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## ECOMORPHOLOGICAL DIVERSIFICATION IN LOWLAND FRESHWATER FISH ASSEMBLAGES FROM FIVE BIOTIC REGIONS<sup>1</sup>

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**Abstract.** This study investigates the relationships among species diversity, community structure, and convergent evolution among divergent fish faunas. Morphological traits can be used as surrogates for ecological data in the comparative study of community niche relationships. In the present study I examined 30 morphological features related to the ecology of the dominant fish species from lowland stream and backwater habitats in five widely separated geographic regions: nearctic Alaska, temperate North America, Central America, South America, and tropical Africa. The study regions exhibited a general gradient of species richness from a minimum of 6 dominant species at one of the high-latitude sites (65° N) to a maximum of 43 numerically dominant species at a neotropical site (8° N). Fishes from Alaskan sites near the edge of the polar circle tended to be larger than fishes at other sites. Mean values for most morphological characters varied little between regions, indicating similar faunal centroids in morphological space. Morphological diversification within fish assemblages was estimated from species similarities based on Euclidean distances plus species projections on the principal axes from multivariate analysis. The total morphological space encompassed by ichthyofaunas in both stream and backwater sites was generally concordant with the latitudinal and species-richness gradient, with low-diversity nearctic assemblages exhibiting little morphological diversification relative to high-diversity tropical faunas. The Central American assemblages showed a greater range of ecomorphological diversification than African assemblages that contained a few more species, and this pattern may be related to greater seasonal stability at the Central American site. Phenetic patterns of dispersion reflect ecological relationships in which greater numbers of coexisting species are associated with higher levels of niche diversification and ecological specialization, leading to enhanced resource partitioning.

Without additional ecological information, a community morphological analysis cannot directly determine whether or not increased ecological specialization is associated with the addition of new resources on the fringes of resource space or with increased subdivision of previously utilized core resources. Based on ecological information gathered concurrently with the fishes used in this analysis, I conclude that close species packing in morphological space is associated with niche generalists rather than with niche compression. With the possible exception of the two high-latitude sites, assemblages that contained more fish species generally did not exhibit tighter packing in niche space than species-poor assemblages, and this result was observed for comparisons both within and between regions. In contrast with several earlier studies, I interpret the lack of correlation between species richness and the average minimum distance between species in assemblage morphospace as being entirely consistent with the observed expansion of morphospace with species richness and latitude. Morphological patterns show that average spacing is held more or less constant as the variety of ecomorphological configurations increases in more-speciose fish assemblages. Even though morphological characters reflect community relationships, tight packing near the center of faunal morphospace actually indicates the opposite of species packing (niche compression) in the traditional sense of resource-utilization curves. The analysis supports the thesis that species interactions are important determinants of community morphological features, particularly in species-rich tropical regions. Relative to assemblages in the other four regions, the two Alaskan fish assemblages were hyperdispersed within a comparatively small morphological space. The Alaskan fish assemblages probably formed via geologically recent, and perhaps repeated, colonizations of polar freshwaters by species with evolutionary histories in more diverse southern and coastal fish faunas. I interpret evidence of greater niche diversification at lower latitudes within a habitat type as being derived primarily from the influence of competition and predation, whereas differences between habitats within regions seems to be associated with the com-

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bined effects of biotic interactions and differences in habitat volume and heterogeneity. Even though different regions within ecomorphological space were dominated by different fish orders, numerous ecomorphological convergences and several one-for-one ecological equivalents were identified within different biotic regions.

*Key words:* communities; ecological convergence; freshwater fish communities; intercontinental comparisons; morphological diversification; niche diversification; orders; phylogeny; resource partitioning; species packing; species richness.

## INTRODUCTION

The relationship between form and function in fishes is well documented for a variety of gross mensural features (Gosline 1971, Lagler et al. 1977, Webb 1984) and for a large number of specific morphological characters (Gatz 1979a, 1981). Keast and Webb (1966) were among the first to discuss the ecological correlates of morphological variation in a freshwater fish fauna. Many aspects of a fish's ecological niche can be reliably inferred from examination of morphological features. For example, relative orientation of the mouth (e.g., superior vs. terminal vs. inferior) indicates the relative water-column depth at which feeding normally occurs. Dentition characters provide a reasonable index of diet, with short conical teeth corresponding to carnivores, multicuspid teeth correlating with omnivory, and flat incisor-like teeth indicating periphyton grazing. Relative gut length is small in piscivores and extremely large in detritivores, the latter utilizing slower elimination rates to facilitate processing of relatively energy-poor food resources (Gatz 1979a, 1981, Bowen 1983). Fin dimensions and body shape are reliable indicators of the swimming behavior and habitat preferences of fishes (Keast and Webb 1966, Lagler et al. 1977, Webb 1984). In addition, laboratory studies of the functional morphology of feeding (Alexander 1970, Liem 1974, Winemiller and Taylor 1987) and locomotion (Webb 1984) in fishes provide direct evidence of the functional properties of a number of morphological features (see also Gatz 1979a).

Given our high level of understanding of many relationships between form and function in fishes, it is reasonable to assume that, at some level, ecological relationships can be inferred from an analysis of morphological features (Hespenheide 1973, Karr and James 1975). Hutchinson's (1959) examination of size ratios of body size and feeding apparatuses represents an early exercise in ecological inference based on morphology. Fenton's (1972) and Findley's (1973, 1976) studies of bat assemblages represent some of the earliest uses of multivariate morphological approaches in the analysis of community niche relationships. Similar tests of community morphological patterns quickly followed and were based on other phylogenetic groups, including birds (Karr and James 1975, Ricklefs and Travis 1980, Travis and Ricklefs 1983, Miles and Ricklefs 1984, Miles et al. 1987), lizards (Ricklefs et al. 1981, Pianka 1986), and fishes (Gatz 1979a, b, 1981, Mahon 1984, Moyle and Senanayake 1984, Page and Swofford 1984,

Watson and Balon 1984, Douglas 1987, Strauss 1987, Motta 1988, Wikramanayake 1990). Multivariate statistical methods condense large numbers of morphological features into summary measures of lower dimensionality, which in turn can be used to determine interspecific ecological similarity. Investigations have shown higher levels of ecomorphological diversification (Findley 1973, Ricklefs and Travis 1980, Ricklefs et al. 1981) as well as greater species packing (Watson and Balon 1984) in more species-rich assemblages. Based largely on the conceptual framework of limiting similarity as outlined by MacArthur and Levins (1967), both of these trends have been interpreted as revealing an historical effect of interspecific competition for resources.

Theoretically, as new species are added to a saturated community, they could reduce interspecific competition during periods of resource limitation by using novel means to exploit new resources and diverge away from the shared use of core resources. Alternatively, competition for core resources could be held constant with the addition of new species if niche compression (specialization) resulted in a more fine-scaled use of core resources (i.e., species packing). The examination of niche relations via morphological features assumes that (1) in the short term, local species assemblages interactively exclude certain regional elements, or (2) in the long term, the evolution of phenotypes is affected, at least in part, by the presence of coexisting species. In any given setting, each of these factors would likely affect the characteristics of species assemblages to varying degrees. In this regard, the concept of convergent evolution provides an important interface between ecology, morphology, and phylogenetics. For example, Karr and James (1975) and Ricklefs and Travis (1980) evaluated the convergent evolution of morphological features for equivalent ecological functions in bird assemblages. Although several remarkable examples of ecomorphological convergences among phylogenetically distinct fishes have been discussed in the literature (Roberts 1972, Lowe-McConnell 1975, 1987), few specific tests have been attempted.

Here I report findings from an ecomorphological analysis of 10 lowland fish assemblages from five distantly separated geographical regions containing taxonomically distinct fish faunas. The five regions lie on three continents and show a latitudinal gradient in species richness. Within each region two environments were chosen for comparison: a lowland stream and a

lowland swamp or backwater. Evolutionary independence in recent geological time coupled with the biotic diversity gradient among sites allows comparative tests of hypotheses explaining species packing and niche diversification in response to greater numbers of potential biotic interactions. Do more species-rich fish assemblages in the tropics exhibit greater ecomorphological diversification, as might be predicted based on their greater number of potential pathways for direct and indirect biotic interaction? Do fishes tend to be more similar or less similar to one another in species-rich assemblages compared with fishes in species-poor assemblages? Are observed relationships between patterns of dispersion in morphological space and species richness the same within and between geographical areas, and are observed ecomorphological patterns largely independent of phylogenetic and geographical factors, or are they explained by them? In addition to addressing these questions, this study also identifies freshwater fish ecomorphological guilds, their taxonomic affiliations, and evolutionary niche convergences between regions. I also discuss conceptual problems with an earlier interpretation of patterns of species dispersion in community morphological space.

#### MATERIALS AND METHODS

Morphological measurements were made on fish specimens from the Texas Natural History Collection (TNHC) of the Texas Memorial Museum, Austin, Texas, USA. With the exception of two east Texas sites that were sampled by C. Hubbs and associates in 1953 and 1985, I collected all of the specimens and recorded field data at each site (I also observed and collected most of the east Texas species at other sites not chosen for this study). The sites compared here were all relatively pristine at the time of sampling. Each location was sampled on at least two separate dates, and most sites were collected numerous times as part of long-term field studies (Winemiller 1989a, 1990a, 1991). Only numerically dominant species (approximately equivalent to "core species", sensu Hanski 1982) were included in the morphological analysis. Dominant species were defined operationally as the most common species at a site whose relative proportions (by number of individuals), when summed by order of their ranks, formed 99% of all individual fishes collected over the full sampling period. Similarly, rare species were defined as species comprising the 1% tail of smallest relative abundances contributing to the numerical total for a site. Whereas this criterion for membership could exclude a few rare, but perhaps significant, community elements, it was designed to eliminate most of the rare fugitive and transient species that were essentially non-interactive components of the core community. Even if the operational rule for species inclusion were to eliminate a few rare species with significant potential for influencing the dynamics of their communities (e.g., large predators), each assemblage would likely be af-

TABLE 1. Total number of species, genera, and families comprising each freshwater fish assemblage, and regional total.

Seward Peninsula, Alaska (65° N)			
	Rivers	Backwaters	Total
Families	2	5	5
Genera	5	6	8
Common species	7	6	10
Rare species	0	0	0
Newton County, Texas (30° N)			
	Creek	Bayou	Total
Families	7	12	12
Genera	8	18	19
Common species	13	26	31
Rare species	0	0	0
Tortuguero Park, Costa Rica (10° N)			
	Creek	Caño	Total
Families	7	13	15
Genera	11	23	25
Common species	13	30	32
Rare species	9	28	29
Western Province, Zambia (15° S)			
	Creek	Backwaters	Total
Families	6	11	12
Genera	8	19	22
Common species	18	33	39
Rare species	14	32	35
Estado Portuguesa, Venezuela (9° N)			
	Creek	Caño	Total
Families	6	19	19
Genera	12	40	46
Common species	13	43	50
Rare species	7	40	45

ected in a similar manner, since distributions of species relative abundances showed very similar negative exponential patterns (Winemiller 1987). Large but rare predatory species eliminated from the present analysis by the operational definition were as follows: Caño Agua Fria Viejo—*Atractosteus tropicus* (Lepisosteidae), *Strongylura timucu* (Belontiidae), *Centropomus ensiferus* (Centropomidae), *C. parallelus*, *C. undecimalis*; Zambia backwater—*Clarias gariepinus*, *C. ngamensis*, and *Serranochromis altus* (Cichlidae); Caño Maraca—*Hoplerythrinus unitaeniatus* (Erythrinidae), *Acestrorhynchus microlepis* (Characidae), *Serrasalmus irritans* (Characidae), *S. medini*, *S. rhombeus*, *Ageneiosus vittata* (Ageneiosidae), *Pseudoplatystoma fasciatus* (Pimelodidae), and *Crenicichla saxatilis* (Cichlidae). About half of these rare predators were transient species represented by one or a few individuals collected during only one or two months out of a year's regular sampling. Table 1 gives the numbers of common and rare species collected from each assemblage, and the Appendix provides a complete list of the dom-

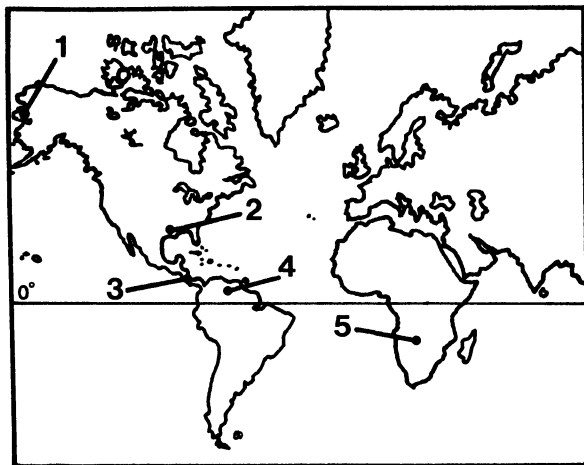


FIG. 1. Map showing locations of the five study regions compared in the ecomorphological analysis: 1 = Seward Peninsula, Alaska (65° N); 2 = Sabine River drainage, Texas (30° N); 3 = Tortuguero Park, Costa Rica (10° N); 4 = western llanos region, Venezuela (9° N); 5 = Barotse or Upper Zambezi floodplain region, Zambia (15° S).

inant species at each site and their taxonomic affiliations.

