

EVOLUTION OF FISH SPECIES FLOCKS

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INTRASPECIFIC MACROEVOLUTION: FUNCTIONAL BIOLOGY OF THE POLYMORPHIC CICHLID SPECIES *CICHLASOMA MINCKLEYI*

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INTRODUCTION

Recently Kornfield et al. (1982, 1983) gave unequivocal evidence that *Cichlasoma minckleyi* is a distinctly polymorphic species, confirming an earlier hypothesis by Sage and Selander (1975). The differences between these two morphs led earlier workers to recognize them as distinct species (Taylor, Minckley 1966; Minckley 1969; La Bounty 1974; Kornfield, Koehn 1975). This striking intraspecific morphological and trophic differentiation, exceeding that found among many closely related and sympatric cichlid species has profound implications for evolutionary biology. 1) It might be associated with macroevolution and the formation of species flocks. 2) It may give us the best evidence yet as how very simple epigenetic mechanisms can produce rapid and quantum structural changes. 3) It gives us a unique opportunity to study incipient functional differentiation within a species. 4) Ecologically, such a polymorphic species behaves differently from a conventional species and may demonstrate fundamental mechanisms of the formation of species flocks by means of phenotypic tracking of the trophic resource abundance. We will review these four evolutionary implications in a detailed laboratory analysis of the deep-bodied forms of the papilliform and molariform morphs of *Cichlasoma minckleyi*.

MORPHOLOGY

Morphological differences between the two morphs can be summarized as follows: 1) The lower pharyngeal jaw in papilliform morphs is more delicate, possessing a significantly narrower outline with smaller horns (Figure 1: LPJ, PM, MM). 2) The gut in the molariform morph is significantly shorter (Smith 1982).

3) The neurocranial articulation of the upper pharyngeal jaw in the molariform morph is greatly expanded posteriorly and laterally, and is more massive (Kornfield, Taylor 1983; Figures 1, 2: AP). 4) Correlated with the hypertrophied pharyngeal jaw apparatus, head width is significantly greater in molariform morphs (Kornfield, Taylor 1983).

To these, we add the following important differences between the two morphs. The upper pharyngeal jaws in the molariform morph are more massive and significantly expanded posteriorly and laterally, with a distinctly convex posterior contour (Figure 1: UPJ). The fourth epibranchial bone in the molariform morph is not only enlarged, but has a more concave posterior outline, providing a larger tunnel for the passage of the hypertrophied fourth levator externus muscle (Figure 1: EB₄). The branchial musculature (Figures 2, 3) exhibits the most dramatic dichotomy between the morphs. In both morphs the levator externus 4 (LE₄), levator posterior (LP), retractor dorsalis (RD), obliquus posterior (OP), obliquus dorsalis (OD), and transversus dorsalis anterior (TDA) are hypertrophied when compared with those of more generalized cichlids. However, in the molariform morph, the levator externus 4 (LE₄), levator posterior (LP), and the retractor dorsalis (RD) undergo an immense increase in cross-sectional area (Figure 2), and undergo a complex differentiation in muscle architecture with the appearance of numerous tendinous elements and pinnations (Ono, Kaufman 1983; Figure 3). The hypertrophy and increased areas of origin and insertion of the fourth levator externus, levator posterior, and the retractor dorsalis have pronounced influences on the form and architecture of the neurocranium and

papilliform molariform

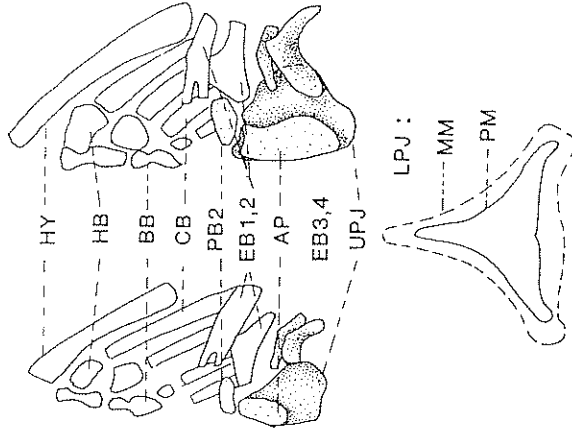
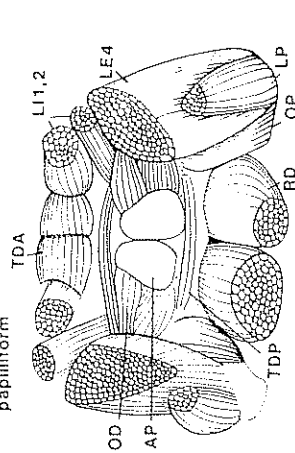


Figure 1. Dorsal view, right half of branchial arches of *Cichlasoma minckleyi*. First pharyngobranchial removed. 6.9 cm SL, each specimen. Lower pharyngeal jaw (LPJ) outlines on bottom are ventral views of molariform morph (MM) and papilliform morph (PM). Code: AP, pharyngeal apophysis of upper pharyngeal jaw; BB, basibranchial; CB, ceratobranchial; EB1-4, epibranchial 1-4; HB, hypobranchial; HY, hyoid; LPJ, lower pharyngeal jaw; MM, molariform morph; PB2, second pharyngobranchial; PM, papilliform morph.

lower pharyngeal jaws (Figures 1,4). The enlarged sites of origin of the fourth levator externus and levator posterior (Figure 4:LE4, LP) in the molariform morph are correlated with an increase in neurocranial width behind the orbit and the expansion of the posterolateral corner of the neurocranium. Similarly, the hypertrophied retractor dorsalis (Figure 3:RD) is correlated with an enlarged fourth vertebral apophysis and changes in the form and architecture of the first four vertebrae. The insertion site of the hypertrophied fourth levator externus, levator posterior, and retractor dorsalis muscles have also undergone concomitant hypertrophy as is evident from the massive horns of the lower pharyngeal jaw in the molariform morph (Figure 1:LPJ, MM, PM).

