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# THE CICHLID FISH OF CUATRO CIENEGAS, MEXICO: DIRECT EVIDENCE OF CONSPECIFICITY AMONG DISTINCT TROPHIC MORPHS

IRV KORNFIELD, DAVID C. SMITH, AND P. S. GAGNON
*Migratory Fish Research Institute and Department of Zoology, University of Maine at Orono, Orono, Maine 04469*

AND

JEFFREY N. TAYLOR
*Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida 33431*

The idea that different individuals within a biological species may have radically different morphologies and distinct feeding modes has commanded attention because of its profound implications for evolutionary biology. If individuals from a panmictic population are recognized as species by standard taxonomic criteria, organismal diversity in nature may be more apparent than real. This concern is particularly germane to the great diversity seen within assemblages of tropical freshwater fishes such as cyprinids and cichlids, where endemic specializations are extreme (Myers, 1960; Greenwood, 1974; Reid, 1980). Several examples of substantial dichotomous morphological divergence have been reported among sympatric collections of closely related fishes (Roberts, 1974; Sage and Selander, 1975; Vrijenhoek, 1978; Turner and Grosse, 1980). The cichlids of Cuatro Ciénegas, Mexico are particularly interesting and their study by Sage and Selander set a precedent which has had a significnat impact on subsequent systematic studies (Kirkpatrick and Selander, 1979; Graves and Rosenblatt, 1980).

By any phenetic criteria, the extreme distinctiveness of sympatric cichlids in Cuatro Ciénegas suggests the presence of two discrete species. A "small tooth" form with papilliform pharyngeal dentition feeds on plant material and possesses a relatively narrow head, slender pharyngeal jaw, and long intestine. A "large tooth" form with molariform pharyngeal teeth feeds on snails and has a wider head, relatively stouter jaw, and short intestine. The morphological and trophic differentiation between these two forms exceeds that observed among many closely related biological species and precisely mimics the differences which define numerous cichlids in the African Great Lakes (Fryer and Iles, 1972). Further, it is this type of variation that might be associated with incipient macroevolution (Greenwood, 1979). The magnitude of differences between these forms has thus historically caused them to be treated as two distinct species (Taylor and Minckley, 1966; Minckley, 1969; LaBounty, 1974; Kornfield and Koehn, 1975). Alternatively, on the basis of the segregation of both types within wild-caught broods, complete electrophoretic similarity, and concordant patterns of allozymic variation between forms, Sage and Selander (1975) suggested that both forms belong to a single polymorphic species. However, this evidence did not provide a definitive test of the two species hypothesis (Hutchinson, 1978).

We present in this article the results of complementary studies of genetics and reproductive biology initiated to resolve the biological status of these fishes. Our allozyme data and observations of mating in natural populations verify the insight of Sage and Selander and attest to their accurate electrophoretic evaluation of conspecificity. This demonstration of substantial morphological variation within a single species has significant implications for ecology and conventional taxonomic characterization.

TABLE 1. *Foreign phenotypes of fry in guarded cichlid broods.*

| Brood | Number of fry | Phenotype | *Ldh-1* | *Ldh-2* | *Ldh-3* | *Pgi-1* | *Pgi-2* |
|---|---|---|---|---|---|---|---|
| GY50 | 145 | Mother | — | — | FF | FF | SS |
| | | Offspring | — | — | FF | FF | SS |
| | | Foreign fry no. 1 | — | — | FF | FF | **FF** |
| | | Foreign fry no. 2 | — | — | FF | FF | **SF** |
| GY51 | 54 | Mother | — | — | FF | FF | SS |
| | | Offspring | — | — | FF | FF | SS |
| | | Foreign fry no. 1 | — | — | FF | FF | **SF** |
| GY01 | 74 | Mother | — | — | — | — | — |
| | | Offspring | SF/FF | SS | FF | FF | SF |
| | | Foreign fry no. 1 | **SS** | **SF** | **SF** | **SF** | SF |
| | | Foreign fry no. 2 | SF | SS | **SS** | FF | SF |

Phenotypes of fry in bold type are parentally incompatible. Relative allele mobilities in Sage and Selander (1975).

