

Hybridization and Speciation among Cichlids: The Case of 'Wesafu', an Ecotype Cichlid

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Abstract: Fishes of the family cichlidae are known for spectacular adaptive radiation and therefore serve as a model for evolutionary and ecological studies. They are highly speciated due to hybridization that frequently occur in the wild. The existence of an ecotype cichlid, 'wesafu' in Epe lagoon, Lagos, Nigeria appears to be the result of such hybridization. This paper reviews the profile of wesafu and compare the species with other cichlids, evaluate the probable causes of speciation which includes diversity in feeding morphology, mate choice, adaptation to changes in habitat arising from water level dynamics, eco-phenotypic variation, restricted migration to predation and introgressive hybridization. The implication of such speciation and hybridization were also highlighted.

Key Words: Speciation, Hybridization, Cichlids, wesafu.

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I. Introduction

A cichlid (pronounced sick-lid) is a fish in the family cichlidae family of fishes of almost unbelievable diversity. They differ greatly in size and taxonomic group (Olojo *et al*, 2003). Tilapias are members of this diverse fish family and serve as important components of subsistence fisheries for thousands of years but have gained prominence in recent years in areas where they are not endemic (Modadugu and Bellen, 2008). Fitzsimons (2007) reported that tilapia have become the second most important fish produced in Aquaculture. This show how significant tilapia is to the world fisheries.

Essentially there are three genera in this family, based on reproductive behaviour. They are; *Oreochromis*, *Sarotherodon* and *Tilapia*. *Oreochromis* species are maternal mouthbrooders, *Sarotherodon* species are bi-parental mouthbrooder while *Tilapia* species are substrate spawners (Christian, 2002). The *Tilapia* natural genetic resources are restricted to Africa but the culture industry is predominant in Asia. Compared to many other fish families that remained unchanged for millions of years, cichlids are highly speciated due to hybridization that frequently occurs in the wild (Barlow, 2000).

II. Evolution of African Cichlid Fishes

The natural distribution patterns of tilapia are the result of evolution (Kocher, 2005). Fishes of the family have long been known for their spectacular adaptive radiation and phenotypic plasticity, and have therefore served as a model for evolutionary and ecological studies (Barlow, 2000). In the lakes of East Africa (lakes Victoria, Malawi and Tanganyika), fishes of the family, cichlidae have undergone an extraordinary rapid and extensive radiation (Kocher, 1991). At least 1500 species of fish have arisen from a common ancestor in the last 10 million years (Kocher, 2005). The author maintained that within Lake Malawi over 700 species have arisen within just two million years. It becomes necessary to elucidate the forces which have caused this rapid speciation. A number of forces are at work which includes trophic specialization and sexual selection. We suspect that rapid evolution of male traits and female preference contributes to pre-mating isolating mechanism among local population, facilitating speciation over small spatial scales (Kocher, 2004). It becomes necessary therefore to carry out gene mapping for phenotypic traits associated with speciation, such as jaw morphology and adult colour pattern. This will enable scientists to identify the genes responsible for speciation of these fishes, and to study the geographic distribution of allelic variants among populations and species in the wild, (Kocher, 2005).

Models of ecological speciation would suggest that functional divergence in feeding morphology has contributed to the origin and maintenance of cichlid species diversity (Kocher, 2006). The author estimated the effective number of genetic factors controlling differences in the cichlid head through a comprehensive morphological assessment of two Lake Malawi cichlid species and their F1 and F2 hybrid progenies. A difference in tooth shape (bicuspid vs tricuspid) appears to be controlled by a single major gene. When he went

to identify DNA markers linked to these genetic factors, several chromosomal regions contain a disproportionate number of quantitative trait loci (QTL) indicating a prominent role for genetic linkage in the divergence of this character complex. The result of this implies that the rapid and replicative nature of cichlid trophic evolution is the result of directional selection on chromosomal packages that encode functionally linked aspects of the craniofacial skeleton. Until recently, little attention was paid to riverine species that exhibit pan-African and West African distribution (Yohey *et al.*, 2006). Recent studies have focused on Pan African and West Africa species through the use of nuclear markers (Streelma and Karl, 1998). Such markers evolve more slowly than mitochondrial DNA, which have been employed extensively in previous phylogenetic analyses of East African cichlids. Another topic of interest is whether the evolution of pan and West African cichlids was accompanied by incomplete lineage sorting and/or inter-specific hybridization, which appears to have occurred multiple times during the evolution of cichlids in the Africa Great lakes (Takahashi *et al.*, 2001). Under what circumstance could the speciation of the ancestral lineages of tilapia have accompanied incomplete linear sorting? Lineage sorting tends to be incomplete when successive speciation events occur rapidly (Takahata, 1989). All previous examples of incomplete lineage sorting in cichlids (Open *et al.*, 2000, Takahaskie *et al.*, 2001) occurred in the African great lakes which are known to exhibit explosive rate of speciation.

