

# Ecomorphology of Freshwater Fishes

KIRK O. WINEMILLER

## Ecological Divergence and Convergence in Freshwater Fishes

*Strong relationships between basic form and ecological function in fishes allow the comparative study of ecological relationships using morphological features. Within-fauna variation and between-fauna similarities of ecomorphological characteristics of freshwater fish assemblages from five regions around the world were compared and contrasted. Ecomorphological features allowed identification of a number of ecologically convergent species from different regions. Based on a relative scale of convergence, tropical fish assemblages exhibited a greater degree of ecological convergence than temperate assemblages. The ecomorphological comparison supports the view that biotic interactions have a greater relative influence on evolution in the tropics compared with temperate regions.*

Figure 1.  
*The body shape, position of fins, and mouth structure of a fish influence its ecological performance. Trout possess a generalized morphology that allows them to use the entire water column and a wide variety of food items in habitats that contain relatively few competing species.*  
PAINTING BY WALTER A. WEBER © NGS

**B**IOLOGISTS AND POLICYMAKERS ARE RACING the clock to document and preserve biological diversity in the face of a growing global human population and alterations of natural habitats. Given the magnitude and rapid pace of changes to natural ecosystems, biologists are challenged with the task of identifying essential features in the organization of biological communities. Notwithstanding the inherent uniqueness of different geographical regions and the evolutionary histories of their flora and fauna, the recognition of common features among communities and the species that comprise them is sometimes possible. This study contributes to our understanding of biodiversity by further examining the ecological characteristics of natural freshwater fish communities from around the world.

One of ecology's greatest challenges is to explain patterns of regional species diversity as well as the ecological, morphological, and behavioral variation among and within populations. Patterns of ecological and morphological diversification are of interest to both ecologists and phylogenetic systematists. Systematists use interspecific variation as the raw material for constructing phylogenies. Ecologists would like to know if interspecific variation in a given trait arises randomly during evolutionary divergence following speciation, or whether this variation is correlated with ecological function. This difficult task is further complicated by unique events. Traits adaptive in a particular ecosystem may be neutral or maladaptive in a new environment. If a maladaptive trait is genetically correlated with one or more strongly adaptive traits, then it might persist in the population for many generations. In one form or another, evolutionary biologists and ecologists seek to identify, interpret, and model patterns of functional (adaptive) variation.<sup>21</sup> Similarities in patterns of individual, population, and community-level variation among different faunas provide evidence that, in many cases, the same deterministic processes organize biological systems.

Biological convergence is the independent evolution of the same feature (physiological, morphological, ecological, etc.) within two divergent phylogenetic lineages. Divergence is the evolution of dissimilar traits between closely related lineages. Remarkable examples of morphological and ecological divergence are well-known in virtually all higher taxa. Examples from the independent adaptive radiation among marsupial mammals of Australia and eutherian mammals of the other continents appear in most introductory biology textbooks. Convergence of ecological niches is seen in rodents and marsupial mice; shrews and marsupial insectivores; and eutherian canines and marsupial wolves. The bony fishes

*I am preparing a report on patterns of resource utilization and guild organization among diverse fish assemblages in Central and South America, North America and Africa. In the interest of communicating with a diverse scientific audience, I have attempted to make the analysis fairly straightforward. This is sometimes difficult to achieve with numerical analyses aimed at revealing temporal trends within species assemblages containing 30 to 70 species.*

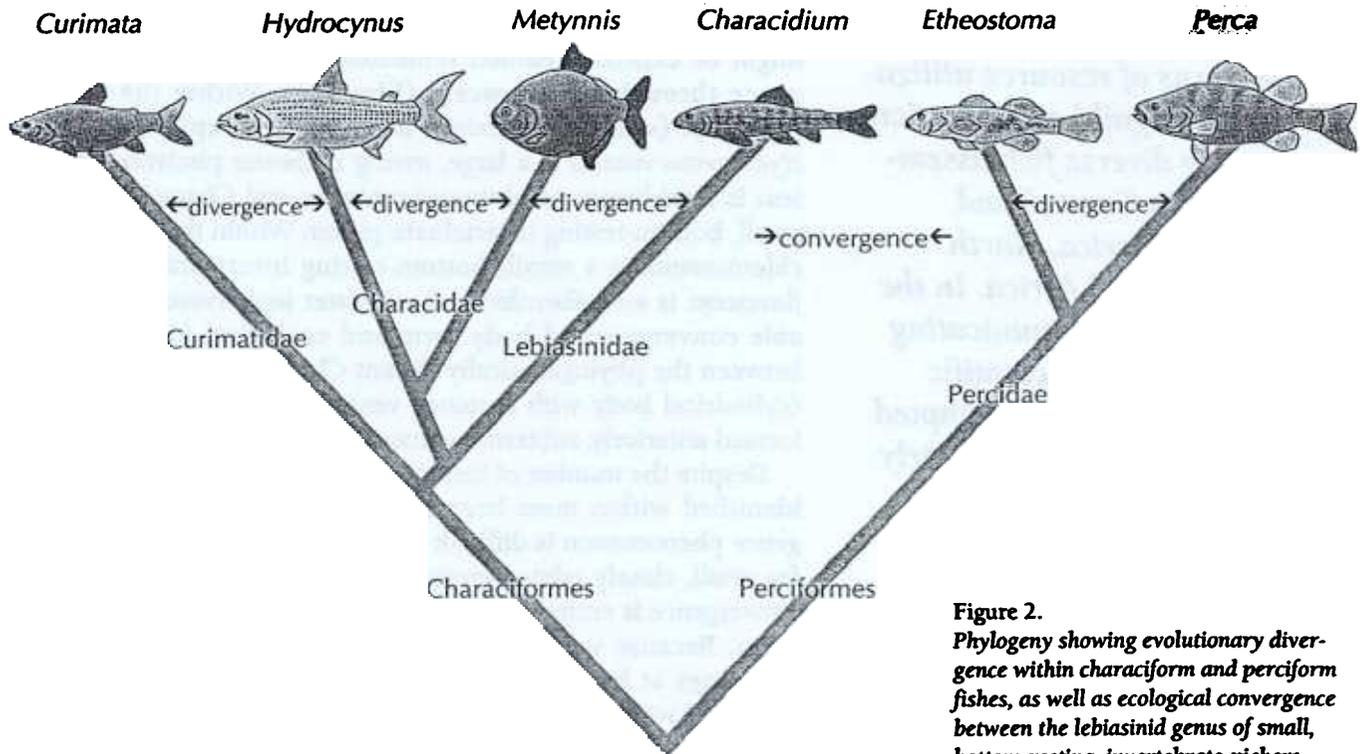
CORRESPONDENCE

(Osteichthys) are a much older and speciose phylogenetic lineage and as might be expected, exhibit numerous examples of evolutionary convergence throughout the world (Figure 1). Within the Characiformes, *Curimata* (= *Steindachnerina*) *argentea* is an epibenthic mud-feeder; *Hydrocynus vittatus* is a large, roving midwater piscivore; *Metynnis argenteus* is a midwater planktivore/granivore; and *Characidium fasciatum* is a small, bottom-resting invertebrate-picker. Within the Percidae, *Etheostoma chlorosomum* is a small, bottom-resting invertebrate-picker; and *Perca flavescens* is an epibenthic and midwater insectivore/piscivore. A remarkable convergence of body form and ecological function has occurred between the phylogenetically distant *Characidium* and *Etheostoma* species (cylindrical body with flattened ventrum, broad pectoral fins, pelvic fins located anteriorly, subterminal mouth, etc.).

Despite the number of instances of remarkable convergence that can be identified within most large taxonomic groups (Figure 3), the convergence phenomenon is difficult to study quantitatively. This is especially so for small, closely related groupings. Our ability to recognize evolutionary convergence is entirely dependent on knowledge of phylogenetic relationships. Because we usually have more confidence in our phylogenetic groupings at broader taxonomic scales, ecological convergence can be identified with greater ease. Within smaller and more recent phylogenetic lineages, it is often difficult to distinguish divergent traits from convergent traits. In fact, a great deal of the methodology of modern phylogenetics seeks to identify the suite of traits that is uniquely divergent versus the suite that is convergent.<sup>2</sup> Phylogenies are based on the information contained in uniquely divergent (derived) characteristics. Convergent traits are seen as potentially confounding characteristics in phylogenetic constructions. Among closely related taxa, the distinction between derived and convergent traits is sometimes unclear and only becomes apparent after phylogenetic hypotheses have been generated and tested.

Here I present results from a comparative study of morphology and ecology of freshwater fish assemblages from five widely separated regions around the world. Study sites span a latitudinal gradient from Alaska (65° N) to the neotropics (9° N), and a tropical longitudinal gradient from Central America (83° W) to Africa (23° E). Like many taxonomic groups, freshwater fishes show a strong latitudinal gradient in species richness, with the highest regional diversity appearing in the neotropics. R. H. Lowe-McConnell<sup>15</sup> counted >1300 freshwater fish species for the Amazon River basin compared with 192 for all of Europe. Since that time, new discoveries have caused most estimates for South American fishes to more than double, while the record for European species remains essentially unchanged. Whereas climatic and biogeographical history are probably the primary underlying agents that produce global patterns of regional diversity, the basic mechanisms that foster coexistence of large numbers of species in tropical faunas are open to debate. The extent to which assemblages from different regions are organized in the same manner indicates the degree to which deterministic processes regulate the populations that comprise communities.<sup>33</sup> Moreover, the relative amount of ecological convergence among taxa from different regions should indicate the strength of similar forms of directional selection in relation to random evolutionary change and evolutionary stasis due to genetic constraints. Here I contrast patterns of morphological divergence within the five local fish assem-

KIRK O. WINEMILLER, assistant professor, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258.



