

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

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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.

CONTENTS

Introduction	
Evolutionary success through key novelties: the pharyngeal jaw apparatus of labroid fishes	280
Morphological adaptation and feeding ecology	280
Intraspecific variation and polymorphisms in cichlids	281
Phenotypic plasticity in cichlid fishes	282
Methods	282
Results	284
I. Morphological description of the polymorphism	284
II. Ecological differences between the trophic morphs	287

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Discussion	289
What causes the expression of different PJA morphs?	289
Phenotypic plasticity of the PJA?	290
Ecological implications of the trophic polymorphism	291
Implications for taxonomy	291
Intraspecific macroevolution and developmental constraints	292
Polymorphisms as intermediate steps during (sympatric) speciation	293
Acknowledgements	295
References	295

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-McConnell, 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.*, 1983; Liem & Greenwood, 1981; Liem & Greenwood, 1983; Liem & Greenwood, 1984; Liem & Greenwood, 1985; Liem & Greenwood, 1986; Liem & Greenwood, 1987; Liem & Greenwood, 1988; Liem & Greenwood, 1989; Liem & Greenwood, 1990; Liem & Greenwood, 1991; Liem & Greenwood, 1992; Liem & Greenwood, 1993; Liem & Greenwood, 1994; Liem & Greenwood, 1995; Liem & Greenwood, 1996; Liem & Greenwood, 1997; Liem & Greenwood, 1998; Liem & Greenwood, 1999; Liem & Greenwood, 2000; Liem & Greenwood, 2001; Liem & Greenwood, 2002; Liem & Greenwood, 2003; Liem & Greenwood, 2004; Liem & Greenwood, 2005; Liem & Greenwood, 2006; Liem & Greenwood, 2007; Liem & Greenwood, 2008; Liem & Greenwood, 2009; Liem & Greenwood, 2010; Liem & Greenwood, 2011; Liem & Greenwood, 2012; Liem & Greenwood, 2013; Liem & Greenwood, 2014; Liem & Greenwood, 2015; Liem & Greenwood, 2016; Liem & Greenwood, 2017; Liem & Greenwood, 2018; Liem & Greenwood, 2019; Liem & Greenwood, 2020; Liem & Greenwood, 2021; Liem & Greenwood, 2022; Liem & Greenwood, 2023; Liem & Greenwood, 2024; Liem & Greenwood, 2025). This species is believed to be responsible for the evolution of the neurocranial structures characters (Trewavas,

I (Meyer, 1988, 1990) jaw structure of a neo-labroid (Barlow, 1976; Barlow, 1977; Barlow, 1978; Barlow, 1979; Barlow, 1980; Barlow, 1981; Barlow, 1982; Barlow, 1983; Barlow, 1984; Barlow, 1985; Barlow, 1986; Barlow, 1987; Barlow, 1988; Barlow, 1989; Barlow, 1990; Barlow, 1991; Barlow, 1992; Barlow, 1993; Barlow, 1994; Barlow, 1995; Barlow, 1996; Barlow, 1997; Barlow, 1998; Barlow, 1999; Barlow, 2000; Barlow, 2001; Barlow, 2002; Barlow, 2003; Barlow, 2004; Barlow, 2005; Barlow, 2006; Barlow, 2007; Barlow, 2008; Barlow, 2009; Barlow, 2010; Barlow, 2011; Barlow, 2012; Barlow, 2013; Barlow, 2014; Barlow, 2015; Barlow, 2016; Barlow, 2017; Barlow, 2018; Barlow, 2019; Barlow, 2020; Barlow, 2021; Barlow, 2022; Barlow, 2023; Barlow, 2024; Barlow, 2025).

