Morphometrics and allometry in the trophically polymorphic cichlid fish, *Cichlasoma citrinellum*: Alternative adaptations and ontogenetic changes in shape

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(With 2 plates and 8 figures in the text)

The Neotropical cichlid fish *Cichlasoma citrinellum* exhibits a distinct trophic polymorphism in the structure of its pharyngeal jaws. Fish have either strong, sturdy molariform pharyngeal jaws or weak papilliform jaws. Intermediate forms are rare among adults. Ontogenetically, however, all fish start as papilliform morphs. Differences in morphology and allometry between morphs in external measurements (25 measurements) and measurements of the lower pharyngeal jaws (nine measurements) were analysed using a multivariate morphometric approach. The ontogenetic growth trajectories for the pharyngeal jaws of the respective morphs start to diverge early in ontogeny and therefore seem to preclude the existence of adult intermediate morphs. The isometric growth of the tooth diameter in molariform morphs (in relation to standard length), versus its relatively retarded (negatively allometric) growth in the papilliform morph, is the main cause for the development of distinct trophic morphs in pharyngeal-jaw morphology. At approximately 50 mm standard length, both pharyngeal morphs can be discerned clearly. In this study only larger fish of determined pharyngeal-jaw morphology were considered ($n = 30$ for molariform morphs, $n = 31$ for papilliform morphs). External morphology differs between morphs as well, but less perceptibly. Principal-components analyses revealed that only a few measures load highly on PC2 and therefore account for most of the differences between the two trophic morphs in the shape of the external morphology. Molariform morphs have blunter, shorter snouts, larger eyes and deeper, shorter bodies than papilliform morphs.

The two external morphologies resemble other known limnetic and benthic body shapes of polymorphic species of fishes, and are believed to enhance the ecological separation of the two pharyngeal-jaw morphs. Evolutionary implications of ontogenetic changes and adult differences in morphology and trophic polymorphism are manifold. The alternative adaptations in this polymorphic species will decrease intraspecific competition by differential niche utilization and habitat choice, thus allowing for larger population sizes. Alternative adaptations may eventually lead to genetic isolation and possibly speciation of the two trophic morphs.

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Introduction

Fishes of the suborder Labroidei possess the most highly modified gill arches of teleost fishes (Kaufman & Liem, 1982; Stiassny & Jensen, 1987). Their branchial skeleton forms a second set of jaws, the pharyngeal jaws, in addition to the oral jaws. These jaws allow the processing of a variety of prey that are not available to fish that use oral jaws exclusively for the same feeding tasks (Slootweg, 1987).

The possession of a highly developed pharyngeal-jaw apparatus may be a key factor responsible for the rapid speciation of cichlid fishes (e.g. Liem, 1973). In the East African Rift lakes, cichlids demonstrated their propensity for speciation and morphological specialization: in each of the three lakes cichlids formed species flocks of up to 500 species (e.g. Lewis, Reinthal & Trendall, 1986). Within some of these cichlid species assemblages, more than 95% of the species are endemic to their lakes (Greenwood, 1974).

Polymorphisms in cichlid fishes

An increasing number of cichlid species that are polymorphic in either coloration or morphology are being discovered (reviewed in Meyer, In press b); therefore, the validity of estimates of the number of real biological species has been called into question (e.g. Turner & Grosse, 1980; Meyer, 1987; Vrijenhoek, Marteinsdottir & Schenck, 1987). The study of polymorphic species provides opportunities to increase our understanding of the evolutionary processes that facilitate the rapid rate of speciation in cichlids. For example, the alternative adaptation hypothesis proposed by West-Eberhard (1986) suggests that, among other conse-quences, polymorphic species should be buffered against extinction and therefore have higher speciation rates.

Study of polymorphic species is important in taxonomy because pharyngeal jaws and proportions of external morphological measurements are commonly used as systematic charac-ters. Polymorphic species provide the opportunity to outline the possible morphospace (*sensu*

Raup, 1966) that can be occupied by a single species. Further, cichlid species assemblages facilitate the study of the evolutionary role of phenotypic variation and developmental mechanisms that produce morphological differences within and between species. Extrapolation to interspecific morphological differences may clarify evolutionary patterns in morphological diversification.

Pharyngeal-jaw morphology is susceptible to environmental influences in at least one species, *Astatoreochromis alluaudi*, (Greenwood, 1965; Hoogerhoud, 1986) but not in *Cichlasoma citrinellum* (Meyer, In press *a*, *b*). In two other species (*Astatoreochromis flaviijosephi* and *Cichlasoma minckleyi*) the polymorphism in pharyngeal jaws is believed to be genetically sex-linked (Sage & Selander, 1975; Kornfield & Taylor, 1983; Spataru & Gophen, 1985).

I reported a trophic polymorphism in one Neotropical cichlid fish, *Cichlasoma haitensis* (Meyer, In press *b*). Here I describe and quantify a polymorphism in the pharyngeal-jaw structure and external morphology in another Neotropical cichlid fish, *C. citrinellum*. In this species, individuals have either molariform (Plate Ia, b) or papilliform pharyngeal jaws (Plate Ic, d). Intermediate pharyngeal-jaw morphs are rare and usually small (see also Meyer, In press *a*).

Molariform fish are adapted for crushing hard prey, such as snails (Hoogerhoud & Barel, 1978; Liem & Kaufman, 1984; Wainwright, 1987, 1988), whereas papilliform fish are adapted to feed on soft diets (Meyer, 1989). Each morph has a performance advantage for the diet to which it seems to be adapted (Meyer, 1989). All young in this species, however, start out being papilliform and only later, probably at a size at which they become biomechanically capable of cracking hard prey, do they develop their molariform dentition and pharyngeal-jaw structure (Hoogerhoud, 1986; Meyer, 1989).

Variation in external morphology in *Cichlasoma citrinellum*

Cichlasoma citrinellum vary tremendously in their external morphology (Meek, 1907; Barlow & Munsey, 1976; Villa, 1976). This was noted as early as 1907 by Meek (1907: 122–123):

'Of all the species (of) fishes in these lakes (Nicaragua), this one is by far the most variable. I made many repeated efforts to divide this material . . . in from two to half-dozen or more species, but in all cases I was unable to find any tangible constant characters to define them. To regard them as more than one species meant to only limit the number by the material at hand, and I have lumped them all in one.

As to form, some individuals are very deep, others quite elongate. . . . On some of the more elongate forms (of about 140 mm) from Lake Nicaragua the nuchal hump is well developed, while on many of the larger individuals it is quite absent. There were no markings or peculiarities that I was able to correlate with sex or size. It is possible that more than one species should be recognized here, and no doubt such will some day be the case, especially if some enthusiastic student of fishes has at his command a far less amount of material than I have had the opportunity to examine.'

This species is also polychromatic (Barlow, 1976), varying from a morph that is grey with striped bars to one that is uniformly yellow or white. This aspect of the biology of this species has been investigated extensively in terms of behaviour by Barlow and co-workers (e.g. Barlow, 1983).

In fish from Lake Jiloa, Nicaragua, it was often possible, on the basis of external morphology, to predict the pharyngeal-jaw morphology (pers. obs.). Molariform fish appeared to have blunter snouts, shorter heads, larger eyes and deeper, shorter bodies than papilliform morphs. The variation in pharyngeal-jaw and external morphology between the two pharyngeal-jaw morphs was investigated in a multivariate morphometric analysis. This analysis was conducted first to test whether differences in pharyngeal jaw morphology and external morphology are correlated, secondly to document ontogenetic trends in the development of pharyngeal jaw and external

morphology in the two trophic morphs, and thirdly to determine which ontogenetic trajectories contribute to the observed differences in adult morphology. Multivariate morphometric studies allow one to separate size from shape (for a discussion on the different meanings of shape see Lessa & Patton, 1989). This separation of size from shape facilitates the study of functionally important changes in shape, which may confer performance advantages, without the confounding effects of size differences (e.g. Bookstein *et al.*, 1985).

