo-Sudanian freshwater fishes. A first record is from the Aswa River in Uganda.[37,38] The presence of *B. apleurogramma* there is not that surprising as, according to Greenwood,[37] the Aswa River has large affinities with the Victoria–Kyoga system, from which it is separated only by a small swampy divide. In addition, it may be highly probable that the upper Aswa River was once part of the Victoria–Kyoga drainage system.[37,40] This record was apparently also overlooked by Banister[41] in his discussion of the distribution of the small *Barbus* species from the Nile system. The second, more remarkable Nilo-Sudanian record is from Aoué (Ennedi Plateau, Chad). The presence of *B. apleurogramma* in this area is considered by Lévêque[42] as a relict of a more ancient fish fauna, the representatives of which later disappeared from Sudanese river basins. However, this statement may have been influenced by the fact that Lévêque (p. 42) assumed that *B. apleurogramma* elsewhere is only known from Lake Victoria and associated river systems (*cf.* Table 1). The presence of a population very similar to or conspecific with *B. apleurogramma* was observed in a tributary of the Lukuga (De Vos, pers. obs.). However, the identity of this population needs to be confirmed.

The only large *Barbus* species present in Lake Kivu is *B. altianalis* Boulenger, 1900. This species is also found in the extreme north of Lake Tanganyika and the Rusizi River. Most probably the fish invaded the Lake Tanganyika system from Lake Kivu through the Rusizi. Other distribution records show a typical East Coast Province distribution (Table 1). Erroneously, De Vos and Thys van den Audenaerde[43] mentioned the occurrence of this species in Lake Albert as a lapsus for Lake George. According to Banister,[44] *B. altianalis* belongs to the *B. intermedius* complex, which is present in the East Coast Province, the Nilo-Sudan Province and the Abyssinian Highlands.

Clarias gariepinus (Burchell, 1822) with its almost pan-African distribution is a bad indicator species for ichthyogeographical relationships and should be treated as a suspect 'primitive cosmopolitan' (sensu Greenwood,[1] p. 193, although the word 'cosmopolitan' in this context may be considered as an overstatement).

Clarias liocephalus Boulenger, 1898 is also rather widespread but is limited to the East Coast and the Zambezi provinces and to small parts of the Zaire Province (Tanganyika–Malagarasi and Bangweulu–Mweru) in close contact with the first two provinces mentioned (Table 1). There is a single, erroneous record from the Tana River in East Africa. This refers to a specimen mentioned by Teugels[45] from the Southern Eusso Nyiro River (also called Ewaso Ngiro or Uaso Nyiro), the northern affluent of Lake Natron. This river does not belong to the Tana system. Most likely, there has been confusion with another Kenyan river of the same name, situated in the north-east of Kenya, close to the Tana system, but apparently not in contact with it.

A single rheophilous *Amphilius* species exists in some affluents of Lake Kivu. This species was described as *A. kivuensis* Pellegrin, 1933, which may tentatively be attributed to *A. uranoscopus* (Pfeffer, 1889) (De Vos, unpubl.), a widespread species in the East Coast Province, the major part of the Zambezi Province and a small part of the Zaire Province;[46] it is present in the lakes Malawi and Tanganyika basins and apparently also in the Lake Victoria system. In Rwanda, a population of *A. uranoscopus* was found in the Nyabarongo system (Upper Victoria basin). In view of the presumed wide distribution of this species and the uncertain taxonomic status of the Kivu *Amphilius*, it currently represents a bad indicator species for ichthyogeographical analyses.

Besides the 28 species currently known from the Lake Kivu system, some other species have been mentioned to be present in the lake. According to Mahy,[47] the large catfish *Bagrus docmak* (Forsskall, 1775) was introduced into the lake, but no records are known of this event. If so, then it would appear that this introduction has failed since the species was never collected in the lake.

The mormyrid *Gnathonemus petersii* (Günther, 1862) was mentioned from Lake Kivu by David and Poll[48] based on a specimen originating from the north of the lake at Gisenyi (Rwanda). In fact this specimen was mislabelled and *G. petersii* definitely does not occur in Lake Kivu.[21,49] Pellegrin[50] described *Varicorhinus babaulti* (currently *V. pellegrini* Bertin & Estève, 1948) from the Kivu region based on a single specimen from a river west of Bukavu, at the extreme south-west of Lake Kivu. Marlier[51] pointed out that this fish most likely originates from the Lowa basin, Upper Zaire system and not from the Kivu drainage.

