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NOTES AND COMMENTS

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GENETIC EVIDENCE FOR ALLOPATRIC AND SYMPATRIC DIFFERENTIATION AMONG COLOR MORPHS OF A LAKE MALAWI CICHLID FISH

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The cichlid fishes of the Great Lakes of Africa are the most spectacular examples of speciation and adaptive radiation within a single vertebrate family. In each of the lakes—Malawi, Tanganyika and Victoria—more species of fish coexist than in any other lake outside of the rift valley region. The exact number of species in each rift valley lake is still unknown, as many undescribed species are being discovered in newly explored areas (Eccles and Lewis, 1977, 1978; van Oijen et al., 1981; Witte, 1981; Witte and Witte-Maas, 1981; Lewis, 1982; McKaye and Mackenzie, 1982; Ribbink, unpubl.). van Oijen et al. (1979), and Barel and Witte (pers. comm.), for example, report that in the Mwanza Gulf of southern Lake Victoria approximately 200 cichlid species coexist, and in Lake Malawi it is estimated that over 500 species are present (consensus of ichthyologists working in Malawi). Further, many of the “species” earlier described are now being recognized to be polyspecific aggregates (Holzberg, 1978; van Oijen et al., 1979; Schröder, 1980; Hoogerhoud and Witte, 1981; Marsh et al., 1981; McKaye et al., 1982). Other outstanding examples of fish speciation in lacustrine environment—the 18 endemic cottids of Lake Baikal (Brooks, 1950; Koshov, 1963), the 18 cyprinids of Lake Lanao (Herre, 1933), and the 14 endemic cyprinodontid species of the genus *Orestias* of Lake Titicaca (Tchernavin, 1944)—achieve but 1/20th of the species diversity of cichlids in Lake Malawi.

However, the high diversity of African cichlid species has been questioned by an electrophoretic study of three trophically specialized Mexican cichlids (Sage and Selander, 1975). This study has often been cited to cast doubt upon the reported species richness of the African cichlids (Kirkpatrick and Selander, 1979; Graves and Rosenblatt, 1980). Electrophoretic data from other fishes such as good-eids “suggest that the number of biological species evolved in several extreme radiations of trophic diversity, most notably those of the cichlids in the African Rift lakes . . . may have been seriously overestimated by morphological references” (Turner and Grosse, 1980).

Besides this skepticism over the total number of species within these lakes, a controversy exists over the modes of speciation responsible for the evolution of these fishes. Fryer (1959, 1977) and Fryer

and Iles (1972) conclude that the diversity of cichlids in Lake Malawi has arisen through microallopatric speciation. This view corresponds with the hypothesis of Marlier (1959) and Matthes (1962), who suggested that populations of ancestral Lake Tanganyika cichlid species were geographically isolated and hence speciated allopatrically. Mayr (1963) cited Fryer’s earlier work in dismissing the possibility that sympatric speciation might, in part, explain the number of cichlids in Lake Malawi. But the allopatric model of speciation may not entirely explain cichlid speciation (Kosswig, 1947; Lowe-McConnell, 1959; Bush, 1975; McKaye, 1978; White, 1978). Most recently Mayr (1982) has suggested that some cichlids provide an “ideal situation” for sympatric speciation by disruptive selection. Recent field and genetic analysis of sympatric color forms of morphologically indistinguishable cichlids from Lake Malawi suggest that differences in color pattern and assortive mating among these entities could theoretically lead to speciation due to intrinsic behavioral isolating mechanisms (Holzberg, 1978; Schröder, 1980; McKaye, 1980; McKaye et al., 1982). To further understand differentiation processes and the importance of color polymorphism in cichlid evolution, an electrophoretic examination of Lake Malawi cichlids was made.

