

Ecological and evolutionary consequences of the trophic polymorphism in *Cichlasoma citrinellum* (Pisces: Cichlidae)

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Received 3 February 1989, accepted for publication 26 May 1989

The neotropical cichlid fish *Cichlasoma citrinellum* is polymorphic in the structure of its pharyngeal jaw apparatus and external morphology. The pharyngeal jaws are either gracile and bear slender, pointed teeth (papilliform) or robust with strong, rounded teeth (molariform). Molariform morphs have a 'benthic', and papilliform morphs a 'limnetic' body form. Furthermore, this species is also polychromatic, with yellow and black morphs. The molariform morphology of the pharyngeal jaw apparatus adapts the fish for cracking and feeding on snails. Based on analysis of stomach contents, 94% of the molariform morph ate snails whereas only 19% of the papilliform morph did so. This result suggests that the morphs occupy different ecological niches. The morphology of the pharyngeal jaw apparatus does not correlate significantly with sex, but it does with body colouration ($P < 0.005$). *Cichlasoma citrinellum* mate assortatively with their own colour; therefore a mating preference for colour may lead to genetic isolation of trophic morphs.

The frequency of the molariform morph differs strikingly among populations of five Nicaraguan lakes and its abundance is correlated with the abundance of snails, the fishes' principal prey item. Among populations the frequency of molariform morphs decreases in the dry season. Morphology possibly changes reversibly within particular individuals between seasons. These results suggest that phenotypic plasticity and polymorphisms may be an adaptive characteristic of cichlid fishes. Patterns of intraspecific morphological variation match patterns of interspecific morphological diversification which suggests that universal developmental mechanisms canalize the possible expressions of morphology. The ability to respond morphologically to environmental shifts, in conjunction with genetically determined trophic polymorphisms and sexual selection via mate choice, could be the basis for speciation through intermediate stages of polymorphism of the impressive adaptive radiation of cichlid fishes.

KEY WORDS: – Trophic polymorphism – seasonal changes in morphology – pharyngeal jaws – intraspecific macroevolution – phenotypic plasticity – speciation through polymorphisms – cichlid fishes – *Cichlasoma* – *Heros* – Nicaragua.

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INTRODUCTION

In each of the three largest East African lakes cichlid fishes form species flocks with more than 500 endemic species (Lewis, Reinthal & Trendall, 1986). These species assemblages represent unrivalled examples of adaptive radiations in vertebrates. Ecologists have viewed these assemblages as paradoxical because they seem to defy accepted ecological principles (e.g. Fryer & Iles, 1972). Evolutionary questions centre around the origin of the species flocks and their mode of speciation (e.g. Trewavas, 1947; Kosswig, 1947, 1960, 1963; Fryer, 1965; Liem, 1984; Lowe-McConnel, 1969; Greenwood, 1974, 1979, 1984; Vrba, 1980; McKaye *et al.*, 1982, 1984; Dominey, 1984; Meyer, 1987, 1988, 1990b).

Despite much theoretical debate, many aspects of the cichlid problem are still unresolved and a consensus has not been reached as to how these fish assemblages evolved or what maintains their biotic diversity (see references in Echelle & Kornfield, 1984).

Evolutionary success through key novelties: the pharyngeal jaw apparatus of labroid fishes

Numerous mechanisms that could explain the evolutionary success of cichlid fishes have been offered, e.g. parental care (Dobzhansky, 1951), sexual selection by mating colouration (Kosswig, 1947; Dominey, 1984; Mayr, 1982), versatile functional design (Liem, 1973, 1978) and phenotypic plasticity and polymorphisms (Meyer, 1987, 1990b). Liem (1973) advanced the idea that the possession of a well-developed pharyngeal jaw apparatus (PJA) in cichlid fishes represents a key innovation (Simpson, 1953) that has increased their 'evolutionary potential' and is responsible for their evolutionary success. Except for the marine family Embiotocidae, which is composed of only about 24 species, other families of the suborder Labroidei which also have PJAs (Kaufman & Liem, 1982) have been very successful evolutionarily (Liem, 1986; Liem & Sanderson, 1986; Stiassny & Jensen, 1987).

All labroids possess highly developed PJAs which act as a second set of jaws located immediately anterior to the oesophagus. The pharyngeal jaws bear highly specialized dentition for the processing of prey. Hypertrophied muscles enable labroid fishes to masticate their diet and to transport it into the oesophagus. The manipulation of prey is accomplished between the pharyngeal jaws by complex movements initiated through contraction of the branchial musculature (e.g. Liem & Kaufman, 1984). The upper pharyngeal jaws contact the skull ventrally via a neurocranial apophysis (Liem & Greenwood, 1981; Stiassny, 1981; Lauder & Liem, 1983).

The PJA frees the oral jaws to become specialized for particular feeding tasks allowing for increased independent, morphological specialization and both

elements (Lauder *et al.*, 1989). The PJA is therefore of utmost importance for ecological specialization and niche diversification (Liem, 1973; Stiassny & Jensen, 1987); this may possibly result in habitat segregation and eventually speciation (see below). The PJA and the functional versatility of cichlids are believed to be responsible for successful and rapid adaptation to shifts in trophic ecology (Liem & Osse, 1975; Liem, 1978; see also Stiassny & Jensen, 1987). The neurocranial structures associated with the PJA are also important taxonomic characters (Trewavas, 1985; but see Greenwood, 1978, 1986).

I (Meyer, 1988, 1990a) described trophic polymorphism in the pharyngeal jaw structure of a neotropical cichlid species, *Cichlasoma citrinellum* (Günther, 1864). This species is variable in colouration and exhibits polychromatism (Barlow, 1976; Barlow & Munsey, 1976; Villa, 1976); the trophic morphs differ in their external morphology as well (Meyer, 1988, 1990a), the fish with molariform PJAs having a blunter head and less elongated body than those with papilliform PJA. Individuals change their external form during ontogeny (Gottfried, 1986; Meyer, 1988). The behavioural biology of this species has been investigated (e.g. Barlow, 1976, 1983; Barlow & Munsey, 1976; McKaye, 1977, 1980, 1986).

