

The Tanganyika problem: comments on the taxonomy and distribution patterns of its cichlid fauna

By J. SNOEKS, L. RÜBER and E. VERHEYEN

With 1 plate, 3 figures and 4 tables in the text

Abstract

The problems encountered in the study of the taxonomy and distribution patterns of Lake Tanganyika cichlids are reviewed. Particular problems for *Lamprologus* s.l., a group of substratum-brooding genera, and for *Tropheus*, a mouthbrooding genus are discussed. Data from our Tanganyika-1992 expedition are compared with reevaluated data from the existing collections. The potential advantages of integrating molecular and morphological techniques are illustrated.

Introduction

The large and ancient lakes of East Africa are characterized by the presence of large numbers of endemic fish species, mainly cichlids. Although these fishes have been and still are the subject of intensive research programs, only an estimate can be given of the number of species in many of these lakes (Table 1) and much taxonomic research remains to be done. This is of particular importance when considered in relation to the study of the speciation, biodiversity and conservation of the ichthyofaunas of these lakes.

The species-level taxonomy of the fishes of the smaller lakes Turkana, Albert and Kivu (SNOEKS 1994) is probably relatively well known and it seems unlikely that the number of taxa will considerably increase in the future. However, Lake Edward probably harbours some tens of undescribed haplochromine cichlid species (SNOEKS, pers. obs.) while, for Lake Victoria, perhaps more than a hundred species – some already extinct – still await their scientific description (BAREL et al. 1991). As many as several hundred cichlid species still have to be described from Lake Malawi (LEWIS et al. 1986, TURNER 1994).

In contrast, Lake Tanganyika is generally assumed to have a rather well-known ichthyofauna. Indeed, as far as can be judged at present, the number of new taxa to be discovered and described is probably lower than for lakes Victoria and Malawi. In the last decades, relatively little research effort has been oriented towards the taxonomy of the Tanganyikan fishes. This is probably related to the limited importance of the majority of these species for the local fisheries. This situation is implicitly reflected in most review papers dealing with the cichlids of the African Great Lakes (e.g. GREENWOOD 1984, RIBBINK & ECCLES 1988, RIBBINK 1991) in which data on the taxonomy and distribution of Tanganyikan fishes are relatively scarce. Substantial progress has been made in other domains, viz. ecology and ethology, due to the effort of the Japanese-Zairean team stationed at Uvira (for more information see e.g. YAMAOKA 1991, KAWANABE et al. 1992).

The present knowledge of Tanganyikan fishes is largely the result of the work of G.A. BOULENGER and M. POLL. Before BOULENGER (1898) published his first account of the Tanganyikan cichlids, only four cichlid species were known from the lake (GUNTHER 1893). In

Table 1. Synopsis of the estimated species numbers in the lakes of eastern Africa (after SNOEKS 1994).

	total	non-cichlids	cichlids
Turkana	39	32	7
Albert	44	35	9
Edward	77	17	60
Kivu	26	8	18
Tanganyika	272	72	200
Malawi	544	44	500
Victoria	338	38	300

Table 2. Species numbers of the various tribes of Lake Tanganyika cichlids, reported in the three major scientific contributions. If different, the number of valid species according to current knowledge is given between brackets. The three families with the highest species numbers (grey zones) at the same time comprise most taxonomic difficulties.

	Boulenger 1915	Poll 1956	Poll 1986
Tilapiini	4	5	6
Haplochromini	2	6	8
Tylochromini	1	1	1
Lamprologini	25 (22)	40 (45)	60
Tropheini	8	13	23 (22)
Eretmodini	2	4	4
Ectodini	18 (16)	22 (26)	30
Trematocarini	3	8	8
Bathybatini	7	8	8
Limnochromini	3	9 (10)	13
Cyprichromini	2	3	4
Perissodini	4	8 (7)	8

+ 20

+ 5

+ 1

+ 10

+ 5

+ 5

+

his impressive Catalogue, BOULENGER (1915) had already described 79 nominal species from Lake Tanganyika (Table 2).

Various parts of the lake were intensively sampled during the Belgian Hydrobiological Expedition of 1946–1947 (POLL 1953, 1956), the results of which made a major contribution to our knowledge of the Tanganyikan ichthyofauna. POLL (1956) (re)described an important number of cichlid taxa from these collections and produced a list of 37 genera containing 127 species and 6 subspecies. More recently, POLL (1986) reviewed the information on the taxonomy of Tanganyikan cichlids and proposed a classification of 173 species in 56 genera and 12 tribes (Table 2). Since then, several new nominal species have been discovered, the majority of which have been described in the aquarist literature.

While it is rather easy to compile a simple inventory of the taxa present in Lake Tanganyika, there is a paucity of more detailed information for each of these taxa. Hence, a reliable basis, on which further research into the taxonomy, distribution patterns and speciation of these cichlids can be developed, is lacking.

- Because of the limited number of specimens available, many taxa are described on the basis of only few specimens. Hence, the variation of morphological characters within the species or even within populations is virtually unknown.
- Often no detailed comparative studies have been made between related species and little (if any) type material has been thoroughly examined. Therefore, even for supposedly valid species, one often has to repeat much of the basic taxonomic groundwork.
- Many areas in the lake are not well explored. BRICHARD (1989) estimates that only one third of the shoreline is superficially investigated. Indeed, large areas of the Zaïrean and Tanzanian shorelines still have to be sampled properly. Hence, the distribution patterns of many taxa reported so far should be regarded as very tentative and represent something of a 'puzzle' in which many pieces are missing. In addition, deep water areas are relatively underexplored.
- Differences in colour patterns and morphology have been documented for allopatric populations of a number of species. However, with the available information it is difficult to assess if these different 'colour races' represent specific, subspecific or infrasubspecific taxa (e.g. *Tropheus* spp., *Neolamprologus brichardi*-complex, *Cyprichromis* spp., *Xenotilapia* spp., *Petrochromis* spp., etc.).
- Even for well-known species and well-explored areas, no effort has been made as yet to review the existing collections. Hence, erroneous data on species identifications and distribution patterns continue to be used in the recent literature.

In this paper we will comment upon some of these gaps in the current taxonomic knowledge of Tanganyikan cichlids. Indeed, 90 years after the first large review of Lake Tanganyika's fauna (MOORE, 1903), one can still retain the same title for the present contribution, though applied to a more restricted framework.

New data – The Tanganyika-1992 expedition

Material and methods

The Royal Belgian Institute of Natural Sciences (RBINSc) and the Royal Museum for Central Africa (RMCA) organized an expedition to sample the cichlid fauna of rocky littoral Tanzanian shores for a multidisciplinary taxonomic study. The ichthyology team of this survey comprised THIERRY BRICHARD and two of his fisherman (Fishes of Burundi), AXEL MEYER and CHRISTIAN STURMBAUER (State University of New York at Stony Brook, USA), JOS SNOEKS (RMCA, Tervuren) and ERIK VERHEYEN (RBINSc, Brussels). Some 46 localities along an estimated 450 km of shoreline were sampled over a period of 12 days (Fig. 1).