## MATERIAL AND METHODS

Collections of specimens and observations were made in Laguna El Mojarral, Cuatro Ciénegas, Mexico in June–July 1979, 1980, and 1981. Broods of free swimming offspring and their female guards were collected simultaneously during daylight hours with fine mesh handnets and spear guns. Adult fish for general electrophoretic studies were collected with coarse mesh handnets two hours after sunset when inactive fish rest on the substrate of the laguna.

For electrophoresis, eyes of adult fish were removed and stored frozen in 0.01 M Tris-HCl pH 7.0 (containing 5 mM dithiothreitol and 0.5% polyvinylpyrollidone-360); cichlid fry were frozen whole in buffer. Material was stored for up to three weeks in a conventional freezer (−6 C) while in Mexico, then transferred to an ultracold freezer (−90 C) upon return to the United States. Starch gel electrophoresis was performed as previously described (Kornfield and Koehn, 1975; Sage and Selander, 1975).

Since the morphological identity of reproducing fish could not be established by underwater observation while they were free swimming, it was necessary to capture individuals to determine trophic morphology. Unfortunately, spawning male cichlids were particularly sensitive to the presence of observers in close proximity to breeding areas and fled when approached. To collect actively mating pairs, we designed a remotely operated trap which, when activated, securely captured both male and female fish (Smith et al., 1981). Traps were set out in ecologically uniform habitats where substantial breeding activity had been previously observed. Additional pairs of breeding fish were collected with the use of spear guns. The pharyngeal dentition of captured fish was determined in the field with an otoscope.

## RESULTS AND DISCUSSION

Information bearing on the extent of genetic control over trophic morphology is limited. Both discrete morphological types developed in laboratory reared fish captured as fry from maternally guarded broods (Sage and Selander, 1975). However, it is questionable whether all fry within single groups are sibs; both New and Old World cichlids may protect unrelated offspring (McKaye, 1979; Ribbink et al., 1980). To evaluate this possibility, isolated groups of free swimming fry and their guarding females were examined for genetic compatibility at five polymorphic allozyme loci. Of 17 broods examined, three contained individuals whose electrophoretic phenotypes indicated that they were either unrelated to the females who guarded them or that they had different fathers than other individuals in their broods (Table 1). This assessment of the magnitude of foster parentage is clearly

TABLE 2. *Frequency estimates of* Pgi-2 (1.00) *in samples of cichlids from Laguna El Mojarral.*

| | Small tooth | | Large tooth | | Total | |
|---|---|---|---|---|---|---|
| | $N$ | $P \pm$ SE | $N$ | $P \pm$ SE | $N$ | $P \pm$ SE |
| 1974 | 20 | 0.70 ± .072 | 15 | 0.57 ± .090 | 52 | 0.63 ± .047 |
| 1980 | 30 | 0.417 ± .064 | 28 | 0.428 ± .066 | 58 | 0.422 ± .046 |

Population estimates of allele frequency differ significantly between years ($t = 2.20$, $P < .05$). Data from 1974 from Sage and Selander (1975).

conservative since some unrelated juveniles may be electrophoretically equivalent (see Hanken and Sherman, 1981). Given the allele frequencies characteristic of cichlids at El Mojarral, over one third of all fish at that locality are indistinguishable from the normal offspring of broods GY50 and GY51 for the loci examined. While it is most probable that foreign fry become incorporated into broods by passive mixing (Lewis, 1980), it is also possible that some individuals with paternally incompatible phenotypes were produced by multiple fertilization (Gross and Charnov, 1980; McKaye, 1980). Regardless, it is clear that inheritance studies based on field-collected offspring can not effectively resolve the systematic problem of the Cuatro Cienegas cichlids.

