Convergent evolution of weakly electric fishes from floodplain habitats in Africa and South America

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Synopsis

An assemblage of seven gymnotiform fishes in Venezuela was compared with an assemblage of six mormyriform fishes in Zambia to test the assumption of convergent evolution in the two groups of very distantly related, weakly electric, noctournal fishes. Both assemblages occur in strongly seasonal floodplain habitats, but the upper Zambezi floodplain in Zambia covers a much larger area. The two assemblages had broad diet overlap but relatively narrow overlap of morphological attributes associated with feeding. The gymnotiform assemblage had greater morphological variation, but mormyriforms had more dietary variation. There was ample evidence of evolutionary convergence based on both morphology and diet, and this was despite the fact that species pairwise morphological similarity and dietary similarity were uncorrelated in this dataset. For the most part, the two groups have diversified in a convergent fashion within the confines of their broader niche as nocturnal invertebrate feeders. Both assemblages contain midwater planktivores, microphagous vegetation-dwellers, macrophagous benthic foragers, and long-snouted benthic probers. The gymnotiform assemblage has one piscivore, a niche not represented in the upper Zambezi mormyriform assemblage, but present in the form of *Mormyrops deliciousus* in the lower Zambezi and many other regions of Africa.

Introduction

It is widely recognized that electrogeneration and electroreception evolved independently in African fishes of the order Mormyriformes (elephant fishes, bottlenoses, stonebashers) and Neotropical fishes of the order Gymnotiformes (cuchillos, or knife-fishes) (Roberts 1972, Lowe-McConnell 1975, Kirschbaum 1984, Marrero & Winemiller 1993). Both groups of tropical freshwater fishes generate weak electric fields that are used for navigation, prey detection, and species and sex identification (Lissman 1963, Hopkins & Bass 1981, Heiligenburg & Bastian 1984). The two phylogentic lineages are very distantly related, with mormyriforms members of an old lineage allied with the bony tongues (infradivision Osteoglossimorpha) and gymnotiforms part of the more recent superorder Ostariophysi (infradivision Euteleostei) that also contains catfishes (Siluriformes) and tetras (Characiformes) (Fink & Fink 1981, Lundberg 1993). This convergent capacity to generate and perceive weak electromagnetic fields should result in convergent ecological niches, and, indeed, both groups are principally nocturnal, benthic, and predaceous on aquatic invertebrates. Both groups tend to be associated with lotic habitats and lentic habitats of river floodplains, and their species richness generally diminishes when rivers are impounded (Corbet 1961, Petr 1968, Balon 1974, Blake 1977, Winemiller 1989).

Recently, Marrero & Winemiller (1993) examined the marked morphological and apparent ecolog-

ical convergence of tube snouted mormyriform and gymnotiform fishes. Two species have independently evolved a highly specialized head morphology that enables the fish to extract benthic insect larvae from tiny holes and crevices in clay nodules and woody debris. We now ask the related question, to what degree do faunas of weakly electric fishes with similar numbers of species from similar habitats show morphological and ecological convergence? Because the two groups occupy the same nocturnal, invertebrate-feeder niche in speciose tropical faunas, one intriguing possibility is that they have evolved similar solutions for foraging and competing. Alternatively, patterns of morphological divergence and resource utilization might be entirely different in the two groups, even when the same number of species occur in very similar habitats in Africa and South America. The latter result is more probable, given the potential influence of differing geological and climatic histories, divergent continental fish faunas, specific differences in resources, and stochastic ecological influences. Here we compare morphological and dietary patterns of mormyriform and gymnotiform faunas from seasonal floodplain habitats. Given that complete (one-for-one) evolutionary convergence at the level of local species assemblages is extremely unlikely, the degree of convergence detected is impressive. We briefly discuss some factors that influence the detection and interpretation of ecological convergence.

