

Ecomorphological diversification and convergence in fluvial cichlid fishes

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Received 15.12.1993

Accepted 24.10.1994

Key words: Adaptive radiation, Convergent evolution, Costa Rica, Diet, Phylogeny, Venezuela, Zambia

Synopsis

We compared ecological and morphological patterns among cichlid faunas from three different biotic regions: the Río Tortuguero/Río Sarapiquí in Costa Rica, the Río Apure drainage in Venezuela, and the Upper Zambezi drainage in Zambia. Cichlids comprise 19 percent of the fish fauna in the Tortuguero and Upper Zambezi drainages and 6.5 percent in the Apure drainage. Cichlid faunas exhibited similar patterns of habitat and food resource utilization, although vegetation-dwelling is more common and detritivory and herbivory are rarer in the Apure fauna. We hypothesize that South American ostariophysan fishes were more preadapted than cichlids to exploit detritivore and herbivore niches. The Zambezi cichlid fauna shows less ecomorphological diversification than the other two faunas, even though the degree of dietary diversification is similar among faunas. *Chaetobranchius flavescens* from the Venezuelan fauna is the only species that specializes on zooplankton as an adult, and algae grazing (*Neetroplus nematopus*) and specialized fruit feeding (*'Cichlasoma' tuba*) were represented only in the Costa Rican fauna. Based on the most recent hypothesized phylogeny for the family Cichlidae, we identified numerous interfaunal ecomorphological and feeding niche convergences. Patterns of ecomorphological divergence in relation to cladogenesis indicate a faster rate of evolutionary niche diversification in Central American cichlids compared with the two other faunas.

Introduction

Ecomorphology is the field of study that examines relationships between functional morphology and ecological performance. Functional morphology is usually studied under controlled conditions in the laboratory (Alexander 1970, Liem 1980, Lauder 1983), however it can be pursued in the field setting (Yamaoka 1982). In contrast and by definition, ecological studies require the investigation of organisms in a field setting. Developments at the theoretical interface between functional morphology and ecology have been, to some extent, hindered by weak linkages between laboratory and field data. For example, Liem & Osse (1975) demonstrated

functional versatility in the feeding apparatus among species of haplochromine cichlids of the African rift lake species flocks. In nearly all cases examined, versatility in motor patterns permitted both specialized feeding modes as well as generalized feeding on a fairly wide variety of prey in the laboratory. Liem (1991) questioned whether or not morphological specializations in these diverse fishes necessarily translated into ecological segregation in the field setting. Several studies have shown variable diets within populations of African lake-dwelling cichlids (McKaye & Marsh 1983, Ribbink et al. 1983, Witte 1984). Other studies have documented specializations in the foraging behaviors and diets of individual fishes within populations of Lake Tan-

ganyika haplochromines (Yamaoka 1982, 1983, 1991, Hori 1983). To date, few field studies have achieved sufficient detail to demonstrate the association between the frequency of utilization of alternative feeding modes, resource utilization, and interspecific niche segregation within fish assemblages.

Imperfect knowledge of phylogenetic relationships poses an additional problem for advances in ecomorphology. Even if ecological specializations can be demonstrated in the field, closely related species might be expected to exhibit similar feeding behaviors and diets due to inherited phenotypic similarities. Adaptive radiations in form, function, and ecology provide evidence of ecomorphological relationships, however interpretations even of the same data can sometimes vary. For example, Liem (1991) and Yamaoka (1991) differed in their interpretations of morphological and ecological diversification in African rift lake cichlids as evidence for adaptive radiation. The demonstration of convergent morphological traits and associated ecological performance is perhaps our most powerful means of documenting ecomorphological relationships (Orians & Paine 1983, Motta & Kotrschal 1992). Studies of convergent evolution require robust hypotheses of phylogenetic relationship, and the lack of a high degree of phylogenetic resolution in large clades has retarded this area of inquiry (Winemiller 1991a, 1992). Meyer et al.'s (1990) molecular study of phylogenetic relationships and parallelism among African rift lake cichlids illustrates how well-resolved phylogenetic data facilitate robust interpretations of morphological diversification.

Motta & Kotrschal (1992) recently outlined the steps for a research program in ecomorphology. They proposed that initial steps should involve: (1) the study of the relationships (covariance) between environmental factors and form, (2) performance testing, (3) examination of optimization and constraints on form-function relationships, (4) investigation of the ontogeny of form-function relationships, and (5) examination of the direction of evolution in form-function relationships. Rarely are all five elements incorporated into ecomorphological research, although Ryan and Rand's studies of predation, sexual selection, and evolution of vocaliza-

tion in the tungara frog (*Physalaemus*) provides an illuminating example (Ryan 1985, Rand et al. 1992). Motta & Kotrschal (1992) also listed several pitfalls in ecomorphology, including: (1) selection of inappropriate characters for the question, (2) selection of an inappropriate analysis, (3) lack of a null hypothesis, (4) lack of knowledge of life history, and (5) lack of knowledge of constraints, both genetic and morphological.

Sparked by Hutchinson's (1959) seminal paper, ecologists have invoked the theory of ecomorphology in studies of community organization (MacArthur & Levins 1967, Fenton 1972, Hespenheide 1973, Karr & James 1975). Gatz (1979a, 1979b, 1981) was among the first to examine the covariance among morphological traits of known function in fish assemblages, and the covariance of morphological traits with ecological traits. Several studies have followed Gatz's paradigm to explore additional aspects of fish community organization (Felley 1984, Moyle & Senanayake 1984, Page & Swofford 1984, Watson & Balon 1984, Grossman 1986, Douglas 1987, Strauss 1987, Wikramanayake 1990, Winemiller 1991a). The success of this community paradigm has resulted in frequent interpretations of patterns of covariation among morphological traits with known functions in the context of ecological interactions. Following this approach, ecomorphological theory is effectively substituted for the absence of mechanistic evidence from field studies (e.g., Werner 1977).

The present study integrates elements 1 and 5 of Motta & Kotrschal's (1992) research paradigm to reveal patterns of ecomorphological divergence and convergence among species assemblages. We examine patterns of morphological and ecological diversification and convergence in river-dwelling cichlids from three biotic regions: south-central Africa, northern South America, and Central America. Morphological traits were selected based on assumptions of optimal performance and functional constraints (Motta & Kotrschal's elements 2-3) from earlier functional morphology (e.g., Alexander 1970, Lauder 1983) and ecomorphological studies of fishes (e.g., Gatz 1979a, Webb 1984). We adopt Winemiller's (1991a) approach for comparing faunas and examining hypotheses of eco-

morphological convergence and divergence. The advantages of using fluvial cichlid fishes for ecomorphological comparisons include: (1) a reasonable preliminary hypothesis of phylogenetic relationship between and within cichlid faunas has been proposed recently (Stiassny 1991), (2) for comparative purposes, many functional morphological studies have been conducted on the feeding of cichlid fishes and similar percomorphs, (3) relevant morphological characters and analytical methods for faunal comparisons have been established, and (4) we have an extensive and reasonably detailed ecological dataset for these ecologically diverse fishes. In addition to revealing a number of regular features in patterns of faunal niche diversification, we demonstrate numerous ecomorphological convergences among all of the basic trophic niches.

Regional cichlid faunas

We relied on the collection records of Winemiller (1990, 1991b, and unpublished data filed at the Texas Natural History Collection, Austin) from numerous locations within each of three river basins located in separate biotic regions: South America, Central America, and Central Africa (Fig. 1). To verify that all known cichlid species had been captured in each drainage, we referred to Bussing (1987) for Costa Rica, Bell-Cross & Minshull (1988) for Zambia, and records in the Museo de Zoología in Guanare, Portuguesa for Venezuela. Our collections uncovered one previously undescribed cichlid species, *Serranochromis altus*, in the Upper Zambezi drainage (Winemiller & Kelso-Winemiller 1991).

We referenced Taphorn (1990) for the total fish species composition and delineation of the Río Apure Basin, except that we omitted cichlid species that occurred only in the acidic clearwater and

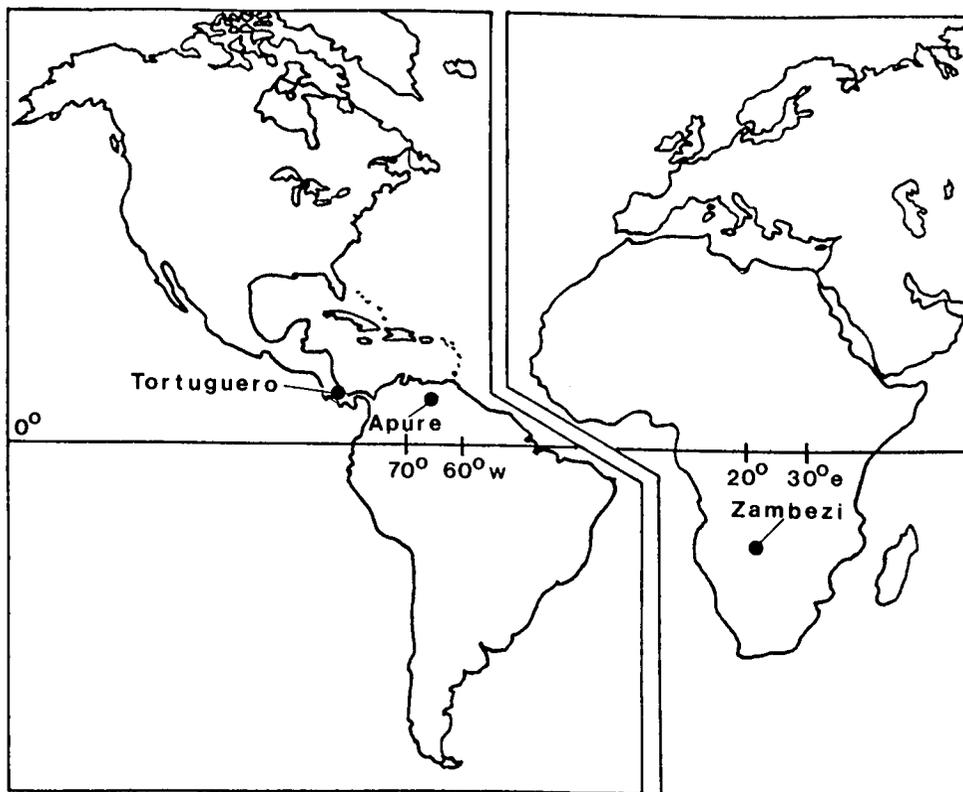


Fig. 1. Map showing locations of Río Tortuguero-Río Sarapiquí (Costa Rica), Río Apure (Venezuela), and Upper Zambezi River (Zambia) drainages.

blackwater Río Aguaro-Guaricito drainages on the eastern fringe of the Apure basin; in acidic streams in Barinas state on the western edge of the Apure basin; or in Las Majaguas, an impoundment in Cojedes state (Taphorn 1990). These areas have distinctive fish faunas that are more characteristic of nutrient-poor acidic ecosystems more commonly encountered in other regions of Venezuela (e.g., the Río Morichal Largo in the eastern Ilanos of Monagas state, Río Capanaparo-R. Cinaruco in southern Apure state, and drainages of the Guyana highlands in Bolivar state and Amazonas territory in the east and south of Venezuela). Although there sometimes is a small amount of overlap in taxonomic composition, the cichlid faunas of these nutrient-poor blackwater streams are quite different from those observed in the more nutrient rich Río Apure fauna (Taphorn 1990). For example *Cichla orinocensis*, *Geophagus* cf. *surinamensis*, and *Mesonauta festivum* occur in either nutrient-poor, highly-acidic waters (pH 4.0–5.9) in southern and eastern Venezuela, or nutrient-rich moderately-acidic waters (pH 6.0–6.9) of the Río Apure drainage in northern Apure state. However, most Venezuelan cichlids typically occur in only one of these aquatic ecosystem categories. For example, '*Aequidens*' cf. *pulcher*, *Apistogramma hoignei*, and *Crenicichla geayi* are widespread in the Río Apure basin, but are replaced by congeneric species in acidic waters in other regions of Venezuela.

We treated the fishes of the northern Caribbean drainages of Costa Rica as one fluvial fish fauna (designated Río Tortuguero/R. Sarapiquí fauna) within Bussing's (1976) Río San Juan ichthyological province. In this comparative study, we elected not to deal with lacustrine fish faunas within the Río San Juan basin. The Río Sarapiquí is actually a north-flowing tributary of the lower Río San Juan with the headwater tributaries located in close proximity to headwaters of northeast-flowing coastal drainages (i.e., Río Chiripó, Río Tortuguero, Río Parismina). Within this region, geographical variation in assemblages is associated primarily with habitat conditions determined largely by fluvial distance from the sea coast and not by individual coastal drainages (Winemiller & Leslie 1992).