Morphological adaptation and feeding ecology

Cichlid fishes are believed to be specialized for particular feeding niches (e.g. Fryer & Iles, 1972; van Oijen, 1982; van Oijen, Witte & Witte-Maas, 1981; Hoogerhoud, Witte & Barel, 1983; Barel, 1983; but see Liem, 1984). However, non-piscivorous cichlid fishes are also known for their functional versatility (Liem, 1978, 1980), which allows even morphologically specialized species to exploit a variety of prey types. Recent field observations support this laboratory finding (Eccles & Lewis, 1977, 1978, 1979; Katunzi, 1983; McKaye & Marsh, 1983). During ecological bottlenecks, specialists may be more efficient predators than generalists and therefore have a selective advantage (Schoener, 1971; Wiens, 1977; Lauder, 1983; Meyer, 1989). Natural selection might act with increased strength during bottlenecks to enhance the tightness of the correlation between morphology and ecology (Grant, 1986; Meyer, 1989; but see Wiens, 1977; Wiens & Rotenberry, 1980).

Intraspecific variation and polymorphisms in cichlids

Traditionally, taxonomic studies of cichlids have assumed that interspecific morphological variation is accompanied by little intraspecific discontinuous (polymorphisms) and continuous variation (e.g. Greenwood, 1967; Barel *et al.*, 1977; van Oijen *et al.*, 1981; van Oijen, 1982; but see Hoogerhoud, 1986a, b; Meyer, 1987, 1990b; Witte & Witte-Maas, in press). This assumption is implied by the use of such characters as differences in body proportions and dentition as well as differences in colouration as taxonomic characters to describe new species (van Oijen *et al.*, 1981; Hoogerhoud *et al.*, 1983).

An example of a traditional adherence to a strictly morphological species concept is seen in the neotropical species *Cichlasoma minckleyi*. This species exhibits a pronounced, genetically determined polymorphism in the structure of its PJA (Kornfield & Taylor, 1983). Researchers initially believed that they were dealing with two distinct species (Minckley, 1969; La Bounty, 1974; Kornfield &

Koehn, 1975). Later, Sage and Selander (1975) and Kornfield *et al.*, (1982) showed convincingly that *Cichlasoma minckleyi* is indeed a single trophically polymorphic species.

Trophic polymorphisms are known from a few other cichlids (reviewed in Meyer, 1990b). The African cichlids *Labidochromis caeruleus* (Lewis, 1982a), *Lethrinops mylodon* (Eccles & Lewis, 1979; Lewis, 1982b), *Hemichromis letourneauxi* (Loiselle, 1979) and *Astatotilapia flavijosephi* (Spataru & Gophen, 1985) are polymorphic in the structure of their PJA.

In polygynous cichlids colouration is often sexually dimorphic (e.g. Fryer & Iles, 1972). Also, cichlids typically change their colouration between reproductive and non-reproductive seasons. *Cichlasoma citrinellum* exhibits a colour polymorphism that is not linked to sex; it can be a 'gold' (yellow) or a 'normal' (black) colour (e.g. Barlow, 1976). Colour polymorphisms may not be as uncommon as previously believed (but see Barlow, 1976, 1983) and may play a role in speciation (McKaye, 1980; McKaye *et al.*, 1982, 1984). In spite of this variation, male breeding colouration is sometimes the only reliable taxonomic character distinguishing closely related African haplochromine cichlids (e.g. Witte & Witte-Maas, in press).