Other dorsal branchial muscles exhibiting

papilliform



molariform

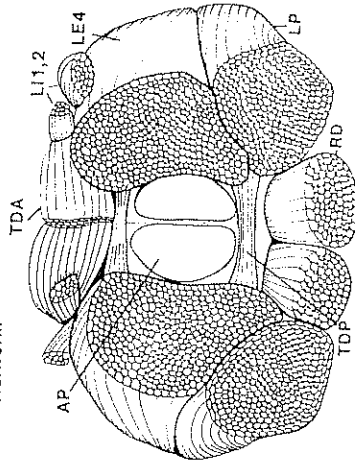


Figure 2. Dorsal view of branchial musculature of *Cichlasoma minckleyi*. Levator posterior, levator externus 4, retractor dorsalis and levatores interni 1, 2 are sectioned. Papilliform morph, 7.2 cm SL; molariform morph, 7.0 cm SL. Code: AP, pharyngeal apophysis; LE4, fourth levator externus; LI 1, 2, levator interni 1, 2; LP, levator posterior; OD, obliquus dorsalis; OP, obliquus posterior; RD, retractor dorsalis; TDA, transversus dorsalis anterior; TDP, transversus dorsalis posterior.

distinct morphological dichotomies are the transversus dorsalis anterior, obliquus dorsalis, and obliquus posterior, all of which are hypertrophied in the molariform morph (Figure 2). However, the levatores interni 1 and 2 (Figure 2:LI1,2) are reduced drastically in the molariform morph.

The ventral branchial musculature (pharyngocleithralis externus and internus, pharyngohyoideus) is identical in the two morphs (Figure 3:PCE, PCI, PH). The pharyngeal and branchial musculature of *Cichlasoma cyanoguttatum*, from its extreme southern and northern localities, Parque, Chapultepec, Mexico, to Chacon Creek,

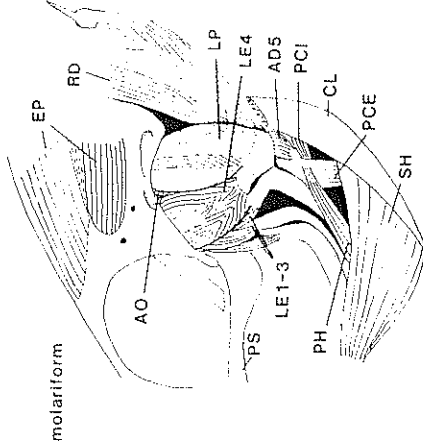
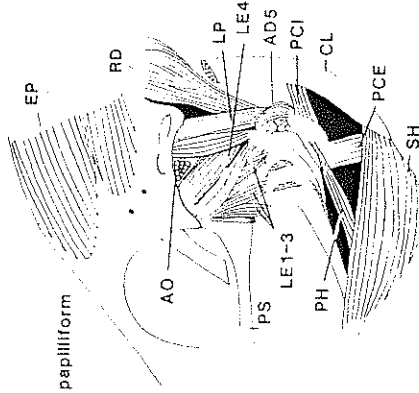


Figure 3. Lateral view of branchial musculature of *Cichlasoma minckleyi*. Code: AD5, fifth adductor branchialis; AO, adductor operculi; CL, cleithrum; EP, epaxial musculature; LE1-3, levatores interni 1-3; LE4, fourth levator externus; LP, levator posterior; PCE, pharyngocleithralis externus; PCI, pharyngocleithralis internus; PH, pharyngohyoideus; PS, parasphenoid; RD, retractor dorsalis; SH, sternohyoideus.

Texas, is virtually identical with that of the papilliform morph of *C. minckleyi*. No major intraspecific differences have been found in other myological and osteological systems. Partial molarization of the pharyngeal jaw apparatus occurs sporadically, but is not accompanied by the specializations so characteristic of the molariform morph of *C. minckleyi*.

FUNCTIONAL ANALYSIS

Prey Capture. The jaw muscles of the two *C. minckleyi* morphs and *C. cyanoguttatum* have been analyzed by high speed motion pictures and electromyography of 5 key muscles: the adductor mandibulae Part A₁, and Part A₂, sternohyoideus, levator operculi, and geniohyoideus. To determine the complete feeding repertoire, the experimental fishes were presented with a wide variety of prey in different positions in the water column (Liem 1980a,b). No major differences were found among the two morphs and *C. cyanoguttatum*. All three exhibited identical kinematic and electromyographic patterns during prey capture (Figure 5), with four feeding patterns:

- 1) Horizontal Suction. This most frequently employed pattern shows relatively little overlap of activity of the abductor and adductor muscles (Figure 5: sternohyoideus, SH; and levator operculi, LO; adductor mandibulae, AM₁, AM₂; geniohyoideus, GH). The upper jaw is protruded as the gape opens, and the mouth is closed with the upper jaw in a protruded condition. This pattern permits prey capture from midwater and from the surface.
- 2) Downwards Directed Suction: Employed during bottom feeding with extended variable and overlapping activity of the sternohyoideus and geniohyoideus muscles (Figure 5: SH, GH). Kinematically, this mode is distinguished by early upper jaw protrusion during the opening cycle. Tubifex worms, chironomid larvae, and benthic invertebrates including snails are captured by this method.