Since our sampling programme was directed particularly at shallow rocky habitats, most fishes were caught by snorkelling in the littoral zone (0–5 meters) on rocky and mixed rocky-sandy substrate. They were

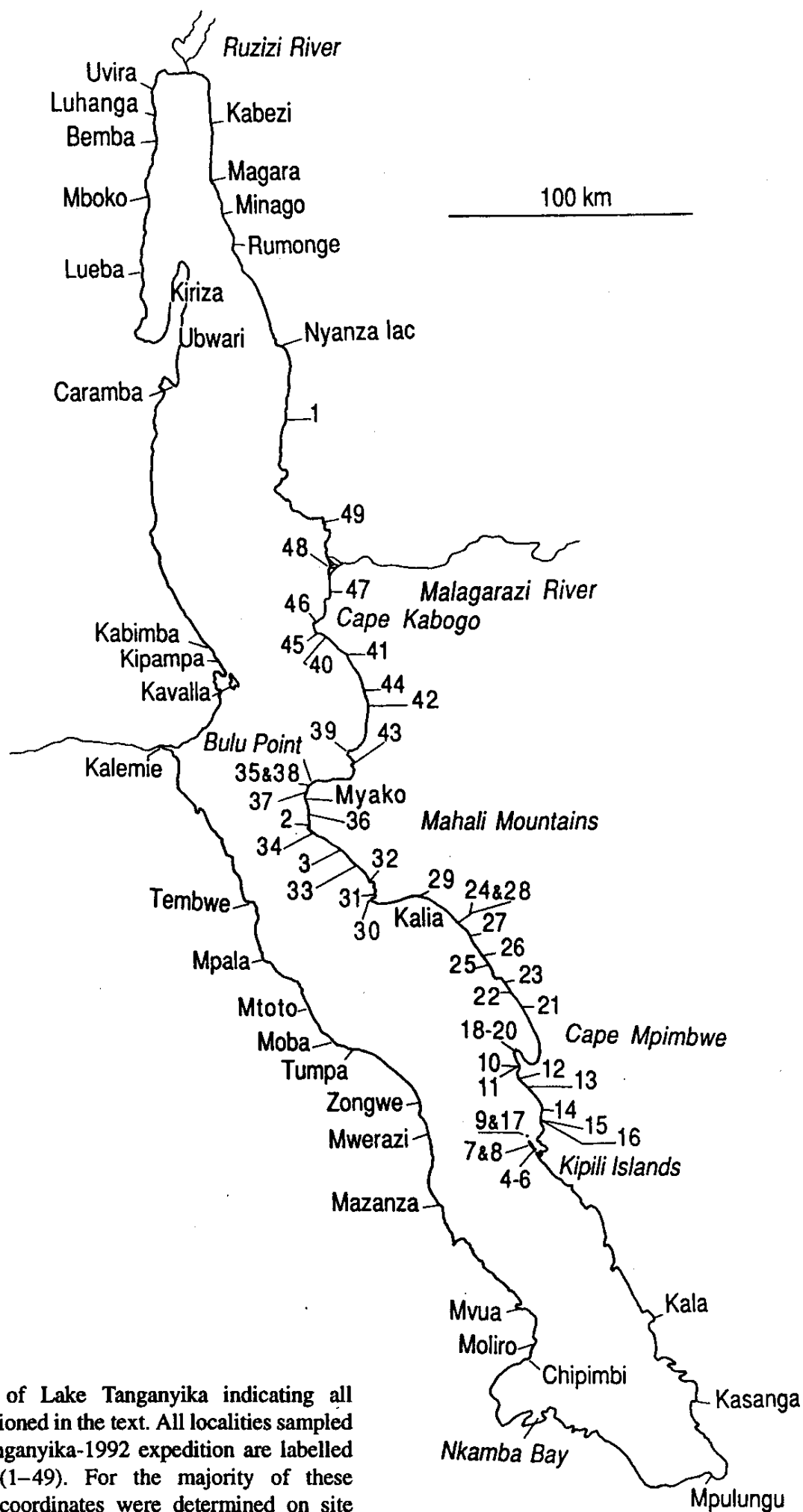


Fig. 1. Map of Lake Tanganyika indicating all localities mentioned in the text. All localities sampled during the Tanganyika-1992 expedition are labelled by numbers (1–49). For the majority of these localities the coordinates were determined on site with a GPS.

chased into small standing nets and then caught by hand. Gill nets were used three times and, on one occasion, fishes were bought from local fishermen.

More than 3000 fishes were preserved for museum-based analyses; 1400 of these are preserved in alcohol allowing tissue samples to be taken for mtDNA analysis and more than 200 photographic slides were made to document the specimens' colour patterns. At present, 88 cichlid and 32 non-cichlid species have been identified from this collection. Part of the gill net catches remains to be analyzed.

As a result of the sampling strategy used, several groups were abundant in our catches whereas others were scarce or absent. The majority of the fishes in the standing net catches were cichlids belonging to the Lamprologini, the Tropheini, the Eretmodini and the Ectodini. Most of the non-cichlid taxa were caught with gill nets; the Ectodini were the best-represented cichlid tribe in these catches. Our collection contains representatives of all cichlid tribes, as defined by POLL (1986), with the exception of the deepwater Trematocarini.

Our study was the first in which such an extensive area of the Tanganyikan littoral zone was the subject of a detailed survey. Consequently, we expected our results to be of importance to particular fields of research, namely the analysis of geographic variation in morphological characters used in traditional taxonomical studies, and the elucidation of distribution patterns along the eastern shoreline of Lake Tanganyika. We will discuss these results for only two groups, (1) the important substratum-brooding group *Lamprologus* sensu lato [= the genera *Altolamprologus* POLL 1986, *Lamprologus* SCHILTHUIS 1891, *Lepidiolamprologus* PELLEGRIN 1904 and *Neolamprologus* COLOMBE & ALLGAYER 1985] and (2) the mouthbrooding genus *Tropheus* BOULENGER, 1898. Other results will be presented elsewhere.

We do not review the distribution of particular taxa in terms of the presence or absence of suitable habitats and ecological niches but rather in terms of broader patterns of geographic distribution that are the results of the geological history of the lake. For information on the micro-distribution and the habitat structure on a rocky shore, see the work of HORI et al. (1983).

Lamprologus sensu lato

Results

During the Tanganyika-1992 expedition, 23 species of *Lamprologus* s.l. were caught, two or three of which possibly represent new species. Only the twenty species caught with the hand-net system (see above) are taken into account for further analysis (see Table 3). We omitted *Neolamprologus furcifer* (BOULENGER, 1898) from our analysis because of its reclusive cave-dwelling lifestyle (KONINGS 1988, BRICHARD 1989). Although it is supposed to have a circumlacustrine distribution we caught it at only two localities. Therefore, we suspect it might also have been present in other localities, where it escaped our collecting efforts. Similarly, the data for *N. tetracanthus* (BOULENGER, 1899), *Lepidiolamprologus attenuatus* (STEINDACHNER, 1909) and *L. elongatus* (BOULENGER, 1898) are not used in this analysis. These species were mainly seen above sandy substrates, which is a habitat that was not intensively sampled. They are reported to have a circumlacustrine distribution (KONINGS 1988) but were only caught at a few localities by our sampling methods.

Although the distribution patterns of the remaining species seem quite complex at first glance, we attempted to group them according to their common patterns (see Table 3).