Materials and methods

Cichlasoma citrinellum were collected from Lake Jiloa in Nicaragua (see fig. 1 in Barlow, 1976). Collections were made in the rainy season of 1969 and 1970 by G. W. Barlow and co-workers and are deposited in the
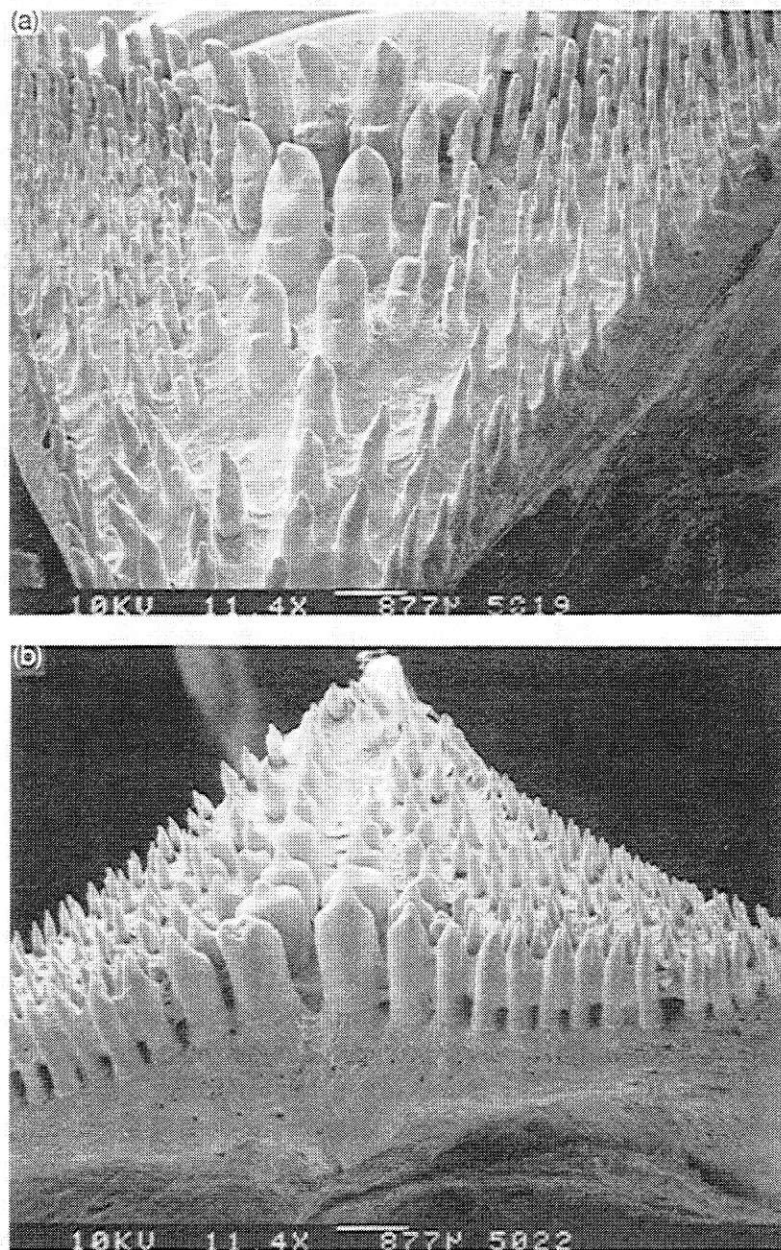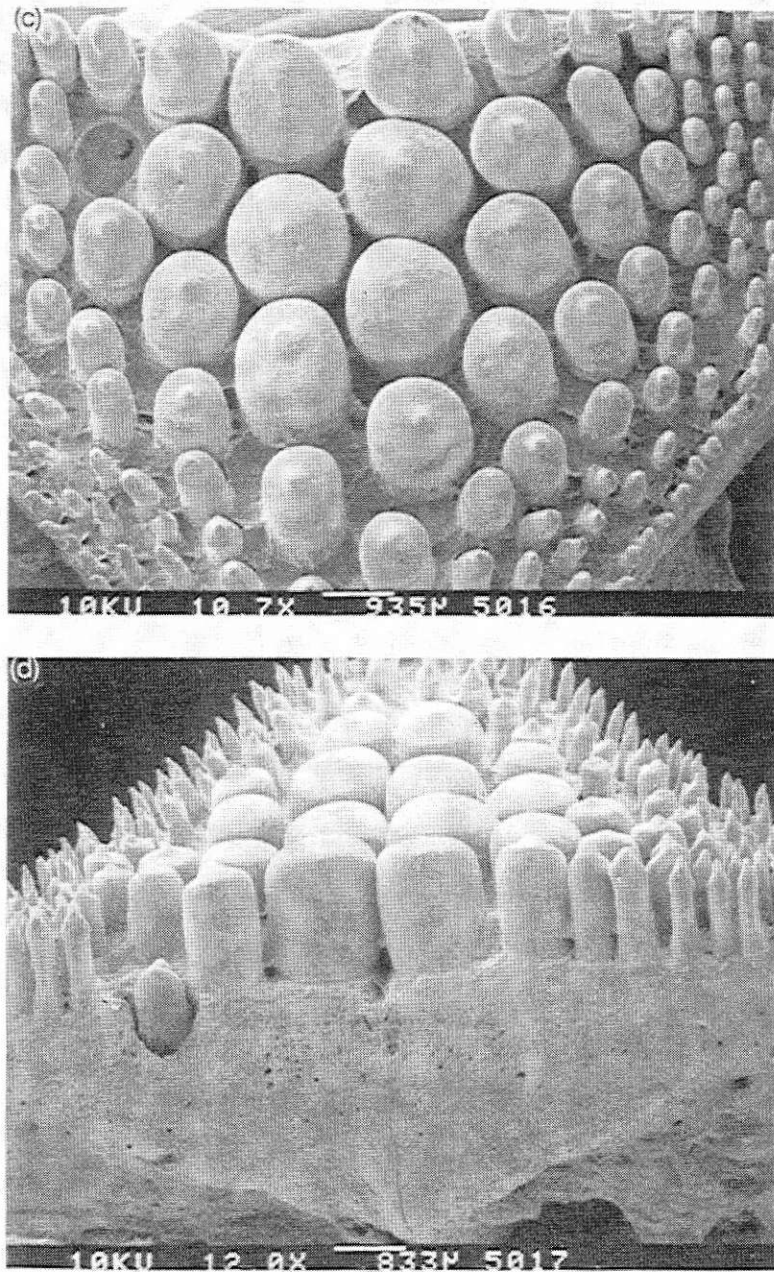

(PLATE 1 a–b)

PLATE I. Scanning electronmicrographs of the lower pharyngeal jaws of *Cichlasoma citrinellum* (from Lake Nicaragua). (a) and (b) are from a papilliform specimen, (c) and (d) from a molariform specimen of almost identical size. (a), (c) View from anterior and above; notice the slender, pointed dentition in the papilliform specimen and the blunt, strong dentition in the molariform specimen. (b), (d) Same jaws from posterior; notice the weak bony support of the pharyngeal jaw in the papilliform specimen and the strong bony support of the molariform pharyngeal jaw. Scales are indicated by the white line and the number under it at the bottom of each SEM.

collections of the University of California at Berkeley (UCB# 909, 910). This study used collections that were made at the south-east shore, at a beach area. Fish were collected by seining.

Twenty-five external distances (Fig. 1) from 30 molariform and 31 papilliform fish were measured with electronic calipers (Fowler Co.). The lower pharyngeal jaws were dissected out and 9 measurements (Fig. 2)
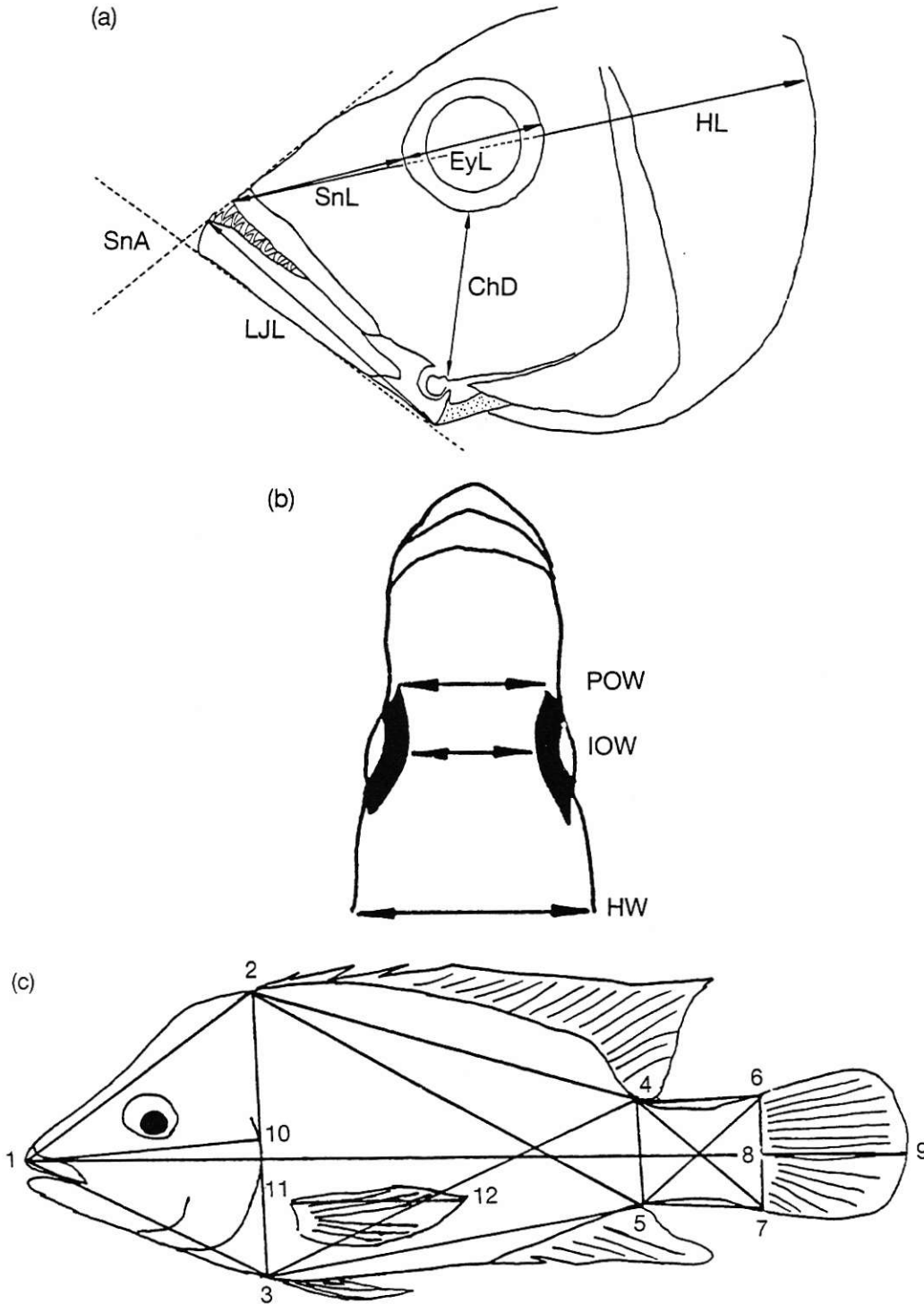
FIG. 1. (a) Head measurements taken as defined by Barel *et al.* (1977): fig. 12). Snout acuteness (SnA), snout length (SnL), eye length (EyL), cheek depth (ChD), lower jaw length (LJL), head length (HL). (b) Head measurements across as defined by Barel *et al.* (1977: fig. 21). Pre-orbital width (POW), inter-orbital width (IOW), head width (HW). (c) External measurements included head length (between points 1 and 10; see also Fig. 1a), pectoral fin length (PFL: 11–12) standard length (SL: between the tip of the snout and the caudal peduncle; 1–8), total length (TL: between the tip of the snout and the end of the caudal fin; 1–9). Thirteen other measurements were taken between 12 landmark points (Humphries *et al.*, 1981) on the outside of the fish: M1 (1–2), M2 (1–3), M3 (2–3), M4 (2–4), M5 (3–5), M6 (3–4), M7 (2–5), M8 (4–5), M9 (6–7), M10 (4–6), M11 (5–7), M12 (5–6), M13 (4–7).