The relative composition of each fish fauna is list-

Table 1. Fish faunas in three river drainages: Río Apure (Venezuela), Río Tortuguero/R. Sarapiquí (Costa Rica), and Upper Zambezi River (Zambia).

Río Apure		
Order	No. species	Percent fauna
Rajiformes	4	
Clupeiformes		
Characiformes	138	
Siluriformes	137	
Gymnotiformes		
Atheriniformes	10	3
Synbranchiformes	1	< 1
Pleuronectiformes	2	< 1
Perciformes	25	
(Cichlidae)	(23)	(6.5)
Total	353 spp.	100%
Río Tortuguero/Río Sarapiquí		
Order	No. species	Percent fauna
Lepisosteiformes		1
Clupeiformes	2	3
Characiformes	8	
Siluriformes		
Gymnotiformes		
Atheriniformes	11	15
Synbranchiformes		
Pleuronectiformes	4	6
Other marine orders	6	8
Perciformes	37	51
(Cichlidae)	(14)	(19)
Total	72 spp.	100%
Upper Zambezi		
Order	No. species	Percent Fauna
Mormyriiformes	7	8
Gonorynchiformes	2	2
Characiformes	7	8
Cypriniformes	25	28
Siluriformes	20	23
Atheriniformes	6	7
Perciformes	21	24
(Cichlidae)	(17)	(19)
Total	88 spp.	100%

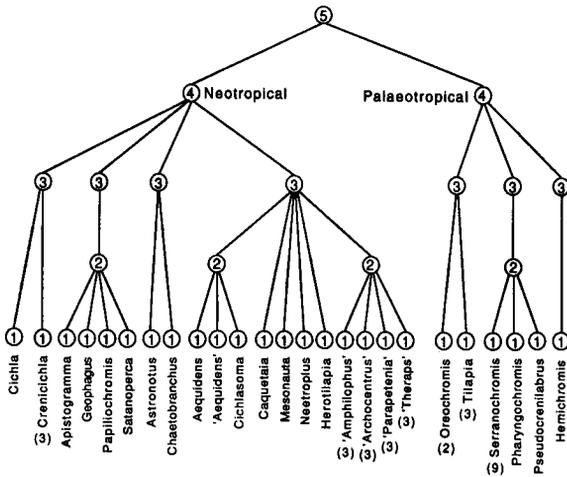


Fig. 2. A phylogeny showing evolutionary relationships among cichlids of the three study regions. The hypothesis of phylogenetic relationship is based on composite phylogenies and information summarized in Stiassny (1991). Numbers of species in those genera containing more than one species appear in parentheses.

ed by family in Table 1. The Apure basin, as defined by Taphorn (1990), has approximately four times more fish species than either the Tortuguero/Sarapiquí or Upper Zambezi basins. As in most large river basins of South America, the Apure ichthyofauna is heavily dominated by ostariophysan fishes of the orders Characiformes and Siluriformes, and cichlids comprise only 6.5% of the Apure ichthyofauna. Following our modification of Taphorn's definition of the Apure ichthyofauna, we excluded eight cichlids with blackwater affinities (*Guianacara* sp., *Aequidens diadema*, *Biotodoma wavrini*, *Hypselecara coryphaenoides*, *Cichla temensis*, *Heros severus*, *Hoplarchus psittacus*, *Satanoperca daemon*) from our intercontinental faunal comparisons. Cichlids comprised 19% of both the Tortuguero/Sarapiquí and Upper Zambezi ichthyofaunas, and were one of the dominant families in each basin, the Tortuguero basin in particular (Table 1).

Methods

Phylogenetic relationships

We used Stiassny's (1991) composite phylogeny as our hypothesis of evolutionary divergence within

the family Cichlidae (Fig. 2). Taxonomy for the Central American species of *Cichlasoma* is in need of modification as a result from Kullander's (1983) revision of the South American *Cichlasoma*. Following Kullander's revision, *Cichlasoma orinocense* is the only valid representative of *Cichlasoma* within our neotropical dataset. Therefore, we designate Central American species formerly placed within *Cichlasoma* as '*Cichlasoma*' species. The true phylogenetic relationships of the Middle American and Caribbean cichlids have not yet been investigated by modern methods of phylogenetic analysis. Therefore, Miller's (1976) sectional assignments within the Central American '*Cichlasoma*' are treated as genera in our phylogeny in accordance with the guidelines proposed by Kullander (1983) and Stiassny (1991).

We also follow Kullander's (1983, 1986) interpretation of the genus *Aequidens*, which yields *Aequidens tetramerus* as the only true representative of this genus within our cichlid faunas. The species formerly recognized as *Aequidens* cf. *pulcher* is designated as '*Aequidens*' cf. *pulcher*. We follow Stiassny (1991) in assuming that Central American '*Cichlasoma*' species are members of a clade derived from an ancestral lineage that gave rise to *Caquetaia*, *Mesonauta*, *Neotroplus*, *Herotilapia*, and a clade comprised of *Aequidens*, *Aequidens*, and *Cichlasoma*. We follow Greenwood's (1979) designation of the African genus *Serranochromis*, and did not deal with any phylogenetic distinctions at the subgeneric level (e.g., subgenus *Serranochromis* vs. *Sargochromis*).

Morphological data

Morphological measurements were made on fish specimens catalogued in the Texas Natural History Collection of the Texas Memorial Museum, Austin. For *Aequidens tetramerus*, we used a collection from Cojedes state that belongs to the Museo de Zoología, UNELLEZ, Guanare, Portuguesa, Venezuela. Basic habitat data (stream width, depth, pH, temperature, etc.) were recorded at each collection site, and most sites were sampled multiple times during long-term field studies (Winemiller

Table 2. Mean values and coefficients of variation (CV) of 29 morphological traits for three cichlid faunas. Except for pigmentation, gill rakers and maximum SL, all measures are ratios (denominators given in Methods).

Character	Apure South America		Tortuguero Central America		Zambezi Africa	
	Mean	CV	Mean	CV	Mean	CV
Body depth	0.42	0.28	0.47	0.13	0.41	0.13
Body width	0.20	0.20	0.20	0.13	0.18	0.10
Peduncle length	0.11	0.36	0.10	0.25	0.14	0.13
Peduncle d.	0.40	0.20	0.32	0.11	0.37	0.08
Peduncle w.	0.29	0.32	0.32	0.30	0.40	0.21
Body d. b. midline	0.53	0.10	0.49	0.18	0.54	0.04
Head l.	0.35	0.09	0.35	0.08	0.34	0.05
Head d.	0.65	0.12	0.60	0.13	0.64	0.07
Eye position	0.63	0.08	0.63	0.11	0.64	0.10
Eye diameter	0.27	0.25	0.27	0.19	0.22	0.20
Mouth position	1.69	0.35	1.96	0.32	1.53	0.34
Mouth w.	0.63	0.30	0.54	0.21	0.64	0.18
Mouth height	0.33	0.41	0.25	0.30	0.28	0.24
Snout l.	0.42	0.14	0.46	0.14	0.41	0.28
Mouth protrusion	1.22	0.06	1.22	0.07	1.19	0.08
Dorsal fin h.	0.20	0.23	0.24	0.19	0.22	0.12
Dorsal fin w.	0.58	0.07	0.59	0.06	0.56	0.05
Pectoral fin l.	0.30	0.24	0.28	0.15	0.27	0.28
Pectoral fin h.	0.15	0.17	0.16	0.14	0.12	0.14
Caudal fin l.	0.27	0.22	0.30	0.10	0.25	0.10
Caudal fin h.	0.31	0.21	0.30	0.14	0.24	0.14
Pelvin fin l.	0.24	0.30	0.27	0.19	0.26	0.16
Anal fin l.	0.20	0.28	0.24	0.17	0.22	0.16
Anal fin w.	0.22	0.31	0.31	0.22	0.20	0.10
Pigmentation	4.07	0.14	3.79	0.15	3.97	0.21
Gill rakers	1.33	0.46	1.36	0.37	1.53	0.51
Gut l.	1.05	0.22	1.49	0.56	2.36	0.97
Swim bladder l.	0.38	0.12	0.36	0.12	0.33	0.10
Maximum SL	151.5	0.62	169.6	0.55	240.1	0.47

1989a, 1990, 1991b). Fishes were collected by a variety of methods, including seines, castnets, dipnets, gillnets, angling, and on occasion rotenone.

Twenty-nine morphological features related to feeding, swimming behavior, or habitat affiliations (Table 2) were chosen based on information presented and findings in Gatz (1979a). Readers should refer to Winemiller (1991a) to obtain a complete description of each morphological attribute. All distance measurements were taken as the straight line distance between points using vernier calipers for measures < 130.0 mm (to nearest 0.1 mm) and a clear plastic ruler for measures > 130.0 mm (to nearest 1 mm). Body length was entered into the multi-

variate morphological analysis as the maximum SL (MSL) recorded for each species at each site. All other linear distance measures were standardized for size. We explored two methods to standardize data for body size differences. First, measurements were converted into various kinds of ratios to serve as components of body, head, and fin shape. The ratios employed in the analysis were chosen based on earlier functional interpretations (Gatz 1979a, Webb 1984, Winemiller 1991a). For example, deeper-bodied and more laterally compressed fishes are more stable in the water column and can turn with greater precision, but have less ability to exhibit rapid burst swimming (Webb 1984). The following

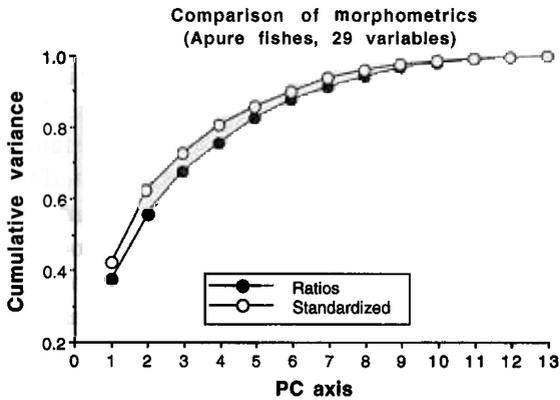


Fig. 3. Comparison of cumulative variation explained by the first 13 axes from PCA performed on cichlid morphological data using two different methods of standardization for linear measures: (1) ratios describing ecomorphological attributes, versus (2) adjustment of linear measures to conform to the grand mean SL.

distances were converted to components of shape using body depth as the denominator: peduncle depth, depth of body below midline, head depth, and mouth height. Body width was the denominator for ratios involving peduncle width and mouth width. Head length was the denominator for the ratio of eye diameter and snout length (mouth closed). Head depth was the denominator for eye position. Snout length with mouth open was divided by snout length mouth closed to provide a measure of relative mouth protrusibility. All other distance measures were divided by SL to yield linear components of morphology.

In the second method, we standardized linear measurements to conform to the interfaunal grand mean SL ($X_{SL} = 150.0$ mm) using $x' = c \cdot x$, where $c = 150.0/SL$. The use of ratios or SL standardized linear measurements allows the first orthogonal axis from principal components analysis (PCA) to be interpreted as primarily a shape determinant rather than solely as a body size axis (Mosimann & James 1979, Bookstein et al. 1985). When raw linear morphological dimensions are entered into PCA, all variable loadings on the first PC axis are of a similar magnitude and positive, indicating the influence of body size on variation in the dataset (Ricklefs et al. 1981, Douglas 1987). Since species scores on principal components axes provide the basis for

ecomorphological ordination and the calculation of distance measures, the use of either ratios or SL standardized measurements reduces the likelihood that the analysis is dominated by a single variable, body size (MSL is employed here as just one of 29 morphological attributes). Allometric bias in the use of ratios as scaling factors in statistics has been debated extensively, especially with regard to between-group comparisons in species with indeterminate growth (e.g., Atchley & Anderson 1978 and references cited therein, Reist 1985, Prairie & Bird 1989, Jackson & Somer 1991). Techniques such as use of regression residuals, log-transformed measures, and log-transformed ratios (Reist 1985) or shearing the first principal components axis derived from untransformed measures (Bookstein et al. 1985) have been used to remove effects of body size on morphological data. Yet, body size is an important factor influencing ecological relationships. We used standardized values for selected ratios as relatively size-independent descriptors of shape that have straightforward functional interpretations (e.g., maneuverability versus burst swimming). Since species scores on the principal components axes are to be used as a basis for ecomorphological ordination and calculation of distance measures, the use of ratios reduces the chance that the analysis is dominated by a single variable, body size. Our analysis seeks to examine variation in the traits of species within and between faunas, as opposed to variation in traits of individuals within and between species and populations, the latter being a common application of multivariate statistics in systematics and ecology. Consequently, we believe that potential allometric effects on the multivariate analysis of ratios are of little consequence to our principal research question. Here we characterize each species as the 'average' adult (in effect treating species as having indeterminate growth), thus the role of allometry and ontogeny on ecological performance is not a focus of the study.