- Three species [*Lamprologus callipterus* BOULENGER, 1906, *Neolamprologus fasciatus* (BOULENGER, 1898) and *Altolamprologus compressiceps* (BOULENGER, 1898)] are considered to be present along the entire shoreline that was explored, which is in agreement with the existing literature. There is, however, one small anomaly, viz. all three species are absent in our catches from the larger part of the Mahali mountains area. This observation may be of minor importance, but could be relevant in view of the special character of this region for other species as well (see below).
- Five species [*N. christyi* (TREWAVAS & POLL, 1952), *N. cylindricus* STAECK & SEEGER, 1986, *N. moorii* (BOULENGER, 1898), *N. 'cf. leloupi'* and *N. sexfasciatus* (TREWAVAS & POLL, 1952)] were observed only in the southern part of the area explored. For all these

Table 3. Overview of the capture data of the species of *Lamprologus* s.l. along the area explored. Only localities at which specimens of this group were caught using standing nets are listed. cal = *Lamprologus callipterus*; fas = *Neolamprologus fasciatus*; com = *Altolamprologus compressiceps*; chr = *N. christyi*; cyl = *N. cylindricus*; moo = *N. moorii*; lel = *N. 'cf leloupi'*; sex = *N. sexfasciatus*; sav = *N. savoryi*; toa = *N. toae*; lon = *N. longior*; bri = *N. brichardi*; mon = *N. mondabu*; lem = *L. lemairii*; tre = *N. tretocephalus*; mod = *N. modestus*. Numbers refer to the localities (cf. Fig. 1). Stars represent actual catches; the grey pattern connects these localities and represents the presumed area of distribution. (t) = type locality of *N. longior*; (m) represents additional observations from KUWAMURA (1987) at Myako, when relevant.

	c a l	f a s	c o m	c h r	c y l	m o o	l e l	s e x	s a v	t o a	l o n	b r i	m o n	l e m	t r e	m o d
1	**		**							**			**			
49	**		**							**		**	**	**		
47			**						**	**			**			
46	**		**							**	(t)					
40,45	**	**	**							**		**				**
41	**	**														
44	**									**						**
43	**	**	**							**	**			**	**	**
35,37-38	**	**	III						III		III	III		III		**
36															**	**
2,34										**					**	
33																**
31										**					**	**
29	**	**							**							**
24,27		**						**								**
26			**													
23		**													**	**
22			**													
21		**	**													
18-20	**											**	**			
10,11														**		
12			**				**									**
15													**			
9,16-17	**	**			**	**	**	**				**	**			
4-8	**	**	**	**	**	**		**								

species, our capture data represent the northernmost area of distribution ever reported [for *N. moorii* the northernmost on the eastern shore]. Remarkably, for three of these species, this northernmost record is at the same area, Kipili Islands. One possible new species, *N. 'cf. leloupi'* was caught. No information is available concerning the extension of its distribution area towards the south.

- Conversely, three species [*N. savoryi* (POLL, 1949), *N. toae* (POLL, 1949) and *N. longior* (STAECK, 1980)] were only collected in the northern part of the area explored. The capture data for *N. toae* also represent an extension of its known range. We found *N. savoryi* only at two localities. In addition, it was observed by KUWAMURA (1987) at Myako, in between these two localities. According to the literature, this species is supposed to be present all around the lake (KONINGS 1988, BRICHARD 1989), although as far as we know, there are no preserved specimens available or written reports of this species from the area south of Kalia towards Kipili Islands; hence, it is possible that the species is indeed absent from this region. On the other hand, since this species is reported to have a secretive life style (BRICHARD 1989) and generally lives between 10 and 40 m (KONINGS 1988), it might have escaped our catching efforts. *Neolamprologus longior* was found just north of the Mahali mountains. The types are from near Cape Kabogo (STAECK 1980), somewhat more to the north; the species has also been reported from Myako [as *L. leleupi* (KUWAMURA, 1987)] somewhat further south of our capture locality. However, further research is necessary to ascertain whether this taxon is a distinct species or whether it is a geographical colour race of a more widespread species (cf. KONINGS et al. 1993a).
- A fourth group contains three species [*N. brichardi* (POLL, 1974), *N. mondabu* (BOULENGER, 1906) and *Lamprologus lemairii* BOULENGER, 1899] that were found in the northern and southern parts of the lake, but not in between these regions. The gap in distribution includes, for all species, nearly the entire Mahali mountains area and the large bay south up to Cape Mpimbwe. *Neolamprologus brichardi* represents a special case as it belongs to a species-complex of which several possible species and geographical races have been reported (BRICHARD 1989, KONINGS & DIECKHOFF 1992). Therefore, it is possible that the populations of *N. brichardi* that we found actually represent different species.
- In contrast, we found two species [*N. tredocephalus* (BOULENGER, 1899) and *N. modestus* (BOULENGER, 1898)] to be present in the central part of the area explored and not in the northern or the southern parts. Thus, their distributions are mainly based in that area where species of the previous group were not found.

We performed data analyses to cluster the localities according to the presence of shared species. 'Joining' (several linkage methods) and 'k-means clustering' have been performed using the CSS: STATISTICA package 3.1. While the results varied somewhat according to the method used, the Kipili Islands (localities 4–9, 16–17) consistently came out as an isolated group. Moreover, the localities north and south of the Malagarazi delta (1 to 46) clustered together and the localities along the Mahali mountains (36 to 31) formed a third cluster. The clustering of the other localities was not as straightforward. The major tendency was a clustering of most localities of the bay north of the Mahali area (40, 45 to 35, 37–38) with those of the northern part of the bay south of the Mahali area (29 to 23). Most localities of the southern part of the latter bay clustered with those of the neighbouring bay between Cape Mpimbwe and the Kipili Islands (26–15).

Discussion

The data on the distribution patterns can be reviewed in a broader context, taking into account the information already published. The seemingly complex patterns of intralacustrine differences between the local species compositions contrasts with the earlier assumption that