- 3) High Velocity Suction. This pattern is invariably employed during the pursuit and capture of agile fish prey. It is characterized by greatly overlapping actions of the abductors and adductors (Figure 5). Gape of the mouth and expansion of the buccal cavity are maximized. The feeding cycle of opening and closing the jaws is shortened to less than 50 msec.
- 4) Manipulating. This variable pattern can best be characterized by continuous adjustments in the neuromuscular actions and kinematic profiles. Multiple overlapping bursts of adductors and abductors which show activity of varying lengths and amplitude produce varying degrees of upper jaw protrusion during both mouth openings and closings (Figure 5). Manipulating is a complex, non-cyclical, and

papilliform

molariform

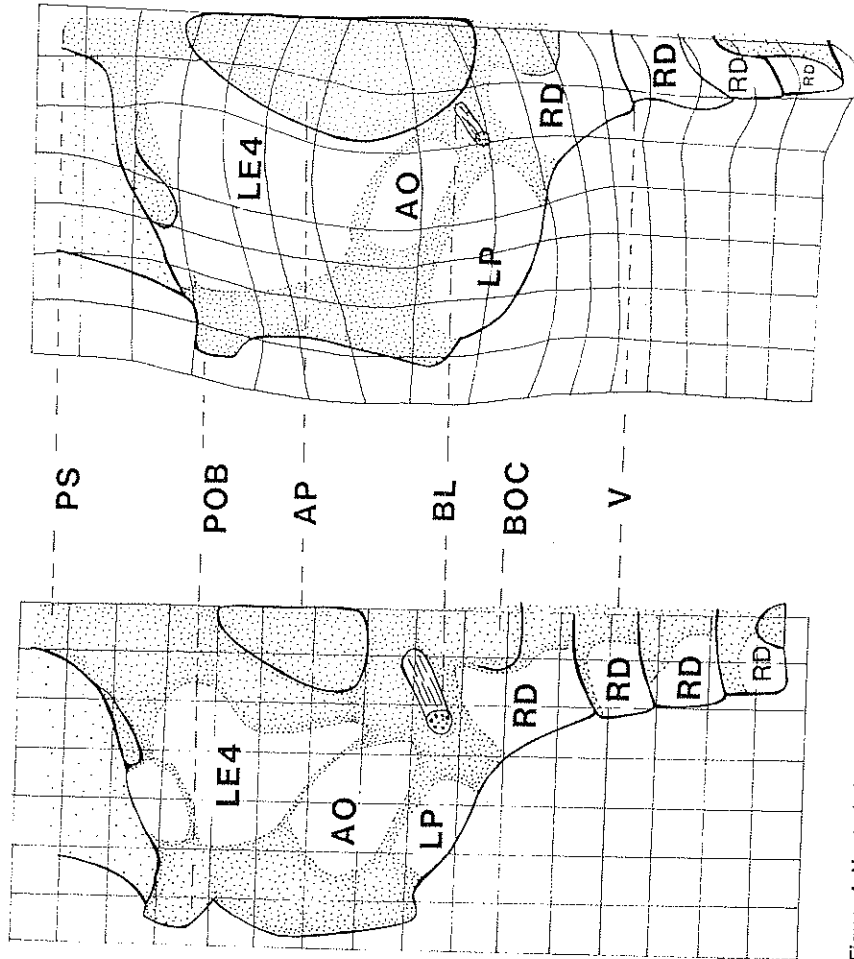


Figure 4. Ventral view, right half of otic region of neurocranium and anterior vertebrae with origins of major muscles (unshaded areas) of *Cichlasoma minckleyi* morphs as projected on the D'Arcy Thompson transformation grid. The papilliform morph is projected as the baseline. Distortion of the grid for the molariform morph expresses the transformation. Standard length, both specimens = 7.4 cm. Code: AO, adductor operculi; AP, pharyngeal apophysis of the parasphenoid; BL, Baudelot's ligament; BOC, basioorbital chamber; FHM, fossae for hyomandibula; LE4, fourth levator externus; LP, levator posterior; POB, postorbital process; PS, parasphenoid; RD, retractor dorsalis; TC, trigeminofacial chamber; V, vertebra.

often extended pattern. Protrusive, retractive, and gripping movements are produced to dislodge sessile prey such as snails.

The two *C. minckleyi* morphs and *C. cyanoguttatum* exhibit an identical repertoire of the four feeding patterns. The intraspecific occurrence of multiple feeding patterns in *Cichlasoma* resembles that of the other "generalized" cichlids (Liem 1980 a,b), and it indicates that the prey capture apparatus in cichlids can meet multiple problems. Thus

profound functional shifts can be realized even if structure of the jaws and associated musculature remain relatively unaltered.