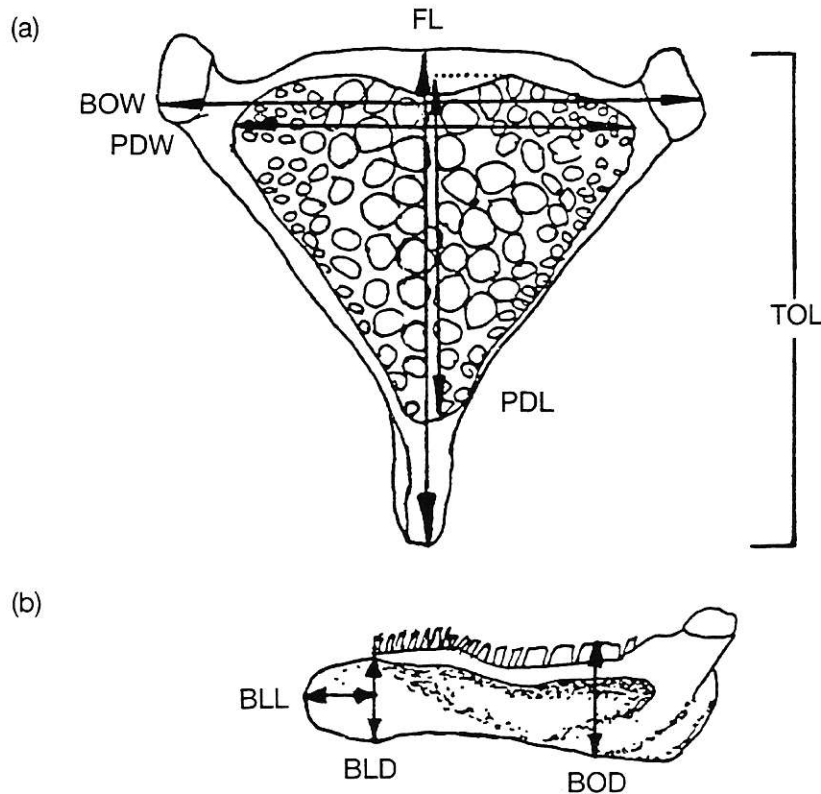FIG. 2. (a) Nine distances were measured from the lower pharyngeal jaws. The fork length (FL) is the distance from the rostral tip of the lower pharyngeal element to its distal end. The total length (TOL) was measured from the rostral tip to a line connecting the distal end of the two horns (same as LPL of Barel et al., 1977). The width (BOW) of the lower pharyngeal jaws was measured as the greatest distance between the ends of the horns (same as LPW of Barel et al., 1977). The length (PDL) and width (PDW) of the dentigerous area of the lower pharyngeal jaw were measured as the maximum anterior to posterior and lateral distances of teeth (or tooth sockets), measurements defined by Barel et al., 1977. The width of the largest tooth (LTW) of the lower pharyngeal jaw was measured as the distance across that tooth (measurement not shown in this figure). (b) Three additional distances from the lower pharyngeal jaws are the depth of the oral area (BOD) measured as the maximum distance between the dorsal side (on top of teeth) and the ventral side of the bone. The length (BLL) and depth (BLD) of the bony blade in front of the dentigerous area of the lower pharyngeal jaw was measured as the maximum distance between the rostral bony tip of the blade and a vertical line drawn in front of the most rostral tooth (BLL), and the depth as the length of this vertical line (BLD).

were gathered from them. From the lower pharyngeal jaws measurements were taken of the fork length (FL), the total length (TOL), the blade length (BLL), the blade depth (BLD), the diameter of the largest tooth (LTW), the depth (BOD), the width (BOW) of the lower pharyngeal element, and the width (PDW) and length (PDL) of the lower dentigerous area. The means and the standard deviations of the raw data are given in **Appendix 1**. From a subset of the fish, the length of the gut and dimensions of some branchial muscles that are important for the function of the pharyngeal jaws were measured and analysed separately.

The morphometric part of this study included only fish of a size that already had a determined molariform pharyngeal-jaw dentition. The smallest papilliform fish were of about the same size as the smallest molariform fish and their mean sizes not significantly different (molariform: mean = 96·7 mm standard length (SL); range: 45·4–133·1 mm; papilliform: mean 114·1 mm SL; range: 50·0–172 mm; $t = 2·38$, $P < 0·05$). The judgement of the development of a molariform dentition was based on visual inspection of the pharyngeal jaws with an otoscope. Molariform fish have distinctly hypertrophied teeth on their pharyngeal jaws (Plate I), which allowed the unambiguous assignment of specimens to morphs.

The external measurements focused on the head region, particularly on distances that are important to the functional morphology of cichlid fish (Barel, 1983). They included the head length (HL), the eye length (EyL), the lower jaw length (LJL), the cheek depth (ChD), the snout length (SnL), and the snout acuteness (SnA). Additionally, measurements were taken of 16 distances in a truss network (Strauss & Bookstein, 1982) among 12 homologous landmark points (Humphries *et al.*, 1981; Bookstein *et al.*, 1985) that are distributed evenly over the body. Details of the measurements are given in the legends of Figs 1 and 2. All original measurements (except SnA, an angle) were logarithmically transformed for subsequent analysis.

Statistical analysis

The data provided in **Appendix 1** show that the differences between the morphs in external morphology are small. Simple univariate comparisons often did not seem to provide enough power to discriminate between the 2 morphs. A more sophisticated multivariate approach seemed appropriate. The pattern of morphological variation was analysed using Principal Component Analysis (PCA). This multivariate technique reduces and 'summarizes' multivariate trends in shape variation to a set of statistically independent variables (PC axes). The eigenvalues of the PC-axes vary in accordance with the amount of original variation that is described in each of the original variables. Statistical procedures were carried out with the SYSTAT statistics package (Wilkinson, 1985) on a personal computer.

Three separate PCAs were conducted for the set of external measurements, and 3 PCAs for the set of jaw measurements. For each set of measurements, the first PCA was obtained from pooled data of both groups and the following 2 PCAs were computed on each of the 2 morphs separately. The PCAs for the jaw measurements were based on a variance-covariance matrix and the multivariate allometric coefficients calculated according to Jolicoeur (1963). Because the external measurements included an angle (SnA) as well as distances, the PCAs were based on a correlation matrix rather than a variance-covariance matrix (Bookstein *et al.*, 1985; Somers, 1986). This precluded the calculation of multivariate allometric coefficients for external measurements.