Analysis of morphological data

Principal components analysis (PCA) was used as a basis for inter-assemblage comparisons of species

distributions in morphological space, as well as for identification of patterns of covariation among morphological characters relating to ecology. PCA produces independent orthogonal axes (uncorrelated axes) from the original matrix of data points, such that the first several components model a major portion of the variation among the original variables. PCA was performed on the combined 46 species data set based on the correlation matrix of morphological attributes. Figure 3 compares the cumulative variation modeled by PCAs based on ratios versus SL standardized data. The two methods produced very similar results and completely converged at PC axis 12. We therefore chose to present results involving the ratio data, because these relative measures have more direct functional interpretations (e.g., lateral maneuverability versus burst-swimming body forms). Species scores on the first eight orthogonal axes were used to calculate pairwise Euclidean distances for comparison with patterns generated by the standardized morphological variables.

For each cichlid assemblage, a matrix of Euclidean distances between species pairs was calculated according to the formula:

$$D_{jk} = \sum^n (x_{ij} - x_{ik})^2]^{1/2}$$

where n is the number of PC axes with eigenvalues greater than 1.0, and x_{ij} and x_{ik} are the character loadings on the same PC axis for the species pair j and k . From each matrix of Euclidean distances, we identified nearest neighbor (NND) and the distance to the assemblage centroid (CD) for each species. Average NND is an index of species dispersion in morphological space, the standard deviation of NND serves as an index of the evenness of species packing in morphological space (Findley 1973, Ricklefs et al. 1981), and average CD provides an index of niche diversification, or the relative size of the morphological hypervolume defined by an assemblage.

Morphological distances were plotted against an index of phylogenetic distance for the 50 smallest and 50 largest pairwise morphological distances. We based phylogenetic distances on Stiassny's

(1991) composite phylogeny for the family Cichlidae. We coded the relative phylogenetic distances between each species pairing in the manner indicated by the nodes of the phylogeny in Figure 2. For example, species in the same genus were assigned a phylogenetic distance of 1, and species united by a node at the next level were assigned a distance of 2, and so on. Among these assemblages, the most distantly related species were any African cichlid versus any cichlid belonging to the neotropical clade, and these pairings were assigned a phylogenetic distance of 5.

Ecomorphological convergence

We used the following modified version of Wine-miller's (1991a) index of ecomorphological convergence:

$$C_{ij} = R_{ij}/M_{ij},$$

where C_{ij} is the convergence index for species i and nearest neighbor j , R_{ij} is the number of more closely related species that are more dissimilar to species i than ecomorphological nearest neighbor j , M_{ij} is the maximum possible number of species that could be more closely related to species i relative to the j th nearest neighbor pairing. The index was calculated from the combined 46 species dataset using NND as the measure of ecomorphological similarity and using Figure 2 as the hypothesis of phylogenetic relationships. The convergence index is equal to 1.0 whenever a phylogenetically distant species is ecomorphologically more similar to the target species than each of the species that are determined to be more closely related. The convergence index equals 0 whenever a species' closest ecomorphological neighbor is actually the most closely related species in the dataset.

Ecological data

Each cichlid species was assigned a basic habitat category based on adult captures and the detailed field data gathered during the long term studies in each river drainage. Because conspecifics are often

found in more than one habitat, species were assigned to habitat where the majority of adults were collected. The habitat categories were (1) river or stream channel, (2) backwater or channel edge, and (3) dense aquatic vegetation or woody debris.

Volumetric proportions of stomachs contents were estimated following the methods in Winemiller (1989b, 1990, 1991b). For interfaunal comparisons, diet items were reduced from approximately 80–160 functional categories (Winemiller 1990) to 19 general categories: substrate, detritus, algae, aquatic macrophytes, terrestrial vegetation, microfauna, molluscs, microcrustacea, crustacea, miscellaneous aquatic insects, Odonata, Hemiptera, Trichoptera, Coleoptera, Diptera, terrestrial insects, tetrapod vertebrates, fish scales, and fishes. This was done in order to reduce bias from having different resources in different local and regional environments. Stomach contents data were summed across all available size classes within a species, and in most cases, across different seasons as defined by precipitation. Because larger individuals have much larger stomach volumes, the aggregate diet data are very heavily influenced by adult diets. Species' sample sizes for stomach contents appear in the Appendix (range 2–677). Species' pairwise Euclidean distances were computed based on dietary proportional volumes of 19 diet items using the combined species dataset.

Analysis of ecological and morphological data

Canonical correspondence analysis (CCA) was used to examine the multivariate relationship between the dietary and morphological datasets. CCA produces linear combinations (canonical variables) for each of two data sets (diet and morphology), with the stipulation that the two canonical variables are maximally correlated. As in PCA, relationships of the original variables to the overall model of variance can be determined by examining the coefficients of the canonical variables (canonical weights) or their correlations with the canonical axes. To test the hypothesis that either head characteristics or body characteristics may be associated with feeding performance, we divided morpholog-

ical attributes into two datasets for CCA: one with attributes associated with the head plus overall body size (i.e., SL), and one with attributes associated with body shape. We assume that head features and size should stress how an organism may capture prey over the habitat where it may forage, whereas body shape should be associated with both how and where a fish forages. In addition, we performed linear regressions on all combinations of morphological traits with diet items, as well as diet Euclidean

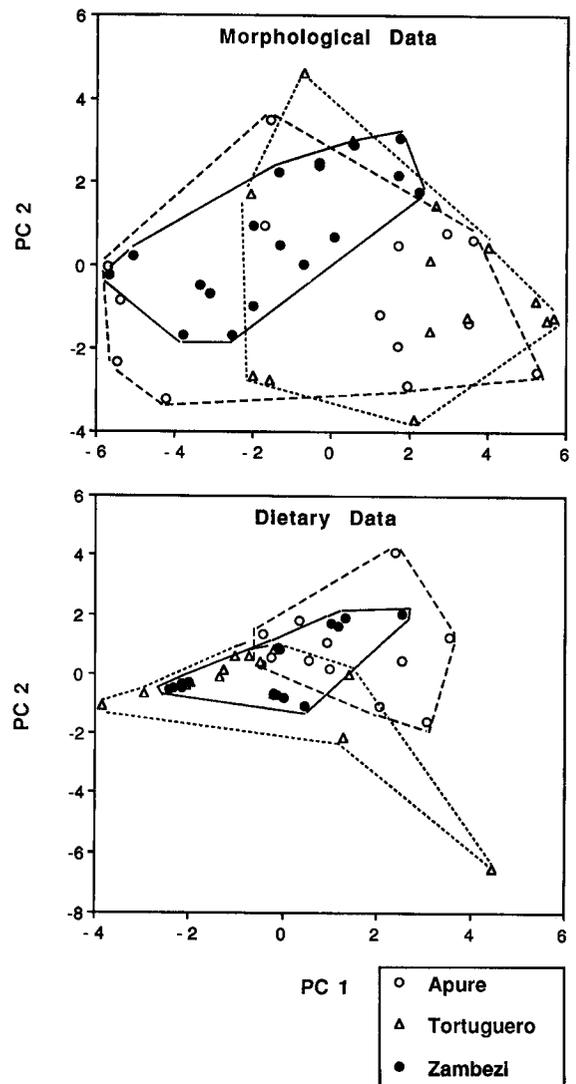


Fig. 4. Plots of species scores on the first two morphology gradients (top) and the first two dietary gradients (bottom) derived from separate PCAs. Polygons bound each of the cichlid faunas. Statistics associated with PCA appear in the Results.

distances with morphological Euclidean distances, both of these based on the combined species dataset.

Results

Patterns of morphological diversification

Univariate comparisons of the 29 morphological attributes between cichlid faunas revealed only a few large differences. Table 2 presents mean values and coefficients of variation for each attribute by fauna. Statistically significant mean faunal differences were obtained for mouth position (Zambezi > Apure, Tortuguero; $t_{Z,A} = 3.05$, DF = 14, $p < 0.01$; $t_{Z,T} = 4.67$, DF = 13, $p < 0.0001$), caudal fin height (Zambezi < Apure, Tortuguero; $t_{Z,A} = 4.16$, $p < 0.001$; $t_{Z,T} = 5.37$, $p < 0.0001$), anal fin width (Tortuguero > Apure, Zambezi; $t_{T,A} = 3.73$, DF = 13, $p < 0.005$; $t_{T,Z} = 6.75$, DF = 13, $p < 0.0001$), log-relative gut length and maximum body length (Zambezi > Apure; $t_{Z,A} = 2.55$, $p < 0.025$). The univariate faunal differences can be summarized by the observation that the Apure fauna generally lacks herbivorous and detritivorous cichlids with long, coiled alimentary canals; and the Zambezi fauna has a relatively greater number of large predatory cichlids with supraterminal mouths and relatively narrow caudal fins compared with the other cichlid faunas (ecological data are presented in following sections).

When species scores on the first two axes from PCA are plotted for the morphological analysis, all three cichlid faunas overlapped in the vicinity of the centroid (Fig. 4). The first PC axis modeled 36% of the total morphological variation (eigenvalue = 10.33) and was most influenced by relative body depth (eigenvector = 0.28), anal fin length (0.25), caudal fin length (0.24), anal fin width (0.24), pelvic fin length (0.24), dorsal fin height (0.23), dorsal fin length (0.23), caudal peduncle length (-0.22), mouth width (-0.22), body width (0.22), caudal peduncle width (-0.21), pectoral fin height (0.21), and eye diameter (0.20). The second PC axis modeled 14% of the total morphological variation (eigenvalue = 3.90) and was most influenced by relative mouth position (eigenvector = 0.34), mouth pro-

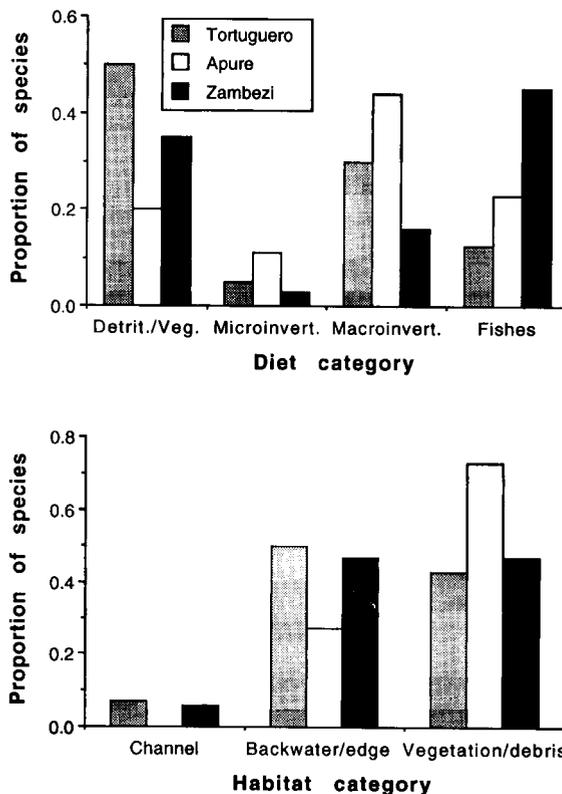


Fig. 5. Histograms showing the proportion of cichlid species in each fauna that were associated with four general diet categories (based on volumetric proportions) and three general habitat categories (based on field collection data). Chi-square contingency test of faunas with habitats was $\chi^2 = 0.147$, DF = 4, $p = 0.997$; and for faunas with diet categories $\chi^2 = 0.525$, DF = 6, $p = 0.998$.

trusibility (-0.31), snout length (0.29), pigmentation (-0.28), depth of the body below the midline (0.26), eye position (-0.25), head depth (0.23), caudal peduncle length (0.23), caudal peduncle width (0.22), and body width (-0.21). The third axis (eigenvalue = 2.62) modeled 9% of morphological variation and had the following dominant variable loadings: maximum standard length (-0.37), relative gut length (-0.35), pelvic fin length (-0.31), pectoral fin height (0.29), eye diameter (0.28), head depth (0.26), dorsal fin height (-0.25), and anal fin length (-0.22). Compared with the Zambezi cichlid fauna, the Apure and Tortuguero faunas tended to have more species with deeper bodies, longer dorsal, caudal, anal, and pelvic fins, wider anal fins, more downturned mouths, shorter jaw protrusion, shorter snouts, and darker pigmentation. Again,

some of these findings seem to be consistent with a larger relative proportion of fusiform piscivores in the Zambezi cichlid fauna.

