

Natural hybridization in tilapias

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Introduction

Tilapia species are well known for their ability to hybridize in captivity, and a large number of crosses have been carried out. Quite often, the F1 are viable but the sex ratio of the descendants is unbalanced. For example, the crossing of a female *Tilapia tholloni* and a male *Oreochromis mossambicus* yields 100% females where the crossing of a female *O. spihurus* and a male *O. leucostictus* yields 98% males. Sometimes the F1 are sterile but they can also be equally fertile. Under natural conditions there are numerous cases of hybridization. However, these hybridizations are not always easily observed and proven. Since the development of genetic techniques, the characterization of tilapia species has not ceased to advance and it is easier today to prove the existence of natural tilapia hybrids.

These natural tilapia hybrids can be classified in three categories: those following species' introduction, those following manmade perturbations of the environment and those which are truly natural. This classification is no doubt purely artificial because the mechanisms occurring during hybridization are probably always the same. One or two factors leads to the rupture of the ethological

barriers between species (when they existed), then competition phenomena between the parent species and their hybrids help the situation to evolve, often, but not always in favor of one of the forms of the parental species.

Hybridization following species' introduction

The majority of wild hybridization cases reported belong to this first category. In certain cases an introduced species hybridizes with a local species, in others, two introduced species hybridize in a new environment.

In Lake Naivasha, *O. spilurus nigra* and *O. leucostictus* were probably introduced in the 1950's. In the beginning of the 1960's, many hybrids were observed with meristic and anatomic characteristics somewhere between those of the parent species. In the 1970's, a few rare hybrids were observed (SIDDIQUI, 1977, 1979) and *O. spilurus nigra* seemed to have disappeared from the lake.

In Lake Bunyoni in Uganda, *O. niloticus* was introduced in 1927 from Lake Edward, *O. spilurus nigra* in 1932 from Lake Naivasha. In 1937 hybrids between the two species were harvested and from 1947 onwards, *O. spilurus nigra* as a pure species had disappeared (LOWE, 1958).

In Lake Naivasha in Kenya, *O. spilurus nigra* was introduced in 1925 and later *O. leucostictus* was also introduced (ELDER *et al.*, 1971). In 1959, the first hybrids between the two species were harvested. In 1972, *O. spilurus* have disappeared from the lake (SIDDIQUI, 1979).

In Lake Itasy, in Madagascar, *O. macrochir* was introduced in 1958 and *O. niloticus* in 1961. In 1965 and 1966 intermediate specimens between these two species were harvested and named 3/4

tilapia (DAGET and MOREAU, 1981). These hybrid individuals had a noticeable pharyngeal bone resembling that of *O. niloticus* but a morphology closer to that of *O. macrochir*. Between 1963 and 1969, the hybrid population in the captures went from 5% to 74%. *O. macrochir* was considered a vanished species in 1971. Finally, the *O. niloticus* became predominant.

On the contrary, in Lake Ihema in Rwanda, *O. macrochir* was introduced near the end of the 1960's, after the introduction of *O. niloticus* in the 1940's. Hybrids were observed in the 1970's. From 1983 to 1987, the proportion of *O. niloticus* decreased from 30 to 20%, that of hybrids increased from 10 to 20 %, the *O. macrochir* population remained stable at 60% (MICHA *et al.*, 1996).

In the 1950's, *O. niloticus* was introduced into Lake Victoria several times (TREWAVAS 1983). The introduction occurred in Uganda with individuals from Lake Edward (BALIRWA, 1992) and numerous stockings took place later. TREWAVAS (1983) believes that even fish from Lake Turkana raised in Uganda were introduced into the lake. During the 1960's, we started to find this species in the fisheries statistics (WELCOMME, 1967; BALIRWA, 1992). WELCOMME (1967), in the mid-1960's described the existence of hybrids between *O. niloticus* and *O. variabilis*. These hybrids were all males. Hybridization with *O. esculentus* were also suspected by other authors. Since then these two species have disappeared from Lake Victoria and *O. niloticus* is suspected of being the cause of these disappearances (WELCOMME, 1967; OGUTU-OHWAYO, 1990). In this particular lake we have begun to compile some genetic data.

Hybridizations following environmental disturbances

Tilapia zillii and *T. guineensis* are two fish species of the subgenus *Coptodon* (THYS VAN DEN AUDENAERDE, 1970) and are genetically very close (POUYAUD and AGNESE, 1995). *Tilapia zillii* and

T. guineensis are present in West African rivers and streams but, while *T. zillii* frequents the upper waters, we find *T. guineensis* in the lower parts of rivers and in the lagoons. Nevertheless, *T. guineensis* is capable of climbing the rivers, sometimes over hundreds of kilometers. Therefore these two species can be considered as sharing a common range. For these two species, we are fortunate to have the genetic analysis of a great many populations: Among the 33 populations studied by POUYAUD (1993), mostly in rivers, no hybrids or gene introgressions were observed in the 25 West African basins studied, except in two places in Côte d'Ivoire. As a result of this work, a more in-depth study was begun (AGNESE and col.) covering the entire territory of Côte d'Ivoire.