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Cichlid fishes are believed to have evolved from a common ancestor (Fryer & Iles, 1972; van Oijen & Liem, 1982; Hoogerhoud, Witte & Liem, 1983; Liem, 1984; Liem, 1985; Liem, 1986; Liem, 1987; Liem, 1988; Liem, 1989; Liem, 1990; Liem, 1991; Liem, 1992; Liem, 1993; Liem, 1994; Liem, 1995; Liem, 1996; Liem, 1997; Liem, 1998; Liem, 1999; Liem, 2000; Liem, 2001; Liem, 2002; Liem, 2003; Liem, 2004; Liem, 2005; Liem, 2006; Liem, 2007; Liem, 2008; Liem, 2009; Liem, 2010; Liem, 2011; Liem, 2012; Liem, 2013; Liem, 2014; Liem, 2015; Liem, 2016; Liem, 2017; Liem, 2018; Liem, 2019; Liem, 2020; Liem, 2021; Liem, 2022; Liem, 2023; Liem, 2024; Liem, 2025).

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Traditionally, taxonomic morphological variation (polymorphisms) and speciation (Meyer, 1987, 1990b; van Oijen & Liem, 1982; Liem, 1984; Liem, 1985; Liem, 1986; Liem, 1987; Liem, 1988; Liem, 1989; Liem, 1990; Liem, 1991; Liem, 1992; Liem, 1993; Liem, 1994; Liem, 1995; Liem, 1996; Liem, 1997; Liem, 1998; Liem, 1999; Liem, 2000; Liem, 2001; Liem, 2002; Liem, 2003; Liem, 2004; Liem, 2005; Liem, 2006; Liem, 2007; Liem, 2008; Liem, 2009; Liem, 2010; Liem, 2011; Liem, 2012; Liem, 2013; Liem, 2014; Liem, 2015; Liem, 2016; Liem, 2017; Liem, 2018; Liem, 2019; Liem, 2020; Liem, 2021; Liem, 2022; Liem, 2023; Liem, 2024; Liem, 2025).

An example of a taxonomic concept is seen in the evolution of a pronounced, genetic polymorphism (Kornfield & Taylor, 1984) dealing with two distri-

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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 &

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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 Jilóa, Apoyo and Masaya are isolated small crater lakes whereas Lake Managua and Lake Nicaragua are large lakes connected to the Atlantic ocean. Because Lake

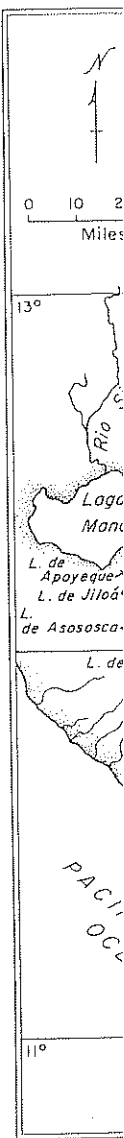


Figure 1. Map of Nicaragua reproduced with permission from Meyer (1987).

Jilóa is the best site for *C. citrinellum* from the Pacific coast. Fish were collected from a lake with a diameter of the tooth-bearing area intermediate in size to other specimens were collected from the Pacific coast.