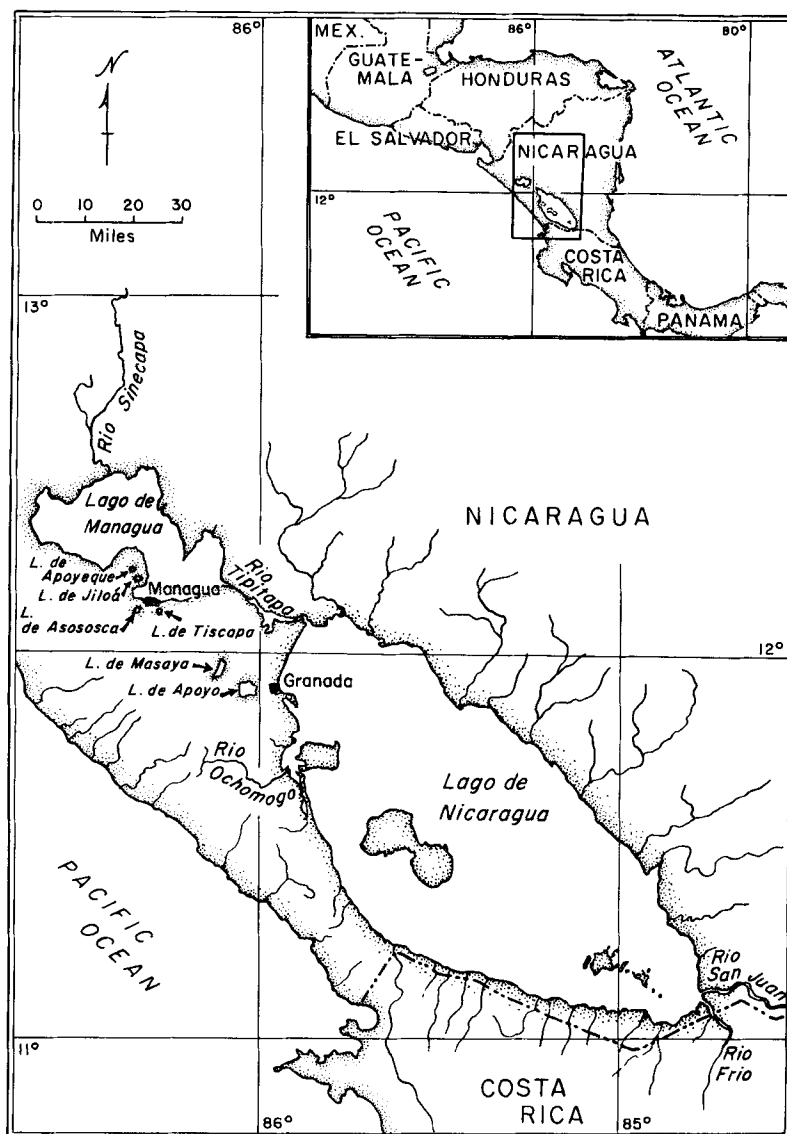
Phenotypic plasticity in cichlid fishes

Evidence is accumulating that many cichlid species are morphologically variable and that much of this variation is ecophenotypic, i.e. environmentally induced (Greenwood, 1965; Witte, 1984; Hoogerhoud, 1986a, b; Meyer, 1987, 1988, 1990b). Laboratory-reared specimens of the African cichlid *Haplochromis squamipinnis* (Witte, 1984) and those of the neotropical cichlids *Cichlasoma citrinellum* and *C. labiatum* (Barlow & Munsey, 1976; Meyer, unpublished) differ from wild-caught specimens in osteological features and body proportions. I reported on the experimental induction of extensive phenotypic plasticity of the entire cranium in the neotropical species *Cichlasoma managuense* (Meyer, 1987). This variation could be induced and reversed by dietary influences (Meyer, 1987). Hoogerhoud (1986a, b) showed unequivocally that the pharyngeal jaws in the African species *Astatoreochromis alluaudi* are phenotypically plastic and hypertrophy of pharyngeal jaws was correlated with snail diet (see also Greenwood, 1965).

This paper addresses the question of the ecological consequences of a trophic polymorphism in *Cichlasoma citrinellum*. It also asks what evolutionary consequences might stem from the ecological separation of the two trophic morphs, and whether this species might be a model explaining the origin of the cichlid radiations in the neotropics and the Old World.

METHODS

I examined the external morphology and the pharyngeal jaws of more than 600 wild-caught specimens of *Cichlasoma citrinellum*. The fish were caught in the centre of their distribution from five Nicaraguan lakes (Fig. 1). Lakes Jiloa, Apoyo and Masaya are isolated small crater lakes whereas Lake Managua and Lake Nicaragua are large lakes connected to the Atlantic ocean. Because Lake



Jilao is the best studied ecologically I have focused the investigation on *C. citrinellum* from this lake when possible (see Results for details).

Fish were collected by seining, except for some from Lake Nicaragua islands which were bought from fishermen. In a subsample of fish from Lake Jilola the diameter of the largest tooth on the lower pharyngeal jaw, and the width of the tooth-bearing area of the lower pharyngeal jaw were measured (Figs 3, 4). These specimens were inspected by eye and classified into papilliform, intermediate or molariform categories. (One small specimen, 44 mm in standard length, was intermediate in the morphology of its PJA.) The lower pharyngeal jaws of the specimens were removed and measured (see above).

In the wet season 1987 (July) bottom samples were collected from Lakes Jilao, Apoyo, Masaya and Nicaragua. Ten samples were collected in 1 m intervals from the shore along transects at right angles to the shore; the sample area was 13×6.5 cm for each sample.

RESULTS

I. Morphological description of the polymorphism

Cichlasoma citrinellum exhibits a polymorphism in its PJA which resembles that in its congener *C. minckleyi* (Sage & Selander, 1975; Kornfield & Taylor, 1983; Liem & Kaufman, 1984). The molariform morph possesses heavier lower and upper pharyngeal jaws with a molariform dentition than the papilliform morph (Fig. 2). The teeth in the papilliform morph are more slender and pointed than in the molariform morph, in which the angle of the lower pharyngeal jaw is more acute and the whole PJA is sturdier (Meyer, 1988). In the molariform morph the horns at the caudal end of the lower pharyngeal jaw are shorter and stouter, providing larger attachment areas for the branchial musculature. Correlated with the heavier pharyngeal jaws are differences in some of the branchial musculature. Particularly muscles that are active during the crushing phase (Liem, 1986) are hypertrophied in the molariform morph (Meyer, 1988). In

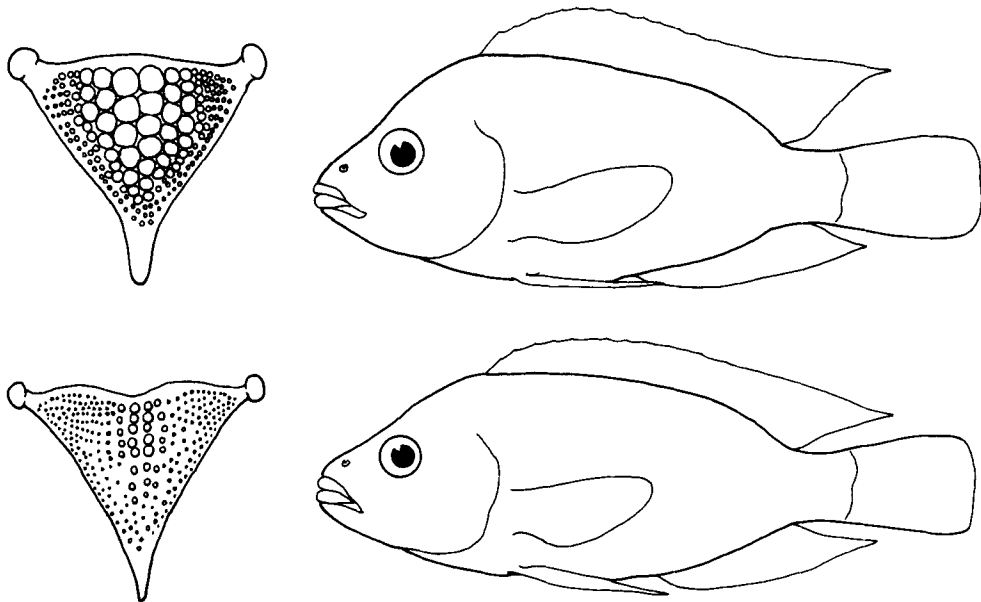


Figure 2. Semi-schematic drawing of the differences in body shape and pharyngeal jaw morphology in *C. citrinellum*. Above: morphs with a molariform type of PJA. Below: morph with a papilliform PJA type. Molariform PJA morphs have a shorter, blunter snout, wider head, larger eye, deeper and shorter body (Meyer, 1990a). The molariform pharyngeal jaws are sturdier, larger, and have larger molariform teeth. Pharyngeal jaws are seen from above.