Based on results from the multivariate methods, the Zambezi cichlid fauna appears to be less diversified morphologically than either of the two neotropical cichlid faunas. As defined by species scores on the first eight PC axes (Fig. 3), the size of the faunal morphological space as defined by species' Euclidean distances to the faunal centroid was smaller for the Zambezi fauna than the other two faunas, and the Apure space was largest (mean CD for Apure = 1.83, Tortuguero = 1.42, Zambezi = 1.26; F for faunal CDs = 8.66, DF = 2.43; $p < 0.0001$;

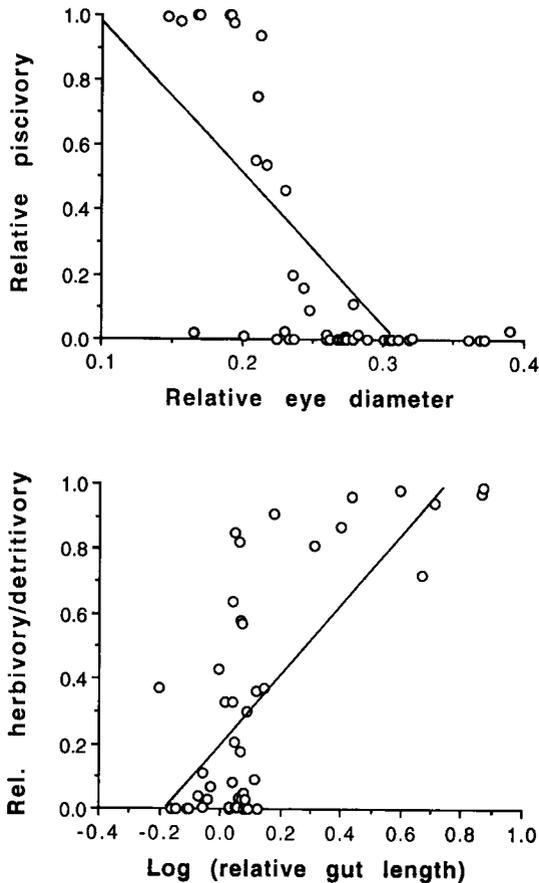


Fig. 6. Two examples of simple bivariate relationships between morphological attributes and diet (relative fraction of aggregate item by volumetric proportion): (top) relative piscivory = -4.73 [log relative eye diameter] + 1.45, $r^2 = 0.49$; (bottom) relative herbivory and detrivory = 1.06 [log relative gut length] + 0.19, $r^2 = 0.53$.

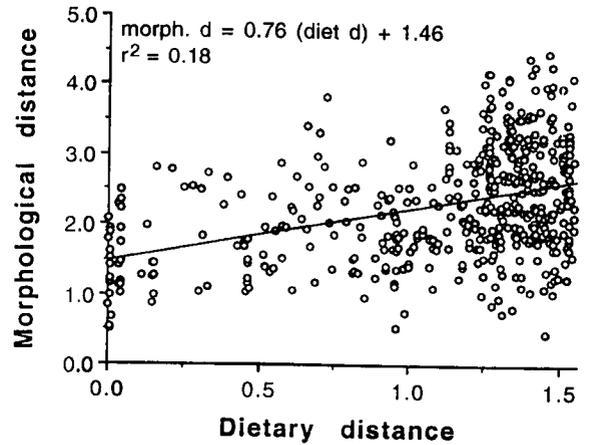


Fig. 7. Plot of morphological Euclidean distance (based on species loadings on first 8 PC axes) by dietary distance (based on volumetric proportions for 19 diet items) for dietary distances < 1.55 among all possible species pairings in the combined fauna dataset (regression $F = 95.52$; $DF = 1,482$; $p < 0.0001$).

Tukey HSD test of mean differences Apure $>$ Zambezi, Tortuguero at $p < 0.025$). Based on mean nearest neighbor distances using species' scores on the first eight PC axes, Apure and Tortuguero cichlids tended to be more dispersed in morphological space than Zambezi cichlids (mean NND for Apure = 2.63, Tortuguero = 2.09, Zambezi = 1.79). The three faunas were more or less equivalent in the evenness of dispersion in morphological space (standard deviation of NND for Apure = 0.76, Tortuguero = 0.66, Zambezi = 0.65).

Patterns of ecological diversification

Frequency distributions of species in four general diet categories were not significantly different between cichlid faunas (Fig. 5), however Apure cichlids tended to consume less detritus and vegetation and more macroinvertebrates, and Zambezi cichlids tended to consume more fishes than the other faunas. When species scores on the first two PC axes are plotted for the diet analysis, the three cichlid faunas again overlapped in the vicinity of the centroid (Fig. 4). The first PC axis modeled 16% of the total diet variation (eigenvalue = 3.05) and was most influenced by algae (eigenvector = -0.34), detritus (-0.34), terrestrial insects (0.32), substrate

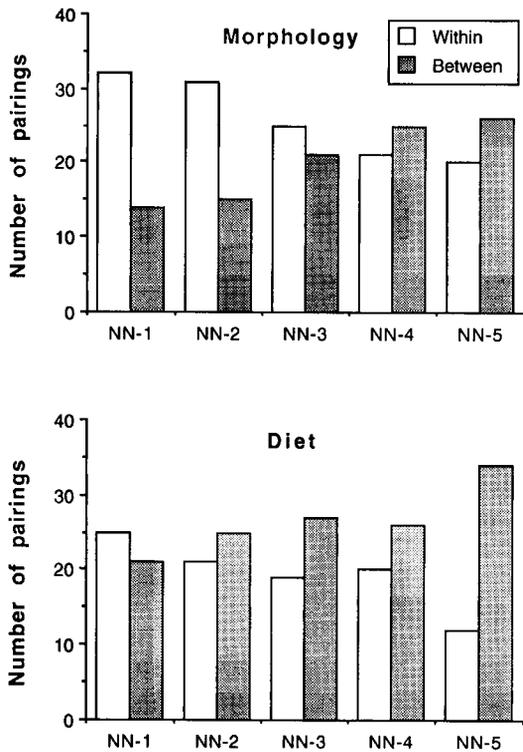


Fig. 8. Frequency histograms of the number of species pairings within-fauna versus between fauna for the first five ecomorphological nearest neighbors and the first five dietary nearest neighbors. Plot is based on Euclidean distances among all possible species pairings in the combined fauna dataset.

(-0.32), Crustacea (0.32), Odonata (0.30), Coleoptera (0.27), Ephemeroptera (0.27), Hemiptera (0.23), and tetrapod vertebrates (0.22). The second PC axis modeled 12% of the total diet variation (eigenvalue = 2.23) and was most influenced by tetrapod vertebrates (eigenvector = -0.44), Trichoptera (0.41), terrestrial insects (-0.39), Crustacea (-0.36), Hemiptera (0.29), fish scales (0.27), Diptera (0.23), and fishes (-0.21). The third axis (eigenvalue = 1.92) modeled 10% of diet variation and had the following dominant variable loadings: fishes (-0.61), substrate (0.37), algae (0.34), detritus (0.29), terrestrial insects (0.26), tetrapods (0.23), and Coleoptera (0.21). The Apure cichlid fauna tended to have more species that consumed large amounts of terrestrial insects, crustacea and odonata nymphs, and more species that ate less detritus, algae and substrate, compared with the Tortuguero and Zambezi faunas. A single species from Tortu-

guero, *Cichlasoma loisellei*, was unique in its consumption of lizards (volumetric percentage = 2.7) and was an outlier on the second PC axis (Fig. 4).

In contrast to results from the multivariate analysis of morphology, cichlid faunas exhibited similar diet diversities and species dispersions in diet space. As defined by species scores on the first eight PC axes (eigenvalues > 1.0, modeling 74% of the total variation), mean CDs for diets were 1.25 (Apure), 1.36 (Tortuguero), and 0.97 (Zambezi). Zambezi cichlid diet diversity was not statistically significantly lower than diet diversities of the two neotropical cichlid faunas (F for faunal CDs = 2.34, DF = 2.43; $P > 0.05$). Mean nearest neighbor distances based on the first eight PC axes were 1.78 (Apure), 1.81 (Tortuguero), and 1.37 (Zambezi), and standard deviations of NND were 0.63 (Apure), 0.91 (Tortuguero), and 0.67 (Zambezi). Frequency distributions of species in four general habitat categories were not significantly different between cichlid faunas (Fig. 5).

Faunal ecomorphological relationships

Bivariate relationships between morphological traits (log-transformed) and diet proportions (categories aggregated into three broad categories: fish, invertebrates, and plants/detritus) were relatively weak with r^2 values ranging between 0 and 0.55 (Fig. 6). In some instances, much of the variation observed around the least squares regression models could be explained by the simultaneous influence of other morphological and ecological variables, and this was examined by PCA and CCA.

We used the species scores on the first eight PCA axes from the morphological dataset to calculate Euclidean distances among all possible pairwise species combinations, both within and between faunas. We used the dietary proportions for 19 prey categories to calculate pairwise Euclidean distances, and plotted the bivariate relationship of morphological distance and dietary distance for each species pair having a dietary distance < 1.5 (Fig. 7). The relationship between morphological similarity and diet similarity had a positive slope, but the correlation was weak ($r^2 = 0.18$). Two factors should operate here to reduce the correlation between morph-

Table 3. Statistics associated with the first three canonical axes of Canonical Correlation Analysis performed on 9 head morphology features and body size with 19 diet features and 6 body morphology features with 19 diet features. Features with eigenvectors between -0.40 and 0.40 are not shown.

	Diet	Diet 2	Diet 3		Diet 1	Diet 2
Canonical correlation	0.98**	0.94**	0.89*		0.96**	0.95*
Proportion of variance	0.55	0.16	0.08		0.31	0.24
Head, size features:				Body features:		
Head length		0.41	-	Peduncle height	- 0.55	-
Head depth	-	-	0.62	Dorsal height	-	0.48
Eye position	- 0.68	-	-	Dorsal length	-	0.50
Eye diameter	0.67	-	-	Pectoral length	-	0.58
Mouth position	0.88	-	-	Anal length	-	0.55
Mouth height	- 0.46	-	-	Pigmentation	- 0.46	- 0.43
Mouth protrusibility	- 0.49	-	-			
Gut length	-	- 0.65	-			
Maximum length	- 0.63	-	-			
Diet composition:				Diet composition:		
Detritus	0.51	- 0.54	-	Detritus	-	0.49
Algae	0.52	-	-	Ephem., Plecopt.	- 0.44	
Aquatic vegetation	-	- 0.48	-	Odonata	- 0.42	
Ephemeroptera, Plecoptera	-	0.46	-	Coleoptera	- 0.45	-
Trichoptera	-	-	0.60	Fishes	-	- 0.69
Fishes	- 0.90	-	-			

* $p < 0.0001$; ** $p < 0.005$; probabilities based on Wilks' lambda for the null hypothesis that the current and all subsequent canonical correlations are zero.

ological similarity and dietary similarity: phylogenetic constraints on gross morphological changes, and regional differences in the distribution of resource availabilities. Adaptive divergences and evolutionary convergences in response to ecomorphological constraints should operate to increase the positive slope and the correlation between morphological distances and dietary distances.

The distributions of nearest neighbor pairings were examined in relation to within-fauna matches versus between-fauna matches for the first five nearest neighbors of each species. This analysis was first performed on the morphological Euclidean distance matrix, then on the dietary matrix. For the morphological data, most of the pairings were within fauna for the first three nearest neighbors, however many between-fauna pairings were encountered (14, 15, and 22 between-fauna matches respectively among the first 3 nearest-neighbor ranks; Fig.

8). Between-fauna matches actually exceeded the number of within-fauna matches for nearest-neighbor ranks 4 and 5 based on the morphological data (Fig. 8). The evidence for interfaunal ecological convergences was even more pronounced in the dietary data. The numbers of between-fauna matches actually exceeded those for within-fauna matches for all nearest neighbor ranks except the first one (Fig. 3). Among first dietary nearest neighbors, the numbers of within- and between-fauna matches were very similar (21 between, 25 within).