Methods

Electric fish assemblages

We define the spatial boundaries of the two local fish assemblages in the following manner: Caño Maraca, a low gradient creek and its associated floodplain in the savanna (llanos) of Venezuela's Portuguesa state (Winemiller 1990); and the Upper Zambezi river and associated floodplain wetlands in the savanna of Zambia's Western Province (Winemiller 1991a). The two sites were chosen for comparison because they have similar aquatic habitats, seasonal hydrology, and numbers of electric
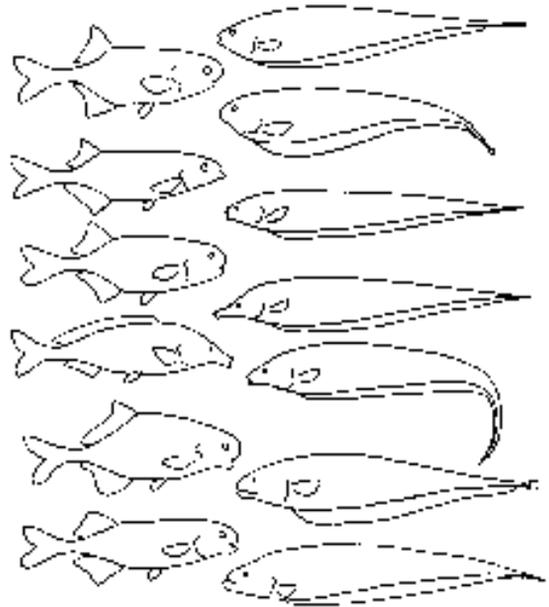

Figure 1. Mormyriform (left column) and gymnotiform (right column) electric fishes from the Zambian and Venezuelan study sites. Left column from top to bottom (all members of the Mormyridae): *Petrocephalus catastoma*, a small midwater swimmer; *Marcusenius macrolepidotus* , a medium size benthic and vegetation forager; *Pollimyrus castelnaui*, a small vegetation-dweller; *Mormyrus lacerda* , a large benthic and vegetation forager; *Hippopotamyrus dischorhynchus* , a medium-size benthic forager; and *Hippopotamyrus ansorgii* , a medium-size benthic forager. Right column from top to bottom: *Eigenmannia virescens* (Sternopygidae), a medium size midwater swimmer; *Adontosternarchus devananzii* (Apteronotidae), a medium-size vegetation dweller; *Brachyhypopomus occidentalis* (Hypopomidae), a medium-size vegetation dweller; *Rhamphichthys marmoratus* (Rhamphichthyidae), a large benthic and vegetation forager; *Sternopygus macrurus* (Sternopygidae), a large benthic forager; *Apteronotus albifrons* (Apteronotidae), a medium-size benthic forager; and *Gymnotus carapo* (Gymnotidae), a large midwater and vegetation forager.

fishes; 7 gymnotiforms from Caño Maraca and 6 mormyriforms from the Upper Zambezi (Figure 1). These similarities notwithstanding, the area of the Upper Zambezi floodplain is vastly greater than that of Caño Maraca. Most sites were sampled multiple times during long-term field studies (Winemiller 1996), and habitat data were recorded (channel width, depth, pH, temperature, etc.). Fishes were collected by a variety of methods, including seines, castnets, dipnets, traps, and gillnets, with the objective of capturing all species present at a site in

Figure 2. Branching diagram illustrating the presumed phylogentic relationships of species included in the study and the integers used as estimates of phylogenetic distance for the convergence index. This phylogeny is based on recent taxonomy (e.g. Daget et al. 1984, Mago-Leccia 1994) and is intended to have low resolution since our primary interest is interfaunal convergence and because new phylogenetic research is likely to alter relationships within orders. For example, a recent analysis of genetic, morphological, and electrophysiological data by Alves-Gomes et al. (1995) removed *Eigenmannia* from the family Sternopygidae and placed it in a clade (suprafamilial) containing *Apteronotus* and *Adontosternarchus*. A similar analysis by Van Der Bank & Kramer (1996) revealed greater phylogenetic divergence between *Hippopotamyrus ansorgii* and *H. discorhynchus* and suggested reinstatement of the latter within the genus *Cyphomyrus*.

numbers that reflected their relative abundances. With the exception of a presumptive second species of *Brachyhypopomus* that is virtually identical to *B. occidentalis* in gross morphology [possibly *H. diazi* listed as *Hypopomus* sp. 2 in Winemiller (1990)], we include all electric species collected at each site, however one of the included species was rare in the Upper Zambezi (*Hippopotamyrus ansorgii*) and two were rare at Caño Maraca (*Apteronotus albifrons, Sternopygus macrurus*).

Phylogenetic relationships

We coded the relative phylogenetic distances between each species pairing in the manner indicated

by the nodes of the phylogeny in Figure 2. Species currently assigned to the same genus were given a distance of 1, species in the same family were given a distance of 2, and species in the same order were given a distance of 3. In this dataset, the most distantly related species were any African mormyrid versus any Neotropical gymnotiform; these pairings were assigned a phylogenetic distance of 4.