#### Sites and sampling schedules

Two types of lowland aquatic environments—streams and backwaters—were sampled in each of the following five study regions (Fig. 1): Alaska (North America), Texas (North America), Costa Rica (Central America), Venezuela (South America), and Zambia (Africa). Sites were selected in an attempt to minimize differences between aquatic habitats for comparisons of fish assemblages in different regions. All of the backwater environments had soft substrates, an abundance of aquatic vegetation, and minimal or no flow during periods of low precipitation. Stream sites were dominated by soft substrates or, in the case of the Alaskan streams, a mixture of stones, sand, and litter substrates. Except for the Alaskan stream sites, midchannel flow was always very slow during periods of low precipitation. Backwater sites contained aquatic vegetation in dense patches, and live vegetation was sparse in stream sites, except for Kataba Creek in Zambia, which had dense shoreline vegetation.

Stream channel and backwater fish assemblages were sampled from the Nuikluk and Fish River drainages of Alaska's Seward Peninsula during June–July 1990. A creek assemblage (Little Quicksand Creek) and a swamp/backwater assemblage (Big Cow Bayou) were sampled within the Sabine River drainage of Texas in June 1953 and June 1986. Creek (Quebrada) and swamp/backwater (Caño Agua Fría Viejo) assemblages were sampled in Tortuguero National Park in the Caribbean lowlands of Costa Rica throughout 1985 (Río Tortuguero drainage). Creek (Caño Volcán) and swamp (Caño Maraca) assemblages were sampled in the west-

ern llanos region (Río Apure drainage) of estado Portuguesa, Venezuela, throughout 1984. From May to December 1989 fishes were sampled from a creek (Kataba Creek) and backwaters of the Upper Zambezi River floodplain (Barotse Plain) in Zambia's Western Province. Fishes were collected by a variety of methods at each site, with reasonable effort to ensure that common species were well represented and that few rare species eluded capture (additional details appear in Winemiller 1990a). The primitive agnathan fish *Ichthyomyzon gagei* (Petromyzontidae) was included as a member of the Texas bayou fish assemblage based subjectively on traditional taxonomic criteria (i.e., lampreys are fish). By including the lamprey and excluding birds and other tetrapod vertebrates, a strict phylogenetic interpretation of taxonomically defined limits of the assemblages was violated. Adult size classes of salmon, *Oncorhynchus keta* and *O. gorbuscha*, were collected but not included in this analysis, since they had entered the streams for spawning and feed normally in the marine environment. Later in the summer, large numbers of a third salmon species, *O. kisutch*, enter streams of the region for spawning. As opposed to adult salmon which enter streams only to spawn and die, adult char (*Salvelinus malma*) and juvenile salmon can be considered normal consumer species in coastal stream food webs. Juvenile *Oncorhynchus* were observed in the streams, but were not collected because of their special protected status. I made morphological measurements on juvenile size classes of *O. gorbuscha* and *O. kisutch* from British Columbia (Canada) streams (TNHC specimens). *Oncorhynchus keta* is not included in the present analysis, because no juvenile specimens were readily available. Juvenile *O. keta* and *O. gorbuscha* are very similar and would be expected to map very closely to one another in ecomorphological space.

#### Morphometrics

Measurements were made to the nearest 0.1 mm using vernier calipers for measures <130.0 mm and to the nearest 1 mm with a clear plastic ruler for measures >130.0 mm. Three specimens corresponding to adult size classes (except for *Oncorhynchus* spp.) were measured, and values were subsequently combined and expressed as means for each trait and each species. Thirty morphological features related to feeding, swimming behavior, or habitat were chosen based on information presented and findings in Gatz (1979a). All distance measurements were taken as the straight line distance between points. These characters were measured and coded as follows:

- 1) maximum standard length (MSL)—largest standard length for specimens collected at a site;
- 2) maximum body depth (BODD)—maximum vertical distance from dorsum to ventrum;
- 3) maximum body width (BODW)—maximum horizontal distance from side to side;
- 4) caudal peduncle length (PEDL)—distance from

the posterior proximal margin of anal fin to the caudal margin of the ultimate vertebra;

5) caudal peduncle depth (PEDD)—minimum vertical distance from dorsum to ventrum of the caudal peduncle;

6) caudal peduncle width (PEDW)—width of the caudal peduncle in horizontal plane at midlength;

7) body depth below midline (BDBM)—vertical distance from midline to ventrum, midline defined as the imaginary line passing from the pupil of the eye through the center of the ultimate vertebra;

8) head length (HEAL)—distance from tip of the upper jaw to the most-caudal extension of the operculum;

9) head depth (HEAD)—vertical distance from dorsum to ventrum passing through the pupil;

10) eye position (EYEP)—vertical distance from the center of pupil to ventrum;

11) eye diameter (EYED)—horizontal distance from eye margin to eye margin;

12) mouth position (MOUPO)—coded as 1 for superior (imaginary vertical plane tangent to both upper and lower jaws with mouth closed between 10°–80°), coded as 2 for terminal (tangent plane at ≈90°), coded as 3 for inferior (tangent plane between 100° and 170°), and coded as 4 for bottom (tangent plane at ≈180°);

13) mouth width (MOUW)—horizontal distance measured inside of fully open mouth at widest point;

14) mouth height (MOUH)—vertical distance measured inside of fully open mouth at tallest point;

15) snout length shut (SNTL)—distance from the pupil of the eye to tip of the upper jaw with mouth shut;

16) snout length open (SNTO)—distance from the pupil to tip of the upper jaw with mouth fully open and extended;

17) dorsal fin height (DORH)—maximum distance from proximal to distal margin of the dorsal fin (excluding filaments);

18) dorsal fin length (DORL)—distance from anterior proximal margin to posterior proximal margin of the dorsal fin;

19) pectoral fin length (PECL)—maximum distance from proximal to distal margin of the pectoral fin;

20) pectoral fin height (PECH)—maximum vertical distance across the fully spread pectoral fin;

21) caudal fin length (CAUL)—maximum distance from proximal to distal margin of the caudal fin (excluding filaments);

22) caudal fin height (CAUH)—maximum vertical distance across the fully spread caudal fin;

23) pelvic fin length (PELVL)—maximum distance from proximal to distal margin of the anal fin;

24) anal fin height (ANAH)—maximum distance from proximal to distal margin of the anal fin;

25) anal fin length (ANAL)—distance from anterior proximal margin to posterior proximal margin of the anal fin;

26) pigment code (PIGM)—coded as 0 for transparent, 1 for silvery/reflective, 2 for silvery with dark lateral stripe or spots, 3 for uniform light coloration with countershading, 4 for lateral or vertical bars with background countershaded, 5 for mottled, densely spotted, or uniform dark with countershading, and 6 for black;

27) tooth shape (TSHA)—coded as 0 for absent, 1 for unicuspid (rasping), 2 for multicuspid (crushing), 3 for short conical (grasping), 4 for long conical (piercing), and 5 for triangular serrated (shearing);

28) gill raker (GRAK)—coded as 0 for absent, 1 for short, blunt, or toothlike, 2 for intermediate or long and sparse, and 3 for long and comb-like;

29) gut length (GUTL)—measured from the beginning of the esophagus to anus (fully extended without stretching);

30) swim bladder length (SWBL)—maximum straight line distance from anterior to posterior margins.

Body length was entered into the multivariate morphological analysis as the maximum standard length (MSL) recorded for each species at each site. All other linear distance measures were converted to ratios to serve as components of body, head, and fin shape. The ratios employed in the analysis were chosen based on earlier functional interpretations (Webb 1984, Gatz 1979a) and were standardized (method given below) to yield equal variances prior to use in comparisons. Allometric biases in the use of untransformed ratios as scaling factors in statistics have been debated, especially with regard to applications in biological systematics (e.g., Acthley and Anderson 1978, and references cited therein). However, some have argued against the use of numerical techniques designed to completely remove all subtle effects of body size on ecomorphological data, because body size is known to be an important factor influencing ecological and evolutionary relationships (e.g., Ricklefs et al. 1981, Douglas 1987). I elected to use standardized values for certain ratios as relatively size-independent dimensions of shape that have straightforward functional interpretations (e.g., relative body height and width influence a fish's capability to remain stable in the midwater column and to turn sharply, vs. its ability to rest on the substrate in an upright position or slither through dense mats of vegetation). This use of ratios allows the first orthonormal axis from principal components analysis (PCA) to be interpreted as a shape determinant rather than a size axis (note again that MSL was employed as one of the morphological variables). When raw linear morphological dimensions are entered into PCA, all variable loadings on the first PC axis are large and positive, which yields the interpretation of an overall body size component modeling most of the variation in the data set (Douglas 1987). Since species scores on the PC axes were to be used as a basis for ecomorphological ordination and calculation of distance measures, use of ratios reduces the chance that the analysis is dominated by a single variable, body size. The fol-

lowing distances were converted to components of shape using body depth as the denominator: PEDD, BDBM, HEAD, MOUH. Body width was the denominator for ratios involving PEDW and MOUW. Head length was the denominator for the ratio of EYED and SNTL. Head depth was the denominator for EYEP. SNTL was divided by SNTL to provide a measure of relative mouth protrusibility (MOUPO). All other distance measures were divided by SL to yield linear components of morphology.

Studies of fish shape for phylogenetic analysis sometimes employ the truss network or a related method of measuring shape elements based on linear measurements between homologous anatomical landmarks (Bookstein et al. 1985). By restricting linear measurements to a set of genetically constrained landmarks, the method often performs better than ratios in demonstrating morphological separation among closely related taxa. However, the anatomical landmark method is clearly undesirable for asking ecological questions of morphological data, because the use of strictly homologous landmarks places severe constraints on the ability of the analysis to detect general features of form related to ecological function. For example, it may matter little whether or not a relatively deep-bodied fish is deepest through the anterior origin of its dorsal fin or through a more posterior region of its dorsum, as long as hydrodynamic features afforded by a deep body are fulfilled. Linear components of shape based strictly on homologous landmarks would usually force a species to be phenetically more similar to its closest phylogenetic relatives—even those with very dissimilar body forms in comparison to more distantly related fishes with convergently evolved morphologies. For example, the darter, *Etheostoma chlorosomum* (Percidae), would exhibit more similarity with other perciforms, such as sunfishes (Cichlidae) and cichlids (Cichlidae), than with ecological equivalents from other zoogeographical regions belonging to distant orders (Fig. 11A).

Strauss (1987) employed homologous anatomical landmark measures in an ecomorphological investigation of North American and temperate South American freshwater fish assemblages, and found high concordance of morphological patterns within regions but very low concordance between regions. His conclusion that phylogeny has the dominant effect on assemblage-wide ecomorphological patterns would be expected, given the predictable effect of the method on comparisons involving taxonomically divergent assemblages. Since the current study seeks to test hypotheses related to species diversity, community structure, and convergent evolution among divergent faunas, ratios provide more appropriate components of shape than a truss network. In other words, if interregional concordance is to be possible, methods of analysis must permit the possibility that a porpoise could cluster with fishes rather than terrestrial mammals.

### Morphological distances

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

$$D_{jk} = \left[ \sum_{i=1}^n (x_{ij} - x_{ik})^2 \right]^{1/2}$$

where  $n$  is the number of attributes, and  $x_{ij}$  and  $x_{ik}$  are standardized values of the same character for the species pair. In order to adjust for the influence of differential scale on distance measures, all calculations were performed on data sets fitting a Gaussian distribution, with a mean of zero and an SD of one, according to the equation:

$$x'_{ik} = (x_{ik} - \bar{X}_k) / \text{SD}_k,$$

where  $x_{ik}$  is the mean value of character  $k$  for species  $i$ ,  $\bar{X}_k$  is the mean value for all  $x_{ik}$ , and  $\text{SD}_k$  is the standard deviation of character  $k$ . From each matrix of Euclidean distances, I identified nearest neighbor (NND) and the distance to the assemblage centroid (CD) for each species. Average NND is an index of *species dispersion* in ecomorphological 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.

Principal components analysis (PCA) was used as one basis for interassemblage comparisons of species distribution in morphological space, as well as for identification of patterns of covariance among morphological characters relating to ecology. Species scores on the dominant orthogonal axes were used to calculate pairwise Euclidean distances for comparison with patterns generated by the standardized morphological variables. PCA was performed on the total 160-species data set based on the correlation matrix of standardized morphological variables (SAS Institute 1985). PCA is a form of factor analysis that produces independent orthogonal axes (principal axes) from the original multivariate swarm of data points, in such a way that the first several components (usually the first three or four) model a major portion of the variation among original variables.

Based on a random subsample from the pooled set, morphological distances were plotted against an index of phylogenetic distance. No definitive phylogenetic scheme yet exists that spans the taxonomic breadth of species employed in the current study. Therefore, for an estimate of phylogenetic distance, I coded the relative distances between each pair of nearest neighbors plus a random sample of 160 species pairings from the pooled data set as follows: phylogenetic distance = 1 if two species belong to the same genus, 2 if same subfamily or tribe, 3 if same family, 4 if same suborder, 5 if same order, and 6 if two species do not belong to the same order. Phylogenetic relationships of higher

taxa are based primarily on Nelson (1984), except for families within the Characiformes and Gymnotiformes, which follow Mago (1970) for neotropical families and Géry (1977) for African characiforms. Assignment of genera within families and species within genera follows Mago (1970), Lee et al. (1980), and Bell-Cross and Minshull (1988).