To serve as a morphological dataset associated with feeding behavior and diet selection, we entered 9 head features and body size (SL) into CCA with an ecological data set consisting of the volumetric proportional utilizations of 19 diet categories. All 46 species were included in CCA. Canonical correlations and proportions of variance modeled by the CCA axes are given in Table 3. The first morphological axis was associated with large eyes

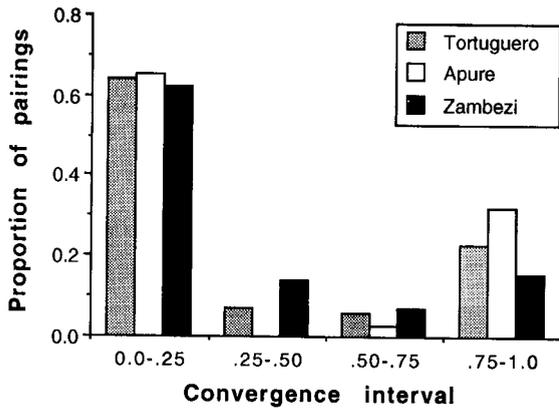


Fig. 9. Proportions of species in each cichlid fauna associated with four ecomorphological convergence intervals calculated in relation to each species' first nearest neighbor. The convergence index is defined in the Methods.

positioned relatively low on the side of the head, a small compact mouth located terminally or subterminally, and a short body. This first morphological axis was paired with a first dietary axis that was most influenced by algae and detritus feeding and avoidance of fish prey. The second morphological axis was associated with a long head and a short gut, and was paired with a dietary axis largely influenced by avoidance of detritus and vegetation and feeding on mayfly and stonefly nymphs. The third pair of CCA axes were largely influenced by greater head depth in association with feeding on caddisfly larvae.

We entered 6 morphological features associated with body dimensions into a separate CCA as components of shape associated with swimming performance and habitat selection. All 46 species were included, and the same dietary data were entered into this CCA as the ecological dataset. The first pair of body dimension and dietary axes were influenced by narrow caudal peduncle and light pigmentation in association with avoidance of several major groups of aquatic insects (Table 3). The second body dimension axis was most influenced by large dorsal fin, long anal and pectoral fins, and light pigmentation. The second dietary axis was most influenced by detritus feeding and avoidance of fish prey. The canonical correlation for the third pair of axes was not statistically significant ($p > 0.05$).

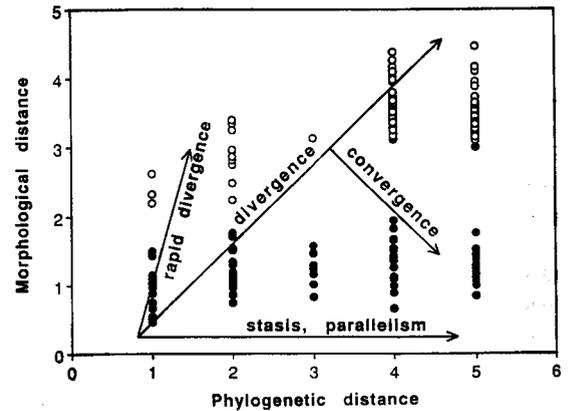


Fig. 10. Plot of ecomorphological Euclidean distance by phylogenetic distance for the 50 smallest and 50 largest nearest neighbor distances (based on ecomorphological species pairings the combined fauna dataset) and showing evolutionary divergence, stasis and convergence. The phylogenetic distance between two species is equal to the highest nodes separating the species in Figure 2.

Community and species-level convergences

Distributions of the convergence index, calculated for each species' nearest ecomorphological neighbor, are plotted as intervals for each fauna in Figure 9. For simplicity, we plotted the index as intervals, however it is important to note that the index represents a continuum representing varying degrees of evolutionary convergence. Cases of remarkable ecomorphological convergence are indicated by the high index values (0.75–1.0). Each fauna contained species showing a high degree of convergence. Even relatively low values on the convergence scale represent ecomorphological convergences, because the null hypotheses (closest relatives are morphologically most similar) predicts that $C_{ij} = 0$. Convergence was also widespread and distributions of the convergence index were qualitatively similar in distance matrices involving lower ranking nearest neighbors.

We plotted morphological Euclidean distance against phylogenetic distance for the 50 largest and 50 smallest morphological distance scores from the matrix containing 1035 unique species pairings (Fig. 10). If we assume that large morphological distance values represent ecological divergences, then large morphological distance scores in association with

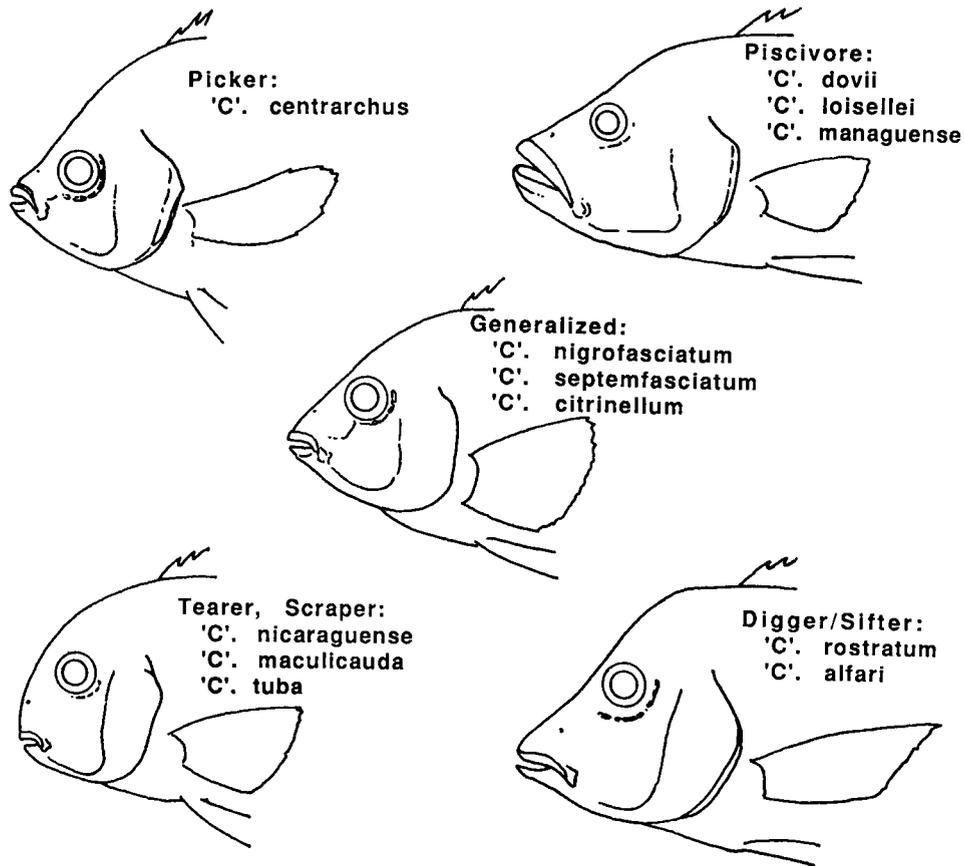


Fig. 11. Examples of rapid evolutionary divergence in head morphology and feeding ecology within the clade of Central American '*Cichlasoma*' species.

small values for phylogenetic distance indicate relatively fast ecomorphological divergence. Most of the species pairings in this upper left-hand regions of Figure 10 involved the Tortuguero '*Cichlasoma*' clade, and several points were derived from ecologically divergent *Serranochromis* from the Zambezi. The degree of morphological and ecological diversification observed among the sympatric species within the Central American '*Cichlasoma*' clade approaches that observed among more phylogenetically divergent cichlids viewed both within and between other regions. Examples of basic ecological niches are listed and their associated external head morphologies are illustrated for Central American '*Cichlasoma*' in Figure 11.

Species pairings associated with small values on both axes of Figure 10 indicate closely related species (congeners) that have diverged little in their

ecomorphological features. Examples would include the herbivorous and detritivorous *Tialpia sparrmani* and *T. rendalli* from the Zambezi, although the latter attains a greater maximum size than the former. Additionally, small detritivorous and omnivorous '*Cichlasoma*' *nigrofasciatum* and '*C.*' *septemfasciatum* are each placed in Miller's *Archocentrus* section and have similar appearances, sizes, and ecologies. Even so, the species in each of these congeneric pairs have different habitat preferences.

Species pairs that exhibit small morphological distances but large phylogenetic distances indicate ecological stasis, parallelism, or convergences (Fig. 10). The evidence for ecological diversification among recently divergent taxa renders the hypothesis for stasis in the evolution of ecomorphological phenotypes an unlikely option. Neither this analy-

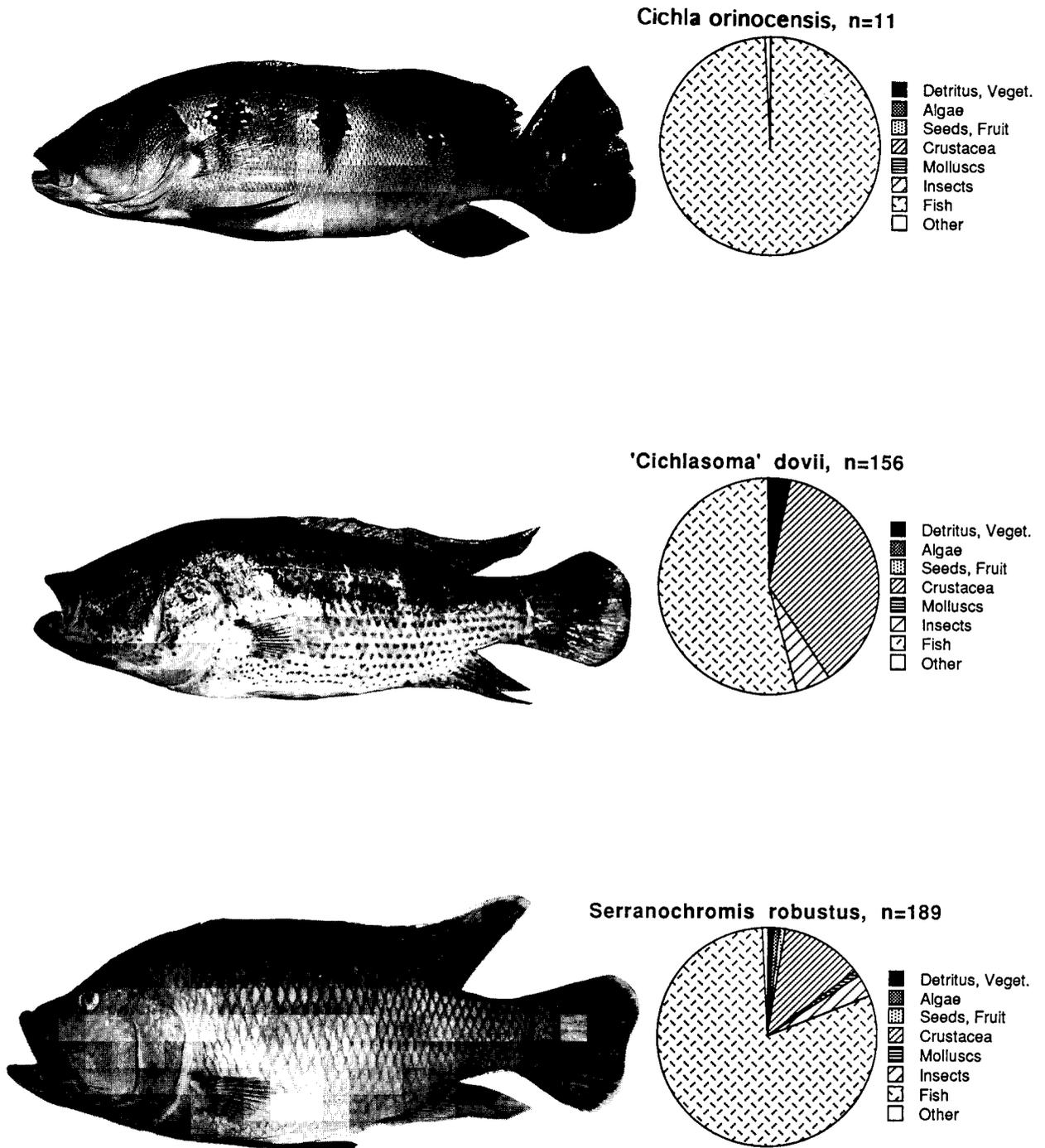
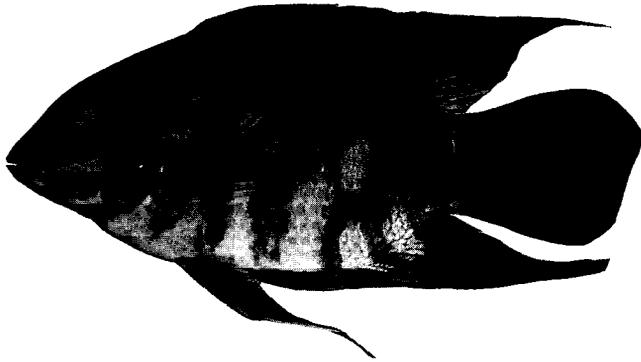
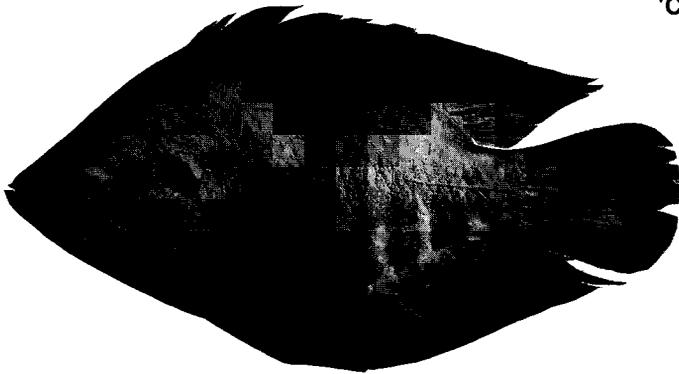
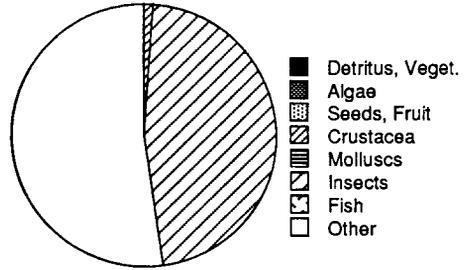