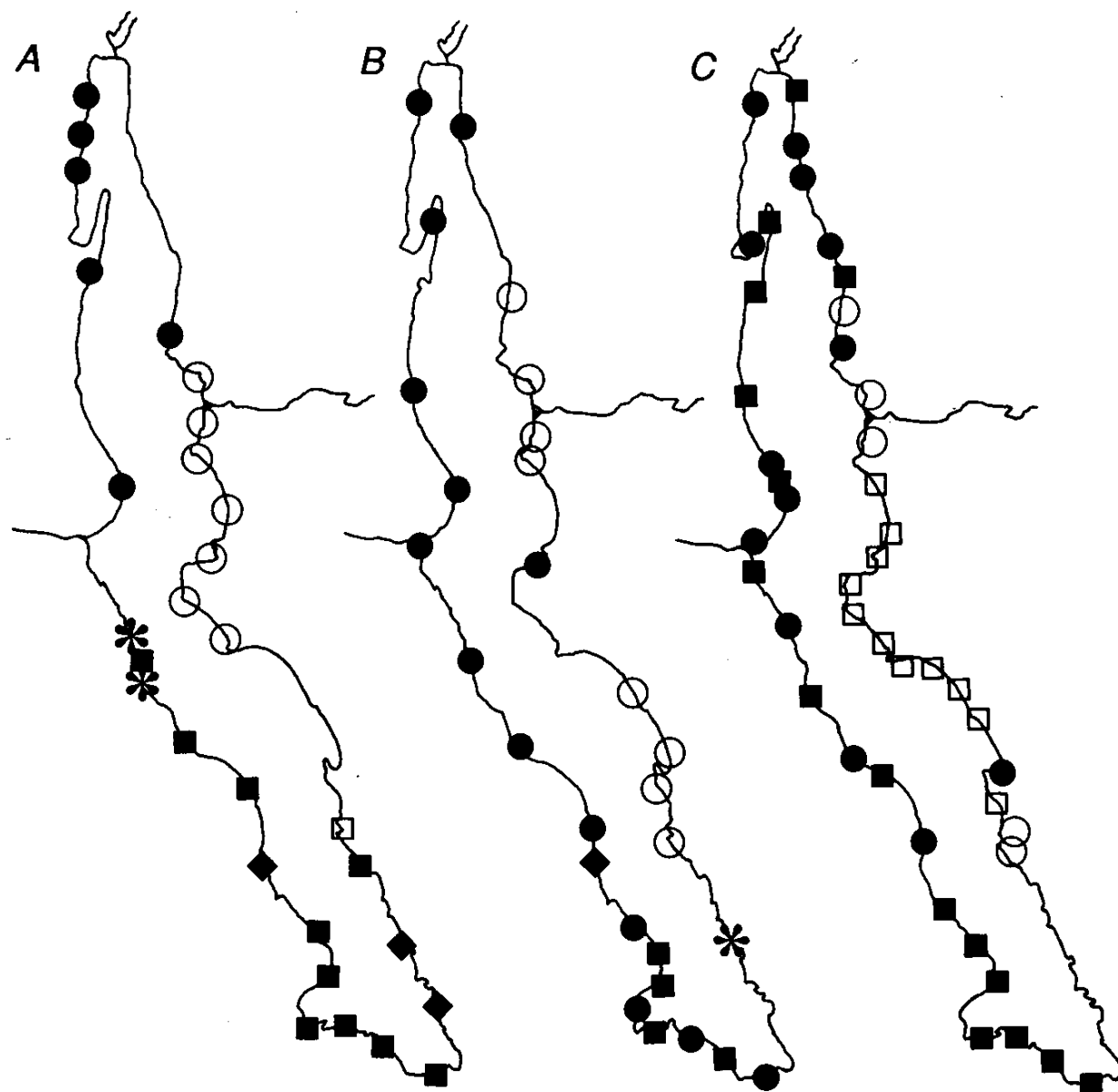


Fig. 2a. Distribution map of *Neolamprologus toae* and *N. moorii*.

- (●) *N. toae*, collections RMCA and RBINSc
- (○) *N. toae*, Tanganyika-1992 collection
- (*) *N. toae*, additional data from KONINGS & DIECKHOFF (1992)
- (■) *N. moorii*, collections RMCA, RBINSc and BMNH
- (□) *N. moorii*, Tanganyika-1992 collection
- (◆) *N. moorii*, additional data from KONINGS & DIECKHOFF (1992)

Fig. 2b. Distribution map of *Altolamprologus compressiceps* and *A. calvus*.

- (●) *A. compressiceps*, collections RMCA and RBINSc
- (○) *A. compressiceps*, Tanganyika-1992 collection
- (*) *A. compressiceps*, additional data from KONINGS & DIECKHOFF (1992)
- (■) *A. calvus*, collections RMCA and RBINSc
- (◆) *A. calvus*, additional data from KONINGS & DIECKHOFF (1992)

Fig. 2c. Distribution map of *Neolamprologus mondabu* and *N. modestus*.

- (●) *N. mondabu*, collections RMCA and RBINSc
- (○) *N. mondabu*, Tanganyika-1992 collection
- (■) *N. modestus*, collections RMCA and RBINSc
- (□) *N. modestus*, Tanganyika-1992 collection

the majority of cichlids are present in all suitable biotopes of the lake (POLL 1950, 1956). However, POLL (1956) has already drawn attention to some north-south distribution patterns of 'species couples' which were at that time reported as subspecies [viz., *Callochromis melanostigma* (BOULENGER, 1906) and *C. macrops* (BOULENGER, 1898), *Lestradea perspicax* POLL, 1943 and *L. stappersi* (POLL, 1943)]. POLL related the distributions of these species to the presence of two separate sub-basins during the lake's geological history. To this list POLL & MATTHES (1962) added *Ophthalmochromis ventralis heterodonta* [= *Ophthalmotilapia heterodonta* (POLL & MATTHES, 1962)] and *Ophthalmochromis ventralis ventralis* [= *Ophthalmotilapia ventralis* (BOULENGER, 1898)]. In 1978, POLL mentioned some 'twin species couples' ("plusieurs couples d'espèces géminées") of *Lamprologus* [*N. leloupi* (POLL, 1948) and *N. caudopunctatus* (POLL, 1978), *N. savoryi* and *N. brichardi*, *A. compressiceps* and *A. calvus* (POLL, 1978), *N. tretocephalus* and *N. sexfasciatus*, *N. modestus* and *N. petricola* (POLL, 1949), *N. hecqui* (BOULENGER, 1899) and *N. meeli* (POLL, 1848)] considering them to have resulted from geographical isolation during the previous existence of separate sub-basins.

The subject of intralacustrine endemism has also been discussed by BRICHARD (1989), who pointed out that this phenomenon is more widespread among substratum-brooders than among mouthbrooders and who listed 84 endemic taxa, indicating their presence in the northern, central and southern parts of the lake. More recently, KONINGS & DIECKHOFF (1992) discussed the distribution of several cichlids in relation to the evolution of the lake. For a better understanding of the events related to the geological history of the lake, we refer to COULTER (1991) and the introductory chapter on Lake Tanganyika of this volume (COULTER 1994).

Below, some examples are given of how the revision of existing collections together with carefully planned additional samples may alter the existing concept of a typical intralacustrine north-south distribution.

- A classical example of this type of distribution is represented by *Neolamprologus toae* and *N. moorii*. The data shown here (Fig. 2a) are based on the collections of the RMCA-Tervuren and the RBINSc-Brussels, including the recent Tanganyika-1992 collection, and supplemented by data from the BMNH-London collection and some relevant data presented by KONINGS & DIECKHOFF (1992).

After analyzing the capture data for *N. tretocephalus* (BOULENGER, 1899) and *N. sexfasciatus* (TREWAVAS & POLL, 1952) from the RMCA-Tervuren and the RBINSc-Brussels collections, we found almost identical distribution patterns for these species; the former is present in the northern part of the lake, the latter in the southern (cf. BRICHARD 1989). However, a recent survey reveals that these species do occur sympatrically at one locality at least between Mazanza and Mvua (BUSCHER, H.H., pers. comm.). This is yet another example indicating that even for well-known cichlid taxa much more sampling will be required to obtain reliable distribution patterns within Lake Tanganyika.