PCA was utilized to differentiate size and shape effects between the 2 groups. Recently, many alternative and refined multivariate approaches to PCA have been published that will remove the effects of size from shape changes, e.g. sheared PCA (Humphries *et al.*, 1981; Bookstein *et al.*, 1985), canonical discriminant analysis (Mosimann & James, 1979), the common-art-removal technique (Wood, 1983), Multiple-Group Principal Components Analysis (MGPCA; Thorpe, 1983). For PCA in the present study, shearing was not necessary because the individual within-group scores on PC2 and PC3 were parallel to those for PC1 (Bookstein *et al.*, 1985); based on a regression analysis, slopes are not significantly different from zero. Furthermore, the groups did not differ significantly in size ($P > 0.05$).

Results

The Neotropical cichlid fish *Cichlasoma citrinellum* exhibits a polymorphism in its pharyngeal-jaw apparatus (PJA) which resembles the previously described polymorphism of its congener *C. minckleyi* (Kornfield & Taylor, 1983; Liem & Kaufman, 1984). The polymorphism in the pharyngeal jaws is linked with a polymorphism in external morphology. Molariform morphs have blunter, shorter snouts, wider heads, larger eyes, deeper and shorter bodies than papilliform morphs.

Pharyngeal jaws

The molariform morph possesses heavier lower and upper pharyngeal jaws with a molariform dentition (Plate I). The teeth in the papilliform morph are more slender and pointed than in the

molariform morph, in which they are stouter and sturdier (Plate I). In the molariform morph the horns at the end of the lower pharyngeal jaw are shorter and stouter, providing larger attachment areas for the branchial musculature.

Branchial musculature

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 through contraction of the branchial musculature (e.g. Liem & Kaufman, 1984). Correlated with the heavier pharyngeal jaws are differences in the musculature: the levator externi IV, the levator posteriori, and the retractor dorsalis muscles are significantly hypertrophied in the molariform morph (Table I). These muscles are active during the crushing phase of the pharyngeal-jaw movements (Liem, 1986). The diameter of the muscle and the angle of muscle fibres in pinnate branchial muscles determine the maximum force exerted by the muscles during the crushing phase (Wainwright, 1987, 1988) and the control of the PJA (see Liem & Greenwood, 1981; Liem, 1986; Liem & Sanderson, 1986, for nomenclature of pharyngeal-jaw musculature).

Neurocranium

In *Cichlasoma citrinellum* the differences in the PJA extend to the neurocranium. The upper pharyngeal jaws contact the skull ventrally via a neurocranial apophysis (Liem & Greenwood, 1981; Stiassny, 1981; Lauder & Liem, 1983; Liem & Sanderson, 1986). The molariform morph has a more massive pharyngeal apophysis; it provides a larger articulation surface with the upper pharyngeal elements (Plate II).

TABLE I

Comparison of branchial muscles and gut length between morphs. Measurements (in mm) of functionally important branchial muscles and gut length of molariform and papilliform C. citrinellum. Given are means and standard deviations. LE4 is the levator externi muscle IV, LP is the levator posteriori muscle, RD/HL is the ratio of the diameter of the retractor dorsalis (RD) muscle divided by the length of the head (head length, HL). Specimens were from Lake Jiloa, Nicaragua (see **Materials and methods***) and laboratory-reared specimens from Lake Masaya, Nicaragua (n = 17). The standard length (SL) of the groups did not differ significantly (t = 0·966, P = 0·338); (molariform: n = 22, range 44·5–124·9, mean 93·5, S.D. 19·8; papilliform: n = 33, range 48·9–199·5, mean 102·6, S.D. 40·9). ANCOVAs could not be conducted because slopes were heterogeneous. The sample sizes for the muscle measurements are n = 13 for molariform, and n = 18 for papilliform morphs. Sample sizes for the gut length are n = 22 for molariform and n = 16 for papilliform morphs*

Trait	Molariform		Papilliform		t	P
	Mean	S.D.	Mean	S.D.		
Area of LE4	30·7	12·2	16·5	13·5	2·98	0·006
Area of LP	9·3	3·7	4·7	3·0	3·87	0·001
RD/HL	0·09	0·01	0·07	0·01	3·35	0·002
Gut length	90·5	24·9	85·9	42·8	0·42	0·676
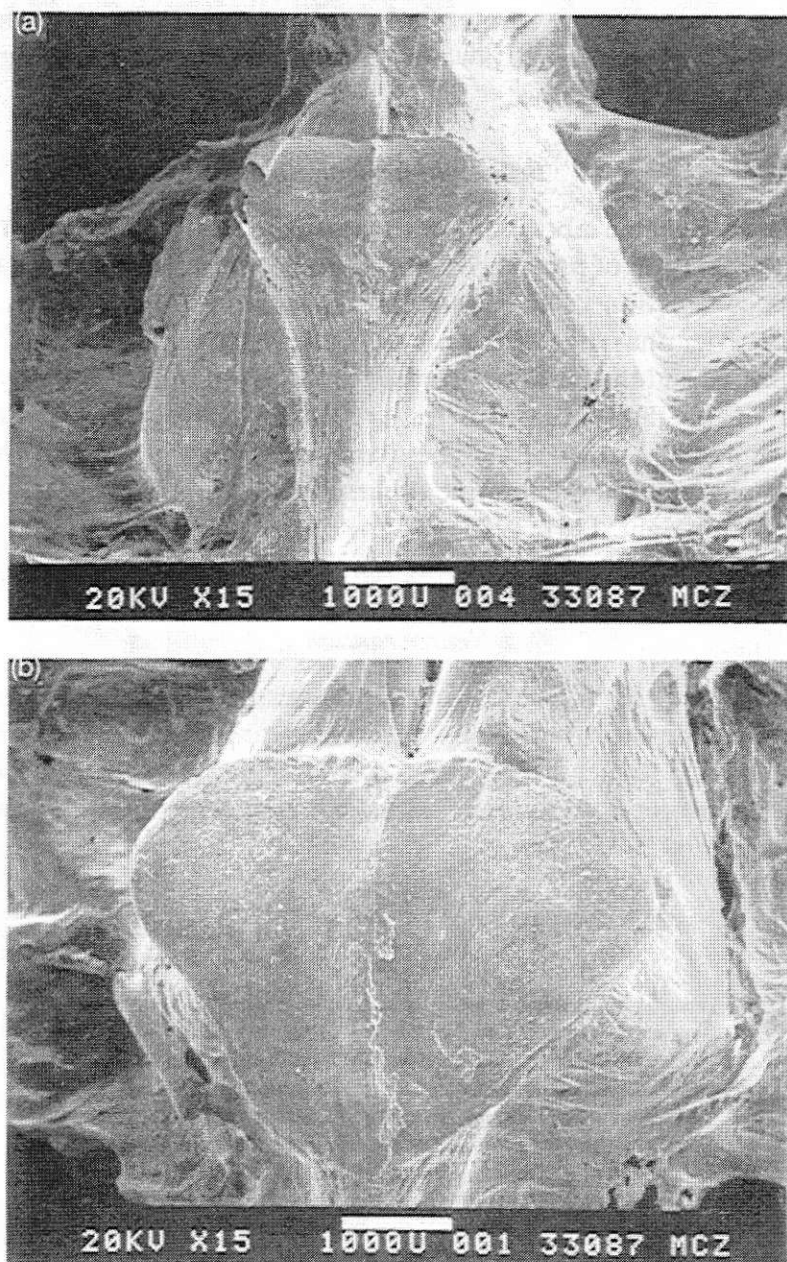
PLATE II. Scanning electronmicrographs of the neurocranial apophysis at the base of the neurocranium. This structure creates an articulation surface with the upper pharyngeal jaw. The fish were of the same size and the SEMs were taken at the same magnification (indicated by the white line and the number under it at the bottom of each SEM). (a) Neurocranial apophysis of a papilliform *C. citrinellum*. (b) Neurocranial apophysis of a molariform specimen.

Gut length

Gut length, which differs between the morphs in *C. minckleyi* (Kornfield & Taylor, 1983), does not differ between the pharyngeal-jaw morphs in *C. citrinellum* (Table I) nor does it differ between sexes ($t = 0.62$, $d.f. = 37$, $P > 0.05$).