Lake Ayamé is an artificial lake built in the 1950's on the Bia river. Observation of captures taken from the lake shows the rarefaction, even the disappearance of two tilapia species: *T. busumana* and *T. discolor*. Another tilapia species, *Sarotherodon melanotheron* was introduced a few years ago. It now represents the largest part of the total biomass harvested. All these phenomena result in a certain number of disturbances which need to be identified and the origins of which can be assumed to be manmade for the most part.

To the samples from the Bia River were added samples from Adzopé, the Aby Lagoon, the Ebrié Lagoon, Bouaké, Lake Kossou, Lake Taabo, Man, Lake Buyo, Lake Dagou, the Valoa River, and from Sassandra (fig. 1).

Concerning Lake Ayamé, the rivers which flow into the lake (including the Bia), are dried up in the dry season (at least in March and April). We must assume that the fish populations of the rivers are temporary and come from individuals from the lake. The situation below the dam is somewhat similar. When the hydroelectric plant does not function for a period of time, the river dries up for several kilometers. Among the loci studied, two are diagnostic loci, which means that the alleles present in one species are all different from those present in the other. These are PGI2 (*T. guineensis* is characterized by allele 100 and *T. zillii* by allele 108) and LDH1 (100 in *T. guineensis* and 250 in *T. zillii*).

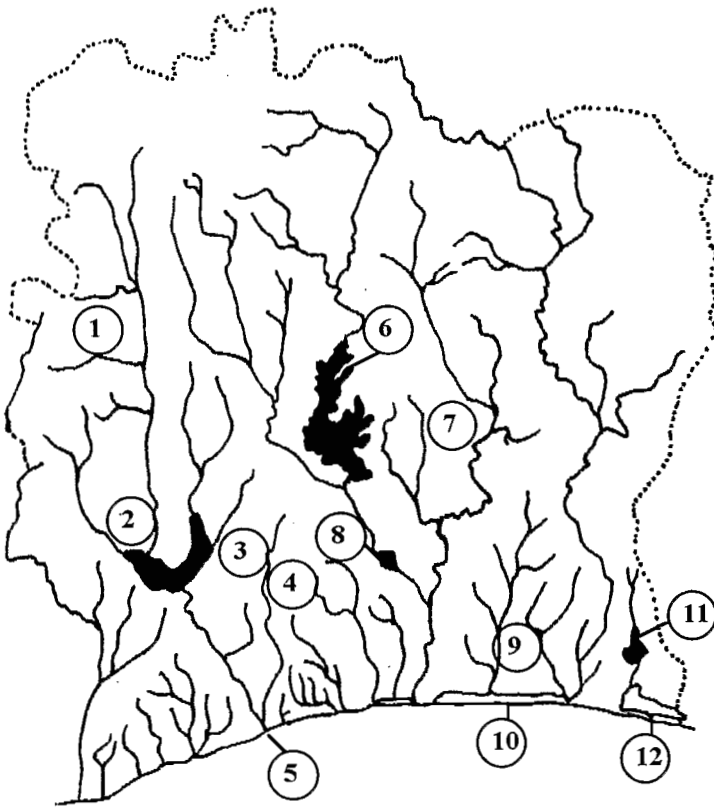


Figure 1
Map showing the collecting sites of tilapias in Côte d'Ivoire : 1, Man, 2, Lake Buyo, 3, Lake Davo, 4, Valoa River, 5, Sassandra River, 6, Lake Kossou, 7, Bouaké, 8, Lake Taabo, 9, Adzopé, 10, Ebrié Lagoon, 11, Lake Ayamé, 12, Aby Lagoon.

For three other loci, we find some alleles only in *T. guineensis*. These are AAT-2 (alleles 50 and 160), ADH (allele 100), and PT1 (allele 70). The samples from Bouaké (7) of *T. zillii* and from Layo (10) of *T. guineensis* were used as controls. We observe the existence of hybrid individuals in all the lake populations with all possible combinations of hybrid genotypes, which seems to indicate that these hybrids are perfectly fertile and have a non-negligible adaptive value. Works are in progress to determine if this observed