### *Electrophoretic Characterizations*

In the absence of breeding information, accurate recognition of separate gene pools can be achieved when sympatric groups exhibit evidence of independent genetic evolution. In the cichlids of Cuatro Ciénegas, estimates of genetic distance are similar to those typical of conspecific populations and do not differentiate the two forms (Kornfield and Koehn, 1975; Sage and Selander, 1975). However, since electrophoretic divergence is probably a time dependent process (Corruccini et al., 1980), very recently evolved species may be expected to be almost indistinguishable. In fish, several studies have demonstrated extreme genetic similarities between valid biological species (Avise et al., 1975; Johnson, 1975); African cichlids in particular exhibit these extremes (Kornfield, 1978; Kornfield et al., 1979).

A more convincing assessment of reproductive isolation involves geographic or temporal comparisons of gene frequencies. Because gene pools of reproductively isolated species respond independently to populational and environmental processes, dissimilar gene frequencies are to be expected (Futuyma and Mayer, 1980). However, frequency differentiation need not be indicative of genetic isolation. For example, significant intraspecific heterogeneity has been reported among age classes in fish (Williams et al., 1973; Koehn and Williams, 1978) and lizards (Tinkle and Selander, 1973). Nevertheless, homogeneity of gene frequencies should generally be characteristic of single species samples regardless of the manner in which individuals are grouped for comparison. Exploiting this approach, Sage and Selander (1975) demonstrated concordant geographic variation of gene frequencies at several allozyme loci for the two Cuatro Ciénegas cichlids. These observations thus implied the existence of a single gene pool.

We re-examined the frequency of four of these loci previously studied by Sage and Selander in fish from Laguna El Mojarral. At Esterase, Lactate dehydrogenase-3, Phosphoglucoisomerase-1, and Phosphoglucoisomerase-2, genotypic proportions were homogenous among the small tooth and large tooth forms. All individual genotypic ratios fit Hardy-Weinberg-Castle expectations. However, allele frequencies were not temporally stable. Between 1974 and 1980, a significant change in frequency was observed at *Pgi-2* (Table 2).

Patterns of coordinated geographic and temporal frequency variation argue against the two species hypothesis. However, it is possible to remain skeptical of this conclusion because of the lack of direct evidence for reproductive isolation. In particular, species may have concordant patterns of allozyme variation in response to common selection pressures (Borowsky, 1977). At single loci, identical patterns of geographic variation in gene frequency have been observed among sympatric populations of reproductively isolated fishes (Johnson, 1974) and molluscs (Koehn and Mitton, 1972; Koehn et al., 1980). It is improbable, of course, that such parallel selective responses occur simultaneously at numerous loci. But if reproductively isolated taxa are of *very* recent origin, differences in allozyme frequencies may be very limited. Thus, it is essential to examine reproduction under natural conditions to directly test the hypothesis of two biological species.

### *Reproductive Observations*

Isolated gene pools evolve independently only if significant gene flow does not occur between them (Crow and Kimura, 1970; Jackson and Pounds, 1979). A limited amount of interspecific gene exchange can be tolerated and still maintain reproductive isolation if selection is relatively strong. In general, though, the number of interspecific matings in sympatric populations should approach zero.

In Cuatro Ciénegas, actively reproducing male-female cichlid pairs were identified by observing standard behaviors of spawning and nest guarding (Baerends and Baerends-Van Roon, 1950). A sample of 33 reproductively active pairs were collected in Laguna El Mojarral during 1979, 1980, and 1981. If the two forms were completely isolated reproductively, we would have expected to see no matings between forms. Examination of the pharyngeal jaws revealed that 19 mating pairs (57%) involved fish with unlike trophic morphologies (Table 3). Further, given the relative proportion of the small tooth cichlid in this population, the observed number of homotypic matings was much less than that expected under reproductive isolation. Mixed morphological matings were also observed at three additional localities: Pozo de la Becerra, Laguna Churince, and Rio Mesquites. Clearly these observations force rejection of the two species hypothesis.

TABLE 3. *Observed association of trophic morphology in breeding pairs of Mexican cichlids.*

| | Male | |
|---|---|---|
| | Papilliform | Molariform |
| Female | | |
| Papilliform | 13<br>(11.85) | 10<br>(11.15) |
| Molariform | 5<br>(5.15) | 6<br>(4.85) |

Expected number of pairs under the random mating hypothesis in parentheses. Note the difference in the relative frequencies of the tooth types between sexes.