**Figure 2.** Phylogeny showing evolutionary divergence within characiform and perciform fishes, as well as ecological convergence between the lebiasinid genus of small, bottom-resting, invertebrate-pickers, *Characidium* (*C. fasciatum*, South America), and the percid genus of small, bottom-resting, invertebrate-pickers, *Etheostoma* (*E. chlorosomum*, North America).

blages. A substantial literature illustrates the correlations between a number of basic morphological features of fishes and ecological performance (summarized in P. W. Webb<sup>27</sup>), and morphology has been used successfully as a surrogate for ecology.<sup>6-8,11,20,26,28,32</sup> In addition, I compare the relative degree of ecomorphological convergence between fish species from different regional faunas.

## Methods

### SAMPLE COLLECTION

Each of five study sites was sampled on at least two separate dates, and most locations were visited numerous times as part of long-term field studies.<sup>29-31</sup> Only numerically dominant species were used for the morphological analysis. Dominant species are defined in this study as the most common species at a site that (by number of individuals), when summed by order of rank, formed 99% of all individual fishes collected over the full sampling period. Rare species were defined as those comprising the 1% tail of smallest relative abundance contributing to the numerical total for a site. Whereas this criterion for assemblage membership could exclude a few rare, but perhaps strongly interactive, community elements, it was designed to eliminate most of the rare fugitive and transient species that were essentially non-interactive components of the core assemblage (Table 1).

Two types of lowland aquatic environments—streams and backwaters—were sampled in each of the following study regions: Alaska (North America), Texas (North America), Costa Rica (Central America), Venezuela (South America), and Zambia (Africa). This paper compares assemblage patterns of morphological and ecological divergence among

Table 1. Species within Each Family Comprising Each Freshwater Fish Assemblage

FAMILY (common name)

SEWARD PENINSULA, ALASKA

	RIVERS spp.	BACKWATERS spp.	TOTAL spp.
SALMONIDAE (salmon, whitefishes)	6	2	6
ESOCIDAE (pikes)	0	1	1
UMBRIDAE (blackfishes)	0	1	1
COTTIDAE (sculpins)	1	1	1
GASTEROSTIIDAE (sticklebacks)	0	1	1
NO. GENERA	5	6	8
NO. DOMINANT SPECIES	7	6	10
NO. RARE SPECIES	0	0	0

NEWTON COUNTY, TEXAS

	CREEK	BAYOU	TOTAL
PETROMYZONIDAE (lamprey)	0	1	1
CLUPEIDAE (shads)	0	1	1
ESOCIDAE (pikes)	0	1	1
CYPRINIDAE (minnows)	6	6	9
CATOSTOMIDAE (suckers)	1	2	2
ICTALURIDAE (catfishes)	0	2	2
APHREDODERIDAE (pirate perds)	1	1	1
CYPRINODONTIDAE (killifishes)	1	1	2
POECILIIDAE (livebearers)	1	1	1
ATHERINIDAE (silversides)	0	1	1
CENTRARCHIDAE (sunfishes)	3	6	7
PERCIDAE (darters)	1	3	3
NO. GENERA	8	18	19
NO. DOMINANT SPECIES	13	26	31
NO. RARE SPECIES	0	0	0

TORTUGUERO PARK, COSTA RICA

	CREEK	CAÑO	TOTAL
CHARACIDAE (tetras)	1	3	3
PIMELODIDAE (catfishes)	1	0	1
CYPRINODONTIDAE (killifishes)	1	0	1
POECILIIDAE (livebearers)	3	5	5
ATHERINIDAE (silversides)	0	1	1
SYNGNATHIDAE (pipefishes)	0	1	1
POMADASYIDAE (grunts)	0	1	1
LUTJANIDAE (snappers)	0	1	1
CENTROPOMIDAE (snook)	0	1	1
CICHLIDAE (cichlids)	3	7	7
ELEOTRIDAE (sleepers)	3	4	4
GOBIIDAE (gobies)	1	2	2
SYNBRANCHIDAE (swamp eels)	0	1	1
SOLEIDAE (soles)	0	2	2
BOTHIDAE (flounders)	0	1	1
NO. GENERA	11	23	25
NO. DOMINANT SPECIES	13	30	32
NO. RARE SPECIES	9	28	1

FAMILY (common name)

WESTERN PROVINCE, ZAMBIA

	CREEK	BACKWATERS	TOTAL
MORMYRIDAE (elephant noses)	1	4	4
HEPSETIDAE (African pike)	0	1	1
CHARACIDAE (tetras)	1	2	3
CITHARINIDAE (African darters)	2	0	2
CYPRINIDAE (minnows)	6	6	8
SCHILBEIDAE (catfishes)	0	1	1
CLARIIDAE (walking catfishes)	0		
MOCHOKIDAE (squeaker catfishes)	0	2	2
CYPRINODONTIDAE (killifishes)	4	4	4
CICHLIDAE (cichlids)	4	10	11
ANABANTIDAE (climbing perches)	0	1	1
MASTACEMBAELIDAE (spiny eels)	0	1	1
NO. GENERA	8	19	22
NO. DOMINANT SPECIES	18	33	39
NO. RARE SPECIES	14	32	35

ESTADO PORTUGUESA, VENEZUELA

	CREEK	CAÑO	TOTAL
ERYTHRINIDAE (guavinas)	1	1	1
CHARACIIDAE (S. Amer. darters)	0	1	1
LEBIASINIDAE (guavinas)	1	1	2
CURIMATIDAE (curimatus)	0	1	1
PROCHILODONTIDAE (coporos)	0	1	1
CHARACIDAE (tetras)	6	12	16
GASTEROPELECIDAE (hatchetfishes)	0	1	1
GYMNOTIDAE (knifefishes)	0	1	1
STERNOPYGIDAE (knifefishes)	0	1	1
PIMELODIDAE (catfishes)	0	3	3
AUCHENIPTERIDAE (catfishes)	0	1	1
TRICHOMYCTERIDAE (parasitic catfishes)	0	1	1
ASPREDINIDAE (banjo catfishes)	0	1	1
CALlichthyidae (armored catfishes)	0	4	4
LORICARIIDAE (armored catfishes)	2	5	6
CYPRINODONTIDAE (killifishes)	0	1	1
POECILIIDAE (livebearers)	1	1	1
CICHLIDAE (cichlids)	2	5	6
SYNBRANCHIDAE (swamp eels)	0	1	1
NO. GENERA	12	40	46
NO. DOMINANT SPECIES	13	43	50
NO. RARE SPECIES	7	40	45

For a complete list of the dominant species at each site and their taxonomic affiliations, see Winemiller.<sup>32</sup>

backwater sites only. A statistical analysis of patterns of ecomorphological dispersion in both backwater and channel assemblages is presented in Winemiller.<sup>32</sup> All of the backwater environments had soft substrates, abundant aquatic vegetation, and minimal or no flow during periods of low precipitation. A bayou assemblage (Big Cow Bayou) within the Sabine River drainage of Texas was sampled in June 1953 and June 1986 by Clark Hubbs and colleagues of the University of Texas at Austin. I sampled a swamp (Caño Maraca) assemblage in the western llanos region (Río Apure drainage) of estado Portuguesa, Venezuela, throughout 1984 and a swamp/backwater (Caño Agua Fría Viejo) assemblage of Tortuguero National Park in the Caribbean lowlands of Costa Rica throughout 1985 (Río Tortuguero drainage). From May to December 1989, fishes were sampled from backwaters of the upper Zambezi River floodplain (Barotse Plain) in Zambia's Western Province. During June and July 1990, fish assemblages were sampled from the Nuukluk and Fish River drainages of Alaska's Seward Peninsula. Using concerted efforts to ensure that common species were well represented and that few rare species escaped capture, fishes were collected by nets and hook and line. Adult size-classes of salmon (*Oncorhynchus keta* and *O. gorbuscha*) were collected in Alaska but are not included in this analysis because they had entered the streams for spawning and normally feed in the marine environment. As opposed to adult salmon, which enter streams only to spawn and die, adult char (*Salvelinus malma*) and juvenile salmon can be considered normal components of 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 specimens of *O. gorbuscha* and *O. kisutch* from British Columbia (Canada) streams.