## RESULTS

### *Regional faunal composition*

Based on the dominant fishes at study sites, the total number of species within regions showed a latitudinal gradient with highest species richness attained at the Venezuelan site (Table 1). These regional totals were influenced primarily by swamp/backwater sites, which had more species than nearby creek sites. The two Alaskan assemblages provided the sole exception. Alaskan assemblages had almost the same number of dominant species ( $N = 6$  and  $7$ ), and the stream environments sampled in Alaska were larger than streams sampled in other regions (sampling in one very small Seward Peninsula stream yielded no fishes; backwater habitats sampled were similar sizes in each region). The five creek sites varied little in fish species numbers (mode 13 species, range 7–18 species), whereas backwaters showed a fairly smooth latitudinal gradient (Table 1). The swamp eel, *Synbranchus marmoratus*, was the only widespread species present within two different biotic regions (Central and South America). Alaskan assemblages were dominated by salmonid fishes and Texas assemblages were dominated by cyprinids and centrarchids, whereas poeciliids, cichlids, and eleotrids dominated Costa Rican fish assemblages. The Upper Zambezi floodplain assemblages were dominated by cyprinid (*Barbus* spp.) and cichlid fishes, whereas Venezuelan llanos assemblages were dominated by characids and other characiform families, siluriforms (i.e., catfishes, especially armored lorica-riids), and cichlids.

### *Morphological variation within and between regions and assemblages*

For the most part, mean values for individual morphological features showed low interregional variation (Table 2), indicating similar faunal centroids in multivariate space. The Zambian floodplain assemblage and both Alaskan assemblages showed bimodal maximum length distributions (Fig. 2). Alaskan fishes tended to be larger than their southern counterparts, and part of this difference was certainly due to the much larger volume of the aquatic environment at the Alaskan stream study sites compared with the creek sites studied in other regions. Nonparametric statistics (Mann-Whitney  $U$ ) were applied in this instance, because data transformations failed to induce normality in the data. A Kruskal-Wallis test indicated that fish size varied significantly among creek sites ( $H = 11.0$ ,

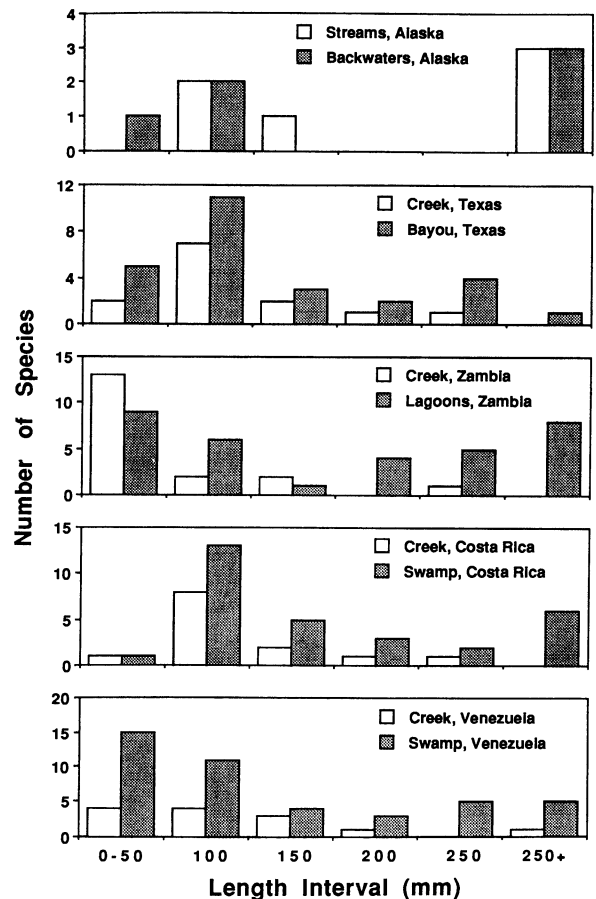


FIG. 2. Maximum standard length (MSL) frequency histograms for the 10 freshwater fish assemblages (two at each of the five study areas shown on Fig. 1).

$P < .05$ ) but not among backwaters ( $H = 3.7$ ,  $P > .05$ ). Since sample sizes were unequal and parametric multiple range tests could not be applied, I conservatively adjusted significance levels by the comparisonwise error rate using  $\alpha/C$ , where  $\alpha$  is the probability for type I error and  $C$  is the number of pairwise comparisons. The Alaskan river channel assemblage appeared to have larger maximum standard lengths (MSLs) than each of the other four creek assemblages (Fig. 2), but only the Alaska stream–Zambia creek comparison contained sufficient degrees of freedom to attain statistical significance ( $Z = 3.0$ , two-tailed  $P < .025$ ). Fishes of the Zambian creek assemblage were significantly smaller than Texas ( $P < .025$ ) and Costa Rican creek fishes ( $P < .01$ ). Within regions, average MSL was significantly greater only for the Zambian backwater assemblage compared with the Zambian small creek assemblages ( $P < .0025$ ). Relative proportions of species in six size intervals (Fig. 2) were significantly different for Costa Rican backwater vs. Zambian backwater ( $\chi^2 = 13.25$ ,  $df = 5$ ,  $P < .025$ ) and for Costa Rican backwater vs. Venezuelan backwater ( $\chi^2 = 11.97$ ,  $df = 5$ ,  $P < .05$ ). Several of the other contingency table tests of inter-



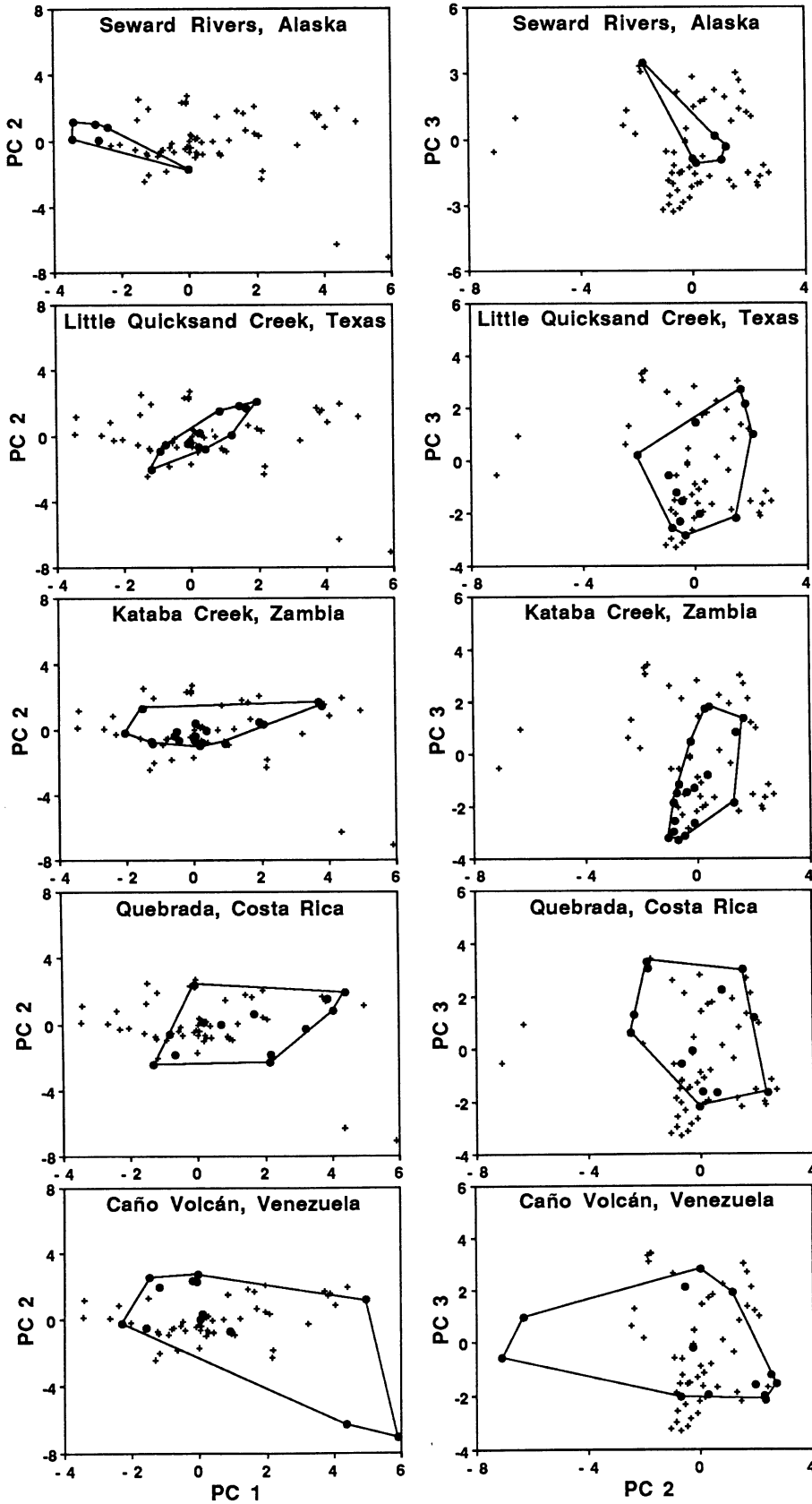


TABLE 2. Values for thirty untransformed morphological characters of pooled freshwater fish assemblages from five geographic regions.

Character*	Alaska		Texas		Costa Rica		Zambia		Venezuela	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
MSL	250.2	242.6	105.4	69.1	151.2	114.8	138.0	107.2	115.8	107.3
BODD	0.19	0.02	0.27	0.10	0.33	0.14	0.30	0.1	0.32	0.13
BODW	0.14	0.05	0.16	0.04	0.17	0.06	0.15	0.04	0.19	0.07
PEDL	0.16	0.03	0.20	0.06	0.15	0.09	0.16	0.06	0.15	0.10
PEDD	0.41	0.16	0.43	0.12	0.41	0.16	0.39	0.11	0.37	0.16
PEDW	0.36	0.11	0.37	0.11	0.29	0.10	0.34	0.11	0.26	0.08
BDBM	0.52	0.08	0.51	0.05	0.49	0.08	0.52	0.06	0.49	0.01
HEAL	0.25	0.03	0.28	0.06	0.30	0.06	0.29	0.05	0.26	0.06
HEAD	0.59	0.08	0.57	0.08	0.58	0.11	0.59	0.07	0.56	0.11
EYEP	0.63	0.08	0.58	0.08	0.62	0.10	0.59	0.09	0.61	0.09
EYED	0.24	0.08	0.26	0.07	0.26	0.08	0.26	0.10	0.29	0.10
MOUPO	2.00	0.71	2.17	0.91	1.88	0.79	2.08	0.90	2.26	1.12
MOUW	0.65	0.21	0.64	0.24	0.56	0.10	0.55	0.17	0.51	0.14
MOUH	0.44	0.14	0.37	0.13	0.40	0.21	0.26	0.07	0.35	0.16
SNTL	0.36	0.05	0.36	0.06	0.39	0.09	0.39	0.06	0.41	0.15
MOUPR	1.04	0.07	1.08	0.09	1.11	0.11	1.07	0.10	1.05	0.10
DORH	0.15	0.02	0.18	0.05	0.19	0.07	0.21	0.06	0.22	0.07
DORL	0.20	0.15	0.24	0.15	0.40	0.26	0.30	0.21	0.20	0.16
PECL	0.15	0.05	0.19	0.06	0.20	0.08	0.20	0.07	0.23	0.08
PECH	0.08	0.04	0.11	0.03	0.11	0.05	0.09	0.03	0.10	0.04
CAUL	0.18	0.03	0.23	0.05	0.26	0.08	0.24	0.06	0.26	0.09
CAUH	0.18	0.04	0.26	0.07	0.27	0.09	0.23	0.06	0.28	0.10
PELVL	0.12	0.04	0.16	0.05	0.18	0.09	0.18	0.07	0.17	0.08
ANAH	0.13	0.03	0.17	0.04	0.19	0.07	0.18	0.05	0.16	0.06
ANAL	0.15	0.06	0.17	0.07	0.27	0.19	0.19	0.11	0.23	0.17
PIGM	2.89	1.76	2.78	1.23	3.69	1.18	3.45	1.38	3.08	1.65
TSHA	2.89	1.27	1.83	1.58	1.97	0.86	2.36	1.40	2.06	1.54
GRAK	2.33	1.00	1.52	0.79	1.13	0.71	1.74	0.79	1.16	1.00
GUTL	0.95	0.17	1.12	1.14	1.06	0.89	1.34	1.57	2.03	3.36
SWBL	0.53	0.34	0.29	0.12	0.32	0.15	0.34	0.07	0.28	0.19

\* Character codes are explained in *Materials and methods: Morphometrics*.

assemblage length differences were nonsignificant due to excessive occurrences of 0-frequency cells.

Alaskan fishes tended to have shallower bodies, longer swim bladders, carnivorous tooth morphology, and shorter alimentary canals than fishes from other locations (Table 2). On average, fishes at the Alaska and Texas sites were lighter colored and more reflective than their tropical counterparts (Table 2: PIGM). Coefficients of variation (cv) were calculated for each morphological trait based on Table 2. The mean coefficient of variation serves as one index of regional morphological diversification. The Venezuelan ichthyofauna exhibited significantly greater morphological variance when compared with each of the other regions (two-tailed *t* tests based on Sidák's multiplicative inequality, *df* = 29, *k* = 10, *P* < .05).