Outcome of the multivariate morphometric analysis

The PCAs confirm that the trophic morphs of *Cichlasoma citrinellum* differ in their external morphology as well as in the structure of their pharyngeal jaws. The scatterplots of the first two components indicate the complete separation, in the case of the jaw measurements, and almost complete separation, in the case of the external measurements (Figs 3, 4). These plots also suggest that little, if any, residual size variation was present in PCs other than PC1.
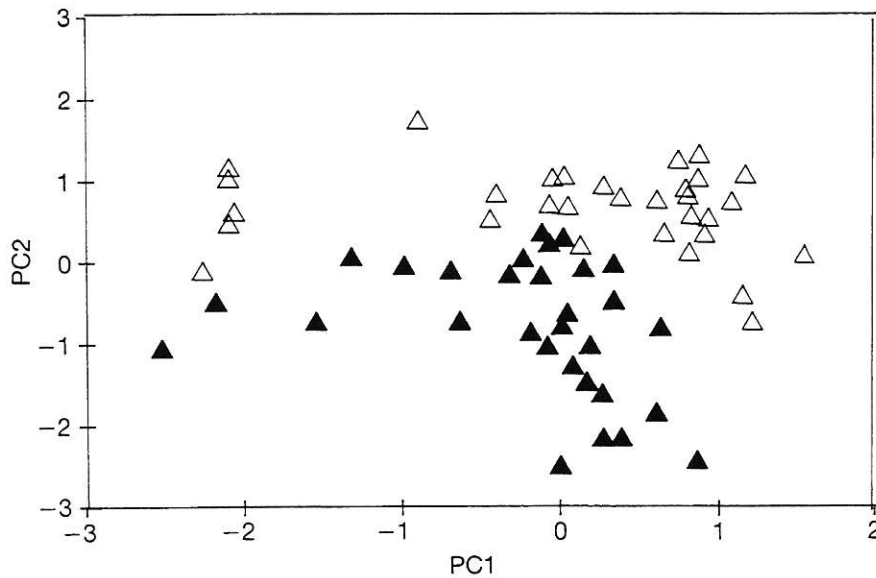

FIG. 3. Scatterplots of first two principal components axes based on between-group-PCA of 25 external distances described in Fig. 1 a–c. ▲ Molariform; △ papilliform.
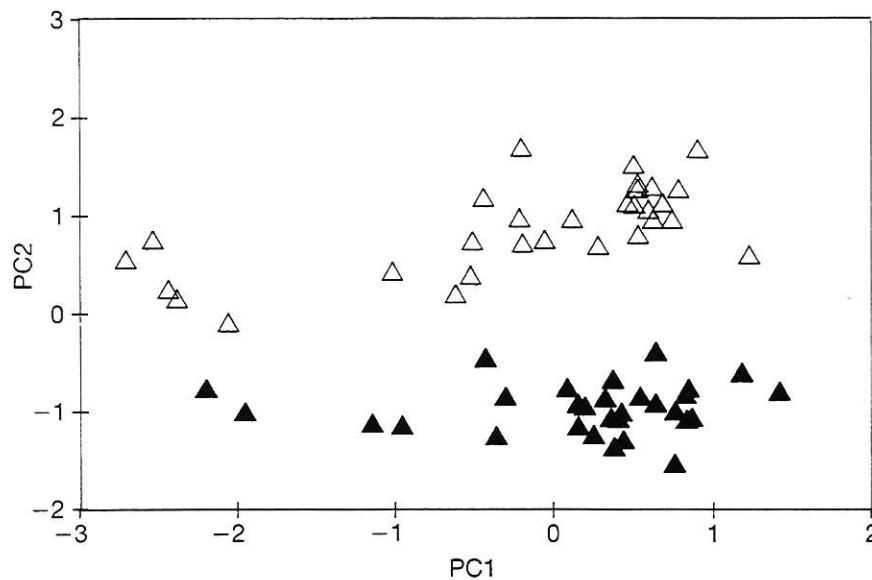

FIG. 4. Scatterplots of first two principal components axes based on 9 measurements from the lower pharyngeal jaw (described in Fig. 2 a, b. ▲ Molariform; △ papilliform.

Separation of size and shape through PCA

The factor patterns (correlation coefficients between individual scores in a measurement and the PC scores) for the first two PC axes from the pooled PCA and the within-group PCAs are reported for the external measurements (Table II) and the jaw measurements (Table III). In all six PCAs conducted, all measured variables correlated highly and positively with PC1. The percentage variation explained by PC1 for the within-group PCAs was always higher than 95%, and it was generally higher in the papilliform morphs, reflecting the larger size-range of fish measured for this morph. These results support the notion that PC1 codes exclusively for size. Few variables correlate highly with the subsequent PC-axes, indicating that few measurements contribute to the discrimination in shape between the two trophic morphs. These measurements are discussed below.

TABLE II

PCA loadings for PCAs of external measurements. Correlation coefficients for log-transformed (except SnA) original variables and the first two principal components (PC) axes

Trait[a]	Between groups		Molariform		Papilliform	
	PC1	PC2	PC1	PC2	PC1	PC2
SnA	0·792	−0·607	0·847	−0·506	0·943	−0·330
SL	0·998	0·034	0·997	0·025	0·999	0·018
TL	0·988	0·025	0·977	0·033	0·999	0·022
HL	0·995	0·020	0·993	0·007	0·995	0·037
EyL	0·979	−0·091	0·979	−0·056	0·989	0·041
SnL	0·988	0·064	0·981	−0·009	0·995	0·09
LJL	0·963	0·100	0·917	0·221	0·983	0·27
ChD	0·991	−0·015	0·983	−0·070	0·995	0·048
POW	0·993	0·038	0·992	0·050	0·995	−0·038
IOW	0·992	0·035	0·986	0·066	0·995	−0·013
HW	0·994	−0·028	0·992	−0·009	0·996	0·018
PFL	0·978	−0·009	0·946	−0·058	0·991	0·005
M1	0·996	0·023	0·933	0·037	0·996	0·006
M2	0·991	−0·041	0·987	−0·021	0·995	0·002
M3	0·995	−0·003	0·992	0·003	0·996	0·024
M4	0·996	−0·008	0·994	0·030	0·998	0·013
M5	0·994	0·057	0·992	0·004	0·996	0·033
M6	0·997	0·021	0·994	0·057	0·999	0·015
M7	0·993	0·012	0·984	−0·034	0·998	0·014
M8	0·995	0·032	0·991	0·007	0·997	−0·005
M9	0·996	0·022	0·995	−0·020	0·997	−0·001
M10	0·971	0·054	0·959	−0·055	0·986	0·030
M11	0·978	0·031	0·965	0·044	0·989	−0·021
M12	0·992	0·035	0·986	0·040	0·995	0·031
M13	0·980	0·083	0·943	0·160	0·997	−0·003
% of variance	96·49	1·67	95·24	1·46	98·55	0·49

[a] For key to abbreviations, see legend to Fig. 1

TABLE III

PCA loadings for PCA of pharyngeal-jaw measurements.
Coefficients for log-transformed original variables and the first
two principal components (PC) axes

Trait	Between groups		Molariform		Papilliform	
	PC1	PC2	PC1	PC2	PC1	PC2
FL	0·996	0·009	0·994	0·016	0·996	0·032
TOL	0·976	0·198	0·990	−0·024	0·997	0·020
BOW	0·979	0·188	0·996	0·012	0·997	0·029
BOD	0·988	−0·080	0·989	−0·046	0·991	0·021
BLD	0·962	−0·171	0·961	−0·184	0·979	0·079
BLL	0·960	0·010	0·953	−0·242	0·959	0·169
LTW	0·707	−0·697	0·940	0·258	0·910	−0·407
PDL	0·969	0·196	0·981	0·120	0·989	0·029
PDW	0·979	0·153	0·985	0·090	0·994	0·001
% of variance	90·24	7·35	95·44	2·05	95·92	2·27

[a] For key to abbreviations, see legend to Fig. 2

Differences between morphs in external morphology

The shape difference in head morphology between the two trophic morphs is largely due to the differences in the angle of the snout (SnA: Table II). The differences between the morphs and the ontogenetic shape trend in this variable is shown in a bivariate plot (Fig. 5). The snouts of both morphs become blunter during ontogeny. The slopes of the SnA-SL relationship are not
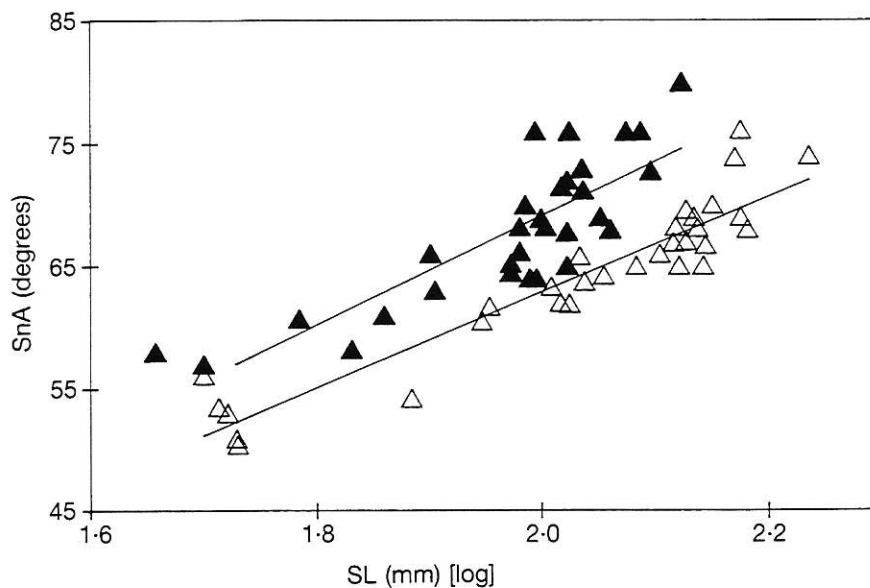

