Tropheus Evolution In Tanganyika Lake

by Robert Toman

General characteristics of the lake and the Tropheus genus

African lakes have produced striking variation in cichlid fish fauna. Lake Tanganyika, whose age is estimated at 9 to 12,000,000 years, is the oldest East African lake and hides morphologically, genetically and behaviorally diverse group cichlid fish. Many of the more than 200 described species is divided into geographically and genetically distinct populations that differ primarily in their coloring. The best example of this phenomenon is endemic genus Tropheus in which it has been described six species and more than 70 different colored local variants. Besides Tropheus duboisi, the overall morphology of this genus is very similar. Tropheus are abundant at the upper coastal zone in all types of rocky habitats where they feed on algae and hide from predators. They strictly avoid sandy and muddy coasts and estuaries. There is evidence that Tropheus are unable to move at long distances, especially over open water, as a result of their strong environmental specificity and fidelity to a particular place and territoriality.

Tropheus are one of the most studied genera of the lake. Ethological studies of Tropheus moori showed complex patterns of behavior and a highly developed social organization. There is not strong sexual dimorphism. Both sexes protect the territory and unlike many other mouthbrooders, Tropheus make temporary pairs during the breeding. Development of eggs and fry takes place only in the female's mouth. Previous phylogeographic studies of Tropheus demonstrated surprisingly large genetic differences between populations. Tropheus duboisi was described as the most original form and 7 different groups came mostly at the same time. Six of them are found in individual coastal areas and one group spread secondary and colonized the rocky sites basically around the lake. Data obtained by analysis of mitochondrial DNA (mtDNA) showed that despite a generally similar morphology, the coloration of fish can be vastly different between genetically closely related populations and vice versa, can be very similar between genetically very distant populations of sister species. These observations are partly explained as a result of parallel evolution of similar color patterns in natural selection or as a result of spatial contact between two genetically distinct populations after secondary contact and subsequent classification of the genus, when the hybrids of these populations and their progeny preferably back crossed only with members of one of the original population.

Historical changes in lake

It is assumed that the rapid formation of large groups of species of East African cichlid is caused by abiotic (physical) factors such as geological processes and climatic events, and biological properties of spreading organisms. Several studies have shown that large fluctuations in lake levels have a serious impact on the rocky environment and species communities in the East African Rift lakes. The lake has been seriously affected by the dry climate from about 1.1 million years, causing a decrease in the level of about 650 to 700 m below current levels. Then the lake dimension gradually increased in the period from about 550,000 years ago. The next level decrease about 360 meters was from about 390,000 to 360,000 years ago, to about 350 m between 290,000 to 260,000 years ago and between

190,000 to 170,000 years ago it was a drop of 250 m. In the nearest history the level decreased during the late Pleistocene of Ice Age, when it was dry climate in Africa. It is a term of 40-35,000 years ago (down by 160 m) and between 23 to 18,000 years ago (probably about 600 m). Any increase in the water level shifts coastline and form a new rocky areas. Once the distance between the newly shaped areas exceeded the ability of the species spreading, gene flow is interrupted and genetic differences between populations accumulate. The subsequent drop in water level can lead to secondary mixing, resulting either in increasing the genetic diversity or relatedness of new species.

