Trends in Ichthyology AN INTERNATIONAL PERSPECTIVE

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GSF-Bericht 7/92

Published by GSF – Forschungszentrum für Umwelt und Gesundheit GmbH

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Trophic Polymorphisms in Cichlid Fish: Do They Represent Intermediate Steps During Sympatric Speciation and Explain Their Rapid Adaptive Radiation?

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ABSTRACT

Accumulating evidence points to the ubiquity of extreme morphological variation, environmentally and genetically caused, in cichlid fishes. Phenotypic variation often is so large that our traditional notion of morphological variation within species may need revising. Trophic polymorphisms in the pharyngeal jaw apparatus of cichlid fishes question whether previously described morphological 'species' in cichlid species flocks really are biological species. Here I review trophic polymorphisms in cichlids and describe a previously unknown one in the Neotropical Cichlasoma haitensis, an endemic to Haiti. Its pharyngeal jaws vary from gracile with slender, pointed teeth (papilliform) to robust with strong, rounded teeth (molariform). Generally, molariform morphology is for cracking and feeding on molluscs. I suggest that trophic morphs occupy different ecological niches; mate assortatively and may then represent intermediate steps during sympatric speciation. The ability to respond morphologically to environmental shifts can, in conjunction with trophic polymorphisms and mate choice, be the basis of the impressive, rapid, adaptive radiation of cichlid fishes via sympatric speciation.

INTRODUCTION

Cichlid fishes underwent a within vertebrate unrivaled adaptive radiation in the East African Rift lakes. Closely related cichlids form 'species flocks' with estimated numbers of 100-300 endemic species in each of these lakes (refs. in Echelle and Kornfield 1984). Ecologists have viewed these assemblages as paradoxical because they seem to defy accepted ecological principles such as competitive exclusion (e.g. Fryer and Iles 1972). Cichlid fishes are believed to be specialized for narrow feeding niches (e.g. Fryer and Iles 1972; Hoogerhoud et al. 1983; but see Liem 1984). However, cichlid fishes are also known for their functional versatility (Liem 1978, 1979, 1980), which allows even morphologically specialized Polymorphisms in cichlid species often went unnoticed and morphs of one species have been interpreted as different biological species. An example of the traditional adherence to a strictly morphological species concept is seen in the case of the Neotropical species *Cichlasoma minckleyi*. This species has a pronounced genetically determined polymorphism in the structure of its PJA. Researchers initially believed they were dealing with two distinct species (Taylor and Minckley 1966; Minckley 1969; La Bounty 1974; Kornfield and Koehn 1975). Sage and Selander (1975) and Kornfield et al. (1982) showed that *Cichlasoma minckleyi* is indeed a single trophically polymorphic biological species.

What has long been recognized for plants (reviewed by Sultan 1987) and insects (reviewed by Harrison 1980; Roff 1986) seems also true for vertebrates in general and for fishes in particular (see references in Meyer 1987): the environment plays an important role in shaping morphology.

Evidence is accumulating that cichlids are morphologically variable and that much of this variation is ecophenotypic (Table 1). Laboratory-reared specimens of the African cichlid Haplochromis squamipinnis (Witte 1984) and the Neotropical cichlids Cichlasoma citrinellum and C. labiatum (Munsey and Barlow 1976; Meyer 1988b) differ from wildcaught specimens in osteological features. Extensive phenotypic plasticity of the whole cranium were induced and reversed through diet in the Neotropical cichlid Cichlasoma managuense (Meyer 1987). Hoogerhoud (1986, in press) showed that the pharyngeal jaws in the African species Astatoreochromis alluaudi are phenotypically plastic; hypertrophy of pharyngeal jaws was believed to be caused by a snail diet. Similarly, the environment probably plays a role in determining the PJA morphology in the trophically polymorphic New World cichlid Cichlasoma citrinellum (Meyer 1988).