structure will remain static or if it will evolve over time. Elsewhere in Côte d'Ivoire other cases of hybridization have been found. In Lake Taabo, of 42 individuals, we found 30 *T. zillii*, 7 *T. guineensis* and 5 hybrids, in Lake Kossou, further upstream, of 130 individuals, 67 were *T. zillii* and 63 were *T. guineensis*, no hybrids were found. In the Sassandra basin, the situation is a little different because *T. zillii* naturally possesses allele PGI 100, only the locus LDH-1 is diagnostic in this basin. If in Man all individuals can be identified as *T. zillii*, in Sassandra, the 9 specimens studied were all *T. guineensis*, confirming the preferential distribution of these two species. In Lake Buyo, we observe a new allele PGI 112 which probably belongs to *T. guineensis* because it is always observed with allele LDH-1 250, typical of this species. Therefore we have 1 *T. zillii*, 24 *T. guineensis* and 30 hybrids. Further South, in Lake Dagou which is a very small lake of a few square kilometers, of the 29 specimens analyzed, we found 5 *T. zillii* 6 whose status is undetermined, 18 hybrids and no *T. guineensis*. In the river a few kilometers below the lake we find 20 *T. zillii*, 9 undetermined, 15 hybrids and no *T. guineensis*. It seems therefore, that in Côte d'Ivoire, the cases of hybridization of *T. zillii* and *T. guineensis* are numerous and closely related to the presence of dams. *T. zillii* is a riverine species and *T. guineensis* is more a lagoon species. The creation of artificial lakes seems to destroy or decrease the ethological barriers between these two species. However, in the largest lake in Côte d'Ivoire, Lake Kossou, these two species do not hybridize, which implies that the mere presence of a dam is not enough to explain this hybridization.

■ Natural hybridizations

In this last case, hybridization did not occur between two species but between three species: *Tilapia zillii*, *T. guineensis* and *T. dageti* (POUYAUD, 1993). *T. zillii* is found throughout the Comoé basin while *T. dageti* is limited to the regions above the Koroboué Falls

and *T. guineensis* to the regions below, the falls acting as the barrier between these two species.

In order to genetically characterize each species, 21 *T. guineensis* from Ebrié Lagoon, as well as 27 *T. zillii* and 22 *T. dageti* from the Abengourou region were analyzed. Among the 23 loci studied, 3 were shown to be diagnostic. *T. guineensis* individuals were characterized by alleles LDH-1 (100), LDH-3 (100) and GPI-2 (100), *T. zillii* individuals were characterized by alleles LDH-1 (250), LDH-3 (100) and GPI-2 (108) and *T. dageti* individuals were characterized by alleles LDH-1 (110), LDH-3 (95) and GPI-2 (112).

Among the 49 individuals which have been analysed below the Koroboué Falls, 24 possessed alleles characteristic of *T. guineensis*, 5 of *T. zillii* and 13 of *T. dageti*. The 7 remaining specimens possessed a combination of the different diagnostic alleles: 4 could be considered as hybrids between *T. guineensis* and *T. dageti*, 2 between *T. dageti* and *T. zillii* and 1 possessed alleles from the three species. After localization of each captured specimen, it was possible to observe the progressive disappearance of the alleles characteristic of *T. dageti* beginning with the second sector below the falls. Therefore these falls truly do play the role of barriers keeping fish from climbing the river. For the moment, the hypothesis retained is of a historical-biogeographical type. *T. guineensis* and *T. dageti* are two very close species, most likely sister species coming from a common ancestral species (POUYAUD and AGNESE, 1995). Other than the fact that the ethological barriers are not well established, it seems that the two species are mutually exclusive in a basin where they may be in cohabitation. *T. dageti* would have colonized the Comoé River from the upper basin thanks to contact with the Volta where *T. guineensis* would have colonized the Comoé from the mouth because it is a species more often found in lagoons. From the river mouth *T. guineensis* would have colonized upriver, stopping at the impassable falls at Koroboué. There, a hybridization phenomenon occurred with individuals of the species *T. zillii*. Of course, this study is only preliminary. More work will be necessary to confirm this hypothesis and so that we can better understand the mechanisms that are engaged during this hybridization.

Conclusions

The numerous hybridizations observed in tilapias show just how unfinished the phenomenon of speciation is in this group. In certain cases, the barriers between species are purely ethological, such as those between *T. zillii* and *T. guineensis*. Therefore species' integrity is only maintained in places where they are the only ones to fill a certain ecological niche, lagoons for *T. guineensis* and rivers for *T. zillii* for example. If the environment is modified, as in the creation of an artificial lake for example, then these barriers may disappear. However, in the majority of cases there are post-zygotic barriers. If sometimes they are very strong and lead to non-viability of the hybrids, quite often the F1 are viable and in part fertile. In most cases, these hybrids in fact have a lower adaptive value than either of the pure species and these hybridizations usually lead to the disappearance of one of the two pure species and eventually of the hybrids as well. The double experiment of the introduction of *O. niloticus* and *O. mossambicus* in Lakes Itasy in Madagascar and Ihema in Rwanda shows that we cannot predict which species will win the competition. We often also don't know the consequences of the elimination of a species after hybridization with another species. In particular, the vanished species may have left some of its genes in the established species. Such introgression has not yet been established in natural tilapia populations in Africa, certainly because of the low number of genetic studies, but which has been observed in reservoirs in Sri Lanka where the feral *O. niloticus* population has *O. mossambicus* genes (DESILVA and RANASINGHE, 1989). With the development of genetics techniques, the characterization of the tilapia genome is progressing rapidly. Proof of hybridization and introgression is now possible for a great number of natural species and populations.

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