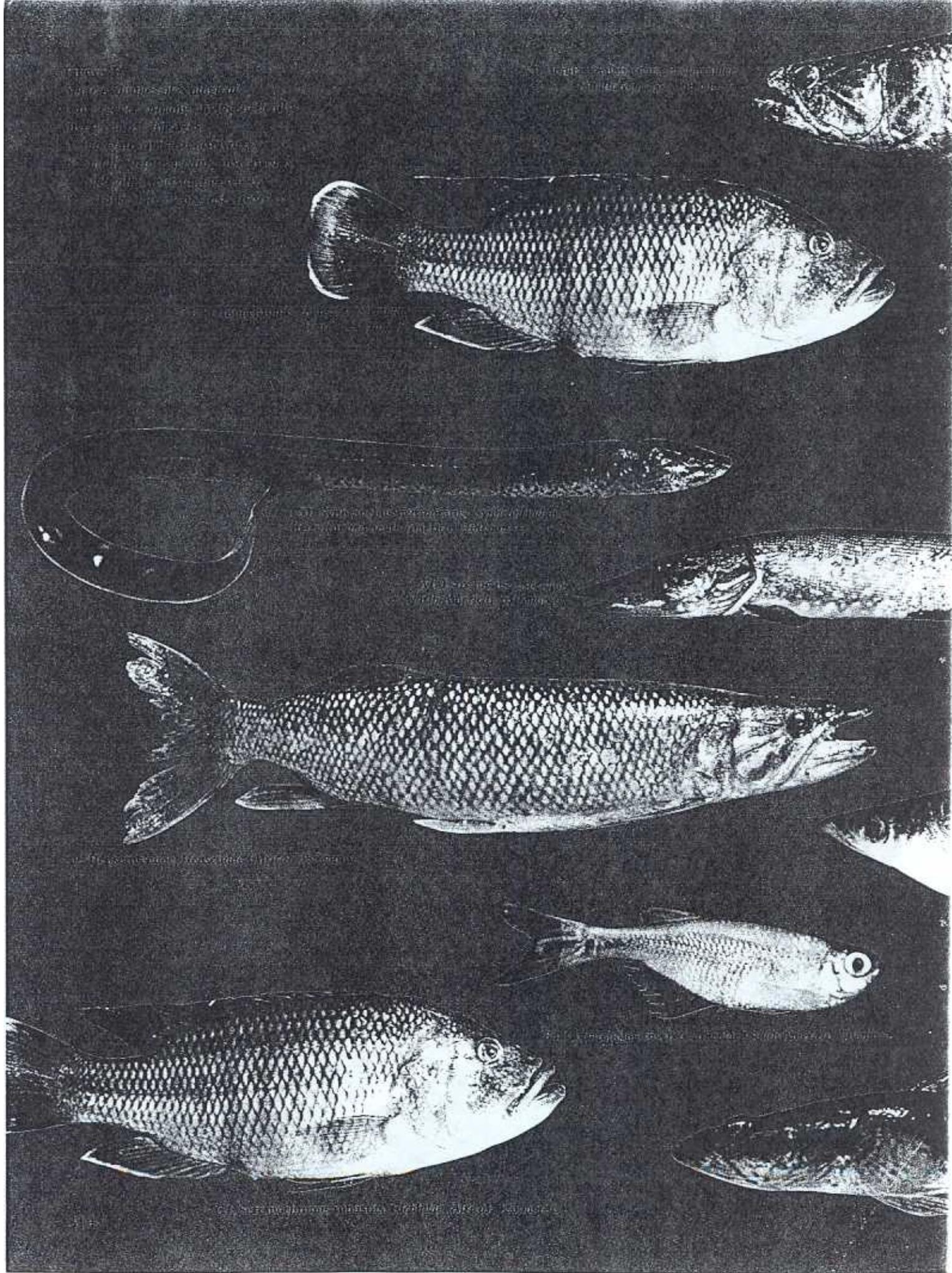
#### MORPHOLOGICAL TRAITS

Morphological measurements were made on specimens deposited in the Texas Natural History Collection of the Texas Memorial Museum, Austin. Three specimens corresponding to adult size-classes (except for *Oncorhynchus* spp.) were measured (to nearest 0.1 mm with vernier calipers, and to the nearest 1 mm with a clear plastic ruler for measures >130.0 mm), and values were later recorded as arithmetic means for each trait and each species. The following morphological features were measured or estimated (detailed explanation of measurements appear in Winemiller<sup>32</sup>): 1) standard length, 2) maximum body depth, 3) maximum body width, 4) caudal peduncle length, 5) caudal peduncle depth, 6) caudal peduncle width, 7) body depth below midline, 8) head length, 9) head depth, 10) eye position, 11) eye diameter, 12) mouth position, 13) mouth width, 14) mouth height, 15) snout length shut, 16) snout length open, 17) dorsal fin height, 18) dorsal fin length, 19) pectoral fin length, 20) pectoral fin height, 21) caudal fin length, 22) caudal fin height, 23) pelvic fin length, 24) anal fin height, 25) anal fin length, 26) pigment code, 27) tooth shape, 28) gill raker, 29) gut length, 30) swim bladder length.

Body length in the multivariate morphological analysis was the maximum standard length recorded for each species at each site (Figure 6). Other linear distance measurements were converted to ratios for use as components of body, head, and fin shape. Ratios employed in the analysis were chosen based on earlier functional interpretations<sup>7,27</sup> and were standardized to yield equal variances before use in comparisons. Standardized ratios served as relatively size-independent dimensions of shape that have

*I am not presenting a detailed analysis of the niche. We used nets to sample within-habitat types (open-water vs vegetation mats) and pool zones (midpool vs pool edge). I directly observed and noted the height at which most individuals of each species swam in the water column. These records allow me to categorize species by predominant habitat with no difficulty.*

CORRESPONDENCE





*Fig. 1. (1) - *Chrysomus (Pezomachus) chrysomus* (Peters), 1844.  
(2) - *Chrysomus (Pezomachus) chrysomus* (Peters), 1844.*

*Fig. 2. (1) - *Chrysomus (Pezomachus) chrysomus* (Peters), 1844.  
(2) - *Chrysomus (Pezomachus) chrysomus* (Peters), 1844.*

*Fig. 3. (1) - *Chrysomus (Pezomachus) chrysomus* (Peters), 1844.  
(2) - *Chrysomus (Pezomachus) chrysomus* (Peters), 1844.*

*Fig. 4. (1) - *Chrysomus (Pezomachus) chrysomus* (Peters), 1844.  
(2) - *Chrysomus (Pezomachus) chrysomus* (Peters), 1844.*

*Fig. 5. (1) - *Chrysomus (Pezomachus) chrysomus* (Peters), 1844.  
(2) - *Chrysomus (Pezomachus) chrysomus* (Peters), 1844.*

*Several studies have failed to detect a strong relationship between morphological traits and ecological performance in fishes and birds. Because resources vary over time, measures of average resource utilization recorded over a long period can result in underestimation of ecological specialization.*

CORRESPONDENCE

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, versus its ability to rest on the substrate in an upright position or slither through dense mats of vegetation). Distances in the vertical dimension were converted to components of shape using body depth as the denominator (e.g., mouth height/body depth). Body width was the denominator for ratios involving peduncle width and mouth width; head length was the denominator for the ratio of eye diameter and snout length; and head depth was the denominator for eye position. Snout length open was divided by snout length to provide a measure of relative mouth protrusibility. The remaining horizontal linear measurements were divided by standard length for use as components of shape.

#### DATA ANALYSIS

Data were transformed to adjust for the influence of differential scale on distance measures. Calculations were performed on transformed morphological data sets approximating a normal distribution, with a mean of 0 and a standard deviation of 1. Principal components analysis was used for inter-assemblage comparisons of species, morphological variation, as well as for identification of patterns of covariance among morphological characteristics relating to ecology. Principal components analysis is a form of multivariate analysis that produces independent orthogonal axes (principal axes) from a multivariate cluster of data points. The first several components (usually the first three or four) identified in the analysis usually model a major portion of the variation among original variables. Principal components analysis was performed on the 160-species data set based on the correlation matrix of standardized morphological variables.

For the entire 160-species data set, a matrix of ecomorphological dissimilarities (Euclidean distances) between species pairs was calculated based on the formula:

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

where  $n$  is the number of attributes, and  $x_{j(i)}$  and  $x_{k(i)}$  are standardized values of the same attribute for the species  $j$  and  $k$ . From each matrix of Euclidean distances, I ranked each species' nearest neighbors from closest (NN1) to most distant (NN159). I also ranked each species' nearest neighbors in terms of their phylogenetic affiliations.

#### CONVERGENCE TEST

No definitive phylogenetic scheme spans the taxonomic breadth of species employed in this study. Figures 2&4 illustrate a hypothesized phylogenetic relationship for the taxa in the data set derived from the 10 assemblages (i.e., both backwater and channel assemblages from each of the five regions). The relationships of higher taxa are based primarily on J. S. Nelson,<sup>18</sup> except for families within the Characiformes and Gymnotiformes, which follow F. Mago<sup>17</sup> for neotropical families and J. Géry<sup>9</sup> for African characiforms. Assignment of genera within families and species within genera follows Mago,<sup>17</sup> D. S. Lee and coworkers,<sup>14</sup> and G. Bell-Cross and J. L. Minshull.<sup>1</sup> For a simple test of the hypothesis of ecomorphological convergence at the species level, I calculated a convergence index for the first- through fifth-nearest ecomorphological neighbors for each of the 160 species. The convergence index was equal to the

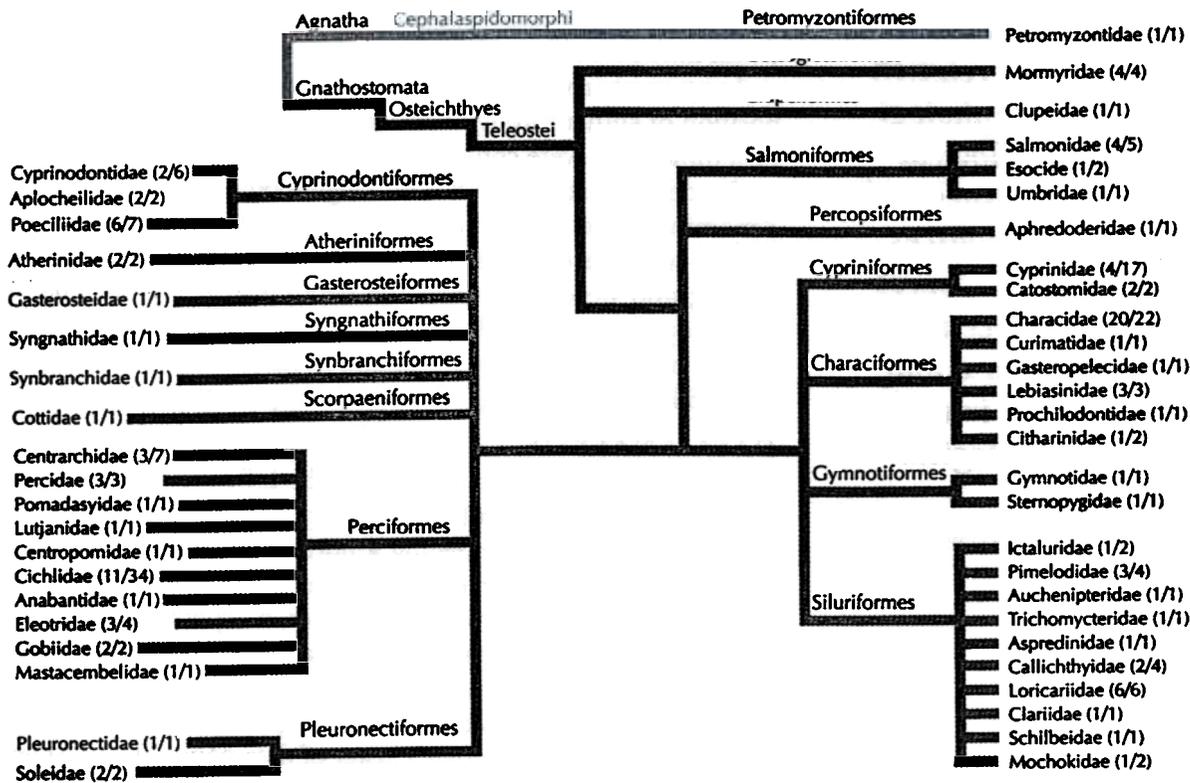


Figure 4. Phylogeny for 160 fish species from Alaska, Texas, Costa Rica, Venezuela, and Zambia used in the morphological analysis of ecological divergence and convergence (higher divisions based on Nelson<sup>18</sup>).

number of closely related species that were actually less similar morphologically to the target species than its morphological nearest neighbor (N) 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 (N/P) was equal to 0 if the nearest neighbor was actually the most closely related taxon, and the index equaled 1.0 if the nearest neighbor was the most distantly related taxon in the entire data set. 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. As a result, the convergence test is very conservative and slightly underestimates the magnitude and frequency of ecological convergences.