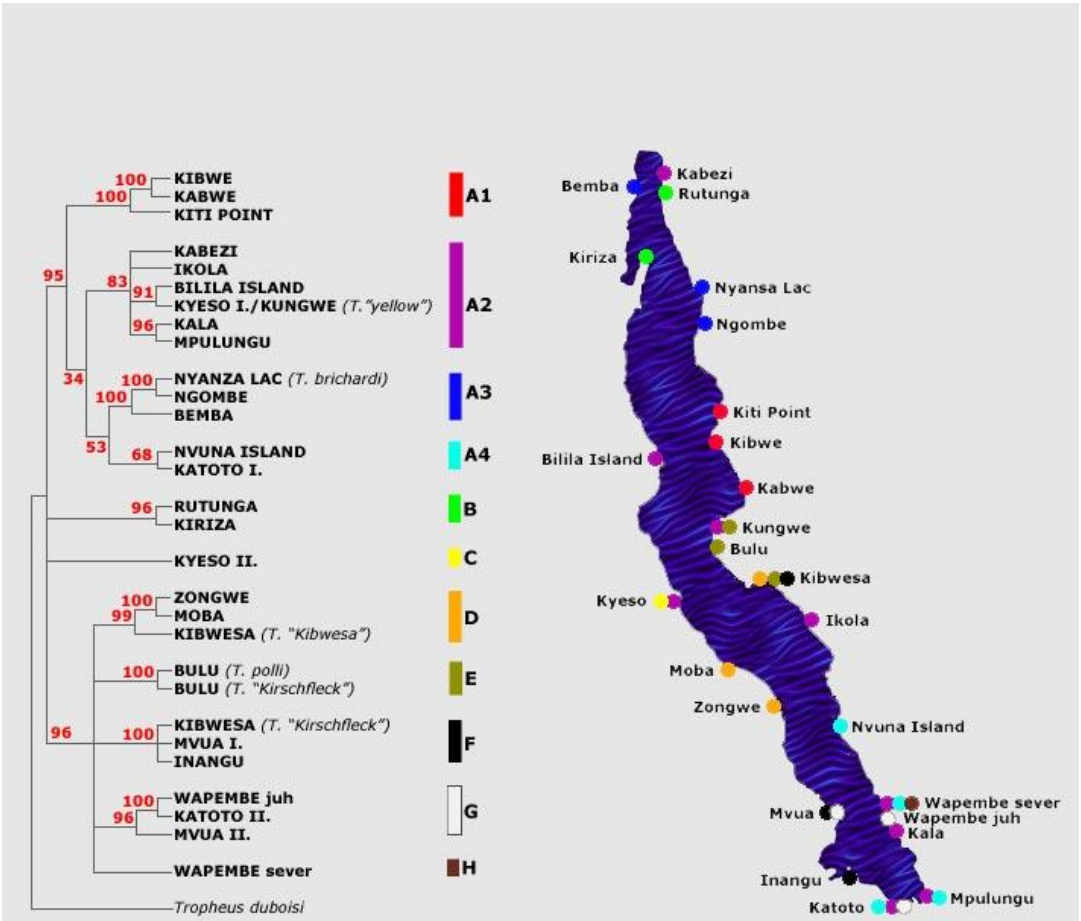
Dissemination of the Tropheus genus in Lake Tanganyika

Based on genetic analysis three periods of Tropheus spreading in the lake were identified. The first period took place during the sea level increase between 1.1 million - 550,000 years ago, the second spreading took place during the level drop between 390,000 to 360,000 years ago and third spreading occurred during the level drop between 190,000 to 170,000 years ago. Climate change from 17,000 years ago caused a dramatic decrease in the levels not only in Tanganyika, but also in Malawi and even drying of Lake Victoria. These events synchronize the diversification of cichlids in all three lakes. Most trusted explanation of Tropheus genetic patterns are 3 periods of low lake levels, when levels fell by at least 550 m, so the lake was divided into three lakes. Tropheus groups were divided into 8 main groups according to mtDNA and by occurrence in various localities of the lake, which was named by settlements on the coast:

Group A1 (Kibwe, Kabwe, Kiti Point)
Group A2 (Kabezi, Ikola, Bilila Island, Kyeso I./Kungwe - T. "yellow", Kala, Mpulungu)
Group A3 (Nyanza Lac - *T. brichardi*, Ngombe, Bemba)
Group A4 (Nvuna Island, Katoto I.)
Group B (Rutunga, Kiriza)
Group C (Kyeso II.)
Group D (Zongwe, Moba, Kibwesa - T. "Kibwesa")
Group E (Bulu - *T. polli*, Bulu - T. "Kirschfleck")
Group F (Kibwesa - T. "Kirschfleck", Mvua I., Inangu)
Group G (Wapembe south, Katoto II., Mvua II.)
Group H (Wapembe north)