III. Speciation Among Tilapias

A species is never stable in nature. It may die out or spread to from another species (Ayinla and Williams, 2005). The author maintained that in taxonomy, species with a very restricted distribution are considered “young” species, and those with wide distribution are considered “old”. According to the author, once a species has a very wide distribution it may fall apart. This happens frequently with fish species when water bodies become mutually isolated and the separated populations change through new mutations and genetic flux. The natural distribution of pattern of tilapia suggests such a situation. Evolution of new strains of the cichlids is making identification difficult. Morphological characters (Meyer *et al.*, 1990) and molecular studies (Kocher *et al.*, 1993) were reported to have failed in resolving some relationship in the cichlid within the last two decades.

The pattern of speciation in *Oreochromis*, *Sarotherodon* and *Tilapia* leads to the conclusion that it has occurred in two ways:

- (i) by ecological diversification in one area (sympatric)
- (ii) by geographical isolation (allopatric).

Sympatric species tend to differ in diet and the associated pharyngeal jaw morphology (Mckaye *et al.*, 2002). Ecological factors play significant role in speciation (Schuter, 2000). Other possibilities are introgressive hybridization, eco-phenotypic variation or local adaptive differentiation in which case synoptic populations of two species should be more similar due to local gene exchange or geographical variation in environmental condition (Christian *et al.*, 2003).

IV. Speciation And Hybridization In Tilapia

Although early experience influences the development of preferences in cichlid mate choice, the same species can be very “tolerant” and spawn with members of other species appearing very different from conspecifics (Caprona, 1986). The conditions under which such inter-specific spawning occurs in captivity are considered to exist in the field.

In nature there are large number of allopatric species inhabiting different river systems or different parts of river systems, sometimes encroaching slightly on each other but rarely hybridize unless brought together artificially in fish ponds where they often hybridize rather easily (Ayinla and Williams, 2005). The author further stressed that this is rather evidence for regarding tilapia as a supra species. Bringing different tilapias together through transfers has a consequences of undoing the work of nature; selection over many thousands of years. From these we can infer that the conventional system nomenclature (genus, species, sub species) is fine for describing a natural situation but inadequate for an aquaculture situation in which interbreeding occurs, as in tilapia (Kocher, 2005).

Many cichlid fishes are genetically similar, and inter-specific spawning often produces fertile hybrids (Caprona, 1986). Professor H.M. Peters (in Trewavas 1982) has artificially fertilized eggs of *Sarotherodon melanotheron* with sperm from *Oreochromis niloticus*. F1 hybrids of both sexes were obtained and 12 of them, 4 males and 8 females of 82-98mm standard length were examined. They resemble *O. niloticus* in most contrasting proportion. The depth of the pre-orbital bone, which is *S. melanotheron* of this size measure 22-25.5% length of head, in *O. niloticus* 15.0-19.0 in hybrids 17.0-20.0. In number of scales, vertebrae and dorsal fin rays they are intermediate the author reported.

With *O. mossambicus* male and *S. melanotheron* female, the hybrids were all female. With *T. tholloni*, hybrids were obtained when the male parent was *S. melanotheron*. The reverse cross resulted in high mortality among the embryos (Trewavas, 1982).

The target of inter-specific hybridization of two species in tilapia is to obtain monosex populations (Beardmore *et al*, 2001). The author observed that the bulk of research on the genetic basis and commercial potential of monosex hybrids has been carried out on tilapia. Many *Oreochromis* hybrids are characterized by a majority of males, the occurrence of all male broods is relatively common and it is where the major interest in hybridization lies. The first report of monosex hybrids created significant interest with the potential for mass production of all male progeny to prevent the serious problem of unwanted reproduction in aquaculture.