The cichlid fish *Pseudotropheus zebra* is endemic to Lake Malawi and is widely distributed over rocky habitats. Fryer (1959), Fryer and Iles (1972), and Holzberg (1978) have given ecological and color descriptions of the four distinct morphs examined in this report. Briefly, the morphs examined are 1) blue and black vertical bars (BB = most common morph), 2) orange-black (OB), 3) homogeneous blue (B), and 4) predominantly white (W). All four morphs are found in sympatry in the Nkhata Bay region of the lake while only the BB and OB morphs are naturally occurring in the southern region (Fig. 1). Ecological and behavioral studies suggest that these four morphs show complete assortive mating, forming two distinct groups (BB + OB vs. B + W) and thus might be considered two sympatric species (Holzberg, 1978; Schröder, 1980). To test this relationship and elucidate possible speciation mechanisms, we examined tissues from all four color morphs of *P. zebra* from Nkhata Bay using starch gel electrophoresis of soluble enzymes (Se-

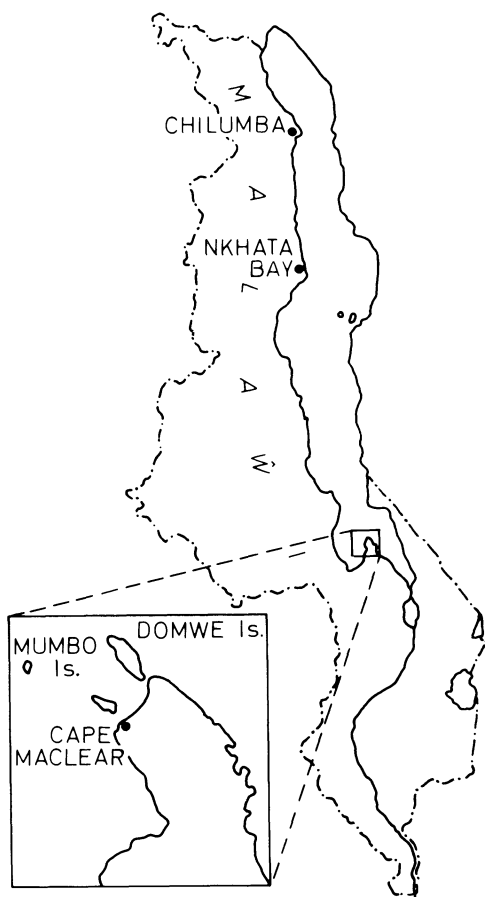


FIG. 1. Map of Malawi and Lake Malawi (=Nyasa). Fish were collected at Chilumba and Nkhata Bay in the north, and Mumbo and Domwe islands in the south.

lander et al., 1971). In addition, to determine if there is geographical differentiation between various demes of the common BB morph, we examined samples from three other sites in different geographic regions of the lake: two sites from the southern region, Mumbo and Domwe islands, and one site further north at Chilumba (Fig. 1).

The electromorph frequencies of the polymorphic loci confirm that the four color morphs are assortatively mating, forming two separate gene pools for this species from Nkhata Bay (Table 1). For all four loci, no differences are found between the BB and OB morphs or between B and W morphs. However, when the BB and OB morphs are combined and compared to the combined B and W morphs, significant differences are noted. For the *Pep* locus (peptidase; E.C.3.4.11), the frequency of the *a* electromorph was 22% for the BB/OB group

and 99% for the B/W group. The results for the three other loci, *Sdh* (sorbitol = iditol dehydrogenase; E.C.1.1.1.14), *Gpi-1* (glucose phosphate isomerase; E.C.5.3.1.9), and *Est-3* (esterase; E.C.3.1.1.1.) also indicate that the morphs are in the same two distinct breeding groups. These data are consistent with the field observations that the various morphs mate assortatively.