### ECOLOGICAL DATA

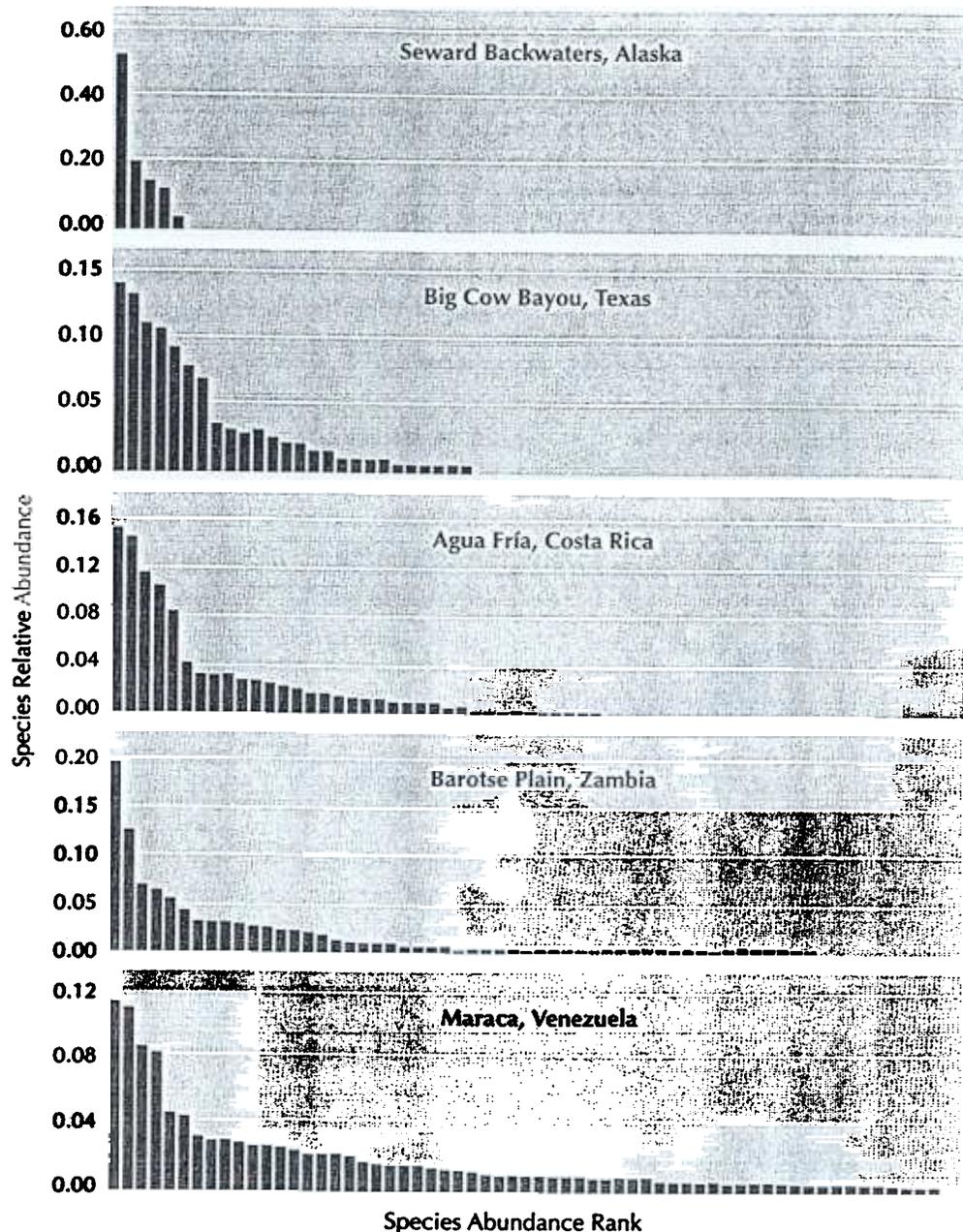
Information on feeding habits of tropical fishes came from earlier long-term studies at the Venezuelan, Costa Rican, and Zambian sites.<sup>29-32</sup> and references therein. Diet was characterized by volumetric analysis of stomach contents based on large samples of formalin-preserved specimens. Those data are summarized here in the form of basic trophic niches: algivore/detritivore, omnivore, invertebrate-feeder, invertebrate/fish-feeder, piscivore. The characterizations of basic trophic niches for Texan and Alaskan fishes were based in part on information in K. D. Carlander.<sup>3,4</sup>

## Results

### ASSEMBLAGE COMPOSITION

Each of the study regions is dominated by different families (Table 1). Salmonids (salmon, grayling, whitefish) are the major components of the

**Figure 5.**  
*Distribution of species numerical relative abundance by rank for five lowland backwater and floodplain fish assemblages.*



Alaskan assemblages, and cyprinids (minnows) and centrarchids (sunfishes) dominate Texan assemblages. In the tropics, cichlids and poeciliids (live-bearers) dominate Costa Rican assemblages; characids (tetras, piranhas) and catfishes (siluriforms) form the largest component of Venezuelan assemblages; and cyprinids and cichlids dominate Zambian assemblages. Within a habitat type (channel or backwater), assemblages show a strong latitudinal gradient in species diversity with the highest diversity occurring in Venezuela.<sup>32</sup> Richness at the genus and family levels also showed strong latitudinal gradients among the five regions, but diversity at the ordinal level was not associated with latitude (Alaska—5 orders, Texas—9 orders, Costa Rica—7 orders, Zambia—6 orders, Venezuela—6 orders).

In all 10 assemblages, distribution of relative abundance among species was strongly skewed in favor of uncommon species (Figure 5). In terms of both individuals and biomass, relatively few species tended to dominate each fish assemblage. With few exceptions, numerically dominant species