Pruginin *et al* (1975) summarized the results of interspecific crosses in tilapia. A high percent (98-100%) of male was reported from: *O. niloticus* X *O. viriabilis*, *O. nigra* X *O. urolepishornorum*, *O. vulcani* X *O. U. hornorum* and *O. vulcani* X *O. aureus* crosses. All male progeny can be produced in *O. niloticus* X *O. U. hornorum* crosses (Wohlfarth *et al.*, 1990). The *O. niloticus* X *O. u.hornorum* cross is not used commercially because of low and inconsistent fry production and the appearance of hybrid fish is not attractive to consumer (Beardmore *et al.*, 2001).

The *O. niloticus* X *O. aureus* cross is utilized commercially in some fish farms in Israel and Taiwan (Liao and Chen, 1983) in Beardmore *et al*(2001). However, there appears to be a problem of inconsistency. Mass spawn between *O. niloticus* female and *O. aureus* males do not produce 100% male progeny, the proportion of males varying between 59% and 81% male (Wohlfarth, 1994).

Hulata *et al* (1993) evaluated the value of different geographical populations in the production of *O. niloticus* X *O. aureus* hybrids and initiated work to improve this technology by selection of broodstock producing high percentage of male progeny.

Table below summarizes the hybrid combinations known to produce monosex male progeny in tilapia.

Female Parent	Male Parent	Note
<i>O. niloticus</i>	<i>O. aureus</i>	Applied commercially but results inconsistent.
<i>O. niloticus</i>	<i>O. macrochir</i>	Majority of broods are all-male some commercial application.
<i>O. niloticus</i>	<i>O. u.hornrum</i>	
<i>O. niloticus</i>	<i>O. viriabilis</i>	All progenies monosex
<i>O. mossambicus</i>	<i>O. aureus</i>	All progenies monosex
<i>O. mossambicus</i>	<i>O. U. hornorum</i>	
<i>O. Spilurusniger</i>	<i>O. macrochir</i>	All progenies monosex
<i>O. spilurusniger</i>	<i>O. hornorum</i>	
<i>O. aureus</i>	<i>O. u. hornorum</i>	All progenies monosex
<i>Tzilli</i>	<i>O. andersonii</i>	

Source: Beardmore *et al* (2001).

V. Implication Of Speciation And Hybridization

The increase in tilapia of genetic and phenotypic diversity due to hybridization may contribute to the uniquely rapid pace of speciation in cichlids (Salzburger *et al.*, 2004). Many *Oreochromis* species utilized in aquaculture were extensively introduced outside their natural range in Africa. Given their recent evolutionary radiation, these species hybridize easily posing a threat to the integrity of local adaptation (De-Amato *et al*, 2006). For instance, where several tilapia species share a body of water, resting areas are usually distinct in place (depth or type of bottom) or time. In substrate spawners the elaborate courtship behaviour probably helps to prevent any hybridization. Courtship behaviour is generally much briefer in the mouth brooders the author reported.

VI. Speciation And Hybridization: The Case Of Wesafu, An Ecotype Cichlid

In Nigeria, there exist an ecotype cichlid called Wesafu in Epe Lagoon, Lagos State where it seems to be highly priced and grow to a size of over 1500g in the wild (Bombata *et al*, 2005). At present 1kg of wesafu sells for N1,200 – N1,500 in Epe, Lagos.

There is, at the present, paucity of information on the origin of Wesafu. Previously it was commonly assumed to be *T. guineensis*, a species that is also found in Epe lagoon. However, the consistently larger size of wesafu and its deep body tend to separate it from the wellknown *T. guineensis* (Bombata *et al*, 2004). The author queried 'could it then be a variant of *T. guineensis*? The study on meristic and morphometrics showed the observed weight range of 495-1500g for wesafu is at variance with that of *T. guineensis* (11 – 352g).