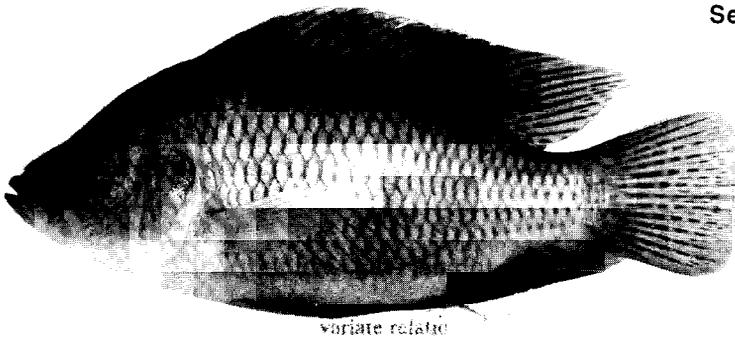
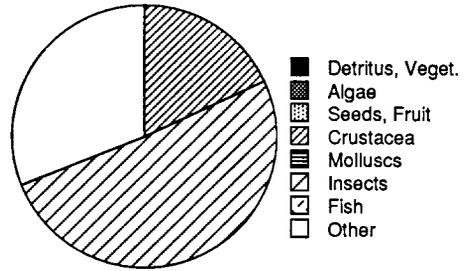
Fig. 12. Piscivorous cichlids (left column) and vegetation-dwelling insectivorous (right column) cichlids and their diets (illustrated by fractional volumes among general diet categories). Cichlids in the top row are from the Río Apure drainage (Venezuela), those in the middle row are from the Río Tortuguero drainage (Costa Rica), and those in the bottom row are from the Zambezi River drainage (Zambia).



Mesonauta festivum, n=25



'*Cichlasoma*' *centrarchus*, n=182



Serranochromis carlottae, n=54

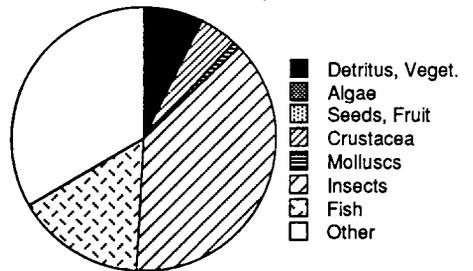


Fig. 12.- right column.

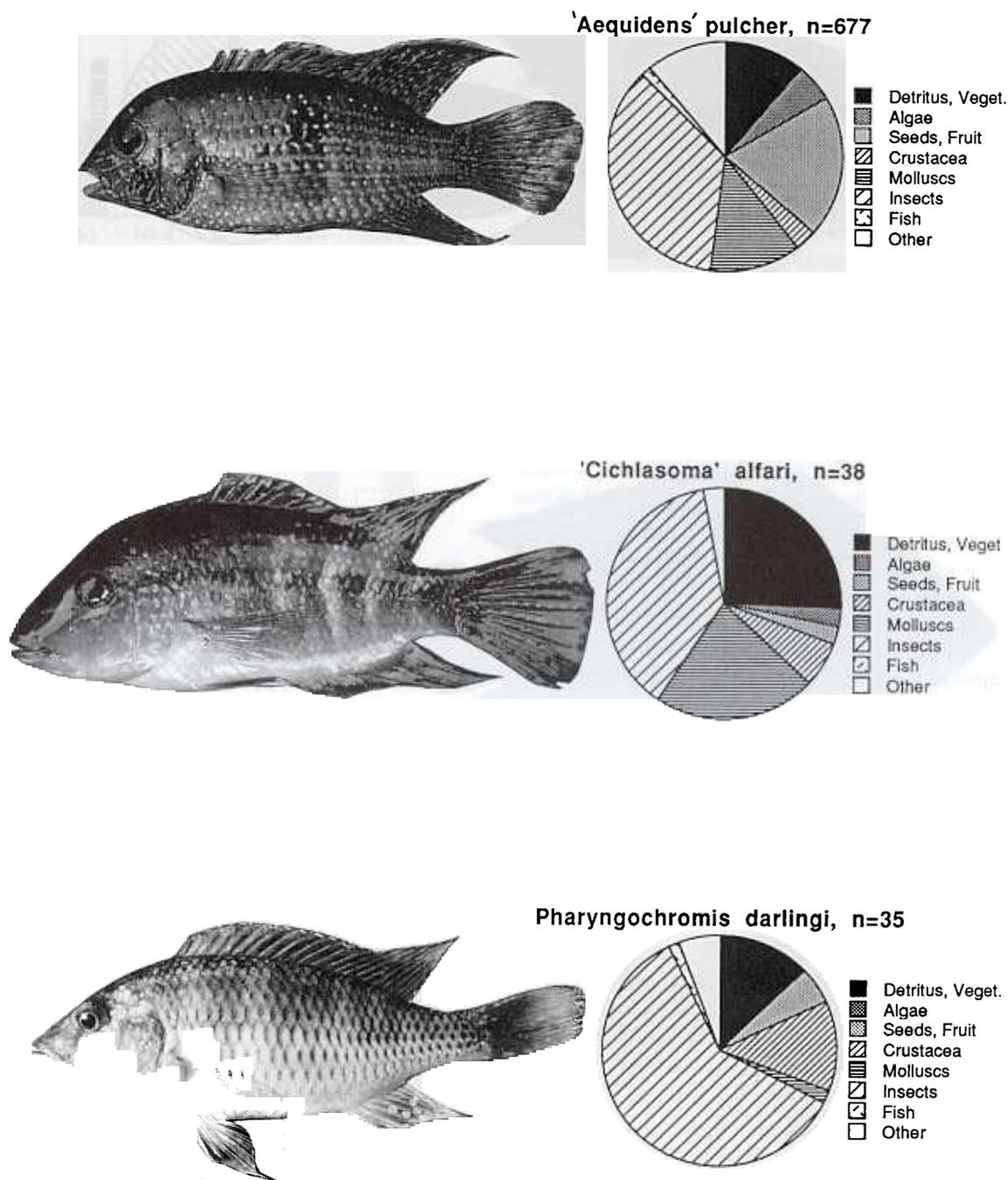
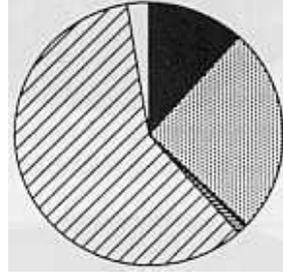
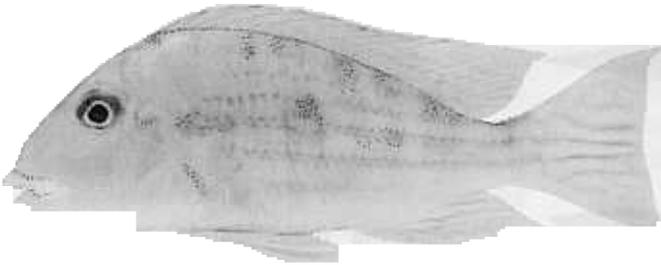


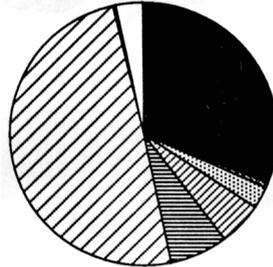
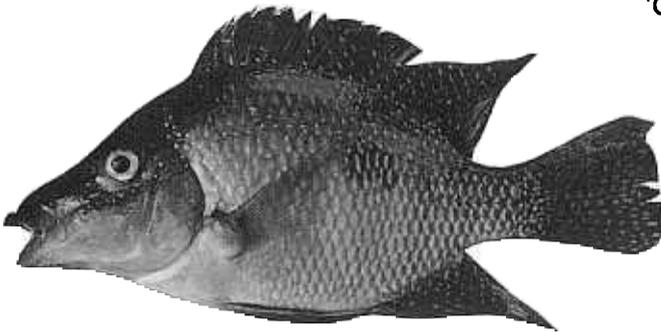
Fig. 13. Epibenthic generalists (left column) and omnivorous digger/sifter (right column) cichlids and their diets. Cichlids in the top row are from the Apure drainage, those from the middle row are from the Tortuguero drainage, and those in the bottom row are from the Zambezi drainage.

Geophagus surinamensis, n=5



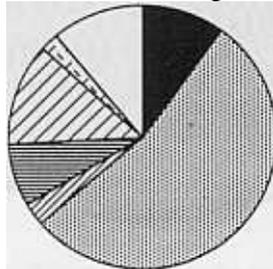
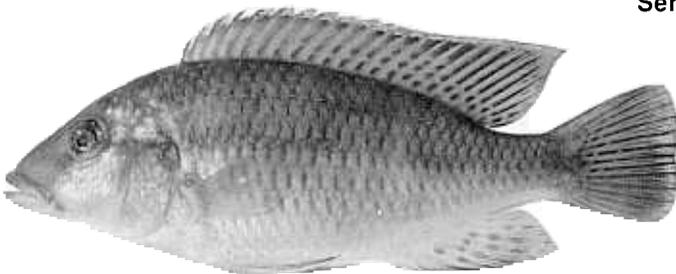
- Detritus, Veget.
- ▒ Algae
- ▨ Seeds, Fruit
- ▩ Crustacea
- ▧ Molluscs
- ▦ Insects
- ▤ Fish
- Other

'Cichlasoma' rostratum, n=13



- Detritus, Veget.
- ▒ Algae
- ▨ Seeds, Fruit
- ▩ Crustacea
- ▧ Molluscs
- ▦ Insects
- ▤ Fish
- Other

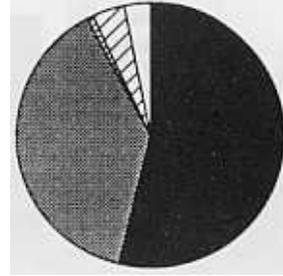
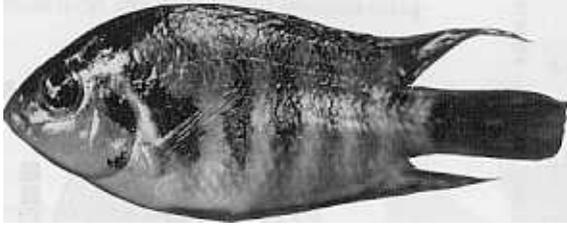
Serranochromis codringtoni, n=163



- Detritus, Veget.
- ▒ Algae
- ▨ Seeds, Fruit
- ▩ Crustacea
- ▧ Molluscs
- ▦ Insects
- ▤ Fish
- Other

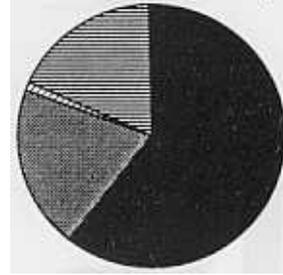
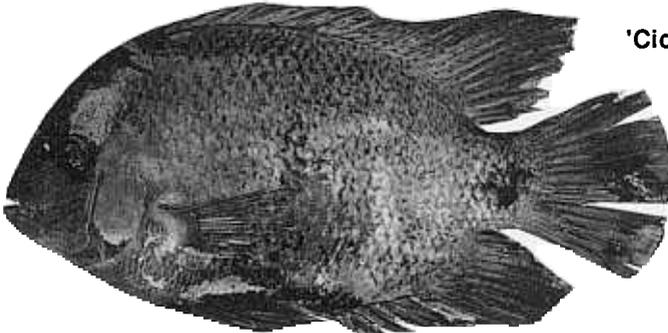
Fig. 13.- right column.