FIG. 5. Bivariate plot of snout acuteness versus standard length. In this and the following graphs regression slopes are provided for each pharyngeal-jaw morph. Tests for homogeneity of slopes were conducted for each set of slopes for each external measurement and each measurement on the pharyngeal jaws (Tables IV, VI). ▲ Molariform; △ papilliform.
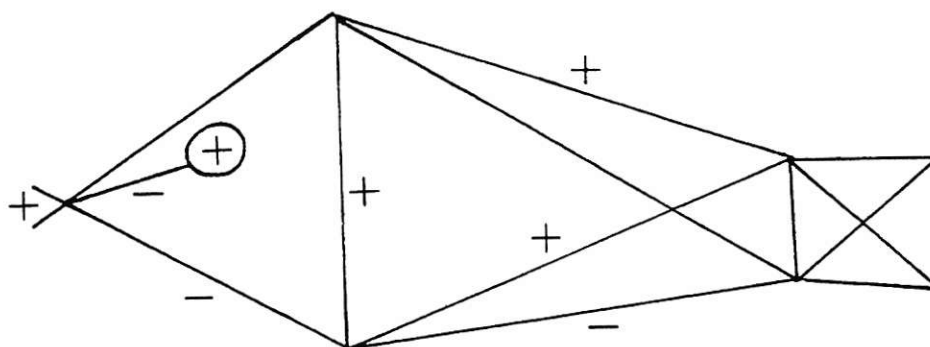
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FIG. 6. External measurements highlighting the differences in external morphology between the molariform and the papilliform morphs. + Indicates a significantly larger adjusted mean (Table IV) of a particular measurement in molariform versus papilliform morphs; — indicates smaller adjusted mean in molariform than in papilliform morphs.

TABLE IV

Bivariate allometric coefficients of external measurements. Allometric coefficients were calculated with log-transformed (except SnA) variables and standard length (SL) as covariate. Tests for homogeneity of slopes, and adjusted means (ANCOVA) were done with SL as covariate (—indicates that ANCOVAs could not be conducted because of heterogeneity of slopes)

	Allometric coefficients		Heterogeneity of slopes		Difference of adjusted means	
Trait[a]	Mo	Pa	F	P	F	P
SnA	(44·34)	(38·88)	0·87	0·355	66·93	0·000
HL	0·92	0·96	1·35	0·250	1·47	0·230
EyL	0·77	0·70	3·27	0·076	24·20	0·000
SnL	1·09	1·12	0·33	0·568	8·22	0·006
LJL	0·76	0·87	2·84	0·097	0·55	0·463
ChD	1·41	1·37	0·33	0·566	3·69	0·060
POW	1·18	1·24	1·66	0·203	0·37	0·545
IOW	1·20	1·28	2·51	0·119	0·36	0·552
HW	1·14	1·13	0·09	0·762	18·70	0·000
PFL	0·93	0·98	0·60	0·442	1·00	0·312
M1	0·98	1·01	0·93	0·338	1·56	0·216
M2	1·03	1·11	2·80	0·100	15·50	0·000
M3	0·99	0·97	0·67	0·417	8·88	0·004
M4	1·02	1·00	1·11	0·296	30·12	0·000
M5	0·97	1·00	2·21	0·143	6·03	0·017
M6	0·98	1·00	1·78	0·187	12·76	0·001
M7	0·99	1·02	0·68	0·415	0·29	0·594
M8	0·93	0·99	2·77	0·102	0·15	0·702
M9	1·05	1·10	3·39	0·071	0·09	0·764
M10	1·37	1·18	5·05	0·028	—	
M11	1·30	1·11	7·41	0·009	—	
M12	1·15	1·13	0·25	0·622	0·01	0·940
M13	1·02	1·12	2·59	0·113	0·51	0·479

[a] For key to abbreviations, see legend to Fig. 1
Mo = molariform; Pa = papilliform

significantly different between both morphs, but the adjusted means (through ANCOVA with SL as covariate) are (Table IV). Only a few other variables contribute noticeably to the shape differences between the morphs (Tables II, IV).

Ontogenetic patterns of differentiation in shape between morphs were investigated through the calculation of bivariate allometric coefficients (Table IV). Tests were carried out for statistical differences in the bivariate allometries (Table IV: tests for homogeneity of slopes, and subsequent tests of the adjusted means between jaw morphs).

The trend of increasing SnA with size of both morphs is apparent on inspection of the allometric coefficients of M1, M2 and M3 in Table IV. M2 is positively allometric (as also is M1 in papilliform fish) while M3 is negatively allometric. These ontogenetic trajectories produce an increase in SnA (see also Fig. 5).

The external morphology of the rest of the body differs between morphs as well. The molariform morphs have blunter snouts, larger eyes, shorter snouts, wider heads, and deeper and shorter bodies than the papilliform morphs (Fig. 6). Papilliform fish grow faster in the midregion of the body, tending to elongate their bodies faster than do molariform morphs (Table IV). In the tail region (M9-M13), the molariform morphs tend to grow faster than papilliform morphs. Allometric coefficients are significantly different in two measurements. The adjusted means of measurements of the tail region are not significantly different between morphs (Table IV).

The overall differences in morphology between the pharyngeal-jaw morphs are remarkably similar to other polymorphisms in body form (e.g. limnetic and benthic forms of bluegill sunfishes; Ehlinger & Wilson, 1988) and interspecies differences in sympatric species of sticklebacks (reviewed in Baumgartner, Bell & Weinberg, 1988).

Differences between morphs in the pharyngeal-jaw morphology

Both morphs differ markedly in pharyngeal-jaw morphology. The single most important variable is the width (diameter) of the largest tooth on the lower pharyngeal jaw (Table III, Fig. 7).
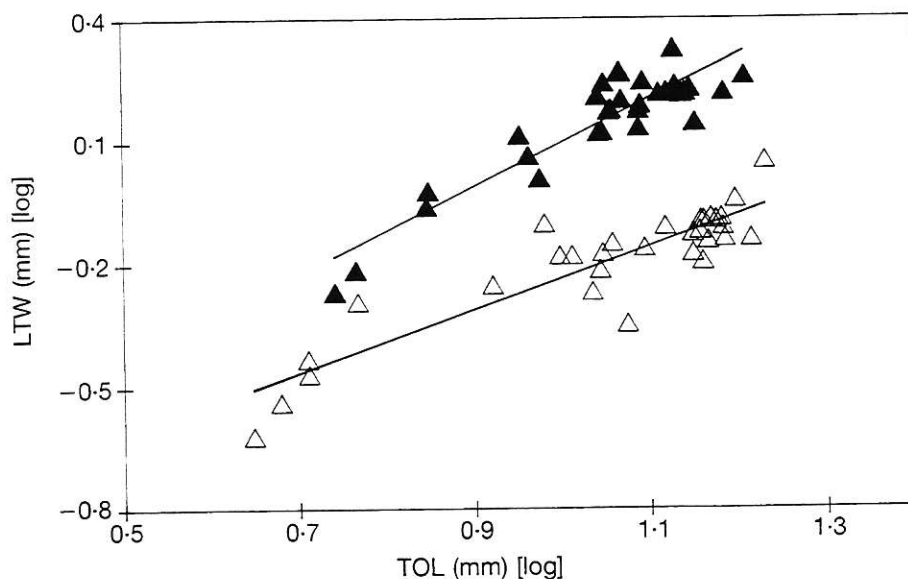

FIG. 7. Bivariate plots of the diameter of the largest tooth width on the lower pharyngeal jaw (LTW) against the total length of the lower pharyngeal jaw (TOL). ▲ Molariform; △ papilliform.

TABLE V

Multivariate allometric coefficients of pharyngeal-jaw dimensions. Derived from within-group PCAs, based on a variance-covariance matrix, rescaling the eigenvectors of the first principal components axis by multiplying each element by the square root of the number of variables (Jolicoeur, 1963)

Trait[a]	Molariform	Papilliform
FL	1·065	1·011
TOL	0·918	1·011
BOW	0·921	1·053
BOD	1·047	1·065
BLD	1·104	1·035
BLL	0·978	0·939
LTW	1·000	0·792
PDL	0·981	0·951
PDW	0·987	1·107

[a] For key to abbreviations, see legend to Fig. 2

TABLE VI

Bivariate allometric coefficients of jaw dimension. (Calculated with log-transformed standard length as predictor variable.) Tests for homogeneity of slopes were conducted and the resulting F- and P-values are reported. All adjusted means between the two morphs (from ANCOVAs) were significantly different, but are not reported here (— indicates that ANCOVA could not be conducted because of heterogeneity of slopes)

Trait[a]	Allometric coefficients		Heterogeneity of slopes		Difference of adjusted means	
	Mo	Pa	F	P	F	P
FL	1·16	1·07	3·66	0·061	31·5	0·000
TOL	1·4	1·07	0·61	0·436	124·2	0·000
BOW	1·12	1·12	0·04	0·831	160·9	0·000
BOD	1·16	1·13	0·66	0·188	365·8	0·000
BLD	1·23	1·10	2·27	0·137	251·2	0·000
BLL	1·10	0·99	1·24	0·271	73·4	0·000
LTW	1·13	0·81	5·73	0·020	—	
PDL	1·09	1·01	3·25	0·077	87·1	0·000
PDW	1·12	1·17	0·79	0·379	142·9	0·000

[a] For key to abbreviations, see legend to Fig. 2
Mo = molariform; Pa = papilliform

This is the variable that exhibits the largest difference between the jaw morphs in the multivariate allometric coefficients (Table V). (Multivariate allometries are rates of growth estimated with respect to overall body size and not simply a bivariate comparison of growth rates: Strauss, 1987.) The isometric growth of the diameter of the largest tooth (LTW) in molariform morphs, as against the retardation of its growth (negative allometry) in the papilliform morph, contributes largely to the observed difference between the morphs in the pharyngeal-jaw morphology (Table V).