*Multivariate analysis*

The first three PC axes modeled 50% of the total variation in morphological space within the pooled data set of 160 species (Table 3). Loadings (eigenvectors) of the original morphological variables on the PC

axes (Table 3) show that PC1 was influenced primarily by relative body width, body depth, fin height, area of caudal and pectoral fins, and relative head length. Species with high scores on PC1 included tall wide-bodied cichlids, centrarchids, and suckermouth catfishes of the neotropical family Loricariidae. *Synbranchus marmoratus*, *Afromastacembelus frenatus*, *Ichthyomyzon gagei*, and other narrow-bodied elongate fishes like gymnotiforms and pikes (Esocidae) scored lowest on PC1. High species scores on PC2 were associated with large relative body depth, short caudal peduncles, relatively compressed heads, superior mouth position, short snouts, long anal fins, light pigmentation pattern, short conical teeth, long gill rakers, and large swim bladders (Table 3). Species scoring high on PC2 were surface or midwater insectivores or planktivores, such as the neotropical species *Gephyrocharax valenciae* (Characidae) and *Alfaro cultratus* (Poeciliidae), plus laterally compressed flatfishes (Bothidae, Soleidae). Several catfishes (Siluriformes) scored lowest on PC2. These species all possess relatively deep heads, inferior mouths, long caudal peduncles, dark pigmentation, and

FIG. 3. Plots of the first three principal component axes based on 30 morphological characters and the pooled species data set for the five stream channel fish assemblages. Species comprising the assemblage of the named creek are highlighted (●) and bounded in each plot. Associated statistics appear in Table 3.

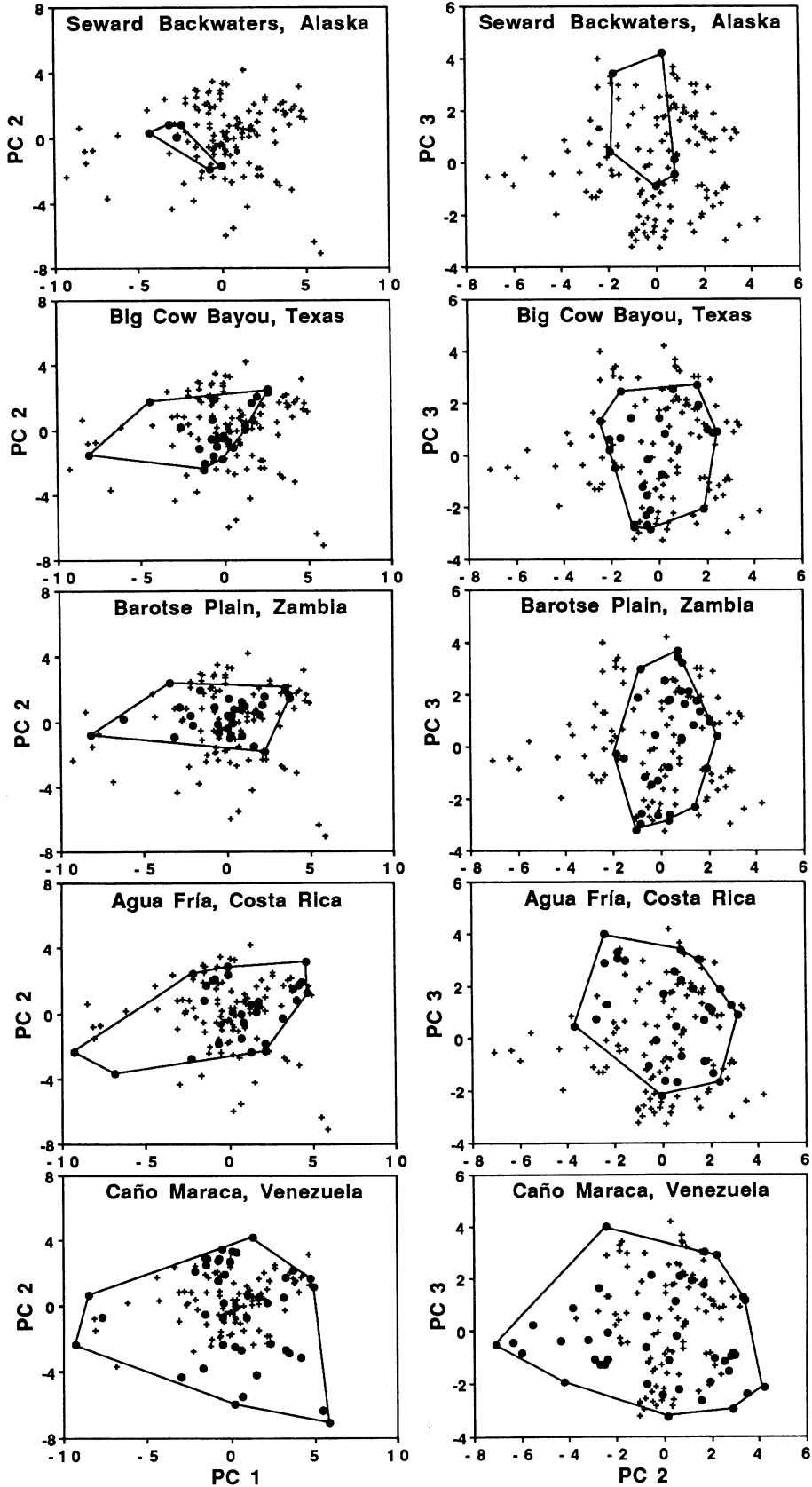


TABLE 3. Axis eigenvalues, proportion variation modeled, cumulative variation modeled, and variable loadings from principal component analysis of 106 freshwater fish species based on morphological characters.\* Eigenvalues  $> -0.20$  but  $< 0.20$  are listed only as positive or negative signs.

	PCA axis		
	1	2	3
Eigenvalue	7.03	4.18	3.59
Proportion of variation	0.24	0.14	0.12
Cumulative variation	0.24	0.38	0.50
MSL	—	+	0.26
BODD	0.23	0.32	+
BODW	0.28	—	+
PEDL	+	-0.27	—
PEDD	+	—	—
PEDW	+	+	—
BDBM	—	+	+
HEAL	0.24	+	0.21
HEAD	+	-0.26	+
EYEP	+	—	0.37
EYED	+	+	-0.35
MOUPO	+	-0.25	—
MOUW	—	+	0.20
MOUH	—	—	+
SNTL	+	-0.26	—
MOUPR	+	+	0.21
DORH	0.28	+	-0.20
DORL	+	+	0.34
PECL	0.30	+	+
PECH	0.28	—	+
CAUL	0.31	—	—
CAUH	0.27	+	—
PELVL	0.33	+	+
ANAH	0.31	+	+
ANAL	—	0.27	+
PIGM	+	-0.20	0.32
TSHA	—	0.25	0.20
GRAK	—	0.26	—
GUTL	+	—	—
SWBL	—	0.25	—

\* Character codes are explained in *Materials and methods: Morphometrics*.

relatively small swim bladders. High scores on PC3 were associated with large body size, a relatively long head, relatively small eyes positioned midway down the head, protrusible jaws, long dorsal fins, and dark pigmentation. Species with high scores on PC3 include the flatfishes, piscivorous perciforms, and eleotrids, whereas low scores were observed for small midwater-dwelling characids and cyprinids.

Two series of plots involving the first three PC axes from the pooled-regions data sets (i.e., one involving stream sites and one involving backwater sites) illustrate the relative positions in morphological space occupied by assemblages and individual species (Figs. 3 and 4). The total multidimensional space occupied by Alaskan assemblages was much smaller than that of other faunas, both for stream and backwater environ-

ments. In each environment, Texas and Zambian faunas spanned comparable regions of morphological space, as defined by the range of species scores for the first three PC axes (Figs. 3 and 4). The Costa Rican assemblages occupied larger spaces than those of Texas and Zambia, but smaller than Venezuelan assemblages in both stream and backwater environments. The Venezuelan assemblages bounded nearly the entire morphological space occupied by assemblages of the other four regions (Figs. 3 and 4). Again, with the exception of the Alaskan sites, the centroids of assemblage hypervolumes in morphological space were similar, but boundary shapes and patterns of dispersion about the assemblage centroid varied considerably between regions for a given habitat category.

#### Distance measures

Patterns of assemblage-wide morphological diversification, as revealed by Euclidean distance measures computed from either standardized variable scores or species scores on the first four PC axes, tended to support the qualitative patterns observed in plots of PCA species loadings. Statistical comparisons of average nearest neighbor distances (NND) can be biased when the numbers of species in the assemblages are unequal. If the total size of the morphological hypervolume were to remain constant with increasing species number, larger assemblages could exhibit greater packing (i.e., reduction in average NND) by virtue of random placement of additional species. Ricklefs and Travis (1980), Ricklefs et al. (1981), and Schum (1984) used a bootstrapping approach to determine whether observed NND were greater or less than those expected by chance. In their randomized cases, assemblages containing many species showed smaller NND than those containing few species. I begin by asking whether or not total dispersion in morphological space is related to region or habitat by examining results from a  $2 \times 2$  factorial ANOVA for centroid distance (ln-transformed CD) as the dependent variable. All statistics are for distances computed from PC loadings. Significant main effects were exhibited by both habitat ( $F = 9.61$ ,  $df = 1$ ,  $191$ ,  $P < .01$ ) and region ( $F = 8.64$ ,  $df = 4$ ,  $191$ ,  $P < .0001$ ). Since total morphological space appears to increase with assemblage size, I performed a similar test for NND (between habitat, NS; between regions,  $F = 3.97$ ,  $df = 4$ ,  $191$ ,  $P < .01$ ). Statistical comparisons of NND for stream vs. backwater sites within regions were not possible, although some trends clearly ran counter to null expectations based on species richness (discussed below). The type I error rate for multiple comparisons within a habitat type was adjusted by Sidák's multiplicative inequality (Sokal and

←

FIG. 4. Plots of the first three principal component axes based on 30 morphological characters and the pooled species data set for the five backwater/swamp fish assemblages. Species comprising the assemblage of the named backwater are highlighted and bounded in each plot. Associated statistics appear in Table 3.

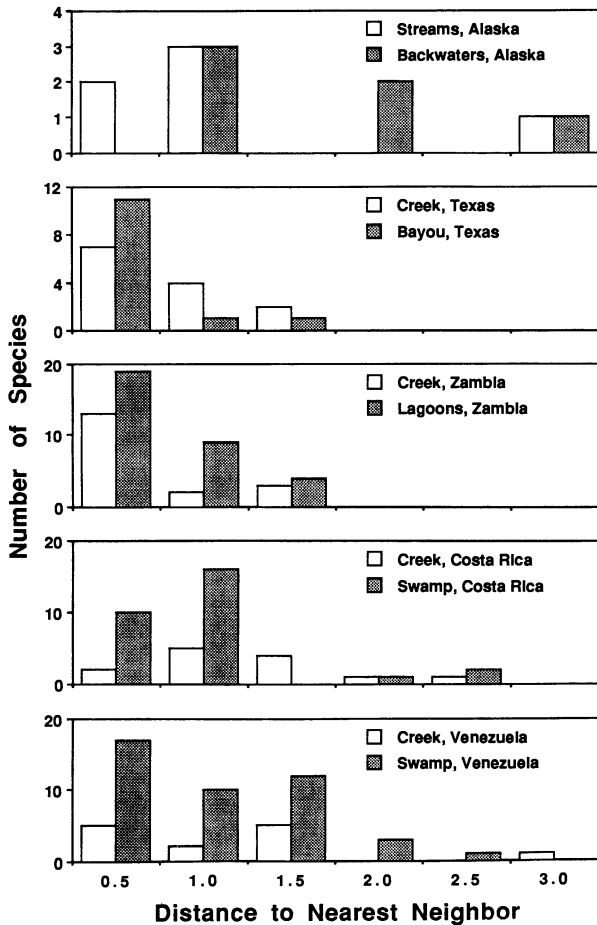


FIG. 5. Frequency histograms of species similarities with nearest neighbors based on Euclidean distances (NND) computed from species projections in principal component space. NNDs (mean  $\pm$  1 sd) computed from standardized morphological variables were as follows: Alaska: river  $4.17 \pm 1.68$ , backwater  $5.43 \pm 1.86$ ; Texas: creek  $2.92 \pm 0.78$ , bayou  $3.29 \pm 1.89$ ; Costa Rica: creek  $3.98 \pm 1.21$ , swamp  $3.80 \pm 1.80$ ; Zambia: creek  $2.55 \pm 0.84$ , lagoons  $3.01 \pm 1.26$ ; Venezuela: creek  $3.99 \pm 1.42$ , swamp  $3.76 \pm 1.32$ .

Rohlf 1981) for pairwise comparisons of assemblage mean NND and CD. Except for CD results for the two Alaskan assemblages, trends and pairwise tests of statistical significance were nearly all the same whether based on standardized variable scores (means and SDs given in legends in Figs. 5 and 6) or species scores on the first four PC axes (Figs. 5, 6, and 7). None of the pairwise within-habitat/between-site comparisons of mean NND in morphological space (Figs. 5 and 7) attained statistical significance. Alaskan assemblages showed the most uneven dispersion of species in morphological space (standard deviation of NND in Figs. 5 and 7). The mean CD, an estimate of morphological diversification, showed only one statistically significant interregional difference, Venezuela backwater > Texas backwater ( $t = 4.28$ ,  $df = 25$ ,  $k = 10$ ,  $P < .05$ ; Fig. 7).