Cichlasoma citrinellum the molariform morph has a more massive neurocranial apophysis for the upper pharyngeal bone; it provides a larger articulation surface for their stronger upper pharyngeal elements (Meyer, 1988, 1990a).

Differences in external morphology are correlated with differences in the PJA morph (Fig. 2, Meyer, 1988, 1990a). Molariform morphs have shorter, blunter snouts, larger eyes, wider heads, and deeper, shorter bodies than papilliform morphs (Fig. 2). Molariform morphs have a 'benthic', papilliform morphs a 'limnetic' body form (*sensu* Ehlinger & Wilson, 1988, Fig. 2). These differences in external morphology might make the molariform PJA morphs more adapted to feeding and manoeuvring in shallow benthic areas of lakes, whereas the external morphology of the papilliform morph seems conducive to sustained swimming in the more open limnetic environment.

Ontogenetic trends

In *C. citrinellum*, as well as in *Astatoreochromis alluaudi* (Hoogerhoud, 1986a), all fish initially exhibit a papilliform pharyngeal dentition during ontogeny (Fig. 3). The smallest specimens that unambiguously had a molariform dentition and molariform "Gestalt" of the PJA were of approximately 40 to 50 mm in standard length. As fish in this species grow, their PJAs will either remain papilliform or become molariform; large fish with an intermediate condition of PJAs are rare. As a result of these distinct ontogenetic trajectories, bimodality is recognizable in the trophic morphs among mature fish (Fig. 4) and differences become more pronounced during ontogeny (Fig. 3).

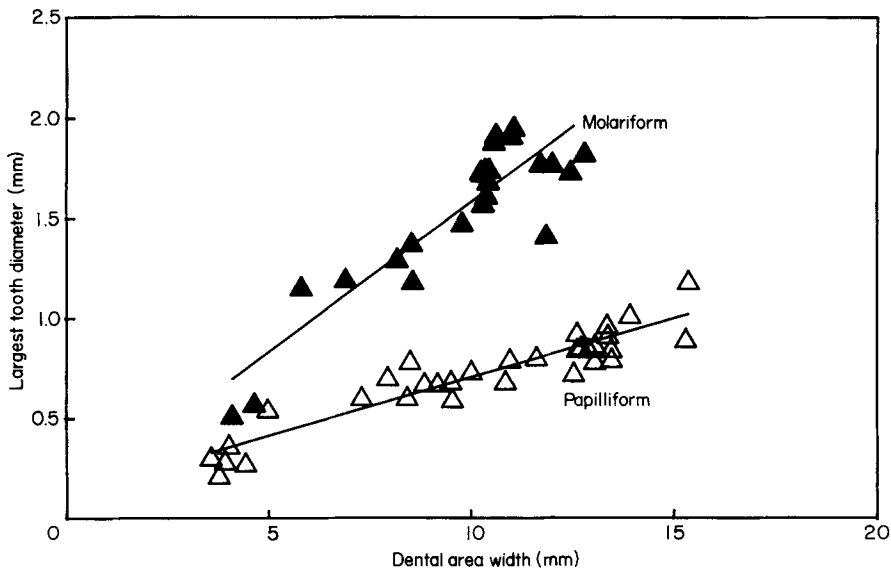


Figure 3. Ontogenetic trends of the developing PJA from molariform and papilliform PJA morphs of *C. citrinellum* from Lake Jilao. The width of the dental area on the lower pharyngeal jaw was measured as defined by Barel *et al.*, (1977: fig. 59). The dental area width does not differ between fish of the same size and is therefore used as a measure of size. The diameter of the largest tooth on the lower pharyngeal jaw differs significantly between the PJA morphs. The only fishes of intermediate morphology are small individuals. During ontogeny the distinctions between the two PJA morphs become more pronounced.

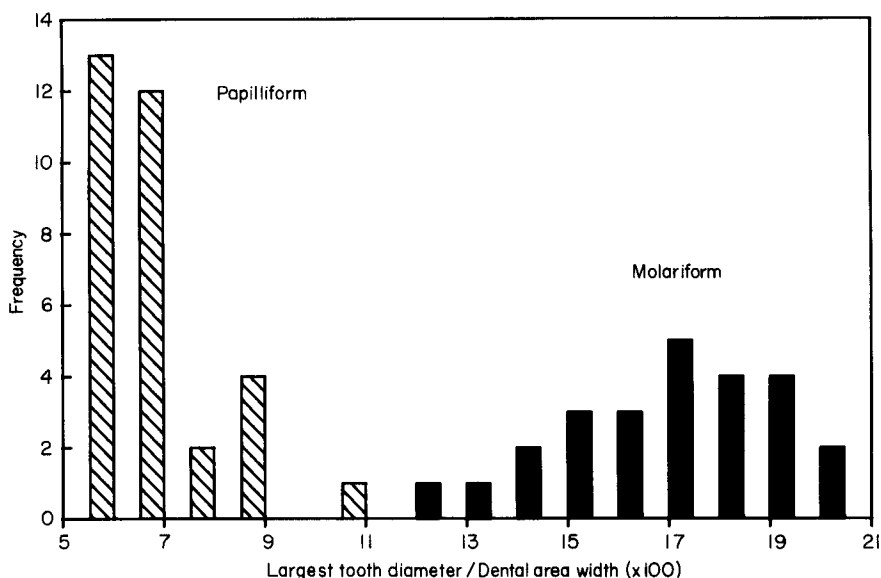


Figure 4. Frequency distribution of *C. citrinellum* from Lake Jilola (measurement: diameter of the largest tooth on the lower pharyngeal jaw, as an indicator of molarity). Notice the extreme bimodality of the distribution of the morphology in the trophic morphs.

Correlation between sex, colour and PJA polymorphism

Both sexes of *C. citrinellum* from Lake Jilola have equal proportions of molariform PJA individuals (Table 1) and I conclude that sex and PJA morph are not associated. Sex linkage, in the strict genetic sense, however, cannot be ruled out; breeding experiments must be conducted to investigate this possibility.