	95	Species	Reference
Old	World:	Astatoreochromis alluaudi	Greenwood 1965; Hoogerhoud
		Haplochromis squamipinnis	1986 Witte 1984
New	World:	Cichlasoma citrinellum Cichlasoma labiatum Cichlasoma manaquense	Barlow and Munsey 1976; Meyer MS Meyer MS Meyer 1987

Table 1: Examples of environmentally induced morphological variation in cichlid fishes:

Implications of Variation for Taxonomy

The pharyngeal jaws and the shape of the neurocranial apophysis of cichlid fishes are important taxomomic characters. Greenwood (1959) described two subspecies of *Astatoreochromis alluaudi* based on differences in the molarity of the PJA-apparatus. Later Greenwood (1965) discovered that this character is phenotypically plastic and suggested that the subspecific status of the two PJA-morphs be dropped. However, Greenwood (1980) used differences of the degree of morphological variation found between the morphs in *C. citrinellum* and *C. minckleyi* to discriminate between two genera of African cichlids (Gaurochromis and Labidochromis; see Hoogerhoud 1984 for a critique of the validity of these genera). Therefore, it has been suggested that many of the morphological 'species' of the African cichlids may actually turn out to be polymorphism (Sage and Selander 1975; Turner and Grosse 1980, Vrijenhoek et al. 1987; Meyer 1987, 1988).

Phenotypic plasticity and trophic polymorphisms are not confined to cichlids. More examples of distinct trophic morphs occur in other groups of fishes (Table 2), although they seem particularly abundant in cichlids. Allendorf et al. (1987) and Vrijenhoek et al. (1987) recently reviewed evidence, primarily for salmonid fishes, that outlines the extent of morphological variation found within single species of fishes. Allendorf et al. (1987) documented that the variation (expressed as coefficient of variation) in morphological traits of fishes surpasses that of other vertebrates by orders of magnitude. They pointed to the "closeness" in which fishes live with their environment as a cause for the morphological variation.

Table 2. Extensive morphological variation in the trophic morphology of fishes:

Reference

Roberts 1974

Salvelinus alpinus Salmo clarki

Ilyodon furcidens

Saccodon

Species

Cichlidae of the Old World: Astatoreochromis alluaudi

Labidochromis caeruleus Hemichromis letourneauxi

Cichlidae of the New World: Cichlasoma mincklevi

Cichlasoma citrinellum Cichlasoma haitensis Greenwood 1965 Hoogerhoud 1986, In press Lewis 1982 Loiselle 1979

Loudenslager and Kitchin 1979

reviewed in Vrijenhoek et al. 1987

Sage and Selander 1975 Kornfield et al. 1982 Meyer 1988 Meyer 1988

Busack and Gall, 1981

Turner and Grosse 1980 Turner et al. 1983

Sometimes environmental influences on morphology will create a discontinuous distribution of phenotypes. Then, the problem of what to call a species is particularly difficult to solve. I recently found that the Neotropical cichlid *Cichlasoma haitensis* (Tee-Van 1935) also displays a trophic polymorphism in the structure of its

pharyngeal jaws (Fig. 1). The molariform morph of trophically polymorphic cichlids typically is characterized by possessing heavier, sturdier lower and upper pharyngeal jaws with molariform dentition. The teeth in the papilliform morph are more slender and pointed than in the molariform morph (Fig. 1). In the molariform morph the horns at the end of the lower pharyngeal jaw are shorter and stouter, providing larger attachment areas for the branchial musculature (Liem and Kaufman 1984). The levator posterior IV, the levator externus and the retractor dorsalis muscle are significantly hypertrophied in the molariform morph of Cichlasoma citrinellum (Meyer 1988). Hypertrophy of the branchial muscles increases the force exerted by the muscles during the crushing phase and the control of the PJA (Liem and Kaufman 1984). The morphological differences between the trophic morphs extend to the neurocranium, with the molariform morph having a larger articulation surface with the upper pharyngeal elements (neurocranial apophysis) (Meyer 1988).



Fig. 1: Scanning electromicrographs of the lower pharyngeal jaws of *Cichlasoma haitensis*. Left side (A): a papilliform specimen, right side (B): a molariform specimen of almost identical size. See text for more details on the morphological differences between the trophic morphs.

Ecological Implications of the Trophic Polymorphism

The molariform morph of *Cichlasoma citrinellum* can crack significantly harder snails than the papilliform morph (Meyer 1988c). But being molariform has its costs: the feeding efficiency of papilliform fish is higher on softer prey. The trophic morphs are ecologically separated (Meyer 1988). In *Cichlasoma citrinellum* the molariform morph feeds predominantly on snails that it can crack with its PJA, the papilliform morph feeds much less frequently on snails but both prefer a softer diet in the laboratory (Meyer 1988c).

Liem and Kaufman (1984) investigated the functional morphology of the trophically polymorphic Neotropicsl *C. minckleyi*. They suggested that the molariform morph has a selective advantage during periods of low food abundance, because it could feed more frequently on snails, the less preferred prey. This finding is important for ecological and evolutionary scenarios that try to explain the origin of specialization; it supports the notion that specialists exploit more efficiently particular types of prey to which they are adapted than generalists and have a selective advantage during ecological crunches. The PJA-morphs of cichlids probably have different fitnesses in their presumed respective feeding niches and habitats.