'Cichlasoma' nigrofasciatum, n=51



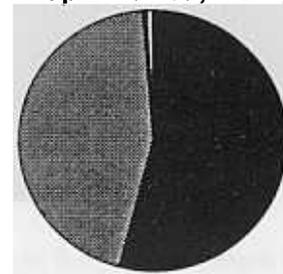
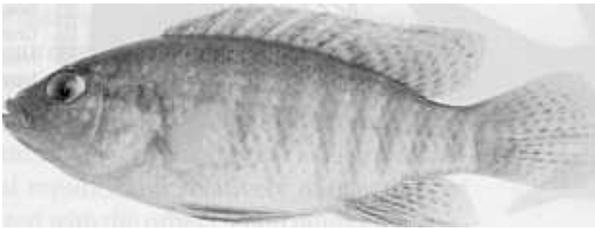
- Detritus, Veget.
- ▨ Algae
- ▩ Seeds, Fruit
- ▧ Crustacea
- ▦ Molluscs
- ▥ Insects
- ▤ Fish
- Other

'Cichlasoma' maculicauda, n=160



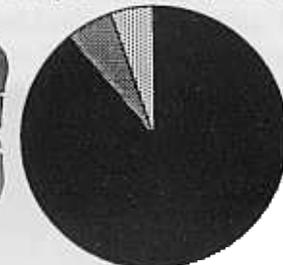
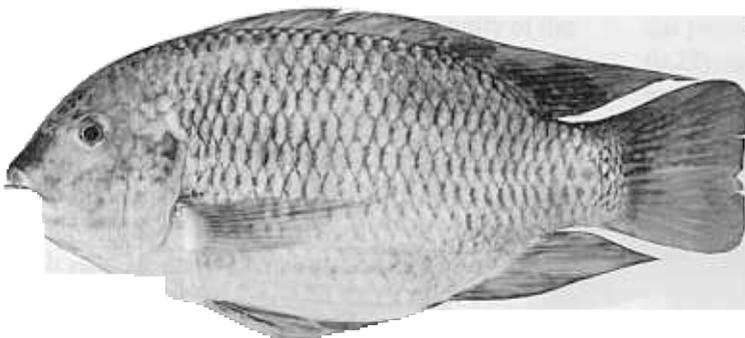
- Detritus, Veget.
- ▨ Algae
- ▩ Seeds, Fruit
- ▧ Crustacea
- ▦ Molluscs
- ▥ Insects
- ▤ Fish
- Other

Tilapia ruweti, n=11



- Detritus, Veget.
- ▨ Algae
- ▩ Seeds, Fruit
- ▧ Crustacea
- ▦ Molluscs
- ▥ Insects
- ▤ Fish
- Other

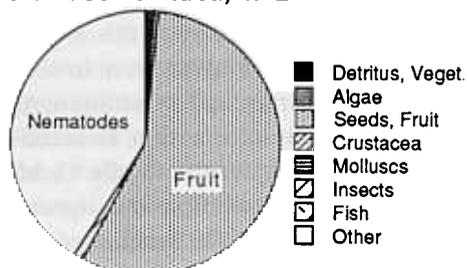
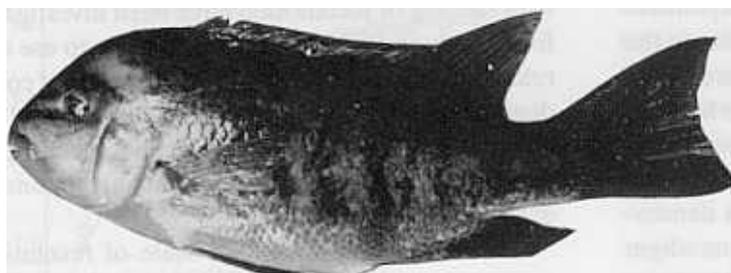
Tilapia rendalli, n=85



- Detritus, Veget.
- ▨ Algae
- ▩ Seeds, Fruit
- ▧ Crustacea
- ▦ Molluscs
- ▥ Insects
- ▤ Fish
- Other

Fig. 14. Detritivorous/algivorous cichlids and their diets (left column). The two top-left cichlids are from the Tortuguero drainage, and the two bottom-left cichlids are from the Zambezi drainage. Two specialized ecological niches from the Central American cichlid fauna: (top-right) '*Cichlasoma*' *tuba*, a rheophilic, epibenthic frugivore from the Tortuguero/Sarapiquí drainages, and (bottom-right) *Neetroplus* *nematopus*, a small epibenthic algae-scraper from the Sarapiquí drainage in Costa Rica.

'Cichlasoma' tuba, n=2



Neetroplus nematopus, n=2

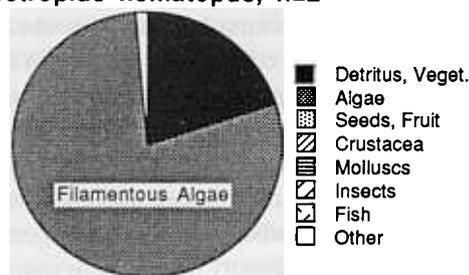
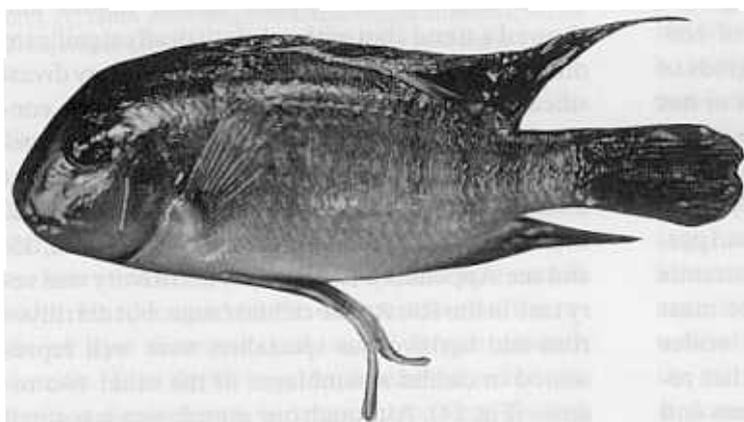


Fig. 14.— right column.

sis, not the convergence index has the power to distinguish between evolutionary parallelism and convergence. (This would require examining ecological traits as characters states in relation to a fully resolved phylogeny.) However given that we are dealing with several related clades, each of which exhibits significant divergence, it seems unlikely that more than a few, if any, of the points in the lower right-hand corner of the plot in Figure 11 could represent parallel evolution. Several examples of morphologically and ecologically convergent cichlids from separate biotic regions are illustrated in Figures 12, 13, and 14.

Discussion

The comparative approach in ecomorphology has been quite successful in establishing patterns of covariance between morphology and ecology. Ecologists have exploited these patterns and have formed a rather vague theory of ecomorphology to serve as a functional link, or intermediary, for causal mechanisms that are difficult to observe and document in the field. Motta & Kotrschal (1992) have outlined a research program designed to test and perhaps strengthen this functional link. Whereas others have focused on the more reductionistic elements of their program (i.e., the study of covariance in morphology and environmental factors, functional morphology, ontogeny), we have presented results of research aimed at the higher-level components of

community structure and the directions of evolutionary change. Research at this level is dependent on information and advances at lower strata in the biological hierarchy and, in addition, requires reliable phylogenetic information. Because our hypothesis of phylogeny for the family Cichlidae lacks a high degree of resolution and rigorous empirical support, we present our results more as a demonstration case for Motta & Kotschal's paradigm rather than a documentation of presumed facts.

The question of faunal and community diversification and interfaunal convergent evolution are central to the basic hypothesis of ecomorphology. If a given morphological configuration has a multiplicity of functions, and none of these functions play a primary ecological role in ecological segregation, then ecologists cannot invoke the theory of ecomorphology for community studies. What kinds of evidence are required to determine whether or not independent faunas have evolved similar patterns of niche diversification in response to similar environmental factors? First of all, a phylogeny is required to distinguish between convergence and parallelism and to identify historical design constraints among contemporary taxa. In addition, one must have reasonably comparable units and scales among: (1) heritable morphological traits that reflect ecologically relevant functions, (2) faunas and taxa, and (3) regions and physical and biotic environments. Because half of the equation involves ecological performance (as distinguished from functional morphology), ecological data must be appropriately detailed and sufficiently replicated within and between different time intervals.

Using fluvial cichlids from three biotic regions, we have attempted to test the nested hypotheses of convergent patterns of community-level diversification involving convergent evolution at the species level. Although the true phylogenetic relationships of all species in the three assemblages are not known, we have a reasonable hypothetical phylogeny based on the work synthesized by Stiassny (1991). The three regions have been well documented, and their historical faunal relationships to adjacent basins have been investigated (Myers 1966, Jubb 1967, Balon 1974, Lowe-McConnell 1975, 1991, Bussing 1976, Taphorn 1990). The functional rela-

tionships between several morphological features with feeding or locomotion have been investigated for cichlids and other fishes, allowing us to use correlative methods with a reasonable degree of confidence. Finally, we have extensive and detailed ecological data for most of the cichlid species plus many of the noncichlid ichthyofaunal components of these three regions.

We found that on a broad scale of resolution, community structure is convergent in that several distinctive niches are represented in the same macrohabitats. For both morphological and dietary data, all three faunas overlapped at the centroid of the total PCA space (Fig. 4). The Zambezi cichlid fauna exhibited significantly less morphological diversification than the neotropical cichlid faunas and showed a trend (but without statistically significant differences in dispersion) toward less dietary diversification. All three regional cichlid faunas contained a variety of specialized piscivores, invertebrate diggers/sifters, mollusc crushers, vegetation-dwelling invertebrate pickers, generalized invertebrate-feeders (examples illustrated in Fig. 12, 13, and see Appendix). Evidence of detritivory was very rare in the Río Apure cichlid fauna, but detritivorous and herbivorous specialists were well represented in cichlid assemblages of the other two regions (Fig. 14). Although our sample size was small ($n = 25$), *Mesonauta festum* was the only Apure cichlid that exhibited significant fractions of detritus in the diet (volumetric percentage = 29.4), and this is probably taken in association with caddisfly larvae most of the time (Trichoptera percentage = 18.3). The correlation between relative length of the alimentary canal and detritivory and herbivory was the strongest bivariate ecomorphological relationship (Fig. 6), and Apure cichlids exhibited a much lower mean relative gut length than cichlids of the other regions (Table 2). We hypothesize that, both on ecological and evolutionary time scales, the abundant and diverse algivorous and detritivorous fishes of the orders Characiformes and Siluriformes have occupied the algae-browsing, algae-scraping, and detritivorous feeding niches to the exclusion of cichlids. In particular, the diverse loricariid catfishes are locally abundant in nearly all Apure basin habitats, and nearly all of the loricariids examined

by Winemiller (1990a, and unpublished data) are specialized for algae-scraping or detritus-feeding (see also Power 1984). We presume that ostariophysan fishes in early South America were more preadapted than cichlids to exploit algae and detritus. Present day characiforms in South America exhibit a vast diversity of ecological niches including numerous detritivores and periphyton browsers, and the latter are especially predominant within the families Curimatidae, Chilodontidae, Prochilodontidae, Anostomidae, and Hemiodontidae (Géry 1977, Bowen 1983).