The only population for which a sufficient number of 'gold' *C. citrinellum* was available in my collections is from Lake Nicaragua. There is a significant

TABLE 1. Correlation of sex and pharyngeal jaw morphs in Lake Jilola. The *C. citrinellum* (N = 38) were collected in the rainy seasons 1969 (UCB # 909, 910 [collection numbers refer to collections deposited at the Department of Zoology at the University of California at Berkeley]) and 1971 (collection Yale University). All fish were of 'normal' (black) colour. Immature fish were excluded from the analysis because sex could not be determined with certainty. The pharyngeal jaw morph is not correlated with sex ($\chi^2 = 0.125$, d.f. = 1, $P > 0.05$)

Sex	Number of individuals		
	Molariform	Papilliform	Total
Female	37 (79%)	10 (21%)	47
Male	24 (73%)	9 (27%)	33
Total	61 (76%)	19 (24%)	80

TABLE 2. Association between jaw morph and colour in *C. citrinellum* from Lake Nicaragua. Fish are from collections made in 1987, and were bought from fishermen and caught off the islands in Lake Nicaragua (see text). Colour is significantly associated with the PJA morph ($\chi^2 = 8.804$, d.f. = 1, $P < 0.005$)

Colour	Number of individuals		
	Molariform	Papilliform	Total
'Gold'	13 (43%)	17 (57%)	30
'Normal'	52 (76%)	16 (24%)	68
Total	65 (66%)	33 (34%)	98

association between the colour of the fish and their pharyngeal jaw morph for this lake (Table 2, $\chi^2 = 8.804$, d.f. = 1, $P < 0.005$); 'normal' *C. citrinellum* have molariform PJAs more frequently.

II. Ecological differences between the trophic morphs

Dietary differences between the PJA morphs

The morphology of the molariform PJA adapts the cichlid for crushing snails (Hoogerhoud & Barel, 1978; Liem & Kaufman, 1982; Hoogerhoud, 1986a; Meyer, 1988). Molariform morphs of *C. citrinellum* can crack significantly larger and harder snails than papilliform morphs (Meyer, 1989). However, papilliform morphs are more efficient at feeding on soft prey (Meyer, 1989). They have a shorter handling time for soft prey than molariform morphs.

I examined the stomach contents of *C. citrinellum* of both morphs from Lake Jilola. The performance differences of both morphs seem to translate into ecological differences: in the wet season 94% of molariform morphs of *C. citrinellum* had fed on hard hydrobiid snails but only 19% of the papilliform

TABLE 3. Presence of snails in the stomach contents. *Cichlasoma citrinellum* were collected at the end of the rainy season 1969 in Lake Jilola (UCB# 909, 910). Thirty-eight stomachs were examined, four were empty (all from fish of the molariform morph). The fish ranged in size from 50.4 mm SL to 116.5 mm SL. The mean SL did not differ between the groups. The differences between the molariform PJA and the papilliform PJA were highly significant ($\chi^2 = 20.037$, d.f. = 1, $P < 0.000$)

Jaw morph	Number of individuals		
	No snails	Snails	Total
Molariform PJA	1 (6%)	17 (94%)	18
Papilliform	13 (81%)	3 (19%)	16
Total	14 (40%)	20 (59%)	34

TABLE 4. Overall frequency of the pharyngeal jaw morphs of *Cichlasoma citrinellum* and the abundances of snails in five Nicaraguan lakes. Fish were collected in the wet seasons of 1969, 1971 and 1987 and the dry season of 1970. Snails were collected in July 1987 (see text). The mean number of snails collected per sampled area is given. 127 jaws were dissected and measured. 498 jaws were inspected optically only (with an otoscope): N=625. (Mo = Molariform; Pa = Papilliform; Pa/Mo = intermediate form; N = sample size of fish collected). Abundance of snails was determined through samples along a transect line; means of ten samples are given (— indicates that that habitat was not sampled)

Lake	Percent of individuals				Abundance of snails
	Mo	Pa	Pa/Mo	N	
Nicaragua (islands)	67%	29%	4%	155	—
Nicaragua (shore)	7%	93%	0%	40	0
Masaya	0%	100%	0%	68	0
Jilola	50%	49%	1%	136	111.5
Apoyo	17%	70%	13%	53	75.5
Managua	21%	71%	8%	79	—

morphs did so (Table 3). The amounts of soft prey present in stomachs were not quantified.

Distribution of the morphs in Nicaraguan lakes

The relative frequencies of the morphs differ among the lakes in a striking manner. In Lake Mayasa all specimens of *C. citrinellum* are of the papilliform pharyngeal morph while in all other lakes, fish of both morphs exist in differing frequencies (Table 4). I also examined specimens of the closely related sister taxa *C. labiatum* (Barlow & Munsey, 1976; Villa, 1976) (endemic to Lakes Nicaragua and Managua; N=29), *C. zaliosum* (endemic to Lake Apoyo; N=14) and laboratory-reared specimens of *C. citrinellum* from Lake Masaya (N=51). All inspected specimens of these three groups were found to be papilliform.

The abundance of snails

The abundance of the main food item, snails, is correlated with the abundance of molariform morphs (Table 4). In 1987, the snails were most abundant in Lake Jilola, less frequent in Lake Apoyo, and totally absent from Lake Masaya and the sampled area of Lake Nicaragua (the shore at the city of Granada). The proportion of fish with molariform PJA caught in the same season in each of these populations, accorded with the abundance of snails.

Seasonal fluctuation in the frequencies of PJA morphs

In the dry season sample the proportion of fish with molariform PJA collected was low compared with the wet season sample. For Lake Jilola this difference was 67% in the wet season compared with 5% in the dry season; for Lake Apoyo the frequency of the molariform morphs dropped from 40% to 21% during the dry season (Table 5). These differences in the frequency of morphs are statistically significant (Table 5).

TABLE 5. Distributions of the molariform and papilliform morphs during the end of the wet seasons 1969 and 1971 and the dry season 1970 for Lakes Jilola and Apoyo. Data from two collections made during the wet season from Lake Jilola were used for the stomach contents analysis. The difference in the frequencies of morphs is significantly different for Lake Jilola ($\chi^2 = 45.9$, d.f. = 2, $P < 0.000$) and Lake Apoyo ($\chi^2 = 7.04$, d.f. = 2, $P < 0.05$).