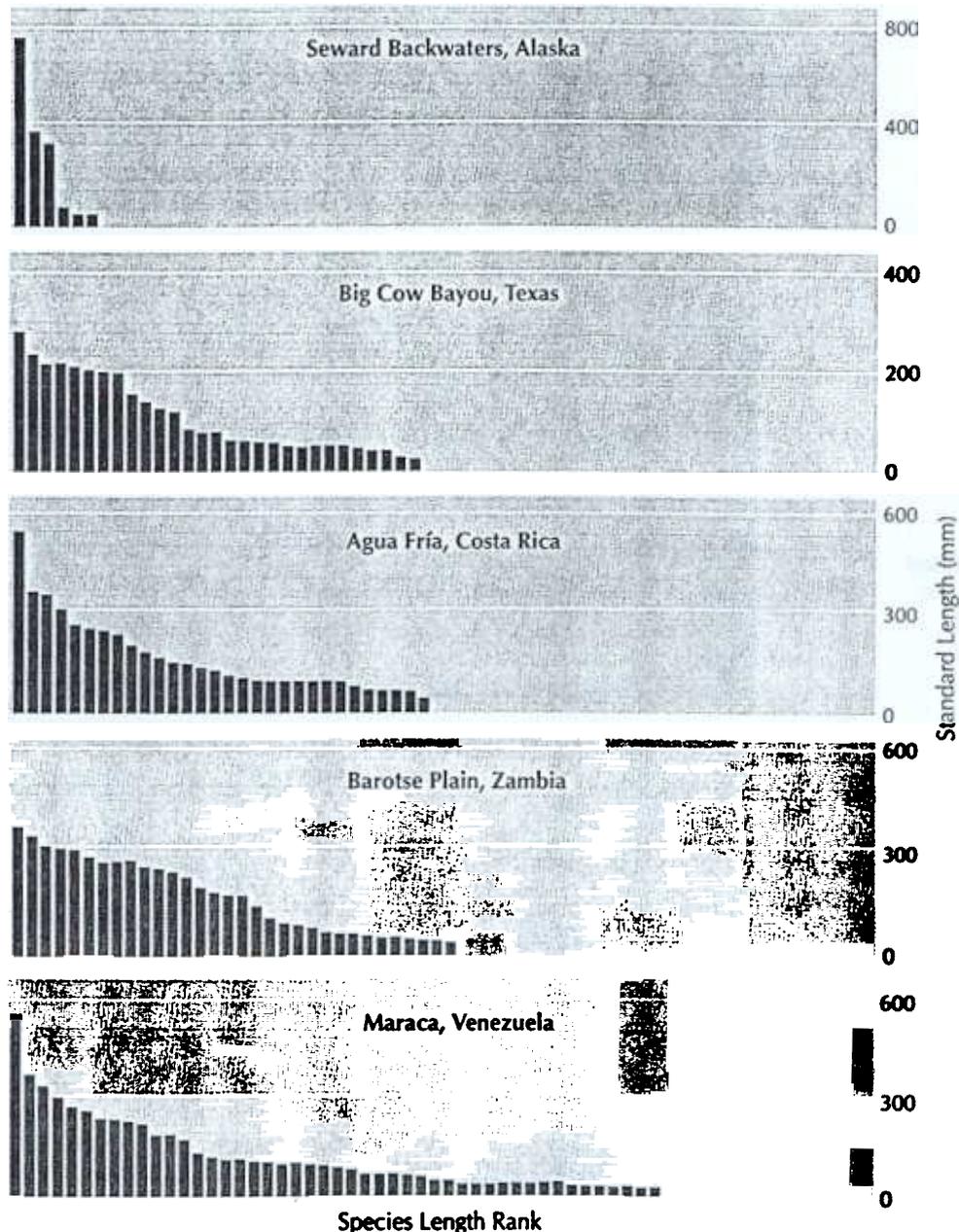
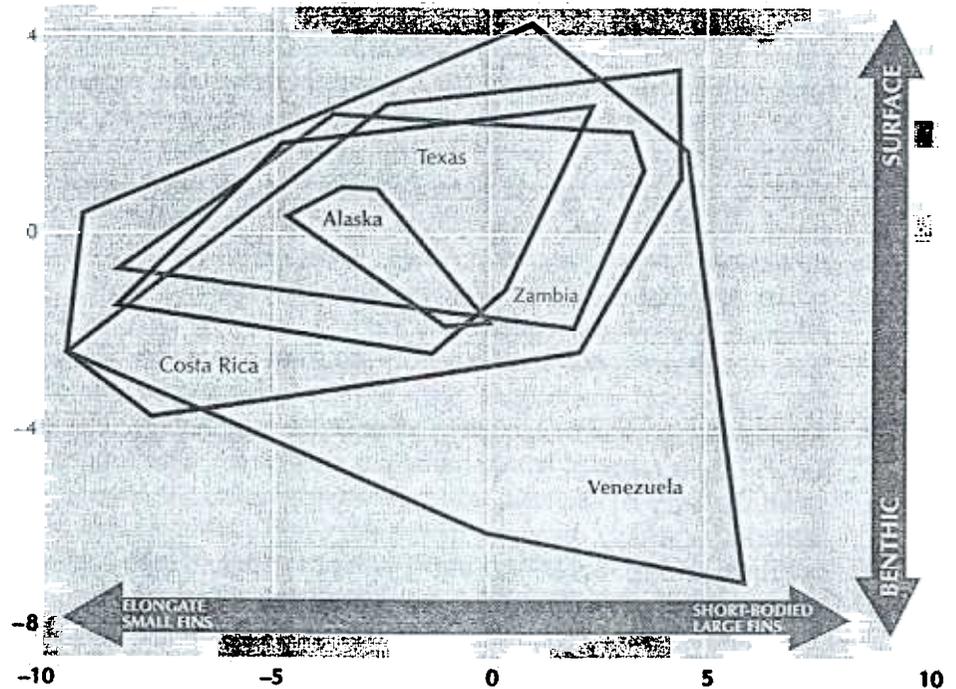


Figure 6. Distribution of species standard lengths by rank for five lowland backwater and floodplain fish assemblages (each species standard length is the maximum recorded among all individuals collected at a site).

fed near the base of the aquatic food web (e.g., detritivores, algivores, granivores, omnivores, planktivores). The predatory northern pike (*Esox lucius*) was the most abundant species in the Alaskan backwater sample. More than for other sites, the relative abundance figures in the Alaskan backwater sample were probably biased to some extent by the collecting methods (dip-netting in shallows, hook and line in depths). The Texas bayou sample was dominated by minnows (*Notropis venustus*, *N. texanus*, *N. volucellus*), mosquitofish (*Gambusia affinis*), and longear sunfish (*Lepomis megalotis*). A tetra (*Astyanax fasciatus*), predatory cichlid (*Cichlasoma loiseliei*), eleotrid (*Eleotris amblyopsis*), and two algivorous live-bearers (*Phallichthys amates*, *Poecilia gilli*) were most numerous in the Costa Rican backwater sample. The Zambian floodplain sample was dominated by a minnow (*Barbus paludinosus*), two catfishes (*Schilbe mystus*, *Synodontis woosnami*), a killifish (*Aplocheilichthys johnstoni*), and two herbivorous cichlids (*Tilapia rendalli*, *T. sparrmani*). The most numerous fish-

**Figure 7.** Results of principal components analysis based on 30 morphological characters and 160 fish species from five lowland backwater fish assemblages. The first PC axis modeled 24% of the total morphological variation (eigenvalue=7.03) and the second axis modeled 14% (eigenvalue= 4.18). Verbal interpretations of the dominant variable loadings appear below the axis labels.



*In highly variable environments, the advantages of a morphological specialization may only be perceived during a very limited period when resources are less abundant, population density is higher, or competitors are more abundant.*

CORRESPONDENCE

es in the Venezuelan swamp included two small characids (*Ctenobrycon spilurus*, *Odontostilbe pulcher*), a mud-feeding curimatid (*Curimata argentea*), a small callichthyid catfish (*Corydoras habrosus*), and an omnivorous cichlid (*Aequidens pulcher*).

#### ECOLOGICAL DIVERGENCE

The shape of species-length distributions (maximum standard length) was similar among backwater sites (Figure 6). Small and intermediate-sized fishes dominated all five assemblages. The average size of fishes did not differ significantly among backwater assemblages, except that Alaskan fishes were larger than fishes from the other four regions.<sup>32</sup> The largest species in the comparative study was the northern pike from the Alaskan assemblage (750 mm). Most of the smallest adult fishes were characids, minnows, and killifishes from the Zambian and Venezuelan systems. The African minnow (*Barbus haasianus*) attained a maximum size of 17.3 mm; the largest specimen of the African killifish (*Aplocheilichthys hutereaui*) was 20.0 mm; and the largest specimen of the benthic citharinid (*Hemigrammocharax machadoi*) was 25.0 mm. Among Venezuelan fishes, the tetra (*Creagrutus* sp.) reaches only 28.0 mm; the catfish (*Corydoras habrosus*) reaches 25.0 mm; and the dwarf cichlid (*Apistogramma hoignei*) attains 30.0 mm. Most these small fishes have short life spans ranging from several months to just over a year. In most instances, these diminutive fishes spawn multiple clutches of only a few to >100 small eggs during the annual spawning period. The largest fishes at all five sites have batch fecundities of tens or hundreds of thousands of eggs and synchronous spawning during relatively short seasons.<sup>29</sup>

Figure 7 summarizes results from principal components analysis of ecomorphological variation in the five backwater fish assemblages. For an extensive statistical analysis of variation in morphological traits associated with ecological performance, see Winemiller.<sup>32</sup> Assemblages containing fewer species at higher latitudes show less morphological variation (i.e., their species cluster near the center of multivariate morphological space in

Figure 7). For the most part, Alaskan fishes have the relatively elongate, fusiform body of habitat generalists.<sup>7</sup> Tropical fishes, and Venezuelan fishes in particular, exhibit a wide spectrum of body shapes (i.e., species are widely scattered with morphological statistical space). Divergent body forms in tropical fishes are often associated with special habitats, subregions within habitats, or specialized modes of locomotion. For example, the eel-like fishes (spiny eel of Africa [*Mastacembelus frenatus*], swamp eel of the neotropics [*Synbranchus marmoratus*], brook lamprey of North America [*Ichthyomyzon gagei*]) are highly adapted for burrowing through bottom sediments and dense mats of vegetation where they forage on benthic insects and crustaceans. With respect to feeding adaptations, most Alaskan fishes possess relatively generalized morphology (e.g., terminal mouth, short rounded snout, numerous small teeth, eyes located midway down the sides of the head, short alimentary canal). In contrast, tropical fishes show widely divergent morphology and a diverse array of feeding specializations including: algae-scraping (e.g., *Hypostomus argus*, Loricariidae, Venezuela); mud-feeding (*Prochilodus mariae*, Prochilodontidae, Venezuela); vascular plant-feeding (*Schizodon isognathus*, Anostomidae, Venezuela); granivory (*Markiana geayi*, Characidae, Venezuela); frugivory (*Brycon guatemalensis*, Characidae, Costa Rica); digging (*Serranochromis codringtoni*, Cichlidae, Zambia); mucus-scraping (*Ochmacanthus alternus*, Trichomycteridae, Venezuela); scale-feeding (*Roeboides dayi*, Characidae, Venezuela); sit-and-wait piscivory (*Hoplias malabaricus*, Hoplerythrinidae, Venezuela); fin-nipping (*Serrasalmus irritans*, Characidae, Venezuela); mutilation piscivory (*Pygocentrus caribe*, Characidae, Venezuela); nocturnal planktivory (*Petrocephalus catostomus*, Mormyridae, Zambia); and piscivory aided by electrosensory physiology (*Gymnotus carapo*, Gymnotidae, Venezuela).

Divergence in feeding behavior and resource usage is seen in the morphology of the pharyngeal mill apparatus of tropical cyprinids and cichlids, and in the tooth morphology of neotropical characids (Figure 8). Much can be inferred about the diet of characids from the shape of their teeth. Omnivores, insectivores, and small granivores have multicuspid teeth for shearing and tearing food items. Large frugivores have multicuspid molariform teeth for crushing and milling. Flat, incisor-like teeth are used for tearing off pieces of aquatic macrophytes and freshwater sponges or for scraping attached algae. Most detritivorous characiforms have microscopic teeth. Piscivorous characids have sharp needle-like teeth for piercing and grasping. Piranhas shear off pieces fish fins or chunks of animal flesh using triangular, razorlike teeth that occlude tightly. Some of the scale-feeding characids (e.g., *Roeboides*, *Exodon* spp.) have external snout teeth used to dislodge scales from other fishes. Similar levels of divergence in tooth morphology are seen in the South American loricariid catfishes and African mochokid catfishes (e.g., specialized dentition used for algae-scraping, omnivory, detritivory, wood-eating, etc.).