- Interestingly, the distribution patterns of the species couples reported by POLL (1978) are not always as disjunct as in the aforementioned examples. In 1978, POLL described *Altolamprologus calvus*, a species closely related to *A. compressiceps* but morphologically clearly distinct. While *A. compressiceps* has a more or less circumlacustrine distribution, *A. calvus* has been found only in the south-western part of the lake where it lives sympatrically with the former species (Fig. 2b). In addition to the fact that several colour forms exist for both species (KONINGS 1988 and pers. obs.), a possible third, shell-dwelling species of the same genus has been found (KONINGS & DIECKHOFF 1992).
- Finally, we note an example where two species were erroneously suggested to have a complementary north-south distribution, viz. *N. mondabu* (BOULENGER, 1906) in the northern and central part and *N. modestus* (BOULENGER, 1898) in the south (KONINGS 1988, BRICHARD 1989). Re-examination of the collections demonstrated that the geographic

Tables 4a and b. Summary of anal and dorsal spine numbers in all *Tropheus* taxa studied to date (NELISSEN 1979, BRICHARD 1989, own data). The localities are listed from north to south for the western (a) and the eastern (b) coastline. Listed are the three taxa that can unequivocally be identified (*T. duboisi*, *T. polli* and *T. annectens*); the other nominal species names have only been mentioned for the specimens from the type localities (*T. brichardi* from Nyanza Lac, *T. moorii* from Mpulungu and *T. kasabae* from Kasaba Bay). When possible, cheironyms have been attributed to the remaining populations according to the codes given by BRICHARD (1989). As shown for the better studied specimens from the Mahali mountains area (between localities 31 and 36) each locality may harbor more than one *Tropheus* taxon. Other populations remain unnamed until they have been studied in more detail.

Localities along western shoreline			Anal spines (%)							dorsal spines (%)				
North to South	Tropheus taxa	N	4	5	6	7	N	18	19	20	21	22	23	
Uvira	XW 3.30 & MW 3.25	52	0	50	50	0	1	0	0	0	100	0	0	
Bemba	MW 3.35	52	0	100	0	0	4	0	0	0	100	0	0	
	<i>Tropheus duboisi</i>	41	0	98	2	0	41	0	0	0	90	10	0	
Mbokolo	MW 3.45	43	0	100	0	0	43	0	0	0	72	0	0	
Lusaba	MW 4.00	7	0	86	14	0	7	0	0	14	86	0	0	
Kiniza	MUN 4.10	14	0	100	0	0	-	-	-	-	-	-	-	
Ubwari west	MUN 4.10	5	20	80	0	0	15	0	7	7	87	0	0	
Banza	XUS 4.15	6	0	83	17	0	6	0	0	33	50	17	0	
Ubwari east	XUS 4.15 & MUS 4.15	12	0	100	0	0	31	0	0	29	71	0	0	
Ubwari south	XUS 4.15 & MUS 4.15	63	0	16	84	0	-	-	-	-	-	-	-	
Caramba	XUS 4.15 & MUS 4.15	56	0	100	0	0	4	25	0	50	25	0	0	
Kabimba	XW 4.50 & LW 5.30	12	0	8	84	8	17	0	0	29	71	0	0	
Kipampa	XW 4.50 & LW 5.40	76	0	0	100	0	-	-	-	-	-	-	-	
Kavalla	XW 4.50 & LW 5.40	12	0	17	67	17	11	0	0	18	73	9	0	
Kalemie	LW 5.55	70	0	2	96	2	9	0	0	11	89	0	0	
Tembwe	LW 6.45 & LW 7.00	2	0	0	100	0	2	0	0	0	100	0	0	
Mpala	<i>Tropheus annectens</i>	5	100	0	0	0	5	0	0	0	100	0	0	
Mtoto	<i>Tropheus annectens</i>	6	100	0	0	0	6	0	0	50	50	0	0	
Moba	<i>Tropheus annectens</i>	130	100	0	0	0	10	0	0	10	90	0	0	
Tumpa	WW 7.15	1	0	100	0	0	1	0	0	100	0	0	0	
Zongwe	WW 7.15	5	0	100	0	0	14	0	0	78	22	0	0	
Mwerazi	WW 7.25	121	0	100	0	0	1	0	0	0	100	0	0	
Mazanza	WW 7.30	5	0	100	0	0	5	0	0	80	20	0	0	
Mvua	KW 7.55	1	0	0	100	0	1	0	0	0	100	0	0	
Moliro	KW 8.10	10	0	0	100	0	10	0	10	0	90	0	0	
Chipimbi	KW 8.18	6	0	0	83	17	5	0	0	20	60	20	0	
Nkamba bay	KW 8.32 & KS 8.30	59	0	5	90	5	10	0	0	20	60	20	0	
Kasaba Bay	<i>Tropheus kasabae</i>	19	0	4	92	4	8	0	0	25	75	0	0	

Localities along eastern shoreline

Dorsal spines (%)

Anal spines (%)

North to south

Tropheus taxa

N

8

N

19

20

21

22

23

North to south	Tropheus taxa	N	4	5	6	7	8	N	19	20	21	22	23
Kabezi	ME 3.35	6	67	33	0	0	0	6	17	83	0	0	0
Magara	ME 3.35	33	0	100	0	0	0	6	17	33	50	0	0
Minago	ME 3.50	5	0	100	0	0	0	5	0	0	100	0	0
Rumonga	ME 3.55	40	0	100	0	0	0	20	20	65	15	0	0
Nyanza lac	<i>Tropheus brichard</i>	106	0	0	100	0	0	21	0	5	95	0	0
1	BE 4.50	10	0	0	100	0	0	10	0	20	80	0	0
	<i>Tropheus duboisi</i>	1	0	100	0	0	0	1	0	0	100	0	0
49	-	6	0	0	83	17	0	6	0	0	67	33	0
	<i>Tropheus duboisi</i>	2	50	50	0	0	0	2	0	50	50	0	0
47	-	8	0	0	100	0	0	8	0	0	0	100	0
	<i>Tropheus duboisi</i>	5	0	100	0	0	0	5	0	0	100	0	0
46	-	9	0	0	89	11	0	9	0	0	22	67	11
	<i>Tropheus duboisi</i>	3	0	100	0	0	0	3	0	0	100	0	0
45	-	2	0	0	100	0	0	2	0	0	50	50	0
	<i>Tropheus duboisi</i>	1	0	0	100	0	0	1	0	0	100	0	0
40	-	11	0	9	91	0	0	11	0	9	91	0	0
	<i>Tropheus duboisi</i>	4	50	50	0	0	0	4	0	0	75	25	0
41	-	6	0	0	100	0	0	6	0	0	67	33	0
44	-	3	0	0	100	0	0	3	0	0	100	0	0
43	-	3	0	33	67	0	0	3	0	0	100	0	0
	<i>Tropheus duboisi</i>	2	0	50	50	0	0	2	0	0	100	0	0
38	T.'yellow fin'	5	0	0	100	0	0	3	0	33	66	0	0
	<i>Tropheus duboisi</i>	11	0	100	0	0	0	11	0	9	91	0	0
37	T.'yellow fin'	5	0	0	100	0	0	3	0	0	100	0	0
	T.'polli-like'	4	0	100	0	0	0	4	0	25	75	0	0
35	<i>Tropheus polli</i>	1	100	0	0	0	0	1	0	0	100	0	0
36	XE 6.10	7	100	100	0	0	0	7	0	57	43	0	0
	<i>Tropheus polli</i>	1	100	0	0	0	0	1	0	0	100	0	0
2	T.'yellow fin'	11	0	9	91	0	0	11	0	9	73	18	0
	XE 6.10	2	0	100	0	0	0	2	0	0	100	0	0
3	<i>Tropheus polli</i>	1	100	0	0	0	0	1	0	0	100	0	0
	XE 6.10	4	0	100	0	0	0	4	0	25	75	0	0
31	XE 6.10	8	0	75	25	0	0	8	0	25	63	12	0
	T.'belge'	3	0	100	0	0	0	3	0	66	33	0	0
	<i>Tropheus polli</i>	3	100	0	0	0	0	3	0	0	66	33	0
27	-	36	0	89	11	0	0	36	0	26	74	0	0
	<i>Tropheus polli</i>	4	75	25	0	0	0	4	0	0	100	0	0
25+26	XE 6.42	26	0	100	0	0	0	27	0	63	37	0	0
22+23	XE 6.42	11	0	91	9	0	0	11	0	0	36	64	0
21	-	10	0	0	100	0	0	10	0	0	10	90	0
19	XE 7.05	7	0	0	100	0	0	7	0	0	42	29	29
10+11	XE 7.05	16	0	0	75	25	0	15	0	0	40	53	7
12	-	17	0	0	82	18	0	17	0	0	12	88	0
14	-	15	0	0	88	12	0	15	0	0	53	47	0
15+16	XE 7.25	27	0	0	81	19	0	27	0	0	58	44	0
9	XE 7.25	11	0	0	64	36	0	11	0	0	18	73	9
7	XE 7.25	5	0	0	80	20	0	5	0	0	0	100	0
4-6	XE 7.25	16	0	0	31	63	6	16	0	6	31	63	0
Kala	-	6	0	0	100	0	0	6	0	100	0	0	0
Kasanga	XE 8.35	5	0	0	100	0	0	5	0	80	20	0	0
Mpungu	<i>Tropheus moorii</i>	60	0	2	91	7	0	8	0	25	75	0	0