Prey Mastication and Crushing. High speed cineradiography during mastication and crushing of prey reveals a stereotypic kinematic pattern common for the two morphs and *C. cyanoguttatum* (Figure 6). The kinematic pattern of mastication starts with a forward, protrusive movement of the upper pharyngeal jaws, and a posterior, retractive

virtually identical, and are independent of the nature of the prey. In all three forms the levator posterior and levator externus muscles are dominant in activity patterns (Figure 7:LP, LE4). Crushing occurs by synchronous activity of the levator posterior, levator externus 4 (elevation of the lower pharyngeal jaw), and retractor dorsalis (retraction of the upper pharyngeal jaw) muscles in an identical pattern in all three forms, regardless of whether the prey is soft, tough, or hard. The electromyographic pattern resembles that of other cichlids, except that the levator posterior plays a more prominent role (Liem 1974, 1978).

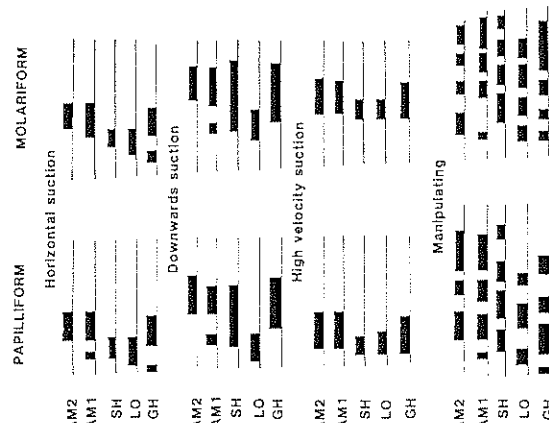
LABORATORY FEEDING BEHAVIOR

Patterns of food utilization in relation to food abundance, food type, and predator morphology were analyzed by offering the predators, *C. cyanoguttatum* and the two morphs of *C. minckleyi*, varied combinations of prey items. Abundant food supply and satiation of the fish were indicated when the different food types were no longer taken by the fish after 10 minutes. Low food abundance was indicated when all food types were ingested before satiation within 3 minutes. Intermediate abundance was indicated when fish were satiated within 10 minutes with all food depleted. Fish were conditioned to the particular abundance level of food seven days prior to the recording of feeding cycles. The number of feeding cycles or "bites" on each type of food were counted during a 10-minute observation period; the cycle was defined as the opening and closing of the oral jaws. Stable estimates of each individual's preference in a given experimental situation were obtained by averaging frequency data from 20 trials. Chi square tests for heterogeneity were applied to test the null hypothesis that patterns of food utilization were random with respect to food type.

Three Individuals of Both Morphs: Two Food Types. Paired food types were presented sequentially to three each of the papilliform and molariform morphs of *C. minckleyi*, 6.9 - 7.5 cm SL, in a single 76 l aquarium. When food is abundant, no significant preferences occurred between the morphs for any of the paired food combinations. Behavioral variations sometimes occurred within morphs. Significant within-morph

Figure 5. Block diagrams of active periods of key jaw muscles of *C. minckleyi* during capture of various prey in various positions in the water column. Code: AM1, AM2, parts A1 and A2 of adductor mandibulae muscle complex; GH, geniohyoideus; LO, levator operculi; SH, sternohyoideus.

movement of the lower pharyngeal jaw (Figure 6:30). This is followed by a retraction of the upper pharyngeals and protraction of the lower pharyngeal jaw. Both jaws are abducted at this stage (Figure 6:35). Crushing is accomplished by elevation of the lower pharyngeal jaw against the retracting upper pharyngeal jaws (Figure 6:40). After crushing, the prey is transported into the esophagus by retraction of the upper pharyngeal jaw and lowering of the lower pharyngeal jaw. This stereotypic pattern is employed regardless of whether the prey is soft, such as brine shrimp, tubifex worms, and dried fish food flakes, or tough, such as live fish, or hard, such as snails. It appears that the pharyngeal jaw movements are governed by a pattern generator in all three forms studied. Further evidence for the concept of a pharyngeal jaw pattern generator can be found in the electromyographic profiles of some key muscles associated with the pharyngeal jaw apparatus of the two morphs and *C. cyanoguttatum* (Figure 7). The electromyographic patterns are