Tropical fishes exhibit far greater habitat specialization than do their temperate counterparts even within a particular feeding guild (Figure 9). In the extreme, surface-feeding fishes have horizontal dorsal profiles, upturned (superior) mouths, keeled chests, and wing-like pectoral fins (e.g., *Gephyrocharax valenciae*). Highly mobile benthic feeders tend to have horizontal ventral profiles, convex dorsal profiles, down-turned (inferior) mouths, and small pectoral fins (e.g., *Creagrutus* sp.). Midwater-

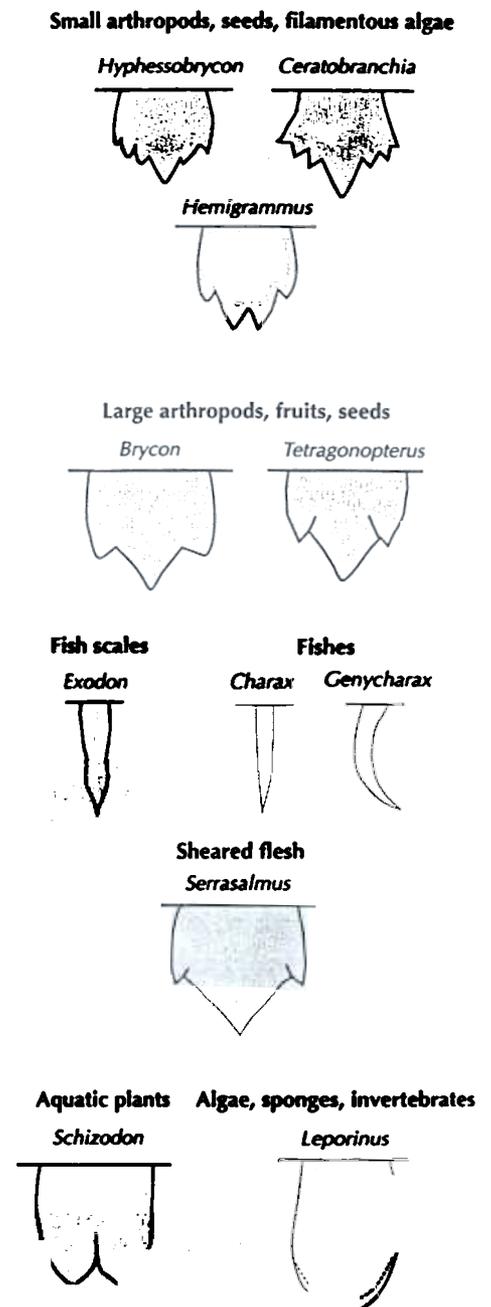
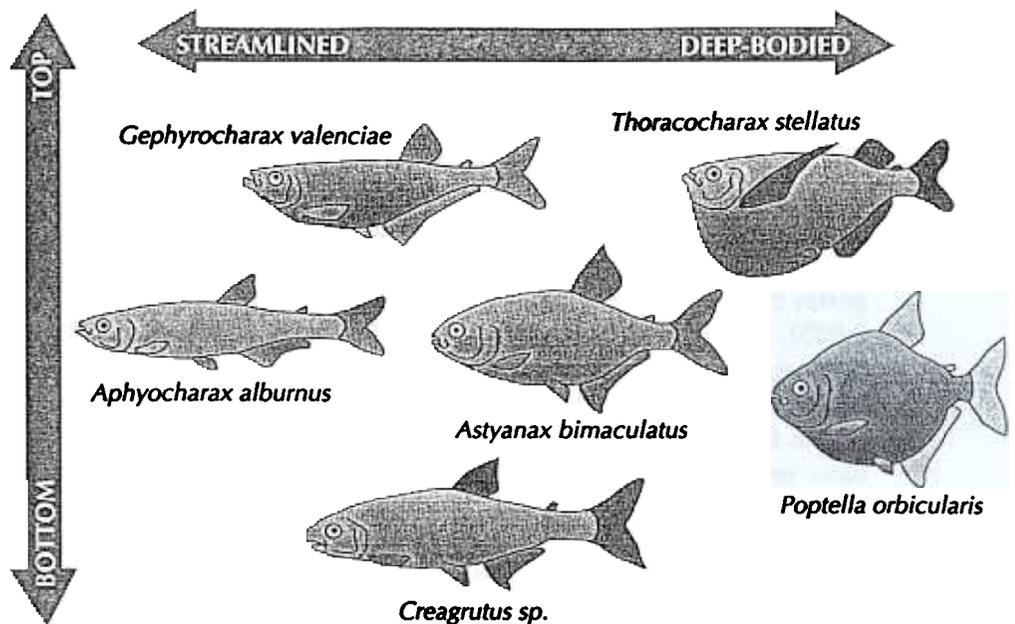


Figure 8. Examples of adaptive divergence in tooth morphology among South American characid and anostomid fishes (Characiformes). DRAWINGS BASED ON GÉRY (1977)

Figure 9.  
Adaptive divergences in body form relative to distribution in the water column and swimming style in small, omnivorous, pool-dwelling characid and gasteropelecid fishes (Characiformes) of South America.



dwellers have fairly symmetrical dorsal and ventral profiles and terminal mouths (e.g., *Astyanax bimaculatus*). Fusiform fishes (e.g., *Aphyocharax alburnus*) are proficient in dashing after food particles that lie several body lengths away; however, they suffer a trade-off in positional stability and ability to perform sharp turning maneuvers. In contrast, deep-bodied fishes (*Metynnis argenteus*) can turn sharply and position themselves in the water column with great accuracy. However, the deep-body morphology carries with it a trade-off in proficiency for rapid straight-line swimming. Extreme forms of the deep-bodied morphology are conspicuous in pelagic fishes of tropical freshwaters, but are essentially nonexistent in pelagic freshwater fishes of the temperate zone. Most of the deep-bodied midwater fishes of the tropics are planktivores or fruit- and seed-eaters. Examples among the neotropical Characidae include the giant pacu (e.g., *Colossoma macropomum*), smaller silver dollars (*Mylossoma*, *Metynnis*, *Myleus* spp.), and tetras (*Tetragonopterus*, *Gymnocorymbus* spp.). During certain times of the year, these fishes compete for seeds, fruits, and terrestrial arthropods that drop or are blown into the water. There is very little aquatic primary and secondary production in the nutrient-poor aquatic systems inhabited by many of these fishes. In such systems, I have observed large schools of *Metynnis* sp. frantically snatching up tiny adult midges that were trapped on the water's surface during the previous night. These feeding frenzies are intense and short-lived as the midges are depleted in a period of several minutes. Similarly, the robust, deep bodies of schooling piranhas (*Pygocentrus* spp.) are well adapted for quick maneuvering at close range during feeding frenzies. In contrast, the long cylindrical bodies of pike-like predators are efficient for swimming by means of brief, rapid bursts along a straight-line trajectory.

I placed each of the species of the five backwater assemblages into five general trophic categories (detritivores/algivores, omnivores, invertebrate-feeders, piscivores, invertebrate-feeders/piscivores) based on dietary data (volumetric proportional usage of general food categories). Species were also assigned to five habitat categories (benthic, epibenthic, midwater, surface, vegetation) based on the field collection records of fishes captured from different habitats and pool zones. The relative frequency of species in

the five trophic categories showed some general similarities across regions (Figure 10). Except for the codominance of invertebrate-feeders and omnivores at the Venezuelan site, invertebrate-feeding was the most common trophic guild irrespective of the region. Algivores/detritivores, piscivores, and species that, as adults, consume a mixture of invertebrates and fishes were also present in all regional assemblages. Nevertheless, there were significant differences in the relative proportions of trophic categories represented in regional fish assemblages ( $\chi^2 = 34.78$ ,  $df= 16$ ;  $p < 0.005$ ). Omnivores (diets consisting of a mixture of algae, seeds, fruits, detritus, insects, crustacea) were just as abundant as invertebrate-feeders in the Venezuelan assemblage yet were entirely absent from the two temperate zone assemblages. Fish assemblages from higher latitudes were more heavily skewed in favor of invertebrate-feeders, whereas trophic categories tended to be more evenly apportioned with decreasing latitude (Figure 10). Habitat categories exhibited fewer interfaunal differences than trophic categories ( $\chi^2 = 12.62$ ,  $df=16$ ,  $p= 0.70$ ). Again, the Venezuelan backwater assemblage tended to have more even distribution of species within the five categories than the high-latitude assemblages. The majority of Alaskan fishes were midwater forms, and none were surface-dwellers. Benthic fishes dominated the Venezuelan swamp assemblage.