Alaskan assemblages had among the smallest CDs

(Figs. 6 and 7), but they had the largest CDs when computed directly from the standardized variables (see Fig. 6 legend). The discrepancy between the two methods is explained by the pattern of dispersion of Alaskan fishes within relatively small multivariate hypervolumes. Fishes of the Alaskan assemblages were almost entirely scattered around the periphery of the morphological hypervolume (Figs. 3 and 4). With a paucity of species near the centroid, the variable-based calculation yielded large mean CD, even though morphological diversification was actually less for the Alaskan assemblages than others. Distances calculated from PC loadings defined the limits of the morphological space for each assemblage relative to the total morphological space occupied by all fishes, and as a result the mean CD for Alaskan assemblages was smaller. Average CDs based on PCA loadings seem to more accurately reflect relative inter-assemblage differences;

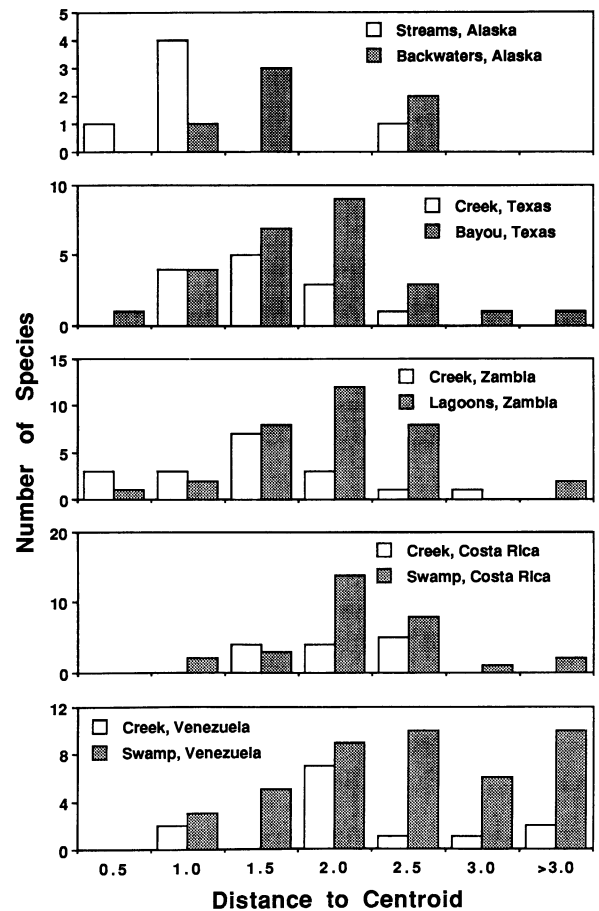


FIG. 6. Frequency histograms of species distances to the assemblage centroid (CD) computed from species projections in principal component space. CDs (mean  $\pm$  1 sd) computed from standardized morphological variables were as follows: Alaska: river  $2.07 \pm 0.60$ , backwater  $2.45 \pm 0.63$ ; Texas: creek  $1.19 \pm 0.13$ , bayou  $1.33 \pm 0.24$ ; Costa Rica: creek  $1.18 \pm 0.15$ , swamp  $1.45 \pm 0.52$ ; Zambia: creek  $1.21 \pm 0.16$ , lagoons  $1.43 \pm 0.24$ ; Venezuela: creek  $1.39 \pm 0.39$ , swamp  $1.55 \pm 0.48$ .

however, the variable-based analysis indicates that Alaskan fishes are hyperdispersed in morphological space compared to the other assemblages.

Trends within habitats showed decreasing mean NND and decreasing standard deviation of NND with increasing species richness, but there were too few degrees of freedom to indicate statistical significance (Fig. 7). Moreover, mean NND would be expected to decline to some extent with increasing richness based on stochastic expectations (Ricklefs and Travis 1980). When all assemblages are combined in linear regressions of mean NND and standard deviation of NND with species richness (Fig. 7), no significant pattern emerges ( $r = 0.47, 0.43$ , respectively;  $P > .05$ ). Contrary to the predictions of null models (Ricklefs and Travis 1980, Schum 1984), mean NND was actually larger for the species-rich Texas bayou assemblage compared with the Texas creek assemblage, and for the Zambia backwater assemblage compared with Zambia creek fishes (Fig. 7). The Alaska backwater assemblage had higher mean NND (1.34) than the Alaska stream assemblage with the same number of taxa (NND = 0.91). Together, the factor analysis and distance measures indicate that more speciose freshwater fish assemblages were not significantly more packed within faunal morphospace than low-diversity assemblages (except perhaps for the two Alaskan assemblages showing overdispersion relative to other sites). In contrast, more species-rich assemblages showed greater morphological diversification and tended to occupy larger regions of ecomorphological space (Figs. 3, 4, and 7). The overall regression for mean CD against species richness was positive ( $r = 0.67$ ) and significant ( $F = 6.53, df = 1, 8; P < .05$ ). Likewise, the degree of latitude was negatively correlated with mean CD ( $r = -0.67, P < .05$ ) when all 10 assemblages were included in the linear model. Within regions, mean CD was always greater for backwater assemblages compared with creek assemblages containing fewer species (Fig. 7).

#### Phylogenetic trends and ecomorphological convergence

Phylogenetic constraints on the evolutionary diversification of form and function are evident in the distribution of species and orders within multivariate morphological space as revealed through factor analysis (Fig. 8). Salmoniforms (wide ranging in nearctic region) and cyprinodontiforms (wide ranging at low latitudes) are both efficient colonizers, and both groups clustered near the center of morphological space (Fig. 8), indicating generalized ecomorphologies. Larger orders tended to occupy larger zones within ecomorphological space, and each one dominated a different peripheral region, usually with considerable overlap with other orders near the pooled fauna centroid. For example, in the plot of the first two PC axes (Fig. 8), characiforms dominate the top-center region (surface and midwater insectivores and omnivores), perciforms dominate the right side (deep-bodied fishes), and siluriforms dominate the bottom region (darkly pigmented, benthic forms). Comprised primarily of African *Barbus* spp. and Texas *Notropis* spp., cypriniform fishes aggregate near the pooled assemblage centroid in the plot of the first two PC axes, but dominate the bottom-center region (small, silvery, midwater-dwellers) in the plot of the second and third PC axes (Fig. 8).

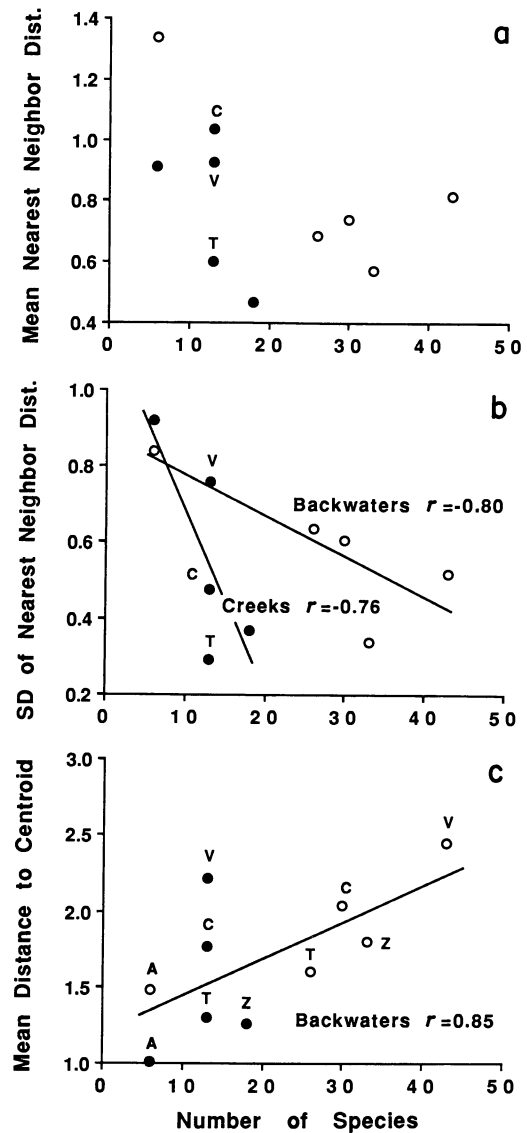


FIG. 7. Three measures of distance between species in niche space plotted as functions of the number of species in the assemblage: (a) mean nearest neighbor distance (NND), (b) standard deviation of NND, and (c) mean centroid distance (CD).  $\circ$  = backwater sites;  $\bullet$  = creek sites. Euclidean distances were calculated from species scores on the first four principal component axes. Only the linear regression involving CD and the five backwater sites was statistically significant ( $P < .05$ ). A regression of CD vs. number of species that combined all 10 assemblages was significant ( $r = 0.67, P < .05$ ). Letters identify sites: Alaska (A), Texas (T), Costa Rica (C), Zambia (Z), and Venezuela (V).

forms dominate the bottom region (darkly pigmented, benthic forms). Comprised primarily of African *Barbus* spp. and Texas *Notropis* spp., cypriniform fishes aggregate near the pooled assemblage centroid in the plot of the first two PC axes, but dominate the bottom-center region (small, silvery, midwater-dwellers) in the plot of the second and third PC axes (Fig. 8).

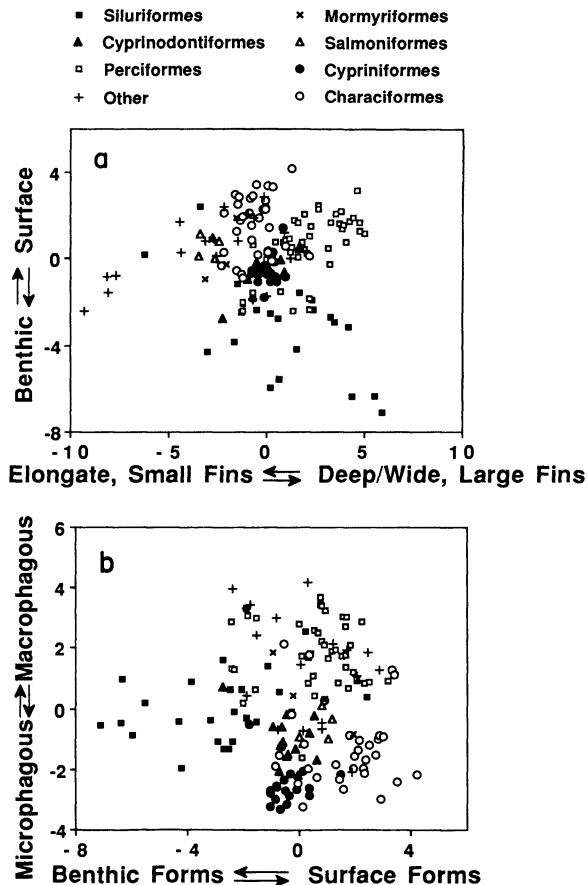


FIG. 8. The distribution of higher taxa (orders) in ecomorphological space. Species ordination is (a) by the first two, and (b) by the second and third principal component axes from the pooled-species data set.

Ecomorphological distance was significantly correlated with phylogenetic distance in plots (Fig. 9) involving 160 nearest neighbors from the pooled data set ( $r = 0.67$ ,  $F = 130$ ,  $df = 1$ ,  $158$ ,  $P < .0001$ ) and 160 randomly chosen species pairings ( $r = 0.40$ ,  $F = 30.1$ ,  $df = 1$ ,  $158$ ,  $P < .0001$ ). These general trends clearly illustrate increasing morphological divergence in association with phylogenetic divergence over geological time. However, considerable variation is observed within morphological distance values associated with large phylogenetic distances (points lying above scores 5 and 6 on the abscissa). The many low morphological distances (i.e., high similarities) associated with large phylogenetic distances in Fig. 9 indicate either of two possibilities: (1) extreme stasis in the evolution of form and function during the course of phyletic divergence, or (2) ecomorphological convergences among distant taxa. The considerable morphological variation at middle-range values of phylogenetic distance (scores of 3–4 on the abscissa) and the dominant positive correlations in Fig. 9 render the stasis hypothesis somewhat untenable. By definition,

two evolutionary lineages must first diverge to some extent before ecomorphological convergences can be identified among their constituents. Products of both processes are visible in Fig. 9.