CINERADIOGRAPHY OF PJA OF MOLARIFORM

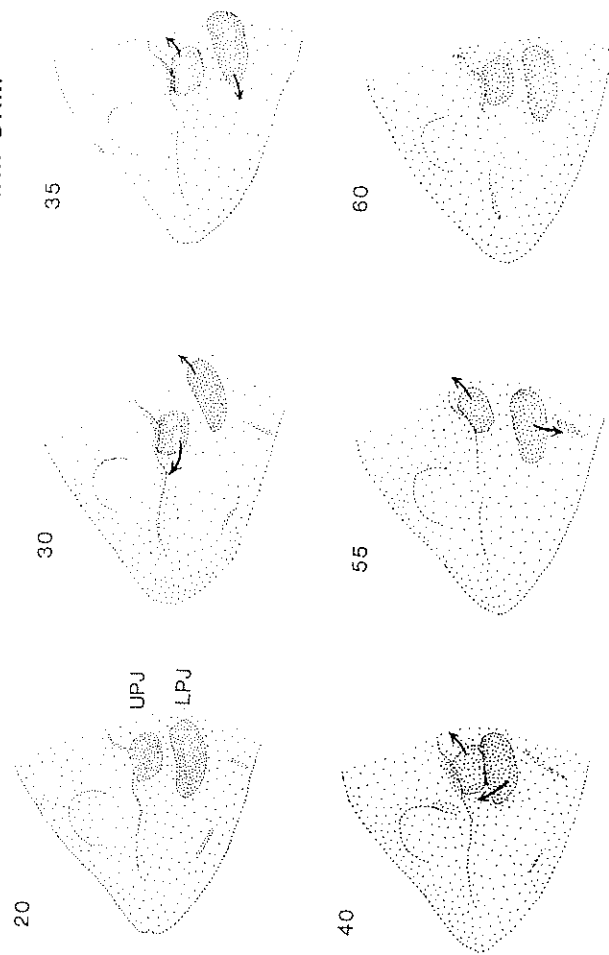


Figure 6. Tracings of images of individual frames of cineradiographic film taken at 150 frames/sec (300 MA, 50 KV) of *Cichlasoma minckleyi* molariform morph during mastication of a snail. Frame numbers indicated. Arrows indicate principal direction of movements on basis of positions of elements prior and just after the frame shown here. Code: LPJ, lower pharyngeal jaw; PJA, pharyngeal jaw apparatus; UPJ, upper pharyngeal jaw.

deviation from random feeding by Chi square test was: snails vs. shrimp, 25.16, $p < .005$; shrimp vs. fish, 11.76, $p < .05$; and fish vs. flakes, 14.78, $p < .025$.

At low food abundance, a different pattern emerged. When offered a choice between fish or snails in low abundance, the papilliform morph fed proportionately on very few snails, while the molariform morph fed heavily on snails as well as fish (Chi square = 11.28; $p < .05$). When the choice was between snails and shrimp in low abundances, the papilliform morph fed preferentially on shrimp, while the molariform morph switched to snails (Chi square = 23.56; $p < .005$). Thus, the effect of lowered food availability is to polarize the feeding behavior of the fishes in accordance with their pharyngeal jaw phenotypes.

Three Individuals, One Morph: Five Food Types. To examine food preference when only one morph is present, three specimens of a single phenotype were offered a range of

five food types in abundant supply (Table 1.1). The results indicate a high degree of behavioral uniformity. Interestingly, snails were the least desirable food types for both the papilliform and the molariform morph.

Three Individuals, Both Morphs: Five Food Types. When three individuals of both morphs in a single 76 l aquarium were offered five food types in high abundance, the feeding behavior did not differ significantly from random expectations either within or between morphs (Table 1.2). However, with low abundance of food the between-morph heterogeneity became highly significant. Papilliform morphs fed more than expected by chance on tubifex worms and dried fish food flakes, while the molariform morphs concentrated their feeding efforts on snails (Table 1.3).

The effects of varied food concentrations on the feeding behavior of the papilliform and molariform morphs under laboratory conditions are shown in Figure 8. The sharp

Table 1.1. Food preference of papilliform and molariform *Cichlasoma minckleyi* when fed separately, and together. (Six specimens)

Morph	Fed separately; Food abundant				
	Shrimp	Flake	Fish	Snail	Tubifex
Papilli:	1	26	34	39	11
	2	40	36	41	15
	3	28	33	33	11
Total	94	103	113	110	475
Ratio	.20	.23	.25	.24	1.00
Chi square = 3.15; $p = .92$					
Molari:	1	31	37	32	12
	2	32	32	36	12
	3	23	37	31	17
Total	95	106	99	41	97
Ratio	.22	.24	.23	.09	.22
Chi square = 2.17; $p = .98$					

Table 1.2. Fed together; Food abundant

Morph	Fed together; Food abundant				
	Shrimp	Flake	Fish	Snail	Tubifex
Papilli:	1	36	29	41	13
	2	22	29	29	14
	3	21	34	29	20
Total	79	92	99	47	71
Ratio	.20	.24	.26	.12	.18
Chi square = 8.65; $p = .37$					
Molari:	1	27	19	33	17
	2	11	26	26	17
	3	17	21	31	11
Total	55	66	90	45	76
Ratio	.16	.20	.27	.14	.23
Chi square = 9.19; $p = .33$					
Between morph: Chi square = 22.23 $p = .33$					

Table 1.3. Fed together; Food low

Morph	Fed together; Food low				
	Shrimp	Flake	Fish	Snail	Tubifex
Papilli:	1	9	7	11	8
	2	7	15	11	1
	3	8	15	10	8
Total	24	37	32	17	33
Ratio	.17	.26	.22	.12	.23
Chi square = 9.56; $p = .30$					
Molari:	1	7	7	11	17
	2	3	3	11	16
	3	4	1	6	13
Total	14	11	28	46	7
Ratio	.13	.10	.26	.44	.07
Chi square = 5.55; $p = .70$					
Between morph: Chi square = 54.83 $p < .001$					

dichotomy in feeding behavior appeared only at a low food concentration. The degree to which papilliform or molariform morphs prey on snails is clearly dependent on the concentration of various food resources.