Further data

Information on other freshwater organisms occurring in Lake Kivu is scarce and mostly still dates from the results of the K.E.A. expedition (1952–54). Verbeke[52] noted that the invertebrate fauna of Lake Kivu is very poor, compared to those of lakes Edward and Albert, with the majority of its elements also present in these two lakes and some originating from Lake Tanganyika. As many invertebrate groups of Lake Kivu are in need of revision, it is currently difficult to assess if this statement still holds for all invertebrate groups. Some more recent information may be taken from a revision of northern African freshwater molluscs.[53] With respect to the distribution of these molluscs in the East and South African subregions and the Sudanian Province, Lake Kivu is placed, together with the lakes Edward, George, Victoria and Albert basins in the sources of the Nile District. Lake Tanganyika and the Malagarasi are placed in a separate province within the West African subregion.

In contrast to Lake Edward, the fossil record of which contains many nilotic elements,[1,2] Lake Kivu does not have a fossil fish record. Hence, it is difficult to speculate about the fish composition of the proto-Kivu Lake, although, most probably, it must have been quite similar to that of Lake Edward at that time.

Discussion

With regard to the presence of Kivu fishes in the Lake Tanganyika basin, Boulenger[11] already assumed that some taxa of certain fish groups (*Polypterus*, characids, cyprinids, silurids, and others) penetrated into Lake Tanganyika from the Nile system via the Rusizi, a hypothesis also supported by Blanc,[54] Roberts[3] and recently discussed by Coulter.[55] This scenario apparently can hold only for those taxa currently present in Lake Kivu as the Rusizi is of a very recent origin (see above). Such possible penetrators could be *Barbus pellegrini, B. apleurogramma, B. altianalis* and *O. niloticus eduardianus*. Hence, it is difficult to accept the suggestion of Roberts[3] (p. 297) that some taxa (*Polypterus bichir* Geoffroy Saint Hilaire, 1802; *P. senegalus* Cuvier, 1829; *Ichthyoborus besse* Joannis, 1835; and *Ctenopoma muriei* Boulenger, 1906) 'entered the Lualaba via Lake Tanganyika as a result of the same transfer of fishes that resulted in the presence of Nilotic fishes in lakes Kivu and Tanganyika when the headwaters were cut off by the elevation of the Mjumbiro or Virunga mountains'. We refer to Poll[56] and Greenwood[1] for a discussion on the distribution of these species and for alternative hypotheses for the presence of the Lualaba 'Nilotics', which is outside the scope of the present contribution.

Following the suggestion of Greenwood[1] regarding the ichthyogeographical status of lakes Edward and George and based on our own observations on the ichthyofauna of Lake Kivu, we propose to include Lake Kivu within the same faunal region as lakes Victoria, Edward and George. With the current state of knowledge, we recommend including these lakes within the East Coast Province, hence removing lakes Edward and George from the Nilo-Sudan Province and Lake Kivu from the Zaire Province (Fig. 1). The reasons for this proposal can be summarised as follows:

1) The origin of the present outflow of Lake Kivu, the Rusizi, is very recent. Before this connection with Lake Tanganyika, and hence the Zaire system, became established, the region of the present lake was connected with the ancient Lake Edward basin.

2) All 15 endemic haplochromines are considered to be part of a super species flock occurring in lakes Victoria, Edward, George and their associated river systems.

3) All other autochthonous species, except *Raiamas moorii*, which invaded Lake Kivu through the Rusizi, are also present in the East Coast Province. In the case of the genus *Barbus*, all species present in Lake Kivu appear to have a mainly East Coast distribution.

4) Lake Kivu does not share a single species with the Zaire Province that is not shared with the East Coast Province, again with the exception of *Raiamas moorii*.

5) The distribution of most of the non-haplochromine taxa, when present in the Zaire Province, is limited to Lake Tanganyika and its associated river system. The exceptions are the two widespread clariid catfishes. *Clarias liocephalus* is also present in the Bangweulu-Mweru system, while *C. gariepinus* has an almost pan-African distribution. If the *Amphilius* species of the Kivu drainage system indeed proves to be *A. uranoscopus*, then it also would have a large distribution, including the upper reaches of the Zaire system.

6) A study of the distribution patterns of freshwater molluscs puts lakes Kivu, Edward, George and Victoria also in the same faunal region, which in contrast to the situation in fishes, also includes Lake Albert. Of course, as freshwater invertebrates have different means of dispersal, their distribution data cannot be compared with fishes. However, this observation can be considered as an extra argument in favour of our hypothesis.

We have benefited from discussions with L. Tack and J. Moeyersons (Africa Museum, Tervuren) on the geological history of the Kivu area.

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