Significant differences are also seen between electromorph frequencies of both adjacent and well-separated demes of the BB morph (Table 2). Differences are noted when the two northern populations (Chilumba and Nkhata Bay) are compared to the two southern populations (Mumbo and Domwe). For *Pep*, 88% and 68% of the electromorphs of Mumbo and Domwe, respectively, are *a*, whereas only 20% and 21% occur in the Chilumba and Nkhata Bay populations, respectively ($G = 58.5$; $d.f. = 3$, $P < .01$). There are also statistically significant differences in the frequencies between the northern and southern populations for *Sdh* and *Est-1* ($G = 24.4$, 23.2; $d.f. = 3$, 6, respectively, $P < .01$). Furthermore, the *Est-3* loci shows a distinct difference between the Mumbo and Domwe island populations (Table 2); the frequency of the *b* electromorphs is 27% for Mumbo and 0% for Domwe and the frequency of the *d* electromorph is 32% for Domwe and 0% for Mumbo.

These results bear on two important issues of cichlid population structure and evolution: the species richness of the African assemblages and the mechanisms of population differentiation and speciation. In contrast to Sage and Selander's (1975) genetic examination of New World cichlid morphotypes, the color morphs of *P. zebra* might be considered two separate species as suggested by others (Holzberg, 1978; Schröder, 1980). How then, can the evolution of assortative mating by sympatric morphs be explained in the context of speciation processes? An allopatric argument suggests that the B and W morphs were at one time geographically isolated from the BB and OB morphs and then subsequently came into sympatry. This requires the extinction of the BB/OB mating group in an area where the B/W group survives, or the colonization of a new area by the B or W morphs where the ubiquitous BB and OB morphs are not present. Alternatively, the sympatric speciation model of Maynard Smith (1966) does not require historical geographic isolation, but instead requires that the morphs mate assortatively, choose different habitats, have different fitnesses in the habitats, and that the heteromorphic offspring be selected against. The results presented here and elsewhere for *P. zebra* (Holzberg, 1978; Schröder, 1980) and other cichlid genera (McKaye, 1980; Marsh et al., 1981) are compatible with this model.

The differences between the demes from the various geographic areas reflect either the amount of gene flow between the populations or varying selective pressures. The slight differences between the adjacent but allopatric populations of Mumbo and

TABLE 1. Electromorph frequencies of color morphs of *P. zebra* at Nkhata Bay, Lake Malawi Africa.¹

Morph	N (alleles)	Allele						Heterogeneity <i>G</i> (<i>d,f</i>)
		<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>	<i>f</i>	
<i>Pep</i>								
BB	34	.21	.79					
OB	34	.23	.77					
B	44	1.00					111.6 (3)**	
W	34	.97	.03					
<i>Sdh</i>								
BB	34	.30	.70					
OB	34	.27	.73					
B	46	.04	.96				18.9 (3)**	
W	36	.03	.97					
<i>Gpi-1</i>								
BB	34	.06	.82		.12			
OB	32		.94		.06			
B	48		1.00				15.8 (6)*	
W	36		1.00					
<i>Est-3</i>								
BB	34		.23	.71	.06			
OB	34		.06	.71	.06	.18		
B	44		.04	.14	.50	.42	110.6 (12)**	
W	36			.06	.36	.47	.11	

* $P < .05$, ** $P < .01$ (*G* test).

¹ Protein electromorphs were studied using standard horizontal starch-gel electrophoresis and histochemical staining procedures (Selander et al., 1971). Liver, muscle, heart, and eyes of adult fish were removed in the field and stored frozen in .01 Tris-HCl, pH 7.0 (containing 5 mM dithiothreitol and .5% polyvinylpyrrolidone-360) at -196°C in liquid nitrogen for 4–6 weeks. The samples were transferred to a freezer (-60°C) on return to the laboratory and remained there 3–8 months until analysis (Selander et al., 1971). Before beginning data collection we surveyed 24 loci to identify polymorphic systems. Our analysis included seven loci which we determined to be discernible and variable. The fish from Chilumba and half the B and W morphs were shipped live and kept in aquaria. The tissues of these fish were quick frozen in liquid nitrogen and then used immediately.