Tests for homogeneity of slopes between molariform and papilliform fish for each of the nine jaw measurements regressed against standard length show that only the slopes of the relative growth of the largest tooth are significantly different between morphs; the adjusted means of all measurements (ANCOVA not possible for LTW) are significantly different between the morphs (Table VI). This indicates that although the respective morphologies are already determined in the size-range of fishes considered in this study, the differences in pharyngeal-jaw morphology continue to increase during ontogeny.

Discussion

It is self-evident that differences in adult morphology between species, particularly in shapes of homologous structures, result from differences in ontogenies (Strauss, 1984; Strauss & Fuiman, 1985; Shea, 1985; Creighton & Strauss, 1986). In a polymorphic species, however, the ontogenetic trends in change in shape can also differ intraspecifically between morphs. Furthermore, the amount of transformational change from juvenile to adult in polymorphic species is especially instructional. It defines the morphospace that can be 'occupied' by a single species. Its dimensions indicate how different other species must be not to overlap in morphology. Of course many species differ only behaviourally and not morphologically. However, the delineation of intraspecific morphospace helps taxonomists assign or deny species rank to morphotypes of unknown taxonomic status.

Ontogeny and phylogeny of shape changes and their functional significance

Barel (1983) proposed a functional morphological model that related relative dimensions of the shape of cichlid skulls to a hypothesized feeding mode. In his scheme, 'biters' are cichlids whose jaws inflict a relatively more powerful bite than those of 'suckers', who suck prey into their buccal cavity without prior manipulation by their oral jaws. 'Biters' have relatively shorter lower jaws, shorter snouts, shorter, more ventrally oriented ethmoid regions of the neurocranium, and deeper adductor-mandibulae muscles. As a result of this morphology the gape of 'biters' is not as wide and cannot be protruded as far as that of 'suckers'.

Barel's terms imply a functional explanation of form; however, the hypothesized feeding mode of 'biters' and 'suckers' has not been tested explicitly. I therefore suggested (Meyer, 1987) the purely descriptive terms 'obtusorostral' for the steep snout of 'biters' and 'acutorostral' for the pointed snout of 'suckers'. These terms cannot be applied categorically but rather denote ends of a morphological continuum.

Cichlasoma citrinellum of both morphs change from acutorostral to obtusorostral morphology during ontogeny (Gottfried, 1986). The lower jaws become relatively shorter, the cheeks deeper (the depth is determined by the adductor mandibulae, which is important for the force of biting), the eyes relatively smaller, and the snouts shorter and the snout acuteness steeper (figs 1, 2 in

Gottfried, 1986; Fig. 5). Compared with the molariform benthic morph, the limnetic papilliform morph retains a more acutorostral morphology throughout its life.

Models of functional morphology (Otten, 1982, 1983; Barel, 1983) predict that this ontogenetic change in head shape has pronounced effects on the feeding mode of the fish. This difference in feeding mode will facilitate ecological differentiation and may decrease intraspecific competition between different ontogenetic stages and also between pharyngeal-jaw morphs.

Limnetic and benthic body forms in polymorphic species

The differences in external morphology between molariform and papilliform *C. citrinellum* show remarkable resemblance to the littoral (benthic) and open water (limnetic) intraspecific morphs that have been found in bluegill sunfish (Ehlinger & Wilson, 1988). Those two morphs are morphologically and behaviourally specialized to feed on different prey and in different habitats within lakes (Ehlinger & Wilson, 1988). Differences in body shape (e.g. elongate papilliform versus deep-bodied molariform morphs; Fig. 8) will also affect fast-start and endurance-swimming performance (Webb, 1978, 1984; Webb & Corolla, 1981; Taylor & McPhail, 1985a, b, 1986).
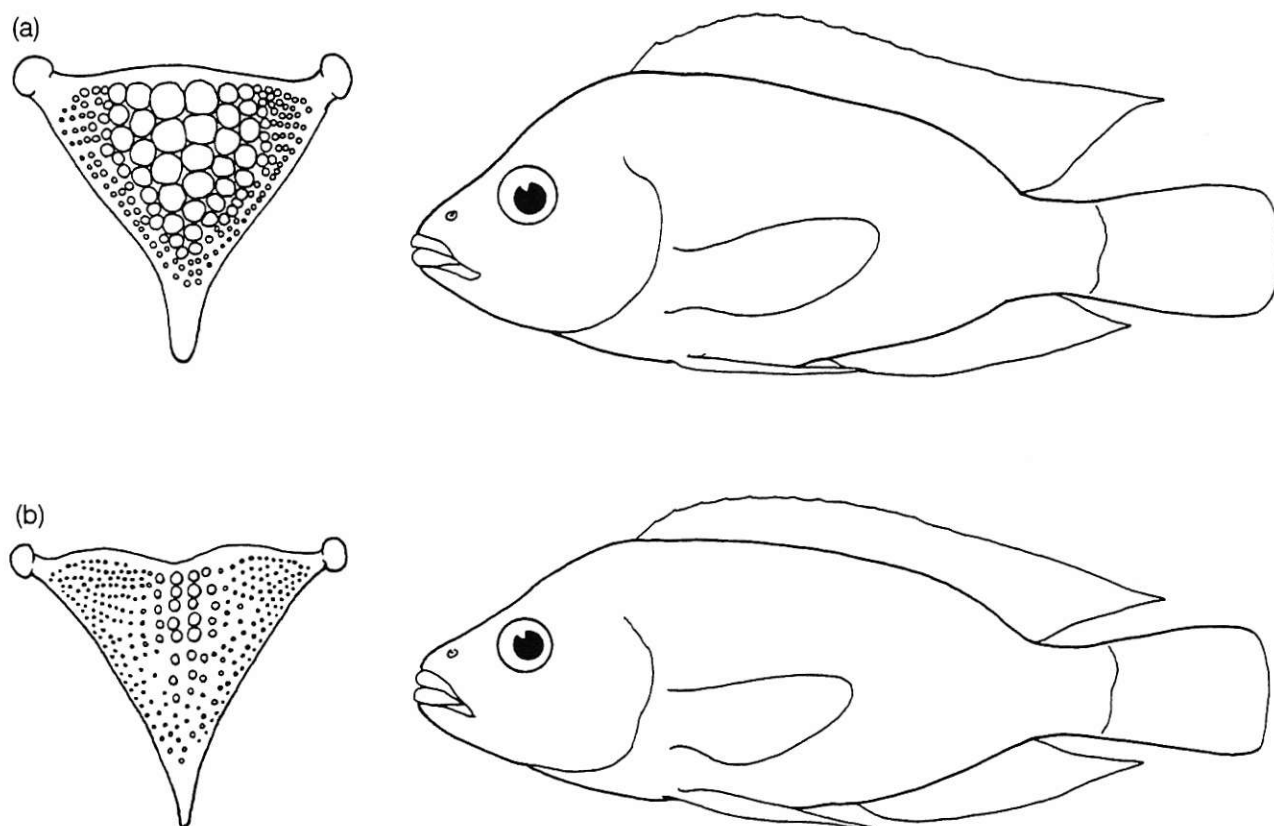

FIG. 8. Semischematic drawing outlining the differences in body shape and pharyngeal-jaw morphology in *C. citrinellum*. Molariform morphs have shorter, blunter snouts, wider heads, larger eyes and a deeper, shorter body than the papilliform morph. Molariform pharyngeal jaws are sturdier and larger, and have larger molariform teeth. Pharyngeal jaws are seen from above. (a) Benthic body form and molariform pharyngeal-jaw morphology. (b) Limnetic body form and papilliform pharyngeal-jaw morphology.

Limnetic and benthic forms are also found in sympatric species pairs of sticklebacks (Larson, 1976; Bentzen & McPhail, 1984; Bentzen, Ridgeway & McPhail, 1984; McPhail, 1984; Ridgeway & McPhail, 1984; Lavin & McPhail, 1985; Baumgartner et al., 1988). The morphs in sticklebacks differ further in migration, escape and foraging specializations (reviewed in Baumgartner et al., 1988).