TROPHIC ECOLOGY IN THE FIELD

Smith (1982) made extensive field observations of the behavioral ecology of the papilliform and molariform morphs in Cuatro Ciénegas, Coahuila, Mexico. His major conclusions are: 1) There is a lack of dietary specialization in the season when food is presumably most abundant. 2) The ecological differences are not as great as expected on the basis of distinct trophic morphologies. 3) Snails may constitute a competitive refugium for molariform morphs as food becomes scarce. These conclusions are congruent with our data on feeding behavior in the laboratory.

DISCUSSION

Our data and the unequivocal evidence that *Cichlasoma minckleyi* is a distinctly polymorphic species shed light on the pattern and processes underlying morphological, functional, and ecological diversification that could be involved in the process of speciation. Because the different morphs belong to the same species, they represent unquestionably a monophyletic clade, providing us the best possible scale for a well-founded evaluation of the processes by which such diversifications evolve. Of the two, the molariform morph is hypothesized to be the more specialized. Morphologically, the papilliform morph resembles most forms of *Cichlasoma cyanoguttatum* very closely. In our analysis we have considered *C. cyanoguttatum* the primitive sister-group of *C. minckleyi*, even though Kornfield and Taylor (1983) proposed that *C. labridens*, *C. bartoni*, and *C. steindachneri* may be the species most closely aligned with *C. minckleyi*. However, because *C. cyanoguttatum* exhibits a sufficiently generalized, primitive morphology, we think that using it as a primitive outgroup is justifiable. Polymorphism in *C. minckleyi* has been considered a differentiating process with the molariform morph as a specialized daughter form, possibly under the influence of a recessive allele for the molariform character (Kornfield et al. 1982). The alternative hypothesis is that the morphs represent disappearance of two or more species by introgression.

Because no other *Cichlasoma* species studied has the complete set of fully developed specializations of the molariform morph,

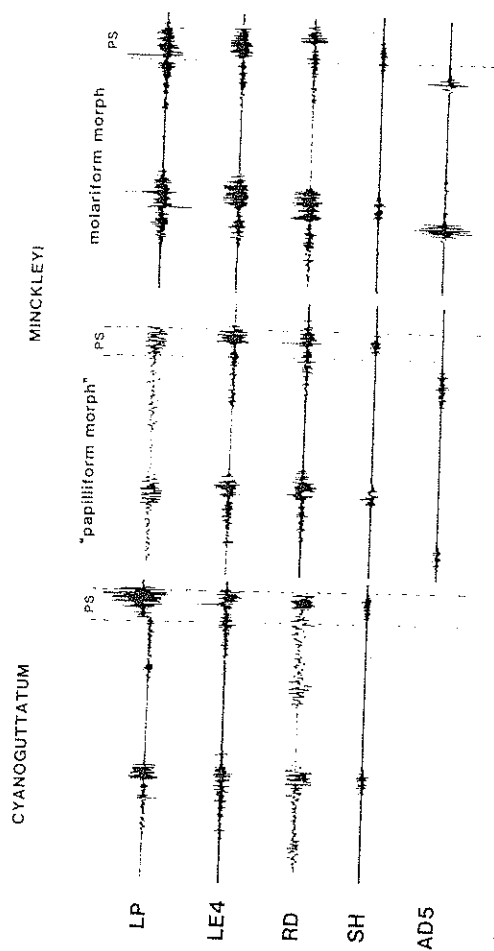


Figure 7. Electromyograms of key pharyngeal jaw muscles during mastication in *Cichlasoma cyanoguttatum* and the two morphs of *Cichlasoma minckleyi*. During PS, the upper pharyngeal jaw occludes against the retracting upper pharyngeal jaw, resulting in crushing action. Time scale, 200 msec. Code: AD5, fifth adductor; LE4, fourth levator externus; LP, levator posterior; PS, power stroke resulting in crushing action; RD, retractor dorsalis; SH, sternohyoideus.

introgression seems less likely than diversification. However, *C. regani* and *C. labridens* do show a high degree of molarization of the pharyngeal jaw apparatus (Miller 1974; Taylor, Miller in prep), but information on the degree of other specializations is lacking. Thus, a hybridization scenario for the origin of *C. minckleyi* cannot be dismissed.

Morphological Transformations: Pattern and Process. It is clear that the specializations in the molariform morph transcend the morphological limits of related species and even of genera. This pattern of extreme intraspecific morphological differentiation strongly supports Greenwood's (1974) notion that simple epigenetic mechanisms influencing ontogeny underlie both the rapidity and diversity of morphological radiations in the cichlid species flock of Lake Victoria. Evolutionary biologists have hypothesized that small changes in the timing of ontogenetic events can lead to distinctly discontinuous changes in phenotype, not just to graded phenotypic changes (Waddington 1969; Alberch 1980, 1982a,b; Gould 1982). The intraspecific morphological shift from papilliform to molariform morph is one of the best examples among vertebrates of Gould's concept that "small inputs give rise to big outputs." Morphological