Polymorphisms as Intermediate Steps During Sympatric Speciation Events

Morphological variation that confers differences in the ecology may have an effect on the mode of speciation that predominated during the evolution of cichlid fishes. The relationship between genetic polymorphisms and sympatric speciation has been dealt with repeatedly in the literature (Knerer and Atwood 1973; Tauber and Tauber 1977, 1978; Rosenzweig 1978; Seger 1985; Kondrashov and Mina, 1986; Wilson and Turelli 1986). However, the relation between trophic polymorphisms and speciation scenarios has not been addressed for cichlids.

Mayr (1982) suggested that the case of *C. minckleyi* and the adaptive radiation of cichlids in Africa may provide ideal situations to test whether sympatric speciation and disruptive selection (see Thoday 1953, 1972 for review) may in part explain the large number of cichlid species.

Frequency dependent competition for resources between distinct phenotypes may lead to sympatric speciation (Rosenzweig 1978; Seger 1985; Wilson and Turelli 1986). Therefore, polymorphisms may be intermediate steps during the formation of new taxa. For this scenario it does not matter whether the polymorphism is a pleiotrophic effect of, for example, a genetically determined habitat preference, or linked to genes coding for color. The crucially limiting step during sympatric speciation seems to be the initial establishment of a stable polymorphism (Maynard-Smith 1966).

Fig. 2 outlines graphically that two trophic morphs have different fitness in their respective habitats/niches and that the fitness of an intermediate morphology is probably lower than the fitness of either morph. Morphological polymorphism may therefore lead to ecological differentiation through morph-specific habitat or prey choice. If the trophic polymorphism were linked to some marker like color, then the morphs could recognize each other and choose their mates morph-specifically. The Maynard-Smith model of sympatric speciation (1966; see also Thoday 1972) predicts that the trophic morphs should, after ecological differentiation occurred, exhibit assortative mating, or be reproductively isolated in some other way bringing about isolated gene pools. In Cichlasoma citrinellum jaw morph is correlated with coloration; and color morphs mate assortatively (Barlow 1983; McKaye 1980, 1986). Hence, genetic barriers between the trophic morphs may arise; a possible case of speciation in sympatry. This possible case of sympatric speciation may not be the only one. If we start to look for them, the number of trophic polymorphisms found will certainly increase which may in

turn point to sympatric speciation as the dominant mode of speciation for cichlid fishes. Maynard Smith (1966) believes that the importance of sympatric speciation will depend on the frequency with which polymorphisms occur, and the second step during the speciation process, the genetic isolation of separate morphs, will occur with relative ease. Sympatric speciation via intermediate steps as trophic polymorphisms may provide a plausible mechanism for the rapid evolution of cichlid fishes.



Morphological Phenotype

Fig. 2: Sympatric speciation scenario in which a single polymorphic population can split into two non-interbreeding populations. The figure shows a hypothetical adaptive landscape of two (homozygous) distinct phenotypic morphs in their respective niches. It is assumed that there will be a heterozygote disadvantage in both niches and that the superior fitness of morph A in niche A and morph B in niche B will lead to a suppression of (heterozygous) morphological intermediates in both niches. Genetic differentiation between the morphs A and B could occur through assortative mating or increased linkage between the gene coding for the morphology and the habitat selection or prey choice (parameters that define the respective niches).

Acknowledgements

G. Barlow, T. Kocher, J. Losos, and D. Wake, provided constructive critisism on an earlier version of the manuscript. Travel to Central America and museum collections was funded through a Noyes grant from the Organization for Tropical Studies, the Center for Latin American Studies at the University of California at Berkeley, a Raney Award from the American Society of Ichthyologists and Herpetologists, and an Ernst Mayr Award from the Museum of Comparative Zoology at Harvard University. Other support came from Sigma-Xi, the American Cichlid Association, and the Chancellor's Patent Fund from the University of California at Berkeley. Fellowships were granted from the German and the American Fulbright-Commissions and the University of California at Berkeley. George Barlow provided advice and support through grant # HD18612 from the National Institute of Child Health and Human Development; his work and that of his students significantly helped in the conduct this study. Specimens from the collections of the American Museum of Natural History and the Field Museum of Natural History were generously provided by those institutions.

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