ranges of these taxa are more complex than previously reported (Fig. 2c). We have, for the moment, disregarded the report of HORI (1983) concerning the presence of *L. modestus* at Luhanga, near Uvira (Zaire). His illustration (Fig. 1, p. 130 and Fig. 5, p. 137) clearly depict a profile and emarginate tail which is not characteristic of *N. modestus* but is typical of *N. mondabu*, which had already been found at Luhanga.

The genus *Tropheus*

Results

In contrast to the very species-rich genus group *Lamprologus* s.l. discussed above, the genus *Tropheus* BOULENGER, 1898 comprises only six nominal species [*Tropheus moorii* BOULENGER, 1989; *T. annectens* BOULENGER, 1900; *T. duboisi* MARLIER, 1959; *T. brichardi* NELISSEN & THYS VAN DEN AUDENAERDE, 1975; *T. kasabae* NELISSEN, 1977 and *T. polli* AXELROD, 1977]. The popularity of these species among aquarists has resulted in their presence in thousands of aquaria around the world. In contrast, relatively few specimens were available for taxonomic purposes until recently and only a few geographical areas had been sampled. Consequently, there is virtually no available information concerning intraspecific variation within these taxa.

We have studied the intralacustrine variation for two sets of meristic characters (number of anal and dorsal spines) that are known to demonstrate a considerable degree of variation within this genus (POLL 1956, NELISSEN 1979, BRICHARD 1989). Our results are a combination of the data provided by M. NELISSEN and P. BRICHARD (NELISSEN & THYS VAN DEN AUDENAERDE 1975, NELISSEN 1977, 1979, BRICHARD 1989) and of the results of the investigation of more recent *Tropheus*-collections of the RCMA-Tervuren, including the specimens from the Tanganyika-1992 expedition. Table 4 shows the anal and dorsal spine numbers for respectively 1367 and 628 specimens from 61 localities around Lake Tanganyika. *Tropheus duboisi*, *T. annectens* and *T. polli*, which are readily distinguishable, are listed but excluded from further discussion.

Our data show that there is a great variation in anal and dorsal spine numbers (Table 4a and b). Moreover, the distribution of these characters shows a distinctive pattern. Discrete groupings of *Tropheus* populations can be distinguished according to their spine numbers (particularly anal spines). Groups with the same modal anal spine numbers are, apparently, separated from other such groups with a different modal anal spine numbers by sharp geographic boundaries. The overall pattern that emerges is far more complex than that suggested by NELISSEN (1979). Interestingly, within most groupings, the majority of constituent individuals (> 80%) have the same anal spine number. There are four areas along the eastern shoreline of the lake [(a) Kabezi, (b) locality 43, (c) locality 31, (d) localities 10–11, 9 and 4–6 in the area between Cape Mpimbwe and the Kipili Islands] where two different anal spine numbers occur with more balanced frequencies within the same group. Along the western shoreline a similar situation is found only at two localities (Uvira and Kavalla). We suggest that the presence of a bimodal frequency distribution for anal spine numbers may indicate the presence of more than one *Tropheus* taxon at the localities mentioned above. This suggestion is supported for at least two localities (31 and 36), by additional observations of the colour patterns and morphology of the specimens (Plate 1; unpublished results).

The variation in spine number is much greater in the dorsal than in the anal fin; nevertheless, this character also permits the separation of certain *Tropheus* populations. The anal spine data (Table 4b) as well as the distribution data (Fig. 3a for *T. brichardi* and *T. duboisi*, cf. KONINGS 1993b) suggests that the Malagarazi river might not have been a major geographic barrier.