### ECOLOGICAL CONVERGENCE

According to the operational definition of ecomorphological convergence (convergence index values ranging from 0 to 1.0), convergence was seen in all five regional assemblages at low frequencies (Figure 11) and was usually not extreme. Most convergence index values were small ( $0 < \text{index value}$

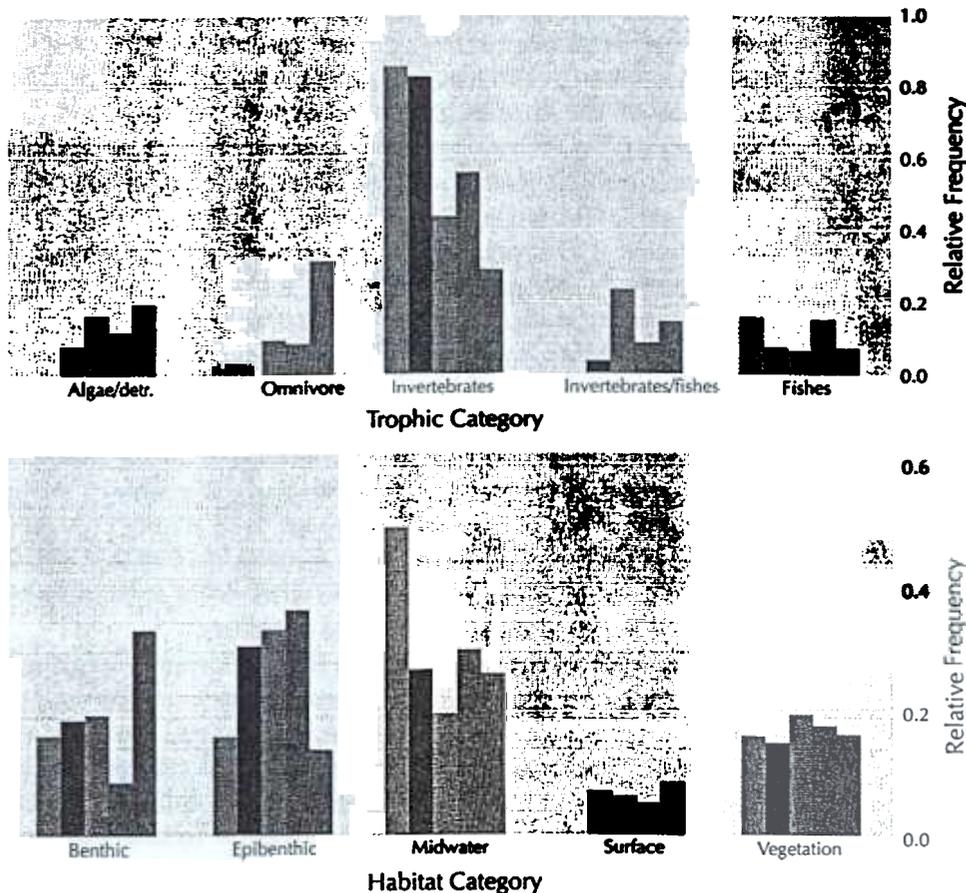


Figure 10. Frequencies of species associated with five general trophic categories (top) and five habitat categories (bottom) for backwater fish assemblages in five biotic regions.

*The ability to shift from a restricted diet to one that incorporates several alternative foods is obviously adaptive when these alternative resources are seasonally abundant.*

CORRESPONDENCE

<0.5), indicating that for the majority of species, the nearest ecomorphological neighbors were actually the most closely related taxa (Figure 3). Yet several species were actually most similar in form to quite distantly related taxa (index value >0.5). Eel-like fishes (*Ichthyomyzon gagei*, *Synbranchus marmoratus*, *Afromastacembelus frenatus*) exhibited extreme convergence (index value ~1.0). The spiny eel, *Afromastacembelus* (Perciformes), is genetically more similar to perches, sunfishes, and cichlids than to other eel-like fishes. The extremely elongate African catfish, *Clarias theodora*, is more similar in morphology and ecology to the eel-like fishes than it is to most other catfishes. A taxonomically diverse group of small, surface-feeding insectivores are ecological equivalents (e.g., *Alfaro cultratus* [Poeciliidae], *Aplocheilichthys johnstoni* [Cyprinodontidae], *Gephyrocharax valenciae* [Characidae]).

A number of instances of extreme ecomorphological convergence were identified even at the family level. Within the family Cichlidae, the large predatory guapote (*Cichlasoma dovii*) was more similar to predatory African cichlids (*Serranochromis macrocephalus* and *S. robustus*) than to more closely related neotropical *Cichlasoma* species (Figure 3). Similarly, the predatory, vegetation-dwelling cichlid *Cichlasoma loisellei* (Costa Rica) was more similar to the African cichlid *Hemichromis elongatus* and the North American sunfish *Lepomis cyanellus* than to most other Central American *Cichlasoma*. Within the Cyprinidae, several African *Barbus* sp. (e.g., *B. paludinosus*) matched most closely with North American *Notropis* sp. (e.g., *N. atrocaudalis*) with similar ecological niches. Numerous other examples of pairwise ecomorphological convergence could be cited among the data that yield the nonzero values in Figure 11. Among Alaskan fishes, extreme instances of convergence with species from other faunas involved the sit-and-wait/stalking piscivore *Esox lucius* (Figure 3). In general, high convergence index values (>0.5) were more frequent among tropical species than temperate species (Figure 11).

## Discussion

.....  
Comparisons among five regional fish assemblages yielded patterns of latitudinal taxonomic diversity that are consistent with most earlier studies involving large groups.<sup>6,8,22</sup> Given the greater number of species in the tropics, it is perhaps not surprising that greater morphological and ecological diversity is observed in tropical fishes than in temperate fishes. In a separate analysis based on the same species, I concluded<sup>32</sup> that the statistical properties of this greater ecomorphological variation in tropical assemblages support an interpretation of evolution in response to deterministic forces. Competition for food resources, either directly or indirectly via microhabitat selection, is probably a major source of natural selection on ecomorphological characteristics in the tropics. Patterns of divergence within the Texan fish assemblage were generally concordant with those observed in tropical fish assemblages, which suggests that deterministic forces are also at work in species-rich temperate faunas.

Compared with tropical faunas, the lesser degree of taxonomic and ecological diversification in temperate faunas most likely results from greater rates of species extirpations in temperate regions on a geological time scale. Most biogeographers agree that the habitat changes associated with the glacial epochs were more severe at higher latitudes. In addition, the

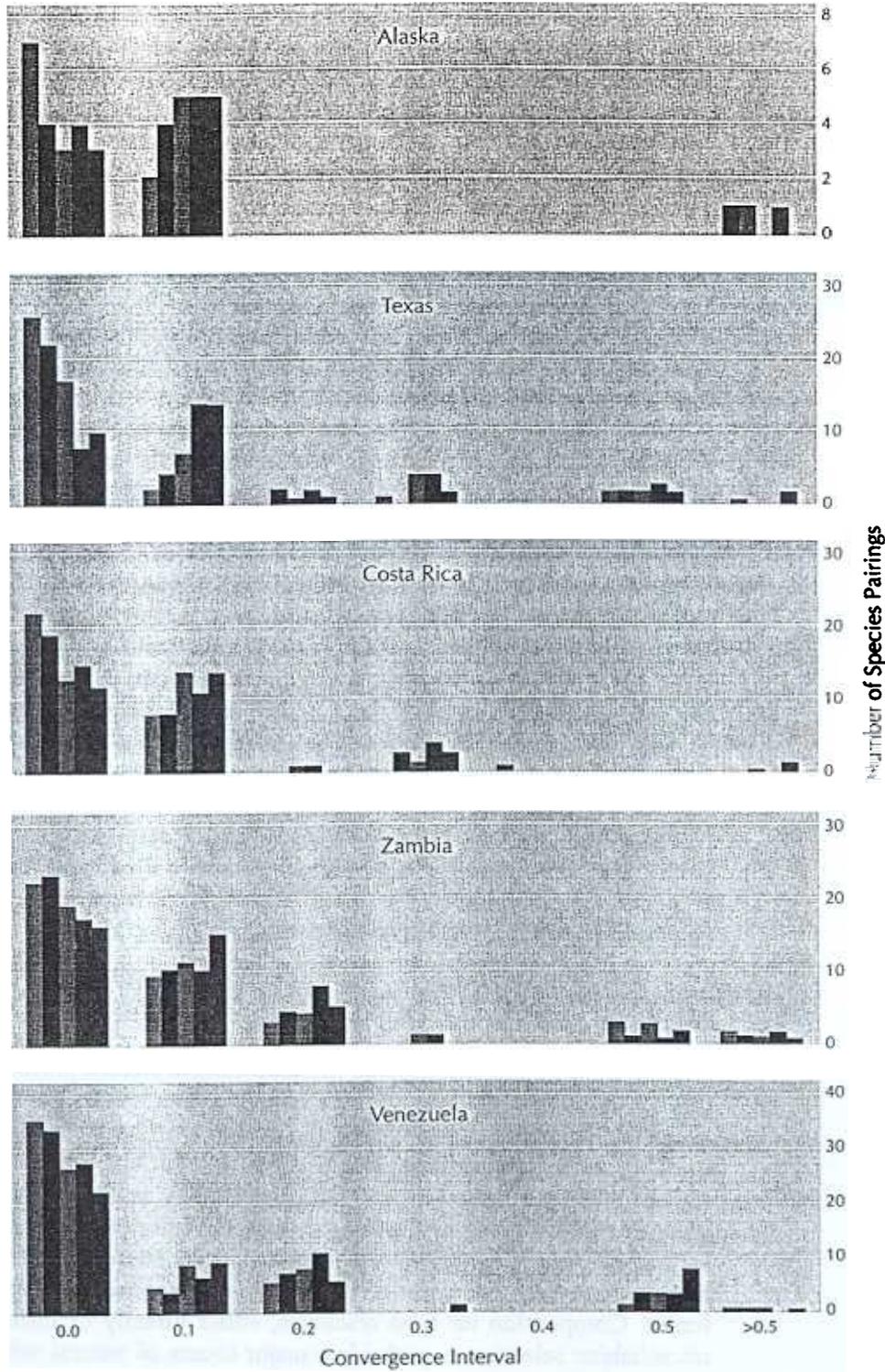


Figure 11. Frequencies of species pairs showing various degrees of ecomorphological convergence based on the relative convergence index. Nonzero convergence values (values are grouped at intervals on the x-axis) indicates that at least one close phylogenetic relative was less similar ecomorphologically than the ecomorphological nearest neighbor. Convergence values >0.2 indicate that >20% of close phylogenetic relatives were less similar ecomorphologically than the nearest neighbor (convergence index defined in text).