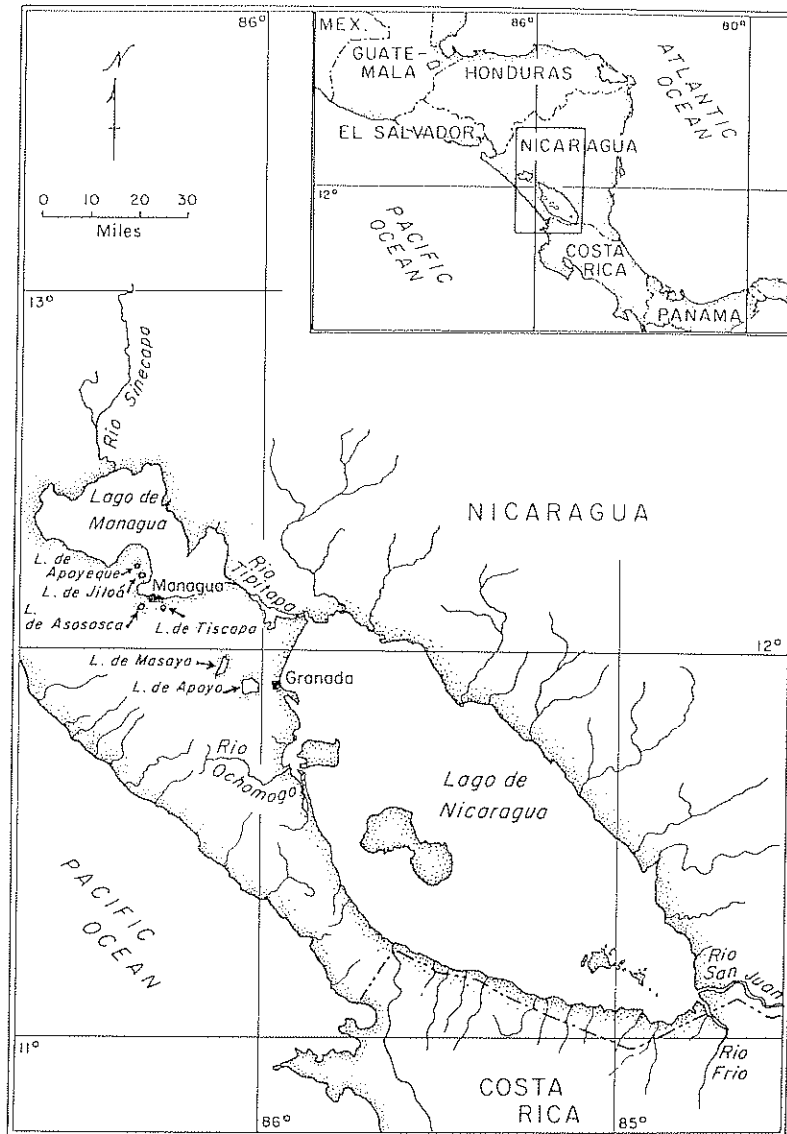


Figure 1. Map of Nicaragua showing the location of the lakes sampled (from Barlow, 1976; fig. 1, reproduced with permission).

Jiloa 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 Jiloa 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).

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In the wet season 1987 (July) bottom samples were collected from Lakes Jiloa, 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

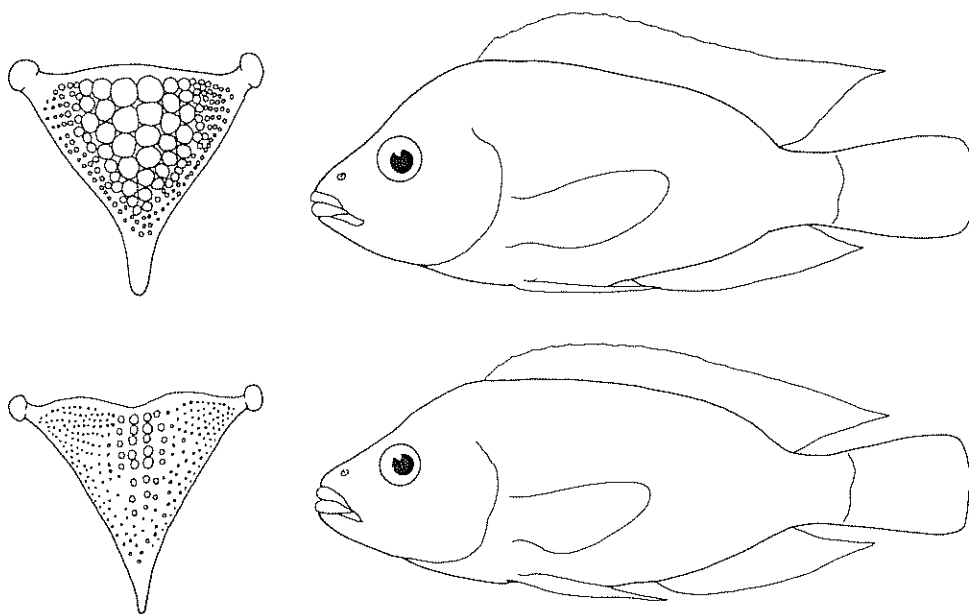


Figure 2. Semi-schematic drawing of the differences in body shape and pharyngeal jaw morphology in *C. citrinellum*. Above: morphs with a molariform type of PJA. Below: morph with a papilliform PJA type. Molariform PJA morphs have a shorter, blunter snout, wider head, larger eye, deeper and shorter body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