Primary spread of Tropheus genus was subjected to a strong increase in the level of the lake from about 700,000 years ago. The first two groups (A and B) came from the northern parts of the lake, group C and D originated on the west coast of the central part of the lake, and group E was developed in the east of central part of the lake. Groups F, G and H are most likely to become established in the south of the lake. It should be noted that recently discovered eighth group C in Kyeso probably represents Tropheus annectens, because Kyeso is located in close proximity to the type of fish samples, which described Boulenger in 1990. These fish lived in the vicinity of fish belonging to group A2, which appeared on both sides of the central part of the lake.

The figure shows the relationships between different groups of the Tropheus genus and their location in the lake.



Príbuznosť skupín rodu Tropheus v jednotlivých lokalitách s označením lokality na mape jazera Tanganika. Čísla na diagrame vľavo označujú príbuzenský vzťah medzi formami (prípadne druhmi) rodu Tropheus v jednotlivých lokalitách. Čím vyššie číslo, tým užší príbuzenský vzťah, ktorý bol zistený na základe mitochondriálnej DNA izolovanej zo svaloviny rýb. Na porovnanie je uvedený aj druh Tropheus duboisi, ktorý je úplne odlišný druh.

Primary spread of Tropheus genus was subjected to a strong increase in the level of the lake from about 700,000 years ago. The first two groups (A and B) came from the northern parts of the lake, group C and D originated on the west coast of the central part of the lake, and group E was developed in the east of central part of the lake. Groups F, G and H are most likely to become established in the south of the lake. It should be noted that recently discovered eighth group C in Kyeso probably represents Tropheus annectens, because Kyeso is located in close proximity to the type of fish samples, which described Boulenger in 1990. These fish lived in the vicinity of fish belonging to group A2, which appeared on both sides of the central part of the lake.

Morphological analysis showed that 6 out of 7 subjects had 4 rays in the anal fin and seventh individual had five rays. A further five individuals caught in the Kyeso had six anal rays and also differed in shape of the mouth and coloration from T. annectens. Interestingly, the fish caught in Kyeso area previously identified as T. annectens, belong to group C, unlike Tropheus polli (group E) from the opposite side of the lake, although they have similar morphology, the number of anal fin rays and coloration.

Most major groups had expanded into neighboring areas during the second expansion to about 400,000 years ago, and groups A and D move to the opposite coast of the central part of Lake Tanganyika. During this period, after the occupation of the east coast, group A was divided into 4 distinct subgroups. Subgroups A1 and A3 are likely to appear after expansion to the north of the east coast. Subgroup A2 was coming from the northwest coast settlement of northern and central part of the lake, while the subgroup A4 probably came from the colonization of the eastern part of the south coast. Group D likely cast a very short section in the Cape Kibwesa, when moved from the western part of the south coast. This was possible only in the period before 400,000 years ago, when the levels decreased of 550 m, because Tropheus are not able to move through open water when the water level increases and thus the distances widened between the rocky parts of the lake. Only a drop of 550 m level is sufficient to get the rocky bottom to a depth of about 50 m. This created conditions for the Tropheus transfer.