If we define ecomorphological convergence as species pairings in which a distant taxon has greater morphological similarity than one or more closely related taxa, then numerous convergences were evident in the  $160 \times 160$  species pooled distance matrix. To serve as just one example, I calculated a convergence index for the first through fifth nearest ecomorphological neighbors of 22 Zambian fishes. To obtain a small sample for this test, one species was selected at random from each of the 22 Zambian fish genera. The convergence index was the number of closely related species that were actually less similar morphologically to

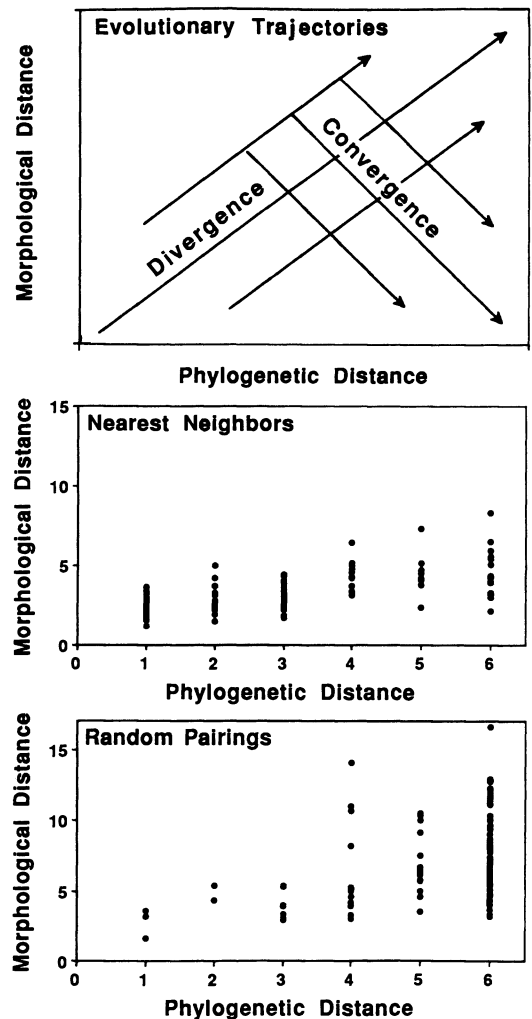


FIG. 9. Plots of morphological distance in Euclidean space against phylogenetic distance for nearest neighbors (middle) and a random set of 160 species pairings (bottom). Species pairings are from the pooled data set in each case. The hypothesized trajectories for species pairs evolving along paths of either ecomorphological divergence or convergence appear in the top plot.

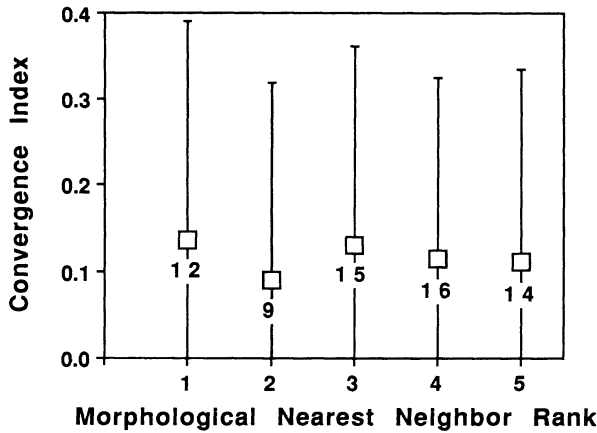


FIG. 10. Convergence index (mean  $\pm$  1 SD) for the first five nearest neighbors in morphological space based on 22 species representing each genus from the African freshwater fish assemblages. The convergence index is equal to the proportion of more recently divergent species that were more dissimilar morphologically than the nearest neighbor. A zero value for the convergence index indicates a complete lack of ecomorphologically convergent species among the fishes studied. Numbers below means are the number of non-zero values among 22 nearest neighbor comparisons.

the target species than its morphological nearest neighbor ( $R$ ) divided by the total number of possible species pairings ( $P$ ).  $P$  was equal to 158 for the first nearest neighbor, 157 for the second, and so on. The convergence index (the ratio  $R/P$ ) was 0 if the nearest neighbor was actually the most closely related taxon, and the index equalled 1.0 if the nearest neighbor was the most distantly related taxon in the entire data set. I used the general phylogenetic scheme described in the *Methods*, and I relied on additional information at the superclass, infradivision, and superorder levels in Nelson (1984). Because I did not distinguish degrees of relatedness between species within a genus, or genera within a family, any bias due to lack of true phylogenetic information was in the direction of no convergence. Therefore, the convergence test should be considered extremely conservative. Even so, ecomorphological convergence was detected about one tenth of the time among the first five nearest neighbors of 22 Zambian fish species (Fig. 10).

A particularly clear example of ecomorphological convergence is seen in the worm-like morphology exhibited by three phylogenetically divergent burrowing fishes: the North American brook lamprey, *Ichthyomyzon gagei* (Agnatha, Petromyzontiformes, Petromyzontidae), the neotropical swamp eel, *Synbranchus marmoratus* (Osteichthyes, Synbranchiformes, Synbranchidae), and the African spiny eel, *Afromastacembelus frenatus* (Osteichthyes, Perciformes, Mastacembelidae). These secretive fishes all burrow in soft substrates and dense mats of litter or aquatic vegetation where they feed primarily on invertebrates. Fig. 11 illustrates some additional convergent ecomorpho-

types (ecological equivalents) from different biotic regions. The Appendix places each fish species in an ecological guild based on diet data (Winemiller 1990a, 1991, and unpublished data) and habitat data from field

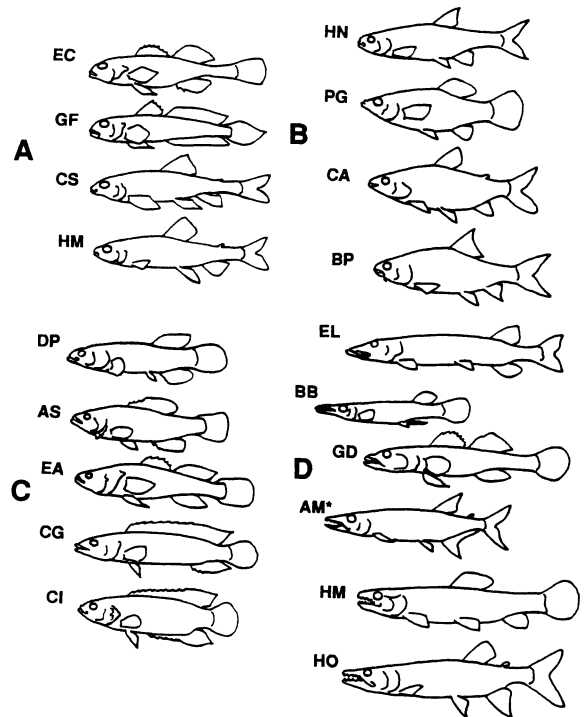


FIG. 11. Examples of ecomorphological convergences among fishes of the five study regions. (Fishes are not drawn to the same scale.) In the pooled-regions data set, these taxonomically divergent species cluster closer to one another than to many, or in some cases all, more-closely related taxa. (A) small, benthic invertebrate-feeders: ED = *Etheostoma chlorosomum* (Perciformes, Percidae; North America), GF = *Gobionellus fasciatus* (Perciformes, Gobiidae; coastal Central America), CS = *Characidium* sp. (Characiformes, Characidiidae; South America), HM = *Hemigrammocharax multifasciatus* (Characiformes, Citharinidae; Africa). (B) small, epibenthic algivore/detritivores with long coiled guts: HN = *Hybognathus nuchalis* (Cypriniformes, Cyprinidae; North America), PG = *Poecilia gilli* (Cyprinodontiformes, Poeciliidae; Central America), CA = *Steindachnerina* (= *Curimata*) *argentea* (Characiformes, Curimatidae; South America), BP = *Barbus poecki* (Cypriniformes, Cyprinidae; Africa). (C) small, cylindrical, vegetation-dwelling invertebrate-feeders: DP = *Dallia pectoralis* (Salmoniformes, Umbridae; Alaska), AS = *Asphredoderus sayanus* (Percopsiformes, Asphredoderidae; North America), EA = *Eleotris amblyopsis* (Perciformes, Eleotridae; Central America), CG = *Crenicichla geayi* (Perciformes, Cichlidae; South America), CI = *Ctenopoma intermedium* (Perciformes, Anabantidae; Africa). (D) fusiform, sit-and-wait/stealth piscivores: EL = *Esox lucius* (Salmoniformes, Esocidae; Alaska), BB = *Belonesox belizanus* (Cyprinodontiformes, Poeciliidae; Central America), GD = *Gobiomorus dormitor* (Perciformes, Eleotridae; Central America), AM = *Acestrorhynchus microlepis* (Characiformes, Characidae; South America [\*denotes a rare species at Caño Maraca not used in the numerical analysis, but included here as a qualitative example]), HM = *Hoplias malabaricus* (Characiformes, Erythrinidae; South America), HO = *Hepsetus odoe* (Characiformes, Hepsetidae; Africa).



collections (K. O. Winemiller, *unpublished data*, C. Hubbs, *unpublished data*). Most guilds had at least one representative in each of the four lower-latitude faunas; however, guilds in the tropics tended to have more representatives, and several guilds (e.g., scale-feeders, mucus-feeders) were unique to tropical assemblages.

#### DISCUSSION

If we assume that the chosen morphological features collectively reflect essential elements of species' ecological niches (Gatz 1979b, 1981, Moyle and Senanayake 1984), then more-speciose tropical fish assemblages encompass a greater diversity of niche characteristics than their temperate counterparts in North America. Although the analysis presented here is essentially inductive in nature, and hence lacks the power to infer causation directly, the ecomorphological patterns observed among the 10 freshwater fish assemblages strongly implicate biotic mechanisms, especially interspecific competition. The more-speciose tropical faunas exhibited larger ranges of values for most morphological characters, and tropical assemblages occupied larger regions within multivariate morphological space than high-latitude faunas in the same kind of environment. This greater ecomorphological volume was not associated with significantly greater levels of species packing in morphological space, although non-significant trends to this effect were seen in separate comparisons based on creek assemblages as a group or on backwater assemblages (Fig. 7). Additionally, speciose tropical assemblages were no less evenly dispersed within morphological space (standard deviation of NND) than temperate faunas in the same habitat (Fig. 7), nor were backwater assemblages more tightly packed in morphospace than channel assemblages of the same region that contained fewer species.

Ecomorphological diversification in freshwater fishes was positively associated with greater species richness and negatively associated with latitude, both when comparisons were based on factor analysis as well as when distance measures were computed from standardized components of morphology. The general pattern was the same for streams/creeks, backwaters/swamps, and a data set combining all 10 assemblages. In contrast, and relying on a smaller suite of morphological characters, Watson and Balon (1984) reported that niche space decreased and species packing appeared greater in a Malaysian stream fauna compared with two north-temperate stream faunas. They hypothesized that intersite differences in levels of species packing might have been more related to habitat differences than to biotic interactions. In the present study only two exceptions ran counter to a perfect positive trend between level of assemblage-wide ecomorphological diversification and species richness: the relatively large mean values for the distance to faunal centroid obtained for Alaskan assemblages calculated from standardized variables (which ran counter to results

based on scores from factor analysis), and the greater hypervolume obtained for Costa Rican sites relative to more species-rich Zambian sites. Historical factors associated with the derivation of modern faunas could also be involved in the generation of these exceptional patterns.

One can reasonably assume that freshwater fish faunas near the arctic circle contain fewer species than the tropical faunas due to greater rates of extinction associated with repeated and severe habitat disturbances during glacial periods, rather than due to lower rates of speciation. Moyle and Herbold (1987) discussed historical effects of Pleistocene glaciations on the composition of North American fish faunas. Western drainages north of the Columbia River experienced extensive and repeated glacial coverage and were recolonized primarily by salmonids and other fishes from coastal environments and freshwater species from the Columbia and Mississippi River watersheds. The fish fauna of northern and western Alaska appears to contain no Mississippi faunal derivatives. If freshwater fish assemblages of the Seward peninsula are comprised of recent colonizers (i.e., recent in the sense of geological time), then most of their evolutionary history, or that of their ancestral lineages, was in association with coastal and freshwater fish assemblages well to the south. The pattern of hyperdispersion within a comparatively small ecomorphological space exhibited by the Alaskan assemblages is likely a reflection of characteristics evolved in association with more-speciose southern faunas. Even if this were the case, both Alaskan fish assemblages were notable in this comparative study for their extreme lack of morphological diversification, with most species possessing a highly generalized fusiform body plan. Only the stickleback, *Pungitius pungitius*, with its unusual dorsal and pelvic spines, and the sculpin, *Cottus aleuticus*, with its dorso-laterally compressed body and benthic habits could be considered mildly specialized ecomorphotypes. Even these forms appear moderate in their level of deviation from a generalized morphology within the pooled-assemblages data set (Figs. 4 and 5). The two relatively specialized Alaskan species were also among the smallest and thus are less likely to disperse long distances over the course of an individual lifetime. If this were so, small body size might increase the likelihood of experiencing a fairly consistent set of environmental interactions throughout individual lifetimes and over the course of generations.