discontinuity between the morphs involves multiple features. Head structural elements in fishes are coupled in specific patterns so that a perturbation in one element will elicit accommodating structural changes in many other component parts (Dullemeijer 1974, 1980; Hoogerhoud, Barel 1978; Liem 1980; Lauder 1981, 1983b). We postulate that a series of regulatory responses are triggered by the genetically induced hypertrophy of the pharyngeal jaws and associated principle muscles, including reduction of the adductor operculi and levatores interni 1-2 muscles, hypertrophy of the fourth epibranchial and basipharyngeal apophyses, and increased cranial width in the postorbital region. This hypothesis is based on the well-documented evidence of regulatory interactions between muscle and bone during ontogeny (Scott 1957), the ability of bones to react to changes in stress regimes (Currey 1968), and Greenwood's (1965) studies on *Astatoreochromis alluaudi*. In the last study, "reduced atypical populations" and normal hypertrophied populations show, respectively, the full extent of genetic control over the development of molariform specializations and the environmentally influenced hypertrophy of the genetically controlled condition.

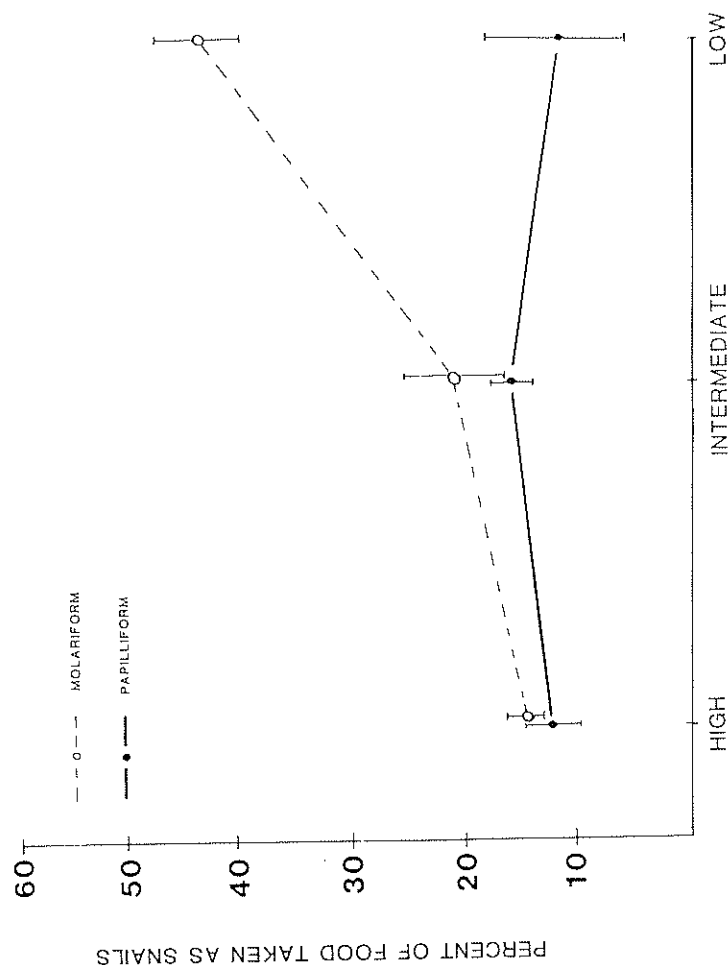


Figure 8. Graphic presentation of feeding behavior of the papilliform and molariform morphs of *Cichlasoma minckleyi* with varying food abundance. Graph expresses the percent of food taken as snails, from the choice of five food types: brine shrimp, flakes, fish, tubifex worms, and snails. Bars denote one standard deviation for three individuals of each morph.

Ontogenetically, the pharyngeal jaw apparatus becomes specialized first, and is followed secondarily by changes in surrounding elements (Greenwood 1965). As growth proceeds, all specializations in the molariform morph become more accentuated. Thus, the morphological dichotomy between the papilliform and molariform morphs is the result of interplay among intrinsic and extrinsic factors (Alberch 1982b) in development. It shows how an intrinsic change in a parameter such as the specialized pharyngeal jaw apparatus in the molariform morph can produce a concomitant series of regulatory changes (head width increase, drastic reduction of spatially related muscles). Phenotypically, the resulting molariform is so different from the papilliform

morph that this could be interpreted as a saltatory or macroevolutionary event.

Strong supporting evidence that small inputs generate big outputs can be derived from strikingly convergent specializations in other molariform cichlid species of Africa (Hoogerhoud, Barel 1978). All specialized characters present in the molariform morph of *C. minckleyi* can be found in a nearly identical condition in the following cichlids that habitually feed on snails by crushing their shells: *Lamprologus iretocephalus* from Lake Tanganyika (Liem 1974); *Tytochromis polylepis* from Lake Tanganyika (Greenwood pers comm); *Astatoreochromis vanderhorsti* from the Luiche River, Tanzania, East Africa (Liem 1974); *Astatoreochromis alluaudi* from

Lake Victoria (Greenwood 1965; Liem, Osse 1975); *Cyrtocara placodon* from Lake Malawi; *Labrochromis mylodon*, *L. mylergates*, *L. pharyngoryllus*, and *L. tegeleai* from Lake Victoria (Hoogerhoud, Barel 1978).