No data exist that demonstrate a habitat segregation between the trophic morphs of C. citrinellum. Nevertheless, one would expect to find higher numbers of molariform morphs in the structurally complex benthic region where their prey, snails, are more abundant than in deeper water (Meyer, In press a). Molariform and papilliform morphs are ecologically separated; papilliform morphs feed less often on snails than do molariform morphs (Meyer, In press a). However, the effect on performance and ecology of the differences in external morphology of the two morphs of C. citrinellum is untested.

Implications of the polymorphism for ecology and evolution

The differences in the morphology of the pharyngeal jaws of the morphs of C. citrinellum have significant effects on the performance of the respective morphs. Each morph is more effective in feeding on the type of diet to which it seems adapted (Meyer, 1989). The molariform morph is able to crack significantly harder prey than the papilliform morph, which in turn is more efficient in feeding on a soft type of prey (Meyer, 1989). The trophic morphs represent alternative adaptations (sensu West-Eberhard, 1986). The molariform morph may represent an additional optional phenotype (sensu West-Eberhard, 1986) which conferred a buffering effect against extinction on this species through its adaptation to feed on alternative prey (snails).

The presumably adaptive differences in external morphology and pharyngeal-jaw morphology are expected to act synergistically to produce ecological separation and might eventually lead to genetic isolation between the two trophic morphs (Meyer, In press a, b). If morphs live in different habitats and mates are chosen in their respective habitats then disruptive selection may bring about speciation in sympatry (e.g. Rice, 1987; Meyer, In press a).

Differences in the ontogenetic trends in shape between morphs

Surprisingly few of the ontogenetic slopes were significantly different between the morphs of the fish of the size used in this study (Tables IV, VI). The fact that although both morphs show the same ontogenetic trends here, they exhibit different adult morphologies, can only be explained by different ontogenetic trajectories of fish of a smaller size-range than considered in this study. This finding suggests an early determination of differential ontogenetic trajectories between morphs, at a time in ontogeny when they are probably not yet separated ecologically. A future study will include small fish (less than 50 mm in SL) that may not yet be committed to their adult pharyngeal-jaw morphology. This study will attempt to determine if the ontogenetic trajectories of the respective pharyngeal-jaw morphs are distinct from the outset or whether an 'ontogenetic switch' may be responsible for the eventual morphological separation of initially identical fish. In Cichlasoma managuense it was found that ontogenetic trajectories could be influenced and reversed through dietary differences (Meyer, 1987). A future study on C. citrinellum should take these findings into consideration and investigate the potential influences of environmental perturbations on morphology.

Environmental influences on shape

In *C. managuense*, it was possible to influence developmental pathways, and to change the morphology of fish during ontogeny and after sexual maturity, by raising groups of siblings on different diets that probably required different feeding modes (Meyer, 1987). The external morphology of other species of cichlids and fishes in general is known to be phenotypically plastic (reviewed in Meyer, 1987, In press *b*).

One morphological feature of *C. citrinellum* is clearly phenotypically plastic: the development of lips. In three of five populations studied in Nicaragua, great variation in the development of this character occurs (figs 1, 2, 7 in Barlow & Munsey, 1976; pers. obs.). When fish with large lips are brought into the laboratory the lips atrophy within three months (G. W. Barlow, pers. comm.; pers. obs.). In this analysis only small-lipped fish were used, to avoid this additional variable. Both molariform and papilliform fish can have strongly developed lips, even at small sizes (50 mm, pers. obs.).

The morphology of the pharyngeal jaws can be changed by environmental influences in at least one cichlid species, *Astatoreochromis alluaudi* (Greenwood, 1965; Hoogerhoud, 1986; reviewed in Meyer, In press *b*). Whether this is the case in *C. citrinellum* is not known; when fish were fed only on a hard diet less than 20–30% of them changed from papilliform to a more molariform dentition within eight months, but this could be due to wearing out of the teeth. However, replacement teeth (Huysseune, 1983) of molariform morphs have a molariform morphology before they erupt (pers. obs.). Breeding experiments are under way to test the genetic influence on the morphology of the pharyngeal jaws.

Barlow & Munsey (1976) investigated the influence of the environment on the external morphology of stock of *C. citrinellum* from Lake Masaya, Nicaragua by means of univariate morphometrics and found some differences; laboratory-raised fish tended (differences were not tested statistically) to have deeper bodies, more shallow heads, smaller mouths, lips and eyes, a longer base of the dorsal fin and a shorter pectoral fin. A multivariate analysis (A. Meyer, unpubl.) of differences between laboratory-raised and wild-caught fish from the same stock found that external morphological characters differ, probably owing to the laboratory environment. The papilliform pharyngeal-jaw morphology of all Masaya stock, however, remained unchanged.

Many organisms exhibit varying degrees of phenotypic plasticity (see Meyer, 1987 for references). Patton & Brylski (1987) found that populations of gophers that grew in different habitats differed markedly in size but not in shape. They believe that plastic responses to environmental influences are pronounced in size but not in shape. This contrasts with the situation in *C. managuense*, and possibly in *C. citrinellum*. *Cichlasoma managuense* clearly is susceptible to environmental perturbations on the ontogenetic trajectories in its development of alternative morphologies. Fish in general may be more susceptible to environmental influences (Allendorf, Ryman & Utter, 1987; Meyer, 1987); yet it is not known why that might be. Additional investigations of this phenomenon are needed.

Evolutionary implications of ontogenetic shape changes

Among cichlids the ontogenetic trend from an acutorostral to an obtusorostral head shape is not universal. In the closely related *C. managuense* the opposite trend in the ontogeny of shape is found; they switch from an obtusorostral morphology to an adult acutorostral morphology (Meyer, 1987). The same ontogenetic trend in morphology is found in other species (e.g. *C. dovii*)

closely related to *C. managuense* (A. Meyer, unpubl.). Whether all adult acutorostral fish start out as obtusorostral and all adult obtusorostral fish as acutorostral juveniles remains to be seen.

Allometric growth is commonplace, possibly because these ontogenetic changes in shape decrease competition between juveniles and adults, because the two age groups differ not only in size but also in shape. Often differences in habitat choice and prey selection will result (Werner, 1974). In general, ontogenetic changes in shape should allow for higher species packing because even if juveniles of one species and adults of another had the same shape they would still differ in size, allowing for ecological separation (Werner, 1977). If this theory is correct, then large intraspecific morphological variation and discrete trophic polymorphisms will tend to decrease intraspecific competition among adults as well.

It would be revealing to test whether the direction of ontogenetic changes in shape generally coincides with systematic trends, provided that the systematic status is based on characters independent of these traits.

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Appendix 1

Means and standard deviations for all measurements of papilliform and molariform fish. Measurements are defined in the legends to Figs 1, 2

Trait	Molariform Mean	Molariform S.D.	Papilliform Mean	Papilliform S.D.	t	P
SnA	67·9	5·89	64·2	6·63	2·34	0·023
TL	127·8	27·02	148·3	43·60	2·21	0·031
SL	96·7	20·91	114·1	34·51	2·38	0·021
HL	35·7	7·34	41·4	12·18	2·19	0·033
EyL	9·7	1·75	10·2	2·31	0·96	0·341
SnL	13·7	3·39	17·2	5·85	2·44	0·018
LJL	13·9	2·66	16·3	4·54	2·44	0·018
ChD	14·2	4·35	17·6	6·82	2·23	0·026
POW	12·7	3·11	15·9	5·95	2·61	0·011
IOW	12·8	3·24	15·9	6·06	2·47	0·016
HW	18·2	4·46	20·9	7·10	1·82	0·074
PFL	29·4	6·41	33·8	10·18	2·04	0·046
M1	41·5	8·70	48·5	14·82	2·25	0·028
M2	44·3	9·83	50·5	16·72	1·78	0·080
M3	41·8	9·15	48·0	14·26	1·99	0·051
M4	57·7	12·51	65·8	20·04	1·89	0·064
M5	48·9	10·25	58·8	17·80	2·12	0·038
M6	63·0	13·19	73·0	22·21	2·12	0·038
M7	56·0	12·15	66·0	20·36	2·31	0·024
M8	14·9	2·99	17·6	5·40	2·45	0·017
M9	13·2	2·99	16·0	5·32	2·49	0·016
M10	9·7	2·86	12·4	4·34	2·83	0·006
M11	11·0	3·09	13·3	4·49	2·24	0·029
M12	17·0	4·23	20·5	6·74	2·42	0·019
M13	17·0	3·99	20·8	6·99	2·61	0·011
FL	10·8	2·67	9·76	3·05	1·38	0·174
TOL	11·5	2·63	11·95	3·74	0·56	0·575
BOW	13·9	3·42	14·48	4·77	0·50	0·619
BOD	5·0	1·28	4·24	1·43	2·11	0·039
BLD	3·6	1·09	2·80	0·97	2·92	0·005
BLL	2·8	0·75	2·52	0·80	1·29	0·201
LTW	1·5	0·37	0·67	0·19	10·65	0·000
PDL	7·9	1·78	8·10	2·48	0·45	0·656
PDW	10·2	2·40	10·34	3·51	0·21	0·835

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