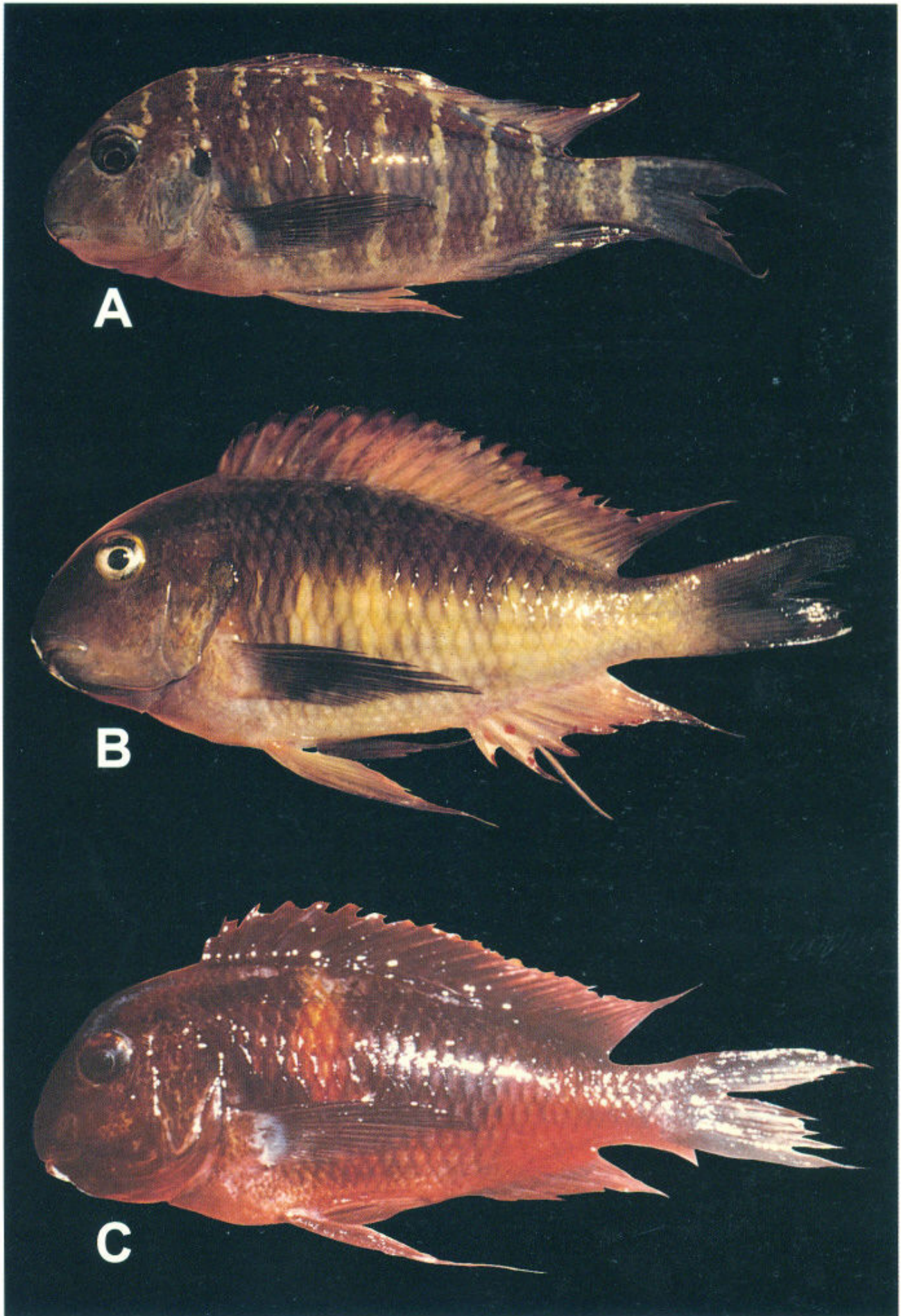


Plate 1. Photograph of the three *Tropheus*-species found at locality 31. In addition to their colour pattern these taxa were shown to be significantly different for six measurements (VERHEYEN, unpubl.). From top to bottom: *T. polli* [4 anal spines (100%)], *T. 'beige'* [5 spines (100%)] and *T. 'XE 6.10'* [= *T. 'kirshfleck'*; 5 spines (75%) and 6 spines (25%)].

Discussion

The last attempt to study geographic variation in the morphology of the putatively circumlacustrine species *T. moorii* was based on only 89 specimens from 13 recorded and a few unrecorded localities (NELISSEN 1979). The specimens originated from the northern part (western shore) and the south-eastern and southern parts of the lake. NELISSEN (1979) demonstrated that the northern and southern populations of what he called *T. moorii moorii* had different anal spine numbers and significant differences in several morphometrics. However, because of the extensive distribution area covered by these two groups, NELISSEN hesitated to describe them as different taxa. Indeed, in view of the fact that the other nominal *Tropheus* taxa were known to have limited distributions, both groups potentially contained several taxa. Therefore, NELISSEN (1979, p. 30) argued that "there is a fair chance that the *T. moorii moorii* with six anal spines represents another taxon than those with five anal spines", and that the number of anal spines is therefore perhaps not as variable as suggested by POLL.

Several useful, recent publications in aquarists' literature report in detail on the distribution of the many, geographically isolated, colour races of *Tropheus* (e.g. well documented in KONINGS 1988, BRICHARD 1989, KONINGS & DIECKHOFF 1992). Although these authors have not always implemented acceptable taxonomical techniques (e.g. synonymy of *T. annectens* and *T. polli* by KONINGS & DIECKHOFF 1992; allocation of a northern *Tropheus* species to *T. moorii moorii* and all the southern *Tropheus* to *T. moorii kasabae* by BRICHARD 1989), they have provided reliable information indicating that *Tropheus moorii* does not have a circumlacustrine distribution (Fig. 3a and Table 4a and b).

This point of view is confirmed by a recent investigation of the distribution of genetic variation within and between populations and species of *Tropheus* (STURMBAUER & MEYER 1992). Divergences among mitochondrial DNA sequences were analyzed using two mitochondrial genes of 54 individuals of 21 localities. The results show that the taxonomy of the genus *Tropheus* is probably complex (Fig. 3b). The authors also concluded that despite the fact that the *Tropheus* populations sampled showed little morphological variation, they are considerably older than the morphologically more diverse cichlids from Lake Victoria and Lake Malawi. There are some conflicts between the mtDNA phylogeny and alternative hypotheses discussed in the recent literature (e.g. BRICHARD 1989, KONINGS & DIECKHOFF 1992, KONINGS 1993b). Hence, STURMBAUER & MEYER's suggestion that the taxonomy of *Tropheus* should be reviewed with molecular data has not been received with much enthusiasm (e.g. KONINGS 1993b). These issues will be the subject of future research.

Interestingly, an overall comparison of the frequencies of the anal and dorsal spine numbers for specimens collected along the Tanganyikan shorelines shows a concordance between the distribution of populations characterized by these meristic characters and (1) the most recent map showing the intralacustrine distribution of the nominal *Tropheus* taxa (Fig. 3a; cf. KONINGS 1993b) and (2) the distribution of mtDNA haplotypes (Fig. 3b; cf. STURMBAUER & MEYER 1992). In virtually all cases, the observed discontinuity of distribution of haplotypes and anal/dorsal spine numbers match along the entire Tanganyikan littoral zone. The only exception is *T. kasabae* which differs in haplotype from *T. moorii* from Mpulungu (type locality) but shows no such differentiation according to the meristic characters considered here. These two meristic characters do not necessarily allow the distinction between all pairs of *Tropheus* taxa; therefore, while the two populations may have the same number of anal and dorsal spines, they can represent separate taxa as indicated by the molecular studies. Unfortunately, only a limited number of localities were sampled for mtDNA data, relative to the number of localities used for meristic characters. Hence, more refined comparisons of the distribution of mt-haplotypes and populations characterized by particular anal and dorsal spine numbers wait until further mtDNA sampling has been conducted.