Collection number	Date	Percent of individuals			Total
		Mo	Pa	Pa/Mo	
Lake Jilola					
Wet season					
909	1 VIII 1969	33%	66%	0%	15
910	1 VIII 1969	74%	26%	0%	23
Yale University	24 V 1971	72%	24%	4%	58
overall:		67%	31%	2%	96
Dry season					
1060	15 IV 1970	10%	90%	0%	20
1081	15 IV 1970	0%	100%	0%	20
overall:		5%	95%	0%	40
Lake Apoyo					
Wet season					
1053	2 VIII 1969	22%	44%	33%	18
961	2 VIII 1969	40%	60%	0%	5
1070	2 VIII 1969	10%	80%	10%	10
overall:		21%	58%	21%	33
Dry season					
963	13 IV 1970	10%	90%	0%	20

DISCUSSION

Cichlasoma citrinellum is trophically polymorphic and the PJA morphs are ecologically separated. The colour morphs of this polychromatic species, which are associated with the PJA morphology, show a mating preference for their own colour (McKaye & Barlow, 1976; McKaye, 1980, 1986). Ninety-five per cent of all mated pairs in the field are of the same colour (McKaye & Barlow, 1976; McKaye, 1980, 1986). Because colour and PJA morphology are associated (Table 2), the ecological separation of the morphs and the mating preference for their own colour may affect the evolutionary future of this polymorphic species. The potential role of the environment in determining the morphology of the PJA in *C. citrinellum* (see below) contrasts with the situation in *C. minckleyi* in which the morphology of the PJA is believed to be entirely genetically determined (Kornfield & Taylor, 1983).

What causes the expression of different PJA morphs?

The occurrence of different frequencies of PJA morphs in the lakes and between seasons within particular lakes may be due to migration or variation in sampling technique—these were identical for the three crater lakes, ruling out sampling differences as causal factors, but the fish from the two big lakes were caught by techniques different at the shore compared to the islands. The

abundance of molariform morphs apparently varies spatially within Lake Nicaragua.

Differences in the proportions of the PJA morphs in the lakes could be caused by interpopulational genetic differences stemming from founder effects, genetic drift or selection, or in part, by sampling error. I am currently using mitochondrial DNA (mt DNA) sequences to investigate genetic differences between populations and morphs. So far no differences in mt DNA sequences of a 360 basepair portion of the mitochondrial cytochrome b gene have been detected either between morphs within Lake Jilola or *C. citrinellum* from Lake Masaya; the sequences are also identical with those from the closely related species *C. labiatum* (Kocher *et al.*, 1989; Meyer, unpublished). Yet, this portion of the cytochrome b gene, contains phylogenetic information that is useful in the establishment of phylogenetic relationships among diverse species of cichlids within the genus *Cichlasoma* and on the level of the whole family Cichlidae (personal observations).

The abundance of snails is correlated with the abundance of molariform morphs of *C. citrinellum* (Table 4). The greatest abundance of snails was expected from Lake Nicaragua where the highest frequency of individuals with molariform PJAs occurs. This lake is the largest, and the distribution of snails is apparently uneven. During the wet season of 1987 (July) snails were absent from the shore of Lake Nicaragua at the city of Granada (Table 4). *Cichlasoma citrinellum* caught in 1987 at the shore off Granada, where the bottom samples were taken, were predominantly of the papilliform PJA type (Table 4).

Most *C. citrinellum* from Lake Nicaragua were purchased in the fish market at Granada. The fish sold at this market are caught with gill nets and hook and line fishing off the islands (Davies, 1976; personal observations). Bottom samples from these areas of the lake were not available, but fishermen from Lake Nicaragua claim that snails are abundant there (personal communication).

Hoogerhoud (1986a, b) found that the abundance of snails correlates with the frequency of molariform PJA morphs of *Astatoreochromis alluaudi* in Africa and believes that they are causally related. In this connection, it should be noted that molluscivorous cichlids appear to be able to influence significantly the abundance of their prey (McKaye, Stauffer & Louda, 1986).

Phenotypic plasticity of the PJA?

One explanation for the morphological differences is environmental influence. During ontogeny the PJAs of all the fish I examined were initially of the papilliform type and only a subset of the population developed a molariform PJA with age.

In an experiment designed to test the influence of the environment on the phenotypic expression of the PJA, I raised a group (N=12) of normally coloured, wild-caught, juvenile *C. citrinellum* with papilliform PJAs from Lake Jilola on a hard-snail diet in an outdoor pond for more than one year. At the start of the experiment the fish were already of a size at which the trophic morphs can be distinguished. Within less than six months the PJA in two fish changed from its originally papilliform type to an intermediate or molariform one. In the control group (N=23), fed on a soft diet, none of the fish showed a change in PJA morphology. I assume that epigenetic mechanisms, through the action of

eating snails, and the different texture of the prey, induced the formation of a more molariform pharyngeal dentition in two of the 12 fish. Phenotypic plasticity of the PJA morphology has been demonstrated in the African cichlid *Astatoreochromis alluaudi* (Greenwood, 1965; Hoogerhoud, 1986a). Since, the teeth on the pharyngeal jaws are replaced constantly in cichlids (Huysseune, 1983) and bone is mouldable and phenotypically plastic (e.g. Watt, 1951; Rubin & Lanyon, 1984; Meyer, 1987) these results are perhaps to be expected.

Further support for the partly phenotypically plastic nature of the PJA is based on the observation that when the offspring of fish from Lake Nicaragua, in which 67% of the population have molariform PJAs (Table 4), were raised on a relatively soft pellet diet for at least two generations; fish developed only papilliform PJAs (personal observations).

If the environmental influence on the PJA morphology were strong, one might speculate that the PJA morphology is not fixed during ontogeny but instead can be reversed, possibly tracking the potentially fluctuating abundance of snails through seasons (Table 5). Gossler (1987) found a seasonal variation in bill morphology within individuals of Great tits, *Parus major*, which seemed to adapt the birds to particular prey items that varied in abundance between seasons.