Morphological data

Morphological measurements were made on fish specimens catalogued in the Texas Natural History Collection of the Texas Memorial Museum, Austin, Texas. Five specimens of each species were measured, except for *Apternotus* (N = 4), *Rhamphichthys* (4), *Sternopygus* (3), and *H. ansorgii* (1). The body plans of mormyriforms and gymnotiforms are radically different (e.g., gymnotiforms are very elongate, have elongate anal fins, usually lack dorsal fins, and caudal fins are absent or vestigial). Assuming these attributes are directly involved in feeding, we restricted our morphological analysis to anterior morphology and the gut. Eleven head attributes, pectoral fin length, and gut length were examined. Head attributes were maximum head depth, maximum head width, eye position, eye diameter, mouth orientation, mouth aperture orientation, mouth width, mouth height, snout length, gill raker length, and number of gill rakers. Most measurements are described fully in Winemiller (1991b). Mouth orientation is the angle (from horizontal) formed by an imaginary line passing through the center of the eye's pupil and the corner of the mouth where the upper and lower jaws meet. Aperture orientation is the angle (from horizontal) formed by an imaginary line tangent to the anterior tips of the upper and lower jaws when the mouth is closed. All distance measurements were taken as the straight line distance between points using vernier calipers (to nearest 0.1 mm).

Linear distance measures were standardized for size. We standardized linear measurements to conform to the interfaunal grand mean HL ($\bar{X}_{HL}$ = 23.3 mm) using x′ = cx, where c = 23.3/HL. The use of HL standardized linear measurements allows the first orthogonal axis from principal components analysis (PCA) to be interpreted as a shape deter-

minant rather than a body size axis. Since species scores on the PC axes provide the basis for eco-morphological ordination and the calculation of distance measures, the use of HL standardized measurements reduces the likelihood that the analysis is dominated by body size. Based on five adult specimens per species, species mean values were computed for each of the standardized attributes.

Analysis of morphological data
Principal components analysis (PCA) was used as a basis for inter-assemblage comparisons of species distributions in morphological space, and to identify patterns of covariation among morphological characters related to feeding. PCA produces independent orthogonal axes (uncorrelated axes) from the original matrix of data points, such that the first several components model a major portion of the variation among the original variables. PCA was performed on the combined 13 species dataset based on the correlation matrix of morphological attributes ($\log_{10}$-transformed species mean values) and diets ($\log_{10} + 1$-transformed proportions).

Species scores on the PC axes with eigenvalues > 1.0 were used to calculate pairwise Euclidean distances among all species in each dataset. Euclidean distances between species pairs were calculated according to the formula:

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

where n is the number of PC axes with eigenvalues greater than 1.0, and x_{ij} and x_{ik} are the character loadings on the same PC axis for the species pair j and k. From each matrix of Euclidean distances, we ranked each species' nearest neighbors. Mean nearest neighbor distance is an index of assemblage dispersion in morphological space, and the standard deviation of nearest neighbor distance serves as an index of the evenness of species distribution in morphological space (Findley 1973, Ricklefs et al. 1981).

Ecomorphological convergence
We used the following modified version of Winemiller's (1991b, Winemiller et al. 1995) index of eco-morphological convergence:

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

where C_{ij} is the convergence index for species (i) and nearest neighbor (j), R_{ij} is the number of more closely related species that are more dissimilar to species (i) than ecomorphological nearest neighbor (j), M_{ij} is the maximum possible number of species that could be more closely related to species (i) relative to the jth nearest neighbor pairing. The index was calculated from the combined 13 species dataset using nearest neighbor distance (Euclidean distance) as the measure of ecomorphological similarity and Figure 2 as the hypothesis of phylogenetic relationships. The convergence index is equal to 1.0 whenever a phylogenetically distant species is ecomorphologically more similar to the target species than each of the species that are determined to to be more closely related. The convergence index equals 0 whenever a species' closest ecomorphological neighbor is actually the most closely related species in the dataset.