The morphological pattern of the morphs of *C. minckleyi* has important systematic implications. In respect to specialized pharyngeal characters, the molariform morph of *C. minckleyi* resembles the mollusc-crushing cichlids of East Africa more closely than its conspecific papilliform morph. This demonstrates the kind of problems that multiple detailed convergences can create in phylogenetic analyses. The occurrence in *C. minckleyi* and in African cichlids, of the same coadaptive character complex of the molariform morph demonstrates how a suite of specialized characters might be inappropriately used as a set of separate synapomorphies. These striking convergences also furnish indirect evidence on how developmental interactions (Alberch 1982b) and the network of interacting constraints (Liem 1980; Lauder 1981) impose limits on the direction and nature of phenotypic transformations during evolution.

Functional Patterns and Evolution of Trophic Specialization. Electromyography of prey capture in the papilliform and molariform morphs of *C. minckleyi* (Figure 5), and in *C. cyanoguttatum* reveals no significant differences among the three forms. All three conform to the cichlid pattern of having a repertoire of varying numbers of programs in their neuronal circuits, producing a wide range of finely tuned movements of the jaws. Each of the three forms have four different programs (Figure 5), and conform to the notion that nonpiscivorous cichlids specializing on prey which cannot be collected by simple suction, tend to expand the number of options in their feeding repertoire (Liem 1980 a,b 1984). This increases their versatility as they specialize. Intraspecific repertoires of programs affecting the motor output to the musculature involved in prey capture may be very important in the evolution of specialized behavioral patterns (Lauder 1983a). Nonpiscivorous cichlids often become specialists but remain generalists. This characteristic functional flexibility may have constrained the extent of polymorphism in the prey capture apparatus of *C. minckleyi*.

alterations rather than by changes in the patterns or sequences of muscle actions.

Implications of Polymorphism on Trophic Ecology. Our data provide a link between functional morphology and ecological tracking of food resources by a polymorphic species. Kornfield et al. (1982) have proposed that simple communities composed of trophically polymorphic species may be more responsive to environmental and biotic perturbations than standard communities. Our laboratory results on feeding preferences and behavior indicate that a different set of selection pressures operates when food is abundant than when food is scarce (Table 1).

Differences in feeding behavior between papilliform and molariform morphs occur only at low levels of food availability (Figure 8). These findings are consistent with the notion that the evolutionary trajectory of vertebrate species is largely determined by occasional bottlenecks of intense selection during a small portion of their history (Wiens 1977; Boag, Grant 1981; McKaye, Marsh 1983). Our observations demonstrate that carefully controlled laboratory experiments can reproduce the proximate effects of bottlenecks. Only during low food abundance does the molariform morph switch to feeding selectively on hard-shelled snails for which its specialized morphology is well adapted (Figure 8). During high food abundance in laboratory conditions, both morphs switch opportunistically to a diversity of energy-rich food types. Again the findings from field studies on *C. minckleyi* (Smith 1982) are congruent with the laboratory data. The capacity of the polymorphic *C. minckleyi* to specialize on available foods when rich ones are scarce insures survival of the polymorphic species under varying conditions. Thus the extremely specialized pharyngeal jaw apparatus of the molariform morph does not necessarily increase efficiency of feeding on preferred food, but enhances the use of a secondary, less preferred food, such as snails in the laboratory and *Mexipygus* snails in the field (Smith 1982). McKaye and Marsh (1983) came to the same conclusion in their analysis of nonpiscivorous algae-scraping cichlids in Lake Malawi. Our studies strongly support the suggestion that a community of polymorphic species is more responsive to environmental and biotic perturbations than is a community

of conventional species (Kornfield et al. 1982).

CONCLUSION AND SUMMARY

Polymorphism as an Incipient Intraspecific Macroevolutionary Transition. Polymorphism in *Cichlasoma minckleyi* could be interpreted as a stage of divergence in specialization with the molariform morph as a specialized daughter form that shows a radically different morphology, function, ecology, and behavior when compared with the ancestral papilliform morph. This polymorphism does not exhibit assortative mating (Kornfield et al. 1982). However we suggest that some degree of trophically based differences in habitat selection may occur during "bottlenecks" or "ecological crunches" (Maynard Smith 1966; Wiens 1977). McKaye et al. (1982) have suggested that this incipient stage of stable polymorphism without assortative mating may be followed first by incomplete and then by complete assortative mating stages under influence of intrinsic behavioral mechanisms in an essentially sympatric setting. Quantum morphological specialization has arisen intraspecifically in *C. minckleyi* by quantitative changes in some basic parameters of development which have caused an interrelated series of alterations in functionally correlated elements. The striking convergences in several different mollusc-crushing cichlids from both Africa and the Americas must be interpreted as results of developmentally canalized variation. Apparently the realm of possible morphologies is determined by the internal network of interacting constraints. The intraspecific functional shift to a purely crushing pharyngeal jaw apparatus is accomplished by a phenotypically discontinuous suite of structural specializations rather than by changes in the motor output of the pharyngeal jaw muscles. In centrarchids, mollusc-crushing is accomplished by a change in the motor output of the pharyngeal jaw muscles (Lauder 1983a,b). The extremely specialized morphology of the molariform morph does not increase efficiency of feeding on preferred food, but enhances exploitation of the secondary, less preferred food during ecological bottlenecks. Our studies of *Cichlasoma minckleyi* have shown how stable polymorphism provides major variants that lead to a saltatory alteration of the phenotype

for certain key features of great importance for macroevolutionary transitions.

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