Domwe islands may indicate restricted gene flow and lend support to Fryer's (1977) model of microallopatric differentiation of populations. The differences between the northern and southern demes are much more pronounced and may be explained by restricted (or no) gene flow between the northern and southern regions. Such restricted gene flow may be the result of habitat segregation by large stretches of sandy beaches in the central region of the lake. Over 95% of the shoreline between Nkhata Bay and the southern populations is sand and marsh (McKaye and Gray, 1984). This represents a formidable barrier and would inhibit migration between populations of this xenotropic, rock-dwelling species. In contrast, the shoreline between the two northern populations is 35% rock substrate, thus facilitating genetic exchange between the populations.

Morphological divergence through variation in coloration is a major component of cichlid evolution. The importance of breeding coloration has been repeatedly recognized in distinguishing cichlid species (Fryer and Iles, 1972; Barel et al., 1977; Greenwood and Barel, 1978). Some cichlid species which lack morphological differences can be distinguished only by unique color patterns (Greenwood, 1974; Barel et al., 1977; Greenwood and Barel, 1978;

Marsh et al., 1981). In the case of *P. zebra*, no diagnostic morphometric characteristic besides color has been discovered to distinguish the different color entities (Fryer, 1959; Holzberg, 1978; Schröder, 1980). Rapid speciation with only marked changes in color has been noted for allopatric cichlid populations separated by only 3,500 years (Greenwood, 1965). Coloration has also been shown to be important in cichlid mate recognition and selection within a species (Fryer, 1959; Greenwood, 1974; McKaye and Barlow, 1976; Eccles and Lewis, 1978; McKaye, 1980).

This study is one of the first to document genetic differences among cichlid color morphs and suggests that variation in coloration may result in genetic isolation (see also McKaye et al., 1982). It demonstrates also that differences are present between various allopatric populations. The field data together with the genetic analysis strongly suggests that these color forms are reproductively isolated. But as we found no fixed alternative alleles at any of the loci we examined, we can not conclusively say that these color entities are completely isolated. Even though the gene frequencies are heterogeneous it is possible that some gene flow is occurring (Allendorf and Phelps, 1981; McKaye et al., 1982).

The hypothesis that sympatric splitting of morphs

TABLE 2. Electromorph frequencies of BB morphs at various localities in Lake Malawi, Africa.

Location	N (al- leles)	Allele				Heterogeneity G (d.f.)
		a	b	c	d	
<i>Pep</i>						
Mumbo I.	34	.88	.12			58.5 (3)**
Domwe I.	34	.68	.32			
Nkhata Bay	34	.21	.79			
Chilumba	54	.20	.80			
<i>Sdh</i>						
Mumbo I.	34		1.00			24.4 (3)**
Domwe I.	34		1.00			
Nkhata Bay	34	.30	.70			
Chilumba	50	.12	.88			
<i>Est-1</i>						
Mumbo I.	34	1.00				23.2 (6)**
Domwe I.	32	1.00				
Nkhata Bay	34	.85	.15			
Chilumba	54	.76	.22	.02		
<i>Est-3</i>						
Mumbo I.	34	.18	.27	.56		50.6 (9)**
Domwe I.	32	.12		.56	.32	
Nkhata Bay	34		.23	.71	.06	
Chilumba	54	.02	.06	.81	.11	

** $P < .01$ (G test).

may be important in explosive radiation has been advanced for both New and Old World cichlids (Kosswig, 1947; Lowe-McConnell, 1959; Trewavas et al., 1972; Barlow and Munsey, 1976; Holzberg, 1978; McKaye, 1980). Clearly, the results presented here do not eliminate either the hypothesis of allopatric or sympatric speciation. Both processes of differentiation and speciation could be occurring simultaneously and may explain the large species assemblages of cichlids. However, more comparative data on the frequency of polymorphism, assortative mating, habitat selection by morphs, survivorship of heteromorphic offspring, and an analysis of possible clinal variation are required to assess properly the speciation processes.

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