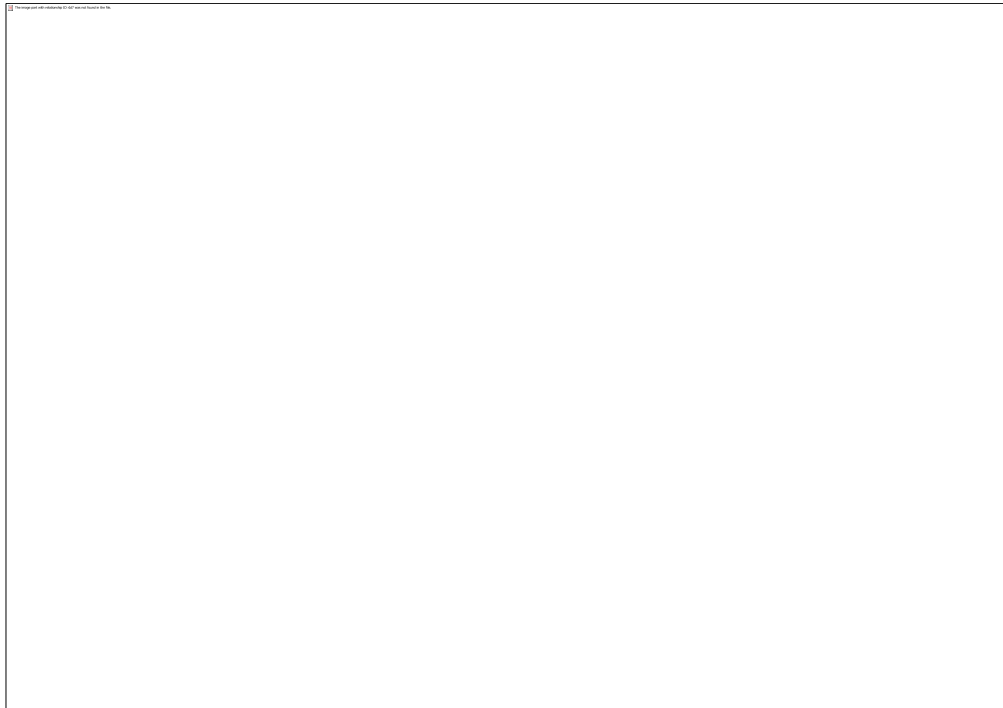


Fig. 1: Figure showing wesafu caught in a net

From the finding of the above study it was observed mean lateral line were the same (28).

Taming 1944 in Bombatta *et al*, (2004) observed that there is a relationship between some meristic characteristics and the environmental condition to which eggs and larvae are exposed. He further showed that the number of rays in the pectoral and the dorsal fins increase with temperature. While speciation cannot be determined by meristic characteristics alone, the unique size of the fish cannot be neglected. Such speciation is one reasons for genetic divergence in lake Malawi, where species evolve through three major selection forces; primary, secondary and tertiary radiation (Danley and Kocher, 2001, Anseeuw *et al*, 1999).

The large size of “Wesafu” coupled with deep body could be of great potentials for filleting, the largest specimen being 1,500g, 414mm TL and body depth of 64mm (Bombat *et al*, 2005). These are higher than the ones reported by other workers for other members of the cichlid family. Holden *etal* (1978) reported that *S. galilaeus* rarely grow larger than 350mm; while blackchin tilapia (*S. melanotheon*) has been noted to reach 24mm (Lee *et al* 1980). The maximum length reported for *Tilapia mariae* was 350mm (Riehl and Baensch, 1991). Olaosebikan and Raji (1998) reported a maximum size of 300mm for *T. guineensis*, which is much lower than the maximum size obtained for wesafu by Bombata *et al*, 2005. See Table 1 below.

Individuals cannot be separated by their meristic characters only but in populations by their differences in mean numbers. It is common to use two or more characteristics in combination for discriminatory functions (Fisher 1935 in Bombatta *et al* 2005). It would, therefore be safe to assume meristic and morphometric variance, based on the variable characters of wesafu and *T. guineensis*.

Radiation of cichlid was recently noticed in the great lakes of Africa (Greenwood, 1991), with unique modes of speciation. Sexual selection has been shown to play a crucial role in the large genetic divergence that make cichlids endemic in the African great lakes (Sturmbaner and Mayer, 1992). Although radiation is not pronounced in Wesafu, it has a distinct and peculiar radiation that is well recognized by the local fishermen, apart from the large size of the individual fish that are landed (Bombata *et al*, 2005).