seasonal changes in environmental conditions are more extreme at higher latitudes and altitudes, but the ecological and evolutionary implications of these proximate fluctuations can be debated. Seasonal interruptions of density-dependent environmental conditions occur in tropical as well as temperate settings.<sup>29,30</sup> All natural communities are influenced by both biotic density-dependent and abiotic density-independent forces, but the relative influence of each varies greatly from one geographical setting to the next. The analysis of fish ecomorphological patterns<sup>32</sup> supports the

*Just as most fishes continue to grow throughout their lives, ecological performance frequently exhibits major changes over the lifespan. Larval fishes generally feed on zooplankton and other microscopic organisms. We find the greatest morphological diversity and ecological diversity among adult size classes, and that is why I restricted my comparative analysis to adult fishes.*

CORRESPONDENCE

general view that biotic interactions have a greater relative influence on evolution in the tropics than in temperate and polar regions.<sup>5</sup>

Ecomorphological convergence among phylogenetically divergent taxa provides powerful evidence for determinism in the evolution of species traits. If two divergent taxa can be shown to have evolved similar solutions for the same problem in different regions, we gain a measure of confidence in our inferences of adaptive functions and that at some level, a set of universal rules exists for the structuring of natural communities. Reports of convergent traits (e.g., fish electroreception,<sup>12,15</sup> lizard toe fringes<sup>16</sup>) and ecologically equivalent species (e.g., fishes,<sup>24</sup> birds,<sup>10,19,25</sup> lizards<sup>23</sup>) abound in the literature. The phylogenetic foundations for hypotheses of convergence are now receiving greater attention and integration with ecological research.<sup>2</sup> Morphological variation among homologous features at a micro-scale (osteology, musculature, ligaments, etc.) provides systematists with evidence of phylogenetic relationships. When subjected to intense scrutiny, many of these small-scale changes in morphology can be shown to cause significant shifts in ecological function; e.g., G. V. Lauder<sup>13</sup> showed how small morphological changes in neuromuscular physiology result in differences in feeding performance in sunfishes.

The simple convergence index used in this study was designed to identify convergence in basic morphological features related to ecological function. This method requires knowledge of phylogenetic relationships. In practice this is never actually the case, because any phylogeny represents only one of several possible hypotheses of relationship. Evolutionary convergences are recognized when similarities in basic form and function emerge from different (analogous) structural components at the micro-scale. Parallel evolution occurs when two divergent lineages independently evolve the same features in response to similar selective environments. The convergence index cannot distinguish between parallel evolution and evolutionary stasis (lack of morphological differentiation in two independent lineages). As new morphological and biochemical data produce larger and more detailed phylogenies, new methods can be developed to test a variety of evolutionary ecological hypotheses.

This study identified a number of convergent species pairs from different geographical regions. The analysis identified many more instances of partial or weak convergences and numerous species that showed no ecomorphological convergence with species from other assemblages. At the level of the species assemblage, morphological diversification was similar among the three regions of intermediate species diversity. The Alaskan fish assemblage showed very little interspecific variation in ecomorphology, and the speciose Venezuelan assemblage showed greater variation than other sites. As a function of the physics of movement through a fluid medium, basic body shape strongly influences ecological performance. In fishes, variation in body form correlates with variation in swimming behavior and partitioning of space within aquatic habitats. Feeding ecology is correlated with morphological features such as tooth shape, mouth size, and mouth orientation. Tropical fishes from species-rich assemblages display the greatest variety of ecological roles. Finally, some morphological traits are associated with defense against predation (e.g., stout spines, cryptic coloration, mimicry) and reproductive biology (fin filaments, flashy coloration, nuchal humps). Tropical freshwater fishes appear to exhibit far greater diversification than temperate fishes in these features as well.

## REFERENCES

1. Bell-Cross, G.; & Minshull, J. L.: *The Fishes of Zimbabwe*. National Museums and Monuments of Zimbabwe, Harare, Zimbabwe; 1988.
2. Brooks, D. R.; & McLennan, D. A.: *Phylogeny, Ecology, and Behavior*. University of Chicago Press, Chicago, IL; 1991.
3. Carlander, K. D.: *Handbook of Freshwater Fisheries Biology*, vol. 1. Iowa State University Press, Ames; 1969.
4. Carlander, K. D.: *Handbook of Freshwater Fisheries Biology*, vol. 2. Iowa State University Press, Ames; 1977.
5. Dobzhansky, T.: Evolution in the tropics. *American Scientist* 38:209-221; 1950.
6. Douglas, M. E.: An ecomorphological analysis of niche packing and niche dispersion in stream fish clades. Matthews, W. J.; & Heins, D. C., editors: *Community and Evolutionary Ecology of North American Stream Fishes*, 144-149. University of Oklahoma Press, Norman; 1987.
7. Gatz, A. J. Jr.: Ecological morphology of freshwater stream fishes. *Tulane Studies in Zoology and Botany* 21:91-124; 1979.
8. Gatz, A. J. Jr. Community organization in fishes as indicated by morphological features. *Ecology* 60:711-718; 1979.
9. Géry, J.: *Characoids of the World*. TFH Publications, Neptune, NJ; 1977.
10. Karr, J. R.; & James, F. C.: Ecomorphological configurations and convergent evolution in species and communities. Cody, M. L. & Diamond, J. M., editors: *Ecology and Evolution of Communities*, 258-291. Belknap Press of Harvard University, Cambridge, MA; 1975.
11. Keast, A.; & Webb, D.: Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *Journal of the Fisheries Research Board of Canada* 23:1845-1874; 1966.
12. Kirschbaum, F.: Reproduction of weakly electric teleosts: Just another example of convergent development? *Environmental Biology of Fishes* 10:3-14; 1984.
13. Lauder, G. V.: Neuromuscular patterns and the origin of trophic specializations in fishes. *Science* 219:1235-1237; 1983.
14. Lee, D. S.; Gilbert, C. R.; & Hocutt, C. H.: *Atlas of North American Freshwater Fishes*. North Carolina State Museum of Natural History, Raleigh; 1980.
15. Lowe-McConnell, R. H.: *Fish Communities in Tropical Freshwaters: Their Distribution, Ecology, and Evolution*. Longman Press, London; 1975.
16. Luke, C.: Convergent evolution of lizard toe fringes. *Biological Journal of the Linnean Society* 27:1-16; 1986.
17. Mago, F.: *Lista de los Peces de Venezuela*. Oficina Nacional de Pesca, Ministerio de Agricultura y Cria, Caracas, Venezuela; 1970.
18. Nelson, J. S.: *Fishes of the World*, 2nd ed. John Wiley & Sons, New York; 1984.
19. Niemi, G. J.: Patterns of morphological evolution in bird genera of New World and Old World peatlands. *Ecology* 66:1215-1228; 1985.
20. Page, L. M.; & Swofford, D. L.: Morphological correlates of ecological specialization in darters. *Environmental Biology of Fishes* 11:139-159; 1984.
21. Pagel, M. D.; & Harvey, P. H.: Recent developments in the analysis of comparative data. *The Quarterly Review of Biology* 63:413-440; 1988.
22. Pianka, E. R.: Latitudinal gradients in species diversity. *American Naturalist* 100:33-46; 1966.
23. Pianka, E. R.: Some intercontinental comparisons of desert lizards. *National Geographic Research* 1:490-504; 1985.
24. Sazima, I.: Similarities in feeding behavior between some marine and freshwater fishes in two tropical communities. *Journal of Fish Biology* 29:53-65; 1986.
25. Schluter, D.: Tests for similarity and convergence of finch communities. *Ecology* 67:1073-1085; 1986.
26. Watson, D. J.; & Balon, E. K.: Ecomorphological analysis of fish taxocenes in rainforest streams of northern Borneo. *Journal of Fish Biology* 25:371-384; 1984.
27. Webb, P. W.: Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist* 24:107-120; 1984.
28. Wilkramanayake, E. D.: Ecomorphology and biogeography of a tropical stream fish assemblage: Evolution of assemblage structure. *Ecology* 71:1756-1764; 1990.
29. Winemiller, K. O.: Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* 81:225-241; 1989.
30. Winemiller, K. O.: Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* 60:331-367; 1990.
31. Winemiller, K. O.: Comparative ecology of *Serranochromis* species (Teleostei: Cichlidae) in the Upper Zambezi River. *Journal of Fish Biology* 39:617-639; 1991.
32. Winemiller, K. O.: Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecology Monographs* 61:343-365; 1991.
33. Winemiller, K. O.; & Pianka, E. R.: Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60:27-55; 1990.

## ACKNOWLEDGMENTS

Numerous persons assisted in the field collections, and special thanks go to L. Kelso-Winemiller, D.C. Taphorn, L.G. Nico, A. Barbarino, E. Urbina, J. Masinja, G. Milini, Mr. Sinda, W. Ritter, and M. Kelso. L. Kelso-Winemiller has my tremendous gratitude for assisting in measurements of many fish specimens. I thank A. Brenkert for assistance in data management. Institutional support abroad was provided by D.C. Taphorn of la Universidad de los Llanos Occidentales in Venezuela, H. Haug and E. Chamorro of el Servicio de Parques Nacionales de Costa Rica, and E. Muyanga and G. Milindi of the Department of Fisheries of Zambia. Collecting and fishing permits were obtained from la Dirección Administración y Desarrollo Pesquero de la Republica de Venezuela, el Servicio de Parques Nacionales de Costa Rica, the Department of Fisheries and National Commission of Development Planning of the Republic of Zambia, and the Alaska Department of Fish and Game. Fieldwork was funded by the National Geographic Society, Tinker Foundation, NSF Dissertation Grant, and a Fulbright Grant for International Exchange of Scholars. Oak Ridge National Laboratory is managed by Martin Marietta Energy Systems, Inc. under contract DE-AC05-84OR21400 with the U.S. Department of Energy.