Cichlasoma citrinellum the apophysis for the upper for their stronger upper

Differences in external morph (Fig. 2, Meyer, snouts, larger eyes, wider morphs (Fig. 2). Molariform 'limnetic' body form (slender external morphology not feeding and manoeuvring morphology of the papilliform the more open limnetic

Ontogenetic trends

In *C. citrinellum*, as with fish initially exhibit a papilliform. The smallest specimens are molariform "Gestalt" in length. As fish in this become molariform; later. As a result of these distinctions the trophic morphs are pronounced during ontogeny

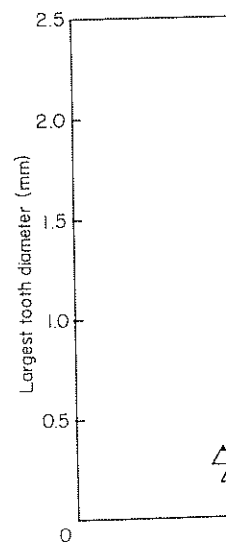


Figure 3. Ontogenetic morphs of *C. citrinellum* jaw was measured and differ between fish of the largest tooth on the. The only fishes of distinctions between

from Lakes Jiloa, in 1 m intervals sample area was

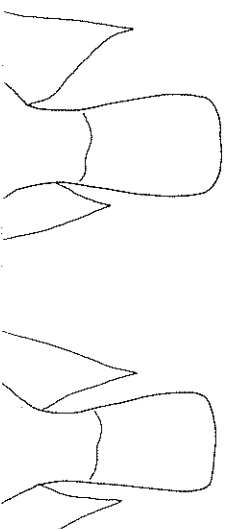
Cichlasoma citrinellum the molariform morph has a more massive neurocranial apophysis for the upper pharyngeal bone; it provides a larger articulation surface for their stronger upper pharyngeal elements (Meyer, 1988, 1990a).

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).

ch resembles that & Taylor, 1983; heavier lower and papilliform morph and pointed than pharyngeal jaw is more molariform morph the shorter and stouter, mature. Correlated of the branchial the crushing phase Meyer, 1988). In



pharyngeal jaw A. Below: morph inter snout, wider pharyngeal jaws seen from above.

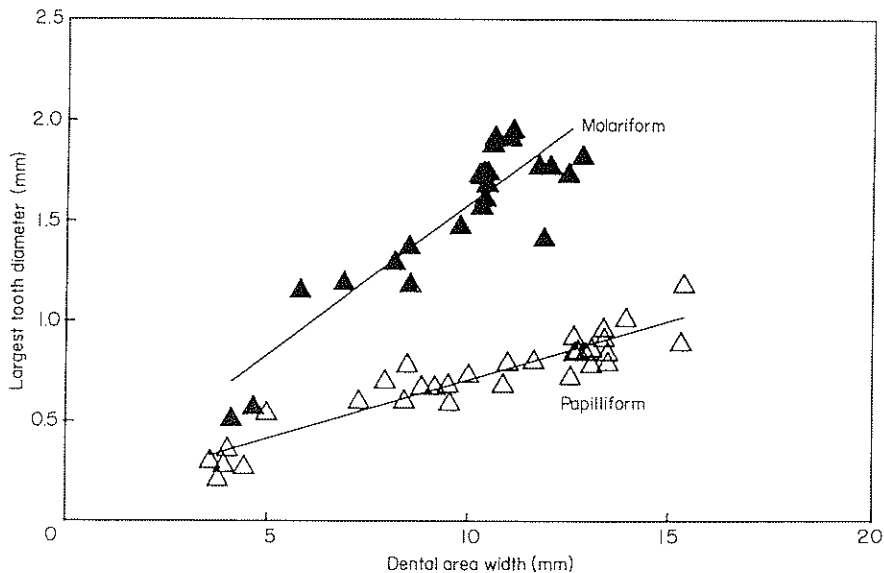


Figure 3. Ontogenetic trends of the developing PJA from molariform and papilliform PJA morphs of *C. citrinellum* from Lake Jiloa. The width of the dental area on the lower pharyngeal jaw was measured as defined by Barcl *et al.*, (1977: fig. 59). The dental area width does not differ between fish of 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.