From the perspective of our fluvial cichlid faunas, three species appear to have evolved unique ecological niches. *Chaetobranchius flavescens* from the Apure drainage is a deep-bodied vegetation-dwelling cichlid with long comb-like gill rakers and was the only zooplankton specialist encountered in our study. '*Cichlasoma*' *tuba* from the Tortuguero fauna is a large epibenthic fruit and periphyton-browser with compact jaws armed with incisor-like anterior teeth (our small sample documented only fruit and associated nematodes, but see also Bussing 1987). Compact jaws and a steeply sloping, convex head profile in '*C.*' *tuba* indicate good capability for biting and tearing (Barel 1983). This unusual cichlid (Fig. 14) appears to favor moderate to swift water currents in rainforest streams where it finds sunken fruits and periphyton that may be less available to smaller omnivorous and herbivorous fishes like *Astyanax fasciatus* (Characidae) or *Poecilia gilli* (Poeciliidae), the two being very abundant in slower marginal areas of the same streams. The large frugivorous characid, *Brycon guatemalensis*, swims higher in the water column than '*C.*' *tuba* and probably takes fruit and seeds most frequently from the surface or water column in deep pools, backeddies along river margins, and backwaters (Winemiller 1990 and personal observations). With its small subterminal mouth, flat incisor-like teeth and convex dorsal head profile, *Neetroplus nematopus* from Tortuguero/Sarapiquí was the only other truly specialized periphyton-browser (Fig. 14) among our 46 fluvial cichlids. Periphyton-browsing has been documented many times among African cichlids of the central Zaire drainage (Roberts 1972, Lowe-

McConnell 1991) and rift lakes (Fryer 1959, McKaye & Marsh 1983, Yamaoka 1991).

Few cichlids exhibited highly canalized foraging specializations, rather most species possess some capability to forage on a wide variety of invertebrate prey when they are available. Functional trade-offs involved in specialized foraging versus generalized invertebrate-feeding were not investigated here, but are hypothesized to exist to some degree in all cases. Meyer (1989, 1990a, 1990b) demonstrated the functional trade-off associated with molluscivory in two feeding morphs of the midas cichlid, '*Cichlasoma*' *citrinellum*, inhabiting lakes in Nicaragua. We did not analyze intraspecific variation in '*C.*' *citrinellum* from the Tortuguero drainage, but small bivalve molluscs comprised a major fraction of its diet (volumetric percentage = 52.3), and it was morphologically convergent ($C_{ij} = 0.71$) with *Serranochromis giardi*, the most molluscivorous cichlid (mollusc volumetric percentage = 50.3) from the Zambezi drainage, and '*Aequidens*' cf. *pulcher* ($C_{ij} = 0.87$), an epibenthic generalist. The most molluscivorous cichlids in the Apure drainage were '*A.*' cf. *pulcher* (mollusc volumetric percentage = 12.7) and *Cichlasoma orinocense* (molluscs = 18.1%), with the former taking mostly small bivalves (bivalves = 7.3%) and the latter consuming mostly snails (snails = 17.0%).

Patterns of habitat affiliation among three basic habitat categories showed interfaunal similarities as well. Within each river basin, cichlid alpha diversity is greatest within low gradient streams of intermediate size, lagoons, and backwaters of larger rivers. Cichlids are not abundant in the channel regions of large rivers (Fig. 5). Jackson (1961) hypothesized that the threat of predation by tigerfish (*Hydrocynus* spp.: Characidae) may restrict the use of river channels by African cichlids. Winemiller (1991b) collected only one of the nine species of *Serranochromis* from the main channel region of the Upper Zambezi with any regularity. Indeed, *S. robustus* was the only cichlid species commonly encountered in the main channel of the Zambezi. The local distribution of *Serranochromis thumbergi*, the other channel-dwelling Zambezi cichlid, appears to correlate with the absence of tigerfish (Bell-Cross & Minshull 1988. Winemiller personal observa-

tion). For example, tigerfish are absent from the Kafue River, and *S. thumbergi* is much more abundant there compared with the upper Zambezi (Lagler et al. 1971). In a manner similar to tigerfish, piranhas (*Pygocentrus*, *Serrasalmus* spp.: Characidae) may also restrict the occupation of South American stream channels by other diurnal fishes, including cichlids (Winemiller 1989b). Habitat selection by cichlids inhabiting larger rivers and lagoons at Tortuguero is probably influenced by large diurnal piscivores as well [i.e., *Megalops atlanticus* (Elopidae), *Centropomus undecimalis* (Centropomidae), and *Atractosteus tropicus* (Lepisosteidae), documented in Winemiller & Leslie 1992].

The percomorph body plan appears to suit cichlids particularly well for life in slack water and vegetated habitats. Except perhaps for *Serranochromis thumbergi*, none of the fluvial cichlids examined here could be considered midwater active fishes (Appendix 1). Most of the species were associated with highly structured edge or vegetation habitats, and others hovered close to the substrate in the more open habitats in lagoons and smaller streams. *Serranochromis thumbergi* is reported to be active at midwater depths in rivers lacking tigerfish and lurks near rocky structure in fast water or inhabits marshy areas in regions where tigerfish are present (Bell-Cross & Minshull 1988). Interestingly, the species that occupied the smallest streams and occupied the greatest range of habitats in each region were all generalized feeders with proclivities for digging and sifting food from the substrate ('*Aequidens*' cf. *pulcher* – Apure, '*Cichlasoma*' *alfari* – Tortuguero, *Pharyngochromis darlingi* and *Pseudocrenilabrus philander* – Zambezi). Males of these species are also among the most strikingly colored of the cichlid species represented in each fauna (Fig. 12). Possibly, the paucity of large piscivores in small streams reduces predation and has permitted intersexual selection to drive the evolution of heightened coloration in males of these generalist species.

Conclusions

Based on fairly broad phylogenetic, ecological, and geographical scales, we have documented morpho-

logical and ecological divergences and convergences in fluvial cichlid fishes from three biotic regions. Based on the best available hypothesis of phylogeny, the rate of ecomorphological divergence appears to have been fast in Central American cichlids relative to South American and African fluvial assemblages. Cichlid fishes of the African rift lakes have provided evolutionary biology with some of the most remarkable examples of rapid phyletic, morphological, and ecological divergence (Witte 1984, Meyer et al. 1990, Meyer 1993). The degree of morphological divergence and ecological specialization among fluvial cichlids is no less remarkable, yet river-dwelling species have not received the intense scrutiny of their lacustrine counterparts for several probable reasons. Cichlids are not the dominant faunal components of rivers where ostariophysan fishes (characiforms, siluriforms, cypriniforms) often outnumber cichlids in terms of species richness and biomass. In contrast to the rift lake fishes, cichlid diversity in rivers is contained within numerous drainage basins covering a very large area of the global landmass. In addition, ecological specializations tend to be more difficult to identify in river fishes, because flooding cycles shift spectra of resource availability and ratios of consumer demand and supply (Winemiller 1989b, 1990). Oftentimes, resource segregation and niche shifts among river fishes can be perceived only in relation to multiple seasonal cycles, which necessitates large field samples and examination of many individuals. Whereas rift lake cichlids appear to be derived from fairly recent common ancestors (Meyer et al. 1990), to deal with the phylogenetic relationships of river cichlids on a global basis essentially requires dealing with the phylogeny of the entire family (sensu Stiassny 1992).

Community ecology and basic evolutionary questions of adaptive divergence and convergent evolution are central issues in ecomorphological theory. In terms of existing systematic and ecological theory and methodology, the study of ecological diversification and convergence is a viable enterprise. Yet to succeed, these studies require much detailed data at several levels of the biological hierarchy, in addition to reliable phylogenetic information. We have explored community organization,

ecological diversification, and convergent evolution using ecological and morphological datasets for fluvial cichlid fishes from three biotic regions and a recent hypotheses of phylogenetic relationships for the family. We expect that the production of a more resolved phylogeny could alter some of our specific findings, especially at the species level. An improved phylogeny with greater resolution would also facilitate tests of parallel versus convergent evolution and aid our understanding of historical and morphological design constraints. In this regard, we consider the present study an initial step in the exploration of adaptive divergence and ecological convergence in fluvial cichlids.

Acknowledgements

Numerous individuals assisted in the field collections, and special thanks go to D.C. Taphorn, L.G. Nico, A. Barbarino, E. Urbina, J. Masinja, G. Milini, Mr. Sinda, and W. Ritter. Institutional support abroad was provided by D.C. Taphorn of the Universidad Experimental de los Llanos Occidentales in Venezuela, H. Haug and E. Chamorro of the Servicio de Parques Nacionales de Costa Rica, and E. Muyanga and G. Milindi of the Department of Fisheries of Zambia. Collecting and fishing permits were obtained from the Dirección Administración y Desarrollo Pesquero de la Republica de Venezuela, Servicio de Parques Nacionales de Costa Rica, and the Department of Fisheries and National Commission of Development Planning of the Republic of Zambia. Field work was funded by the National Geographic Society, the Tinker Foundation, the National Science Foundation, and the Fulbright Program for International Exchange of Scholars. Latter stages of the study were performed under the sponsorship of the Electric Power Institute under contract no. RP2932-2 (DOE No. ERD-87-672) with the Oak Ridge National Lab. ORNL is operated by Martin Marietta Energy Systems, Inc. under contract DE-AC05-84OR21400 with the U.S. Department of Energy. This is publication no. 4242 of the Environmental Sciences Division, ORNL. We thank A. Meyer, S.O. Kullander, and G.R. Smith for critical reviews of earlier drafts.

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Appendix 1. List of species from each river drainage basin (C = common, R = rare). Basic ecological niches are coded as follows: EBI = epibenthic invertebrate feeder, DBI = diurnal benthic invertebrate feeder, GVI = generalized vegetation-dwelling invertebrate feeder, DVI = deep-bodied vegetation-dwelling invertebrate feeder, VIP = vegetation-dwelling invertebrate feeder/piscivore, VDA = vegetation-dwelling detritivore/algivore, EMP = epibenthic and midwater pursuit piscivore, SMP = edge-stalking midwater piscivore, SEP = edge-stalking epibenthic piscivore, EDA = epibenthic detritivore/algivore, EDI = epibenthic digging invertebrate feeder, EAS = epibenthic algae scraper, FRU = frugivore. Numbers inside parentheses are sample sizes for stomach contents analyses.

Venezuela, Río Apure drainage: '*Aequidens*' cf *pulcher* (C, EBI, 677), *Aequidens tetramerus* (R, EBI/EDA, 7), *Apistogramma hoignei* (C, GVI/DVI, 181), *Astronotus ocellatus* (C, VIP, 99), *Caquetaia kraussii* (C, VIP/SMP, 370), *Chaetobranchius flavescens* (R, DVI, 3), *Cichla orinocensis* (C, EMP, 11), *Cichlasoma orinocense* (C, EBI/DVI, 271), *Crenicichla geayi* (C, GVI, 112), *Crenicichla lugubris* (C, SEP, 5), *Crenicichla saxatilis* (C, VIP, 52), *Geophagus surinamensis* (C, EBI, 5), *Mesonata festivum* (C, DVI, 25), *Papiliochromis ramirezi* (C, DVI, 25), *Satanoperca jurupari* (C, EDI, 6).

Costa Rica, Río Tortuguero drainage: '*Cichlasoma*' *alfari* (C, EBI, 38), '*Cichlasoma*' *centrarchus* (C, DVI, 182), '*Cichlasoma*' *citrinellum* (C, DBI/DVI, 88), '*Cichlasoma*' *dovii* (C, EMP, 156), '*Cichlasoma*' *loisellei* (C, VIP, 344), '*Cichlasoma*' *maculicauda* (C, EDA, 160), '*Cichlasoma*' *managuense* (R, SMP, 2), '*Cichlasoma*' *nicaraguense* (C, EBI/EDA, 2), '*Cichlasoma*' *nigrofasciatum* (C, VDA/GVI, 51), '*Cichlasoma*' *rostratum* (C, EDI, 13), '*Cichlasoma*' *septemfasciatum* (C, EBI/EDA, 10), '*Cichlasoma*' *tuba* (C, FRU/EAS, 2), *Herotilapia multispinosum* (C, EDA, 22), *Neetroplus nematopus* (C, EAS, 2).

Zambia, Upper Zambezi River drainage: *Hemichromis elongatus* (C, VIP, 51), *Oreochromis andersoni* (C, EDA, 21), *Oreochromis macrochir* (C, EDA, 48), *Pharyngochromis darlingi* (C, EBI, 35), *Pseudocrenilabrus philander* (C, GVI/DVI, 46), *Serranochromis angusticeps* (C, SMP/DVI, 238), *Serranochromis altus* (C, SMP, 114), *Serranochromis carlottae* (C, DVI, 54), *Serranochromis codringtoni* (C, EDI, 163), *Serranochromis giardi* (C, EBI, 100), *Serranochromis longimanus* (R, VIP, 6), *Serranochromis macrocephalus* (C, EMP, 279), *Serranochromis robustus* (C, EMP, 189), *Serranochromis thumbergi* (R, EMP, 5), *Tilapia rendalli* (C, EDA, 85), *Tilapia ruweti* (C, VDA, 11), *Tilapia sparrmannii* (C, EDA/VDA, 93).