Both Costa Rican fish assemblages contained fewer dominant species than the two Zambian assemblages, yet the former exhibited higher levels of ecomorphological diversification. Of the five regions compared here, Central and South America share the closest historical relationship in the derivation of faunal elements. Ancestral stock lineages of the Poeciliidae and Cichlidae are believed to have had their earliest opportunity for dispersal into nuclear Central America from South

America about  $65 \times 10^6$  years ago (Myers 1966, Bussing 1976). The first Characidae and Pimelodidae probably did not arrive in Central America from the south until the late Pliocene or early Pleistocene (Bussing 1976). Having been derived from much older ancestral colonization events than the characids and pimelodids, the cichlids and poeciliids exhibit greater levels of differentiation from South American relatives and greater niche diversification on a regional basis (Bussing 1976). Therefore, one could hypothesize that morphological characteristics of Central American fish assemblages contain residual effects of their historical ties to the tremendously speciose South American freshwater fish fauna. Because characids and pimelodids dominate the South American ichthyofauna but comprise only minor fractions of the Central American fish assemblages compared with cichlids and poeciliids having longer histories of independent evolution within the region, this hypothesis seems somewhat untenable. Since cichlids and poeciliids obviously underwent adaptive radiations in conjunction with their colonization of Central America, niche diversification in these groups is observed in spite of their historical biogeographical roots (i.e., colonization of the region was initiated from only a few taxonomic stocks) rather than being derived from them. More likely, the explanation for greater niche diversification in Central American fishes compared to Upper Zambezi faunas having similar numbers of species lies in a combination of historical and present differences between regional environments. The region of the Upper Zambezi has experienced considerable fluctuations in rainfall, soil, and terrestrial vegetation throughout a period beginning  $5 \times 10^6$  years ago (Jubb 1967, Balon 1974). Owing to the high elevation ( $\approx 1050$  m) at  $15^\circ$  latitude, the annual temperature profile of the floodplain region in western Zambia is actually more similar to that of southeast Texas than that of lowland Costa Rica. Fish faunas of the Upper Zambezi region exhibit levels of ecomorphological diversification very similar to those of east Texas fish assemblages (Figs. 3, 4, and 7).

Greater niche diversification in tropical ichthyofaunas compared to temperate faunas can be seen on a qualitative level by comparing the suite of characteristics possessed by individual fishes (e.g., Fig. 11), plus the relative numbers of species affiliated with distinctive freshwater fish niches at different sites (Appendix). Some ecomorphotypes are clearly absent from temperate freshwaters, including deep-bodied surface-feeding omnivores (*Thoracocharax stellatus*), deep-bodied midwater omnivores (*Tetragonopterus argenteus*), and broad-finned, benthic aglivo/detritivores (e.g., *Pterygoplichthys multiradiatus*). In fishes, body form is directly related to the manner in which space is utilized. For example, the laterally compressed, deep-body form is most effective for precise turning and positional stability in the water column, especially when coupled with broad medial fins. The deep-body form

is fairly common among epibenthic invertebrate-feeders in North American lowland fish assemblages (e.g., *Lepomis* spp., Centrarchidae), but not found among midwater and surface planktivores and omnivores. The deep-body form was also more prevalent among backwater fishes relative to stream channel dwellers in the same geographical region. With the exception of the Alaskan stream site, the stream channels employed in these comparisons did not exhibit faster current velocities than the backwater sites. Velocities were negligible in all sites during dry months, and except for Alaska, average midchannel current velocities were actually higher for swamp sites than stream sites during periods of high rainfall. Therefore, it seems very unlikely that current velocity constrained colonization of deep-bodied fishes in the small stream channels included in this study. The greater volume and greater habitat heterogeneity created by dense and varied aquatic vegetation in backwaters provide greater opportunities for microhabitat partitioning and the coexistence of a great variety of fish body forms compared with fishes inhabiting small stream channels. Except for greater diversity and densities of floating aquatic macrophytes (greater at three tropical sites than two temperate sites), few differences in habitat structural diversity were observed between the comparative backwater sites at different latitudes. Consequently I interpret many of the within-habitat differences in body form associated with latitude as being derived primarily from biotic factors associated with species diversity and community composition, rather than from the addition of novel resource states in the tropics.

Body form differences between small channel and large backwater fish assemblages are probably derived from the combined effects of biotic interactions and habitat differences, in which competition and predation in backwaters drive larger numbers of species into greater varieties of available microhabitats. This view is consistent with the Schlosser's (1987) interpretation of abiotic and biotic factors that determine fish community composition within longitudinal gradients in midwestern North American streams. Larger stream pools (usually associated with lower reaches) generally support larger sized and greater numbers of predatory fishes, which in turn forces the complement of smaller fishes to forage and compete within restricted microhabitats. The inhibitory effect of piranhas (*Pygocentrus* spp., Characidae) on midpool residence by other diurnal fishes was discussed by Winemiller (1989b), and Jackson (1961) proposed a similar effect for the African tigerfish (*Hydrocynus* spp.). Backwater faunas containing more fish species were not more clustered in morphological space and tended to show greater morphological diversification compared with stream fish assemblages in the same region (Fig. 7). Due to the general disparity in species richness between habitats within regions (Table 1), comparisons based on statistics cannot be extended very far. However, following

Schlösser's model, it is reasonable to assume that niche diversity in the larger backwater sites was associated to some extent with greater structural complexity in the available habitat compared with smaller stream channel sites, and this structural complexity is exploited by small fishes in response to biotic interactions.

If one considers space as a resource (i.e., microhabitat utilization), then space appears to be either more finely subdivided by species-rich tropical assemblages compared with temperate fishes, or the use of space is expanded by tropical fishes. The interpretation depends on how the use of space is defined. In Alaskan backwaters, grayling (*Thymallus arcticus*) and juvenile salmon (*Oncorhynchus* spp.) usually reside at lower midwater depths and feed opportunistically on invertebrates. I found graylings with stomachs packed with benthic immature Ephemeroptera, but the species was frequently observed to rise in pursuit of drifting surface prey. The unspecialized body forms of grayling and salmon would seem to indicate primary utilization of middle water-column depths, yet the species are known to use the entire water column in a more or less opportunistic fashion. Tropical invertebrate feeders in diverse assemblages exhibit a variety of specialized body plans, including pool-dwelling forms associated with dash surface feeding (e.g., *Gephyrocharax valenciae*), agile-maneuvering surface feeding (e.g., *T. stellatus*), dash midwater feeding (e.g., *Astyanax* spp.), agile midwater feeding (e.g., *T. argenteus*), dash epibenthic feeding (e.g., *Creagrutus* sp.), agile epibenthic feeding (e.g., *Aequidens pulcher*), dash benthic feeding (e.g., *Characidium* sp.), and substrate rooting (e.g., *Corydoras* spp.). Further functional subdivisions are apparent even within most of these feeding style groupings (e.g., diurnal vs. nocturnal, and rooting deep into the substrate vs. shallow rooting). The specialized use of space by these tropical species is clearly tied to functional morphology. Whether or not these specializations represent more fine-scaled use of space (resource subdivision) relative to salmonids, or expansion of the primary regions of space utilized (resource expansion) largely depends on how one defines the use of space by salmonids. Since feeding location, rather than total residence time in a microhabitat, is actually what counts here, it seems appropriate to consider niche diversification in morphological features associated with swimming behavior and space utilization as reflecting increased subdivision of the aquatic environment, rather than expanded use of available space. In other words, an expanded morphological hypervolume can reflect either greater subdivision of the same resources (i.e., species packing, sensu MacArthur and Levins 1968) or utilization of an expanded resource spectrum. Without additional ecological information, a strictly morphological analysis cannot distinguish between the two hypotheses.

Some of the feeding specializations seen in South American fishes appear to be completely absent in tem-

perate faunas. Examples of tropical fish feeding specializations include fruit crushing (*Brycon* spp.), flesh shearing (*Pygocentrus notatus*), scale feeding (*Roebooides* spp.), and mucus feeding (*Ochmacanthus alternus*) to note only a few that were involved in the current study (additional discussions of tropical fish feeding specializations appear in Roberts 1972, Lowe-McConnell 1975). Some tropical feeding specializations, such as multicuspid teeth adapted for frugivory and flat incisor-like teeth for highly efficient algae scraping, seem to be associated with expansions of the resource base exploited by temperate fish assemblages. Large fleshy fruits are apparently more available over a greater proportion of the year in tropical forests than temperate forests. Other feeding specializations, like scale feeding, mucus feeding, and wood eating, support the resource subdivision interpretation in the manner already discussed for diversification of body form in relation to space utilization. Presumably, scales and mucus (in most instances these are removed from live fishes with the aid of special adaptations; Sazima 1983, Winemiller and Yan 1989) and woody debris are not much more available in tropical streams compared with temperate streams, yet no temperate freshwater fishes are known to utilize these resources to any significant extent. Depending on specific circumstances, assemblagewide patterns of morphological diversification (expansion of morphospace) for traits associated with food type can be interpreted either as resource expansion, resource subdivision, or a combination of both. Earlier analyses of patterns of community food resource utilization revealed significant levels of resource partitioning in five of the tropical systems included here (Winemiller 1989b, 1991, Winemiller and Pianka 1990).

A number of specialized morphological traits appear to be more related to defense against predation rather than method of food gathering or foraging microhabitat. The banjo catfish (*Bunocephalus amaurus*) of South America is a nocturnal benthic scavenger that mimics a piece of leaf litter or wood. I have observed groups of >70 individual *Bunocephalus* resting in heaps on the bottom during daylight hours at Caño Maraca, this presumably enhancing their mimicry of coarse detritus. The potential role of coloration and fin morphology as defense against fin predators (another tropical specialization) by the South American cichlid, *Astronotus ocellatus*, was discussed by Winemiller (1990b). Special body armor (bony plates or scutes) is another antipredator adaptation found in some temperate zone gasterosteiforms but widespread among certain tropical siluriforms (the Aspredinidae, Callichthyidae, Loricariidae, and Mochokidae, plus the neotropical Doradidae—the last not encountered in this study). In addition, nocturnal navigation and intraspecific communication via bioluminescence and detection of electric fields are traits that appear to be restricted to tropical freshwaters (i.e., Mormyriiformes, Gymnotiformes).

The observation that high levels of species packing in morphological space often can be associated with increased resource sharing by species possessing generalized anatomical features runs counter to some comparatively based interpretations of phenetic distance patterns. Several earlier studies have greatly emphasized measures associated with the average spacing of species (e.g., mean Euclidean [interspecies] distance, mean nearest neighbor distance [NND], SD of NND) rather than patterns of niche expansion. Comparisons of dispersion patterns have little meaning when dissociated from comparisons of the overall morphological space occupied by assemblages. As species numbers increase locally, three outcomes are possible: (1) the average nearest neighbor distance and the pattern of dispersion each remain constant, but the volume of morphospace increases (evidence of niche diversification due to either resource expansion or niche compression); (2) the size of the morphological volume remains constant and nearest neighbor distances decrease, but the pattern of dispersion becomes more even (evidence of response to biotic interactions without niche diversification); or (3) the size of the morphological volume stays constant or decreases, and species are packed closer together in a more random fashion (evidence that there are no interactive biotic effects). Clearly, it is erroneous to equate greater packing within morphological space as a demonstration of greater niche compression in resource space (Schumm 1984, Douglas 1987). If species in an assemblage or higher taxonomic grouping are all very similar to one another, it reflects a lack of niche specialization, rather than the sort of ecomorphological divergence that would be expected in association with high levels of resource partitioning. Travis and Ricklefs (1983) found greater nearest neighbor distances and more-even dispersion of passerine birds within small morphological spaces in island faunas compared with the mainland. They concluded that more-intense interspecific interactions on the small islands containing fewer resources are responsible for producing this pattern. The present study documented greater niche diversification in more species-rich tropical faunas in two different types of habitats. I conclude that, on a global scale, interspecific competition for food resource/foraging space and selection favoring predation defenses greatly influence the evolution of ecomorphological diversity in freshwater fishes.

The concept of ecological convergence and the independent evolution of equivalent ecomorphotypes deserves special attention because of its implications for general ecological and evolutionary theory. Numerous examples of ecological convergence have been known in a variety of plant (Orians and Solbrig 1977) and animal taxa (Pianka 1988) for a long time. Fishes provide some of the best traditional examples of ecomorphological convergence (e.g., pike-like forms in Fig. 11D). Orians and Solbrig (1977) and Orians and Paine

(1983) pointed out that if deterministic factors involved in population regulation and community structure are fairly universal, and the relationship between form and function is fairly conservative, then we might expect to see the evolution of equivalent ecological entities (i.e., species and assemblages), given sufficient time for evolution within very similar environmental conditions. Attempts to rigorously test the hypothesis at the community level have failed, primarily because the ideal conditions for a natural evolutionary experiment (divergent source populations  $\times$  equal environments  $\times$  sufficient time) in actuality are never met, and at best are poorly approximated (Orians and Solbrig 1977, Orians and Paine 1983, Winemiller 1987). Analyses involving specific taxonomic groups exhibiting equivalent ecomorphotypes or habitat associations have resulted in greater success in identifying factors associated with the evolution of convergent ecological niches (Karr and James 1975, Luke 1986, Schluter 1986).

Ecological convergence was defined in this study as greater ecomorphological similarity among phylogenetically divergent species compared with closely related (recently divergent) species (Fig. 10). If one accepts this operational definition for ecological convergence, then convergence appears to be a fairly widespread phenomenon among freshwater fishes from the five biotic regions. A few notable examples of interfaunal niche convergence were illustrated in Fig. 11, and several other remarkable convergent ecomorphotypes were identified by the analysis (e.g., burrowing eel-like fishes, discussed previously—see *Results: Phylogenetic trends . . .*). Obviously, as phylogenetic reconstructions improve and broaden, our ability to perform such comparisons in a rigorous manner will increase. While acknowledging limitations of the phylogenetic data used here to detect convergence, the number of cases identified and the remarkable qualities exhibited by several convergent pairings make the phenomenon difficult to dismiss as arising from stochastic processes. As common as convergence appears here, it should be noted that ecomorphological divergence within lineages is a prerequisite for convergent evolution. Niche diversification within higher taxa was the dominant trend identified in the analysis, as indicated by significant positive slopes in Fig. 9 and the large regions occupied by higher taxa in the PCA scatterplot (Fig. 8).