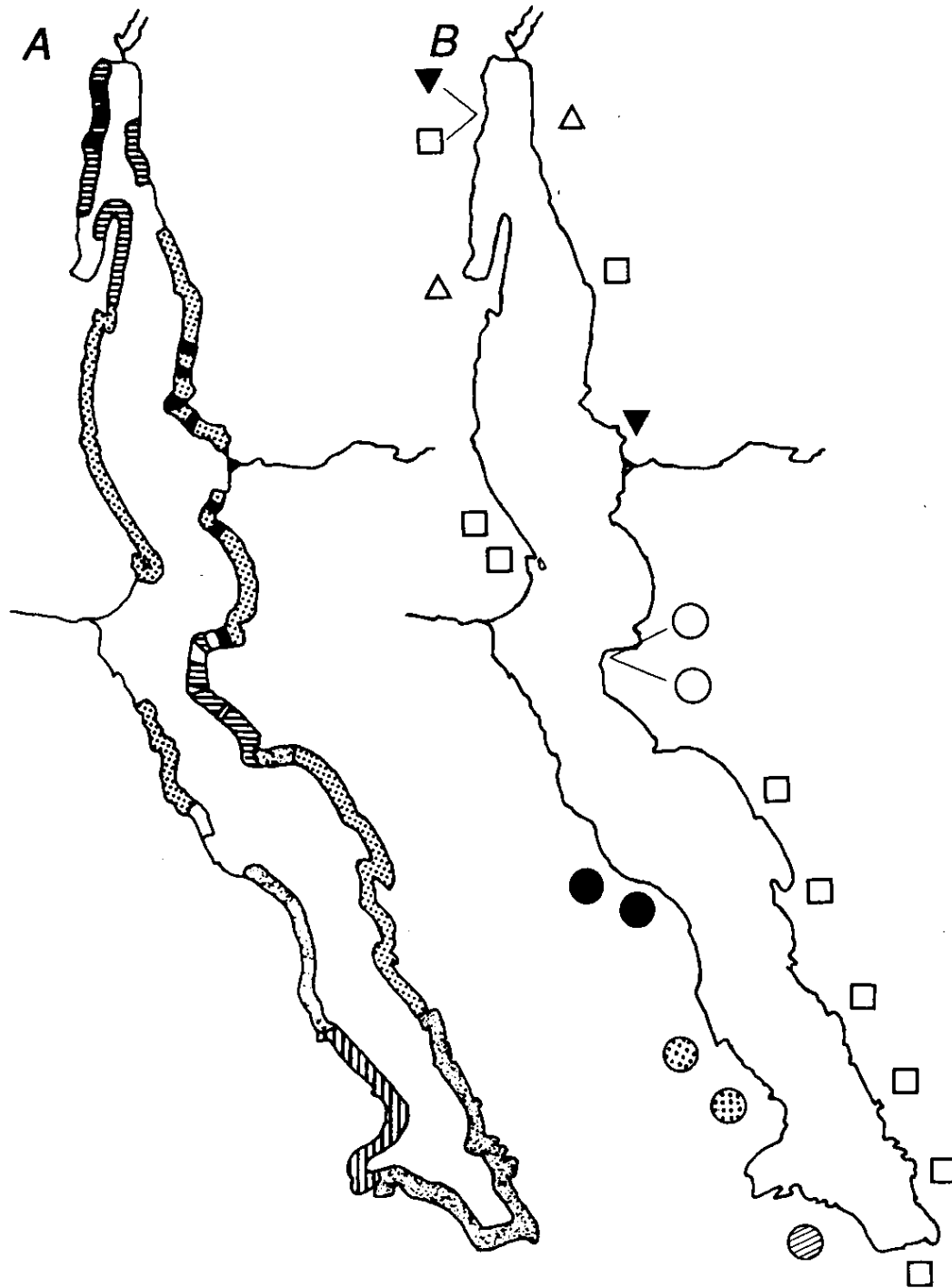


Fig. 3a. Distribution map of the *Tropheus* taxa as considered by KONINGS (1993) (redrawn after KONINGS, 1993).



Fig. 3b. Distribution map of the *Tropheus* taxa studied by STURMBAUER & MEYER (1992) (redrawn after STURMBAUER & MEYER 1992). The symbols represent genetically distinct lineages based upon phylogenetic analyses of mitochondrial DNA sequence data. In all populations from a geographically widespread lineage () only two substitutions were observed in cyt b. Only two sets of sympatric *Tropheus* taxa were studied. In the north western area of Lake Tanganyika *T. duboisi* () is a clearly distinct lineage from the other sympatric *Tropheus* taxon () whereas at the centre of the eastern shoreline *T. polli* and the second sympatric *Tropheus* taxon belong to the same mtDNA-lineage. Remaining symbols refer to other mtDNA lineages (see STURMBAUER & MEYER 1992 for full discussion).

The analysis of spine numbers is too weak a basis for comments on the molecular-based *Tropheus* phylogeny. However, what can be deduced is that the hypothesis that *Tropheus moorii* has no circumlacustrine distribution is now supported by two independent data sets. Moreover, our data also imply that the hypothesis concerning the lack of morphological differentiation between the various *Tropheus* populations is the result of studies based on collections representing *Tropheus* communities from a small number of areas around the lake. Therefore it seems that a successful investigation of the taxonomy of *Tropheus* and other Tanganyikan cichlid taxa will require the study of extensive collections that can only be obtained through a fine-grained sampling program. In addition, it is also clear that the concordance observed between molecular and morphological data suggests that the implementation of molecular data will be useful for the taxonomic revision of the genus *Tropheus* and other Tanganyikan cichlid genera (see STURMBAUER & MEYER 1992).

Conclusion

It is clear that the presence of a well-documented taxonomic account of Lake Tanganyika cichlids is more apparent than real. Indeed, more sound taxonomic knowledge is required before any attempt can be made to explain the biodiversity and intralacustrine distribution of these endemic fishes. The most problematic tribes are those that are most species-rich, such as the Ectodini, the Lamprologini and the Tropheini. Some particular comments on the specific taxonomic and zoogeographic problems of the latter two tribes, representing the Tanganyikan substratum-brooding lineages and one of the mouthbrooding lineages, have been given.

Our study has taken *Lamprologus* s.l. and *Tropheus* as test cases, representing the substratum-brooding and the mouthbrooding lineages of Lake Tanganyika cichlids.

There might be parallels between the patterns of distribution of both mouthbrooding and substratum-brooding taxa (such as the lack of significance of the Malagarazi delta as a geographical barrier and the special character of the Mahali mountains area), but this needs further confirmation.

Our data indicate that: (1) the patterns of the intralacustrine distribution of *Lamprologus* s.l. and *Tropheus* along the Tanzanian shore are more complex than previously assumed. While a few examples of a typical north-south distribution pattern could be confirmed (though somewhat refined) for some species of *Lamprologus* s.l., the patterns of other taxa seem to be much more complex; (2) the Kipili Islands seem to be an important area, acting as the northern limit for the distribution of several lamprologine species; (3) the Malagarazi delta has probably not been a major geographical barrier neither for *Lamprologus* s.l. nor for *Tropheus* (i.e. there is no significant difference between the species compositions north and south of the delta); (4) comparison of morphological and molecular data for *Tropheus* show that both approaches need to be elaborated. Therefore, (5) existing collections need to be reviewed and further analyzed; and (6) more specific 'fine-tuned' sampling is required to ascertain the state of intralacustrine endemism of cichlid taxa in Lake Tanganyika. All such biogeographic information is clearly important for a more comprehensive study of speciation processes in a geographical context.

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Authors' addresses:

J. SNOEKS, Royal Museum for Central Africa, Leuvensesteenweg 13, B-3080 Tervuren, Belgium.

L. RÜBER, Zoological Museum of the University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.

E. VERHEYEN, Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1040 Brussels, Belgium.