Ecological implications of trophic polymorphism

The abundance of snails can vary between seasons in African lakes (e.g. Katunzi, 1983). No data on variation in the abundance of snails between seasons and years in Nicaraguan lakes are available. Yet, in the dry season only 5% of the fish were of a molariform PJA type (Table 5), and only one individual of that type had fed on snails.

Liem & Kaufman (1984) investigated the functional morphology of the trophically polymorphic *Cichlasoma minckleyi*. They suggested that the molariform morph has a selective advantage during period of low food abundance because it feeds more often on snails, the less preferred prey (softer prey are preferred in the laboratory; personal observations). The obvious advantage of the molariform morph raised the question: why are not all cichlids molariform?

The cost of being molariform is that papilliform fish feed more efficiently on softer prey than molariform morphs (Meyer, 1989). However, molariform fish can crack significantly harder snails than papilliform morphs (see above).

These laboratory findings are important for ecological and evolutionary scenarios that try to explain the origin of specialization; they support the notion that specialists can exploit a particular type of prey, which they are adapted to feed on, more efficiently than generalists. The PJA morphs probably have different fitnesses in their presumed feeding niches and habitats. This could translate into different abilities to survive a potential food shortage. Specialists may have a selective advantage during ecological bottlenecks. Selection for morphological specialization should be strongest during these periods and weaker during periods when prey is abundant.

Implications for taxonomy

The pharyngeal jaws and the shape of the neurocranial apophysis of cichlid fishes are important taxonomic characters. Greenwood (1959) described two

subspecies of *Astatoreochromis alluaudi* based on differences in the molarization of the PJA apparatus. Later Greenwood (1965) found that this character is phenotypically plastic and suggested that the subspecific status of the two PJA morphs be dropped. However, he (1980) used differences similar to the degree of differential molarization found between the morphs in *C. citrinellum* and *C. minckleyi* to distinguish between two genera of African cichlids (*Gaurochromis* and *Labidochromis*); he also used other characters, that may not be phenotypically plastic or polymorphic within species. See Hoogerhoud (1984) for a critique of the validity of these genera.

The phenotypic variation that was induced through dietary differences in the neotropical cichlid *Cichlasoma managuense* was large and revealed that the whole cranium of cichlids can be phenotypically plastic (Meyer, 1987). This finding suggests that many more cichlid species of both hemispheres will be found to be phenotypically plastic and/or polymorphic (see also, Meyer, 1987, 1990b; Vriejenhoek, Marteinsdottir & Schenck, 1987; Witte & Witte-Maas, in press). I discovered that *C. haitensis* is also polymorphic in its PJA structure (Meyer, 1990b). The extreme degree of phenotypic plasticity possible in cichlid fishes may be an adaptive characteristic that would allow the fish to track changing ecological (e.g. varying prey densities), and therefore functional-morphological, demands. The amount of variation in cichlid fishes may not be exceptional but may be typical for other fishes and animals in general (Turner & Grosse, 1980; West-Eberhard, 1986; Allendorf, Ryman & Utter, 1987; Gossler, 1987; Meyer, 1987).

Intraspecific macroevolution and developmental constraints

Liem & Kaufman (1984), in referring to the genetically based polymorphism in *C. minckleyi*, emphasized its possible importance for macroevolution (coining the phrase 'intraspecific macroevolution'). Also, Greenwood (1979) cited this case as an example for nascent macroevolution at the intraspecific level, defining macroevolution as the origin and diversification of higher taxonomic categories. These categories are made up of lineages that possess certain key morphological and functional features which allow these taxa to utilize food sources that are denied to others not having these characteristics (Greenwood, 1974). In the case of the cichlids of the East African Rift lakes one may cite the presence of the PJA as a key innovation that allowed them to radiate into uncounted ecological niches, speciate rapidly, and achieve extremely high levels of endemism, whereas members of other fish families did not undergo such impressive radiations.

The importance of internal factors as constraints for macroevolutionary phenomena have recently been re-emphasized (Alberch *et al.*, 1979; Alberch, 1980, 1982a, b; Alberch & Alberch, 1981; Katz, Lasek & Kaiser-Abramof, 1972; Gould, 1982; Atchley, 1987). Liem & Kaufman (1984) suggested that internal constraints during development may canalize the expression of distinct PJA morphs in *C. minckleyi*. The convergent adaptations of the molluscivorous cichlids of both hemispheres have also been cited as evidence in support for this point of view (Hoogerhoud & Barel, 1978; Liem & Kaufman, 1984; Barel, 1983). Epigenetic mechanisms may be canalizing, directing agents of evolutionary diversification.

Adaptations for snail feeding encompass the whole molariform *Gestalt* of the fish (e.g. morphology of the branchial skeleton and the neurocranium). Many features of the molariform morphology are mutually exclusive with a papilliform morphology. This is because perturbations in one structural component will often lead to a cascading sequence of changes in associated structures (Dullemeijer, 1974, 1980) through linkages between functional systems (Lauder *et al.*, 1989).

Intermediates in morphology were rare in *C. minckleyi* (less than 5%, Kornfield & Taylor, 1983) and *C. citrinellum* (Table 4, Fig. 4). During ontogeny the morphology of the two morphs diverges and only young 'undetermined' fish show the intermediate morphology (Fig. 3). The earliest occurrence of a molariform PJA during ontogeny may be determined by a balance of external and internal selection pressures, that is the functional demands of snail cracking, which are determined by the softest, smallest snails available in the environment, and the ontogenetic developmental pathways that can lead to a molariform *Gestalt*.

Polymorphisms as intermediate steps during (sympatric) speciation

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 (for review see Thoday, 1953, 1972) may in part explain the large number of cichlid species. The family Cichlidae probably consists out of more than 1000 species, more than 100 species used to belong to the neotropical genus *Cichlasoma* alone (Kullander, 1983). Colour polymorphisms may, as could be the case in *C. citrinellum*, drive speciation through behaviorally mediated sexual selection as well (Dominey, 1984; but see Kornfield & Taylor, unpublished).