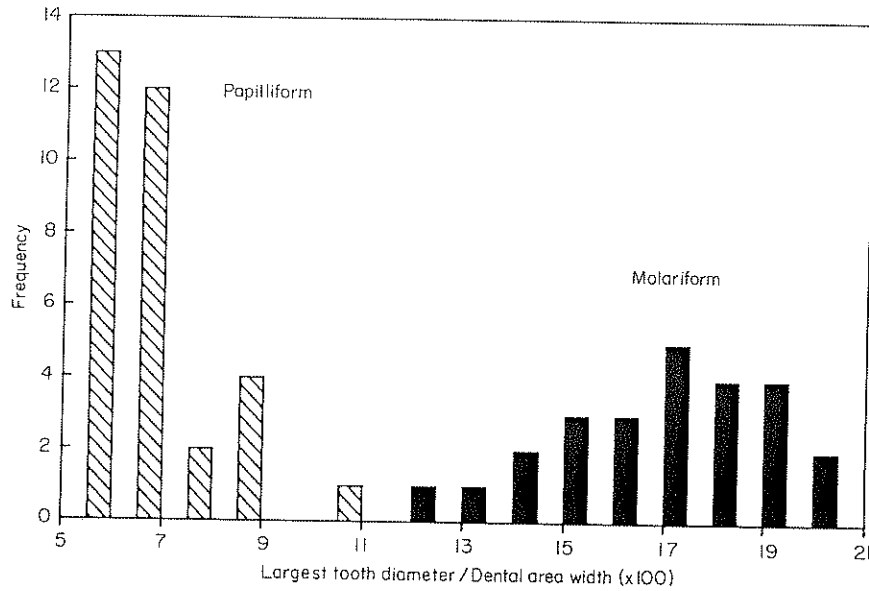


Figure 4. Frequency distribution of *C. citrinellum* from Lake Jiloa (measurement: diameter of the largest tooth on the lower pharyngeal jaw, as an indicator of molarity). Notice the extreme bimodality of the distribution of the morphology in the trophic morphs.

Correlation between sex, colour and PJA polymorphism

Both sexes of *C. citrinellum* from Lake Jiloa 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

association between this lake (Table 2) molariform PJAs n

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TABLE 1. Correlation of sex and pharyngeal jaw morphs in Lake Jiloa. 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

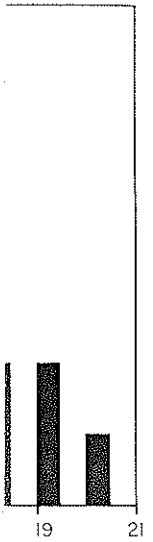
Dietary differences between the PJA morphs

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



diameter of the pharyngeal jaw

proportions of PJA morphs. However, cannot be this possibility. *C. citrinellum* was a significant

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 othoscope): 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			N	Abundance of snails
	Mo	Pa	Pa/Mo		
Nicaragua (islands)	67%	29%	4%	155	—
Nicaragua (shore)	7%	93%	0%	40	0
Masaya	0%	100%	0%	68	0
Jiloa	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 Masaya 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. zaliusum* (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 Jiloa, 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 Jiloa 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. ... during the 1970 for I ... during the contents a significantl

Collection r
Lake Jiloa
Wet season
909
910
Yale Unive
overall:
Dry season
1060
1081
overall:
Lake Apoyo
Wet season
1053
961
1070
overall:
Dry season
963

Cichlasoma citrinellum ecologically separate are associated with t colour (McKaye & all mated pairs in t McKaye, 1980, 19 (Table 2), the ecolog their own colour ma The potential role o in *C. citrinellum* (see l morphology of the (Kornfield & Tayl

Wh

The occurrence between seasons wit sampling technique sampling difference caught by techni