Table 1 shows the summary of meristic and morphometric features of Wesafu (Data from 60 specimens)

Parameter	Mean	Range	Variance	Std deviation	Std error
Body weight(g)	830	495-1500	4421.1	210.8	27.2
Total length (mm)	239	270-414	852.8	29.2	3.8
Std length (mm)	271	223-340	639.1	25.3	3.3
Head length (mm)	85	60-115	109.0	10.4	1.3
Head width(mm)	112	90-138	128.3	11.3	1.6
Eye diameter(mm)	18	13-25	6.2	2.5	0.3
Body depth (mm)	44	25-64	80.0	8.7	1.1
Body width (mm)	127	100-150	119.5	10.9	1.4
Lateral line scales	28	18-35	8.3	2.9	0.4
Dorsal spines	XVI	XVI	0	0	0

Dorsal rays	12	12-13	0.2	0.1	0.1
Anal spines	III	III	0	0	0
Anal rays	10	9-11	0.3	0.6	0.6
Pelvic spines	1	1	0	0	0
Pelvic rays	5	5	0	0	0
Pectoral fin rays	12	11-13	0.2	0.5	0.5

Source: Bombata *et al*, 2005.

The table 2 below the summary of meristic and morphometric features of *Tilapia guineensis* (Data from 60 specimens)

Parameter	Mean	Range	Variance	Stddeviation	Std error
Body weight(g)	92.0	11-352	636.7	73.3	18.1
Total length (mm)	152	76-225	215.3	46.4	6.7
Std length (mm)	122	60-205	139.9	37.4	5.1
Head length (mm)	36	18-60	11.7	10.8	4.5
Eye diameter(mm)	9	4-15	0.8	2.7	0.4
Body depth (mm)	54	28-90	24.8	15.7	2.2
Lateral line scales	28	26-30	0.6	0.8	0.1
Dorsal spines	XVI	XIV-XVI	0.3	0.5	0.1
Dorsal rays	10	9-10	0.2	0.3	0.8
Anal spines	III	III	0	0	0
Anal rays	11	10-13	1.1	1.0	0.1
Pectoral Length(mm)	49	18-79	76.3	27.6	3.8
Pelvic length (mm)	39	17-70	14.4	12	1.6

Source: Bombatta *et al*, 2005

VII. Conclusion

Tilapia has become the second most important fish produced in aquaculture (Fitzsimmons, 2007). It has been introduced to more than 90 countries all over the world except Antarctica (Pullin, 1997). The extraordinary diversity of this fish has fascinated and challenged evolutionary biologists. Many explanations for the rapid evolution of taxonomic diversity have been suggested which include selective mating and brood care, adaptation to changes in habitat arising from water level dynamics, restricted migration to predation and micro adaptation to fragmented habitats (Jeffrey *et al*, 1999). It was further suggested that a combination of extremely low gene flow among populations, coupled with sexual selection could lead to the fixation of distinct mate recognition system within local population.

Jeffrey *et al*, 1999 while working on Malawi cichlid observed that Malawi cichlids have a high level of habitat fidelity (as in the case of “wesafu” in Epe lagoon). He argued that this in combination with patchy distribution of habitat types, could contribute to the evolution of lineage divergence. Increase in water level can open newly flooded habitat patches for colonization and can alter the nature of the existing habitat patches by increasing their depth. A species is never stable in nature. It may die out or spread to form other species. The author opined that once a species has a very wide distribution it may fall apart. This happens frequently with fish species when water bodies become mutually isolated and the separate population change through new mutations and genetic flux. He concluded that the natural distribution of tilapia suggest such situation.

In nature there are large number of allopatric species inhabiting river systems or different parts of river systems, sometimes encroaching slightly on each other but rarely hybridize, unless brought together artificially in fish ponds where they often hybridize rather easily. Bringing different tilapia together through transfer has consequences of undoing the work of nature.

The cichlid, wesafu, which is endemic to Epe lagoon has often times been mistaken for *T. guineensis*. However, the reports of Bombata *et al*, 2005, 2006) revealed that, based on the meristic, morphometric and feeding habits of this ecotype tilapia and exceptionally large size obtained in the wild (larger than 1500g and 414mm TL), this fish should not be mistaken for *T. guineensis*. He therefore queried “could it then be a variant of *T. guineensis*?, Could this variation be as a result of habitat fidelity, selective mating, and adaptation to changes in habitat arising from water level dynamics? To answer the questions above, wesafu opens a window of opportunities for investigation. In the first place, we need to properly characterize the fish using biochemical means such as protein and DNA extraction and profiling. Research should then focus on domestication and hybridization with other cichlids.

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