It appears that in *C. citrinellum*, because colour and jaw morph are associated, we may find a synergistic effect of ecological differentiation and sexual selection. Molariform morphs may have a performance advantage during ecological bottlenecks when other preferred food sources become less available. They appear to occupy an ecological niche different from that of their papilliform conspecifics. This could lead to or be caused by differential habitat utilization by the two morphs, could influence mate choice and eventually lead to reproductive isolation and to speciation. This is similar to Grant's (1986) suggestion for Darwin's finches, namely that reproductive isolation evolved as a correlated effect of the birds' ecological and morphological diversification. Sympatric speciation may have played a role in the evolutionary history of Darwin's finches (Grant, 1986; Grant & Grant, 1979, 1989).

Because snails occur in higher densities in shallow water than in deeper water (personal observation), one might expect to find molariform PJA fish in higher frequencies in shallower water. If mate choice and pair formation took place in the respective habitats of the morphs, then habitat choice will influence mate choice. Therefore, if different morphs chose different habitats, then the possibility exists that genetic differentiation between the two morphs would be enhanced. The association in *C. citrinellum* between colour and PJA morphology, although relatively weak, and the known mating preference for individuals of their own colour seems to support this scenario.

Phenotype-dependent competition for resources may lead to sympatric speciation (Rosenzweig, 1978; Seger, 1985). Therefore polymorphisms may be speeding up speciation events and be intermediate steps during the formation of new taxa. For this scenario it does not matter whether the phenotypic polymorphism is entirely genetically determined, a pleiotrophic effect of, for example, a genetically determined habitat preference, or linked to genes coding for colour.

The Maynard Smith model of sympatric speciation (1966; see also Thoday, 1972) predicts that the trophic or colour morphs of *C. citrinellum* should, in the second step during sympatric speciation, exhibit assortative mating, or should choose different habitats or be reproductively isolated in some other way. Not all necessary data are available to judge whether *Cichlasoma citrinellum* is in the process of speciating in sympatry. However, some observations lend support to a sympatric speciation scenario in this species. The colour morphs of *Cichlasoma citrinellum* breed assortatively in the field and under certain conditions in the laboratory (Barlow, 1983; G. W. Barlow, personal communication). Fewer than 5% of the pairs sighted in the field were heterochromatic (McKaye & Barlow, 1976; McKaye, 1980, 1986). McKaye & Barlow (1976; also McKaye, 1977, 1980) reported different habitat use during the breeding season by the colour morphs of *C. citrinellum* in Lake Jilao, with 'golds' occurring at greater depths than 'normals'. McKaye (1980) believes that *C. citrinellum* is in the process of speciating sympatrically, although he does not provide an ecological mechanism by which the two colour morphs may avoid direct competition for resources. The two PJA morphs seem to be ecologically separated on their dietary differences (Table 3) and their differences in feeding performance (Meyer, 1988). The differences in body morph between 'limnetic' and 'benthic' morphs further suggests ecological separation through differential habitat use (Meyer, 1988, 1990a).

Body morph polymorphisms are known from other species of fishes, e.g. bluegill sunfish (Ehlinger & Wilson, 1988), and the arctic Charr *Salvelinus alpinus* (see recent reviews in Magnusson & Ferguson, 1987; Jonnsson *et al.*, 1988) and are believed to cause habitat segregation between the morphs.

I have no data to suggest that there is a PJA-specific mating preference *per se*. In a large outdoor pool, in which more than 30 specimens of *C. citrinellum* were kept, I found that the only molariform female mated with a papilliform male of the colour. Field collections of pairs and controlled mate choice experiments are needed to establish unequivocally whether mate choice occurs with respect to PJA morphology.

Felsenstein (1981) showed that the genetic linkage between two loci that code for habitat choice and mate choice must be very tight for sympatric speciation to occur. Whether this linkage exists and how strong it is in this species is unknown. It remains to be tested whether this species is in the process of speciation. If it is, it may indicate that this is a common phenomenon in the evolution of species flocks of cichlid fishes. However, the role of colour would only apply to species which are sexually dichromatic; this is not an unusual situation in African cichlid species flocks. I suggest that the scenario introduced in this paper may provide a plausible mechanism that could explain the rapid evolution of cichlid species assemblages.

ACKNOWLEDGEMENTS

I wish to thank L. Safram, M. Rothberg, and M. Conboy from Harvard University and particularly R. Stierwaldt from the University of California at Berkeley for technical assistance in the laboratory. M. Conboy helped during the 1987 field collection in Nicaragua and Karen Klitz for Fig. 2. S. Allison, K. Barel, G. W. Barlow, M. Condic, R. J. C. Hoogerhoud, L. S. Kaufman, I. Kornfield, K. F. Liem, J. Losos, E. Mayr, S. Naeem, W. P. Sousa, M. L. J. Stiassny, D. B. Wake, M. H. Wake and A. C. Wilson provided thoughtful and constructive criticism on earlier drafts of the manuscript. I would especially like to thank my thesis committee: G. W. Barlow, M. H. Wake, W. P. Sousa and A. C. Wilson for all they have done for me during my time at Berkeley. I. Kornfield and J. Taylor and P. R. and B. R. Grant kindly provided unpublished manuscripts. Part of this study was conducted while I was a Visiting Scholar at Harvard University. The hospitality and support of all members of the Fish Department at Harvard University, particularly K. Liem and M. Stiassny, are gratefully acknowledged. Travel to Central America and museum collections was funded through a Noyes grant from the Organization for Tropical Studies, a travel award from 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 by the German and the American Fulbright Commissions and the University of California at Berkeley. George Barlow provided advice and support through NIH grant 18612; his work and that of his students significantly helped in the conduct of this study; the field collections of 1969 and 1970 were his and were generously provided by him for this study. Additional specimens from the collections of the American Museum of Natural History in New York, the Field Museum of Natural History in Chicago and the Yale Peabody Museum in New Haven were generously provided by those institutions. IMPESCA and ENMAR in Nicaragua granted permits and their officers Sergio Martinez and Nussli Ruiz aided in many other aspects of the collections and work in Nicaragua. All persons and institutions that aided this study are gratefully acknowledged.

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