Spreading T. "Kirschfleck" belonging to the group F on the east coast of the central part of the lake and north of Kibwesa seems to be obscure by the present spread of the other members of this group (F) in the southwest around Cameron Bay. In the Kibwesa live three variants of Tropheus (Tropheus polli, T. "Kibwesa" and T. "Kirschfleck"). However, in samples of T. "Kirschfleck" it has been revealed by mtDNA that those individuals belong to two groups, suggesting a crossbreeding probably between the original inhabitants of this area - the group T. polli (E) and moved in T. "Kirschfleck" (F). There are two alternatives: the representatives of the group F were able to move along the western coast to the southern border of the middle of the lake. It remains unclear how the group F could move over a wide area and steeply descending coast on the west side of the southern coast, which is currently inhabited by fish of group D, without leaving any genetic trace or small population. Alternative explanation could be that the group F was originally spread along the southeastern coast of Kibwesa about the Wapembe and later was replaced coming representatives of groups A, so haplotypes (a group of alleles in one chromosome is transmitted from generation to generation together while the child inherits two haplotypes - one from father and one from the mother) of group F in Kibwesa are the remains of the originally much more widespread group. Furthermore, it could be added to this hypothesis that the sub-group F inhabited their present territory near Cameron Bay in the southwest during the main period of lake level rising 400,000 years ago. This would explain the presence of two different haplotypes in the population in Mvua (F and G), as a result of crossing after the secondary contact with representatives of the group F. If this hypothesis is true, this colonization may completely replace the previously occurring group G, which is now centered on the south of the Lufubu estuary. Taking into account the fact that the river Lufubu as the third largest source of water for the lake, is a highly stable ecological barrier that separates the coast of the Chaitika mountains from the Inangu peninsula, then the group G was able to maintain their original area south from the river Lufubu, but was replaced by representatives of the group F in Cameron Bay after declining the water level.

During the third spread around 200,000 years ago, three sub-groups of the group A spread along the coast, where they originally occurred. Subgroup A2 had to move across the lake from the southern edge of the central part to the east coast of the southern part of the lake. Subgroups A2 and A4 were spread along the southeastern coast to the south. In Wapembe on the north, a haplotype was found in one individual which suggest it belongs to a group H, which spread at the primary distribution and all other individuals belong into two A-subgroups. Two distinct Tropheus live in a close relation near Wapembe. In Katoto, the main boundary between groups A and G, about 50% of the population with haplotypes of group G

and 50% of subgroup A2 and A4 was found. Subgroup A2 was found in Katukula site, but the population is made up of mostly fish from the group G.

Summary

Tropheus of 7 groups did not change dramatically the range of their occurrence what may be due to the stability of their environment, which is formed vertically descending coast. These areas were not much affected by fluctuations in lake level, because they only moved downwards and upwards along the cliffs. One subgroup (A2) is found almost all over the lake and also individuals from distant populations are closely related. As similar characteristics and extensions of other genera of Tanganyika cichlids (Eretmodus, Cyprichromis) were revealed, probably the changes in the lake (climate and geology) had also a similar effect on the genetic structure of populations of other species.

Literature

Baric, S. et al.: Phylogeography and evolution of the Tanganyikan cichlid genus Tropheus based upon mitochondrial DNA saquences. *J. Mol. Evol.*, 56, 2003, 54-68.
Cohen, A.S., Soreghan, M.R., Scholz, C.A.: Estimanting the age of formation of lakes: An example from Lake Tanganyika, East African Rift System. *Geology*, 21, 1993, 511-514.
Cohen, A.S. et al.: New palaeogeographic and lake-level reconstructions of Lake Tanganyika: Implications for tectonic climatic and biological evolution in a rift lake. *Basin Res.*, 9, 1997, 107-132.
Gasse, F. et al.: Water level fluctuations of Lake Tanganyika in phase with oceanic changes during the last glaciation and deglaciation. *Nature*, 342, 1989, 57-59.
Sturmbauer, C.: Explosive speciation in cichlid fishes of the African Great Lakes: A dynamic model of adaptive radiation. *J. Fish Biol.*, 53, 1998, 18-36.
Sturmbauer, C., Meyer, A.: Genetic divergence, speciation and morphological stasis in a lineage of African cichlid fishes. *Nature*, 358, 1992, 578-581.
Sturmbauer, C. et al.: Lake level fluctuation synchronize genetic divergences of cichlid fishes in African lakes. *Mol. Biol. Evol.*, 18, 2001, 144-154.