Although the data presented did not deviate from random mating expectations ($G = 0.244$, $d.f. = 1$, $P > .5$), the sample size does not preclude limited assortative mating by morphotype. In fact, if almost 20% of all matings were completely assortative, we would have been unable to demonstrate this given the small sample size. However, assortative mating is unlikely. First, our field observations of natural reproduction did not reveal any obvious habitat segregation. Matings in Laguna El Mojarral occurred on an ecologically monotonous substrate in close proximity to one another. Second, males who sequentially fertilized the eggs of separate females and simultaneously guarded two nests exhibited no mating fidelity to fish of their own trophic type. Two of five males who maintained distinct nests were mated to both small tooth and large tooth females concurrently.

### *Implications*

The confirmed existence of a trophically dichotomous biological species has implications for two areas of evolutionary biology. First, the variation observed between cichlid morphs, and that recently noted in goodeids by Turner and Grosse (1980), forces a critical appraisal of the concept of adaptive radiation; trophic polymorphism may represent a viable alternative evolutionary strategy. The factors controlling the origin of such a system remain unclear. Anatomical flexibility

(Liem, 1980) and/or competition and resource availability may constrain the formation of trophic polymorphisms. Need we reevaluate the niche concept to accommodate such species (Hutchinson, 1978)? Surely their ecological behavior differs significantly from conventional taxa. For example, simple communities composed of trophically polymorphic species may be more responsive to environmental and biotic perturbations than standard communities.

Second, the range of dichotomous morphological variation between cichlid morphs has profound systematic implications. Numerous species exhibit morphological modifications of the pharyngeal dentition and apophysis mirroring the type observed in Cuatro Ciénegas (Greenwood, 1974, 1979; Hoogerhoud and Barel, 1978). If species definitions are primarily based on such phenetic differences, morphology by itself may be generally inappropriate to delimit biological taxa or index actual species diversity. It is of considerable importance that cichlid systematists have begun to emphasize breeding coloration (Barel et al., 1977; Greenwood and Barel, 1978). Cichlid species generally appear to be distinguished by unique coloration (Greenwood, 1974) and assortative mating by color has recently been described for a number of taxa formerly thought to be color morphs of single species (Holzberg, 1978; Schroder, 1980; Marsh et al., 1981). However, color differences, like morphological differences, may not be sufficient to recognize reproductively isolated taxa. In Lake Malawi, trophically equivalent cichlids which differ significantly in breeding coloration and body shape were statistically indistinguishable in allele frequency at three polymorphic isozyme loci (Kornfield, 1974). Clearly resolution of such systematic problems will require direct observations of reproductive isolation or more sophisticated probes for genetic continuity (e.g., Avise et al., 1979). Regardless, differentiation without speciation has received only limited attention by taxonomists. Since this situation exists in fish, it is not unreasonable to suggest that it may occur in other vertebrate groups.

## SUMMARY

Two discrete cichlid fishes endemic to Cuatro Cienegas, Mexico differ significantly in several morphological characters associated with feeding specializations. Conventional taxonomic treatment would suggest the presence of two distinct species, but Sage and Selander (1975) forcefully argued for the presence of a single polymorphic biological species. Biochemical comparisons and observations of reproduction in situ conducted in 1979, 1980, and 1981 revealed gene and genotypic homogeneity between the two types of fishes. A significant change in allele frequency at *Pgi-2* which occurred between 1974 and 1980 was observed in both forms. Of cichlid pairs collected in the process of mating, 57% involved matings between forms, unequivocally suggesting the existence of a single Mendelian population.

Confirmation of a trophically polymorphic biological species has significant ecological and systematic implications. Trophic polymorphism may represent an alternative strategy to adaptive radiation and may inflate estimates of species diversity based solely on phenetically defined taxa.

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Corresponding Editor: D. J. Futuyma