In conclusion, ecomorphological patterns generated by fish assemblages from lowland stream and backwater habitats in five biotic regions indicate that tropical fish assemblages exhibit higher levels of niche diversification and their species are no less evenly spaced than temperate fish assemblages in similar environments. When viewed across both regions and habitats, assemblages containing more species show greater ecomorphological diversity. The 10 assemblages do not show a significant trend of increased species packing

in morphological space with either increasing species richness or decreasing latitude. Even within regions, speciose backwater assemblages were not more tightly packed in ecomorphological space than creek assemblages containing fewer dominant species. Specializations in feeding behavior and microhabitat utilization are clearly implicated in much of the observed morphological diversification. Probably to a lesser extent, antipredator adaptations are also involved in yielding higher variance in morphological traits within more-speciose fish assemblages at lower latitudes. This analysis supports the view that greater species richness in freshwater fish assemblages is associated with greater niche diversification, either through expansion of the total range of exploited food and habitat resources or through finer subdivision of available resources. The morphological analysis alone cannot distinguish between the two mechanisms per se. In addition to forcing increased competition on similar species during times of resource depletion, newly established species in high-diversity communities would provide additional food resources for other species, either as prey directly, or through indirect effects propagated through the more complex food webs. Finally, ecomorphological divergences within higher taxa from the same region and convergences between phylogenetically divergent taxa from different regions were both widespread, particularly among more species-rich low-latitude ichthyofaunas. The phenomenon of ecological convergence has numerous implications for both ecology and evolutionary biology, and the topic should receive increasing attention as the current wave of interest in systematic research begins to yield new phylogenetic hypotheses.

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## APPENDIX

List of orders, families, and common species from the two study sites in each of the five geographic regions used in the ecomorphological analysis. Basic ecological niches are coded for species as follows: AFP = ambush fusiform piscivore, BDA = benthic detritivore/algivore, DBI = diurnal benthic invertebrate feeder, DMI = deep-bodied, midwater invertebrate feeder/omnivore, DSO = deep-bodied surface omnivore, DVI = deep-bodied vegetation-dwelling invertebrate feeder, EBI = epibenthic invertebrate feeder, EDA = epibenthic detritivore/algivore, EMP = epibenthic and midwater pursuit piscivore, EVI = elongate, vegetation or substrate-dwelling invertebrate feeder, GMI = midwater invertebrate feeder/omnivore, GVI = generalized vegetation-dwelling invertebrate feeder, MUCUS = mucus-feeding ectoparasite, NBI = nocturnal benthic invertebrate feeder, NMZ = nocturnal midwater zooplanktivore, SCALE = midwater scale feeder, SDI = surface-dwelling invertebrate feeder/omnivore, SMI = streamlined midwater zooplanktivore/insectivore, SMP = edge-stalking midwater piscivore, and VIP = vegetation-dwelling invertebrate feeder/piscivore. Species are listed according to taxonomic hierarchy.

1) Alaska: Seward Peninsula—Fish/Nuikluk River drainage (R = river channel, B = backwaters):

Salmoniformes, Salmonidae—*Oncorhynchus gorbusha* (R; GMI), *O. kisutch* (R; GMI), *Salvelinus malma* (R; EMP), *Thymallus arcticus* (R, B; GMI), *Coregonus nasus* (R, B; EBI); Esocidae—*Esox lucius* (B; AFP); Umbridae—*Dallia pectoralis* (B; GVI),

Gasterosteiformes, Gasterosteidae—*Pungitius pungitius* (B; GMI/GVI),

Scorpaeniformes, Cottidae—*Cottus aleuticus* (R, B; DBI).

2) Texas: Newton County—Sabine River drainage (B = Big Cow Bayou, C = Little Quicksand Creek):

Petromyzontiformes, Petromyzontidae—*Ichthyomyzon gagei* (B; EVI),

Clupeiformes, Clupeidae—*Dorosoma cepedianum* (B; EDA), Salmoniformes, Esocidae—*Esox americanus* (B; AFP),

Cypriniformes, Cyprinidae—*Hybognathus nuchalis* (B; EDA), *Notemigonus crysoleucas* (C; GMI), *Notropis atrocandalis* (C; GMI), *Notropis emiliae* (B, C; GMI), *Notropis fumeus* (B, C; GMI), *Notropis texanus* (B; GVI), *Notropis umbratilis* (C; GMI), *Notropis venustus* (B; GMI), *Notropis volucellus* (B; GMI); Catostomidae—*Erimyzon sucetta* (B, C; EBI), *Minytrema melanops* (B; EBI); Ictaluridae—*Noturus gyrinus* (B; NBI), *Noturus nocturnus* (B; NBI),

Cyprinodontiformes, Cyprinodontidae—*Fundulus olivaceus* (B; SDI), *Fundulus notatus* (C; SDI); Poeciliidae—*Gambusia affinis* (B, C; SDI),

Atheriniformes, Atherinidae—*Labidesthes sicculus* (B; SMI),

Perciformes, Centrarchidae—*Elassoma zonatum* (B; DVI), *Lepomis cyanellus* (C; VIP), *Lepomis gulosus* (B, C; VIP), *Lepomis machrochirus* (B; DVI), *Lepomis megalotis* (B; DVI), *Lepomis punctatus* (B, C; DVI), *Micropterus salmoides* (B; EMP); Percidae—*Ammocrypta vivax* (B; DBI), *Etheostoma chlorosomum* (B, C; DBI), *Percina sciera* (B; DBI),

Perciformes, Aphredoderidae—*Aphredoderus sayanus* (B, C; GVI).

3) Costa Rica: Tortuguero Park—Río Tortuguero drainage (F = Caño Agua Fria, Q = Quebrada):

Characiformes, Characidae—*Astyanax fasciatus* (F, Q; GMI), *Brycon guatemalensis* (F; GMI), *Roeboides guatemalensis* (F; SCALE),

Siluriformes, Pimelodidae—*Rhamdia guatemalensis* (Q; VIP),

Cyprinodontiformes, Aplocheilidae—*Rivulus isthmensis* (Q; GVI); Poeciliidae—*Alfaro cultratus* (F, Q; SDI), *Belonesox belizanus* (F; AFP), *Brachyrhaphis parismina* (F; SDI), *Phallichthys amates* (F, Q; EDA), *Poecilia gilli* (F, Q; EDA),

Atheriniformes, Atherinidae—*Melaniris milleri* (F; SMI),

Syngnathiformes, Syngnathidae—*Oostethus lineatus* (F; EVI),

Perciformes, Pomadasyidae—*Pomadasys croco* (F; EBI); Lutjanidae—*Lutjanus jocu* (F; EMP); Centropomidae—*Centropomus pectinatus* (F; SMP); Cichlidae—*Cichlasoma al-fari* (F, Q; EBI), *Cichlasoma centrarchus* (F; DVI), *Cichlasoma citrinellum* (F; DBI/DVI), *Cichlasoma dovii* (F; EMP), *Cichlasoma cf. friedrichsthalii* (F, Q; VIP), *Cichlasoma maculicauda* (F; EDA), *Cichlasoma nigrofasciatum* (F, Q; EDA); Eleotridae—*Dormitator maculatus* (F, Q; DVI/EDA), *Eleotris amblyopsis* (F, Q; GVI), *Eleotris pisonis* (F; EVI), *Gobiomorus dormitor* (F, Q; AFP); Gobiidae—*Evorthodus lyricus* (F, Q; BDA), *Gobionellus fasciatus* (F; DBI),

Pleuronectiformes, Bothidae—*Citharichthys spilopterus* (F; NBI); Soleidae—*Achirus lineatus* (F; NBI), *Trinectes paulistanus* (F; NBI),

Synbranchiformes, Synbranchidae—*Synbranchus marmoratus* (F; EVI).

4) Zambia—Upper Zambezi River drainage (B = Central Barotse plain, K = Katamba Creek):

Osteoglossiiformes, Mormyridae—*Marcusenius macrolepidotus* (B; NBI), *Mormyrus lacerda* (B; NBI), *Petrocephalus catostomus* (B; NMZ), *Pollimyrus castelnaui* (B, K; GVI),

Characiformes, Hepsetidae—*Hepsetus odoe* (B; AFP); Characidae—*Alestes lateralis* (B; GMI), *Hydrocynus vittatus* (B; EMP), *Rhabdalestes maunensis* (K; SMI); Citharinidae—*Hemigrammocharax machadoi* (K; DBI), *Hemigrammocharax multifasciatus* (K; DBI); Cyprinidae—*Barbus paludinosus* (B; GMI), *Barbus afrovernayi* (K; GMI), *Barbus cf. annectens* (B, K; EBI), *Barbus bifrenatus* (K; GMI), *Barbus haasianus* (B, K; GMI), *Barbus multilineatus* (B, K; GVI), *Barbus poechi* (B; EDA), *Barbus radiatus* (B, K; EBI),

Siluriformes, Schilbeidae—*Schilbe mystus* (B; EMP); Clariidae—*Clarias theodorae* (B; VIP); Mochokidae—*Synodontis leopardinus* (B; NBI), *Synodontis woosnami* (B; NBI),

Cyprinodontiformes, Cyprinodontidae—*Aplocheilichthys hutereaui* (B, K; SDI), *Aplocheilichthys johnstoni* (B, K; SDI), *Aplocheilichthys katangae* (B, K; SDI), *Aplocheilichthys* sp. (B, K; SDI),

Perciformes, Cichlidae—*Hemichromis elongatus* (B; VIP), *Oreochromis macrochir* (B; EDA), *Pharyngochromis darlingi* (K; EBI), *Pseudocrenilabrus philander* (B, K; DVI), *Serranochromis angusticeps* (B; SMP/DVI), *Serranochromis codringtoni* (B; EBI/DVI), *Serranochromis giardi* (B; EBI), *Serranochromis macrocephalus* (B; EMP), *Serranochromis robustus* (B; EMP), *Tilapia rendalli* (B, K; EDA), *Tilapia sparrmani* (B, K; EDA); Anabantidae—*Ctenopoma intermedium* (B; GVI); Mastacembelidae—*Afromastacembelus frenatus* (B; EVI).

5) Venezuela: Portuguesa—Río Apure drainage (M = Maraca, V = Volcán):

Characiformes, Erythrinidae—*Hoplias malabaricus* (M, V; AFP); Lebiasinidae—*Characidium* sp. (M; DBI), *Lebiasima erythrinoides* (V; GMI), *Pyrrhulina cf. lugubris* (M; SDI); Curimatidae—*Steindachnerina* (= *Curimata*) *argentea* (M; EDA); Prochilodontidae—*Prochilodus mariae* (M; EDA); Characidae—*Aphyocharax alburnus* (M; SMI), *Astyanax bimaculatus* (M, V; GMI), *Astyanax metae* (V; GMI), *Bryconamericus beta* (V; GMI), *Charax gibbosus* (M; SMP), *Corynopoma riisei* (V; SDI), *Creagrutus* sp. (V; EBI), *Ctenobrycon spilurus* (M; DMI), *Gephyrocharax valenciae* (M; SDI), *Hemigrammus* sp. (M; GMI), *Markiana geayi* (M; DMI), *Odontostilbe pulcher* (M; EDA), *Pygocentrus notatus* (M; EMP), *Roeboides dayi* (M, V; SCALE), *Tetragonopterus argentea* (M; DMI), *Triportheus* sp. (M; SDI); Gasteropelecidae—*Thoracocharax stellatus* (M; DSO),

Gymnotiformes, Gymnotidae—*Gymnotus carapo* (M; VIP); Sternopygidae—*Eigenmannia virescens* (M; NMZ),

Siluriformes, Pimelodidae—*Microglanis itheringi* (M; GVI),

*Pimelodella* sp2 (M; NBI); *Pimelodella* sp3 (M; NBI); Auchenipteridae—*Parauchenipterus galeatus* (M; VIP); Trichomycteridae—*Ochmacanthus alternus* (M; MUCUS); Aspredinidae—*Bunocephalus amaurus* (M; NBI); Callichthyidae—*Corydoras aeneus* (M; DBI), *Corydoras habrosus* (M; DBI), *Corydoras septentrionalis* (M; DBI), *Hoplosternum littorale* (M; DBI); Loricariidae—*Ancistrus* cf. *triradiatus* (V; BDA), *Hypostomus argus* (M, V; BDA), *Loricarichthys typus* (M; NBI/DBA), *Otocinclus* sp. (M; DBA), *Pterygoplichthys multiradiatus* (M; BDA), *Rineloricaria caracasensis* (M; BDA),

Cyprinodontiformes, Aplocheilidae—*Rachovia maculipinnis* (M; GVI); Poeciliidae—*Poecilia reticulata* (M, V; EDA), Perciformes, Cichlidae—*Apistogramma hoignei* (M; DVI), *Astronotus ocellatus* (M; VIP), *Aequidens pulcher* (M, V; EBI), *Caquetaia kraussii* (M; VIP/SMP), *Cichlasoma orinocense* (M; DVI), *Crenicichla geayi* (V; GVI),

Synbranchiformes, Synbranchidae—*Synbranchus marmoratus* (M; EVI).