Ecological data
Volumetric proportions of stomachs contents were estimated following the methods in Winemiller (1990). For interfaunal comparisons, diet items were reduced from 160 functional categories (Winemiller 1990) to 13 broad categories. This was done to reduce bias from having different specific resources in the two regions. Stomach contents data were summed across all available size classes within a species, and in most cases, across different seasons. Because larger individuals have greater stomach volumes, the aggregate diet data are very heavily influenced by adult diets. Species' sample sizes for stomach contents appear in the Table 1. Despite the fact that sample sizes for *H. ansorgii, Apteronotus*, and *Sternopygus* were insufficient to achieve highly resolved diet characterizations, we include those data to round out the inter-assemblage comparison of diet.

Analysis of morphological and ecological data
We performed linear regressions on all combinations of morphological traits with diet items, as well as diet Euclidean distances with morphological Euclidean distances, both based on the combined spe-

cies dataset. Due to the small number of species in this dataset (13) relative to the number of morphological and diet variables, we were unable to use canonical correspondence analysis (CCA) to examine the multivariate relationship between the dietary and morphological datasets.

Results

Aquatic invertebrates were the principal food resource for both weakly electric fish assemblages (Table 1). Aquatic dipteran larvae, primarily Chironomidae, were the most important food for 4 of 6 mormyriforms and 3 of 7 gymnotiforms. All 13 species consumed aquatic diptera and vegetation/detritus. None of these fishes have long guts or obvious morphological adaptations for herbivory/detritivory, therefore we conclude that most of the vegetation and detritus was probably debris consumed during suction feeding on benthic and macrophyte-dwelling invertebrates. In numerous instances, vegetative debris was identified as a component of the protective cases constructed by caddisfly larvae, and the volumetric abundances of the diet categories vegetation/detritus and Trichoptera were highly correlated ($r = 0.89$, $p < 0.0001$). Twelve species consumed mayfly nymphs (Ephemeroptera) and aquatic beetles (Coleoptera), and 11 species consumed zooplankton (primarily Cladocera, Copepo-

Table 1. Dietary composition [total volume (ml)] of mormyriform and gymnotiform fishes based on 13 food categories: Veget. = vegetation and detritus; Zoopl. = zooplankton and other microcrustacea; Dipt. = aquatic Diptera larvae; Ephem. = Epehemeroptera nymphs; Odona. = Odonata nymphs; Tricho. = Trichoptera larvae; Hemip. = aquatic Hemiptera; Coleop. = aquatic Coleoptera; Mollus. = molluscs (snails, mussels); Worms = Oligochaeta; Fishes = fishes; Shrimp = shrimp; Terr. Arthrop. = terrestrial arthropods.

| Species Sample size	Veget.	Zoopl.	Dipt.	Ephem.	Odona.	Tricho.	Hemip.	Coleop.	Mollus.	Worms	Fishes	Shrimp	Terr. arthrop.
Mormyriformes:													
Hippopotamyrus ansorgii													
1	0.001	0.002	0.008	0.050	0	0	0	0	0	0	0	0.065	0
Hippopotamyrus dischorhynchus													
40	0.062	0.022	0.650	0.020	0.102	0.611	0.030	0.070	0.196	<0.001	0.009	0	0
Marcusenius macrolepidotus													
92	0.368	0.312	2.679	0.617	0.063	0.497	0	0.022	0.004	0.093	<0.001	0.050	<0.001
Mormyrus lacerda													
120	4.197	0.011	4.666	2.346	1.745	2.825	0	0.030	0.022	0.049	0.046	0.012	0.075
Petrocephalus catostoma													
49	0.013	0.340	0.097	0.013	0.003	0.086	0	0.011	0	0.008	<0.001	0	0
Pollimyrus castelnaui													
61	0.389	0.073	0.741	0.079	0.005	0.065	0	0.001	0	0.003	0	0.025	0
Gymnotiformes:													
Adontosternachus devananzii													
58	0.081	0.945	1.906	0.143	0	0.023	0	0.029	0.003	0.008	0.010	0	0.093
Apteronotus albifrons													
2	0.001	0	0.252	0	0	0	0	0.010	0	0	0	0	0.700
Brachyhypopomus occidentalis													
72	0.030	0.429	0.684	0.119	0	0.004	<0.001	0.082	0	0	<0.001	0	<0.001
Eigenmannia virescens													
138	0.032	2.620	1.136	0.320	0.092	0.056	0.005	0.112	0.001	0	0	0	0.004
Gymnotus carapo													
298	1.846	0.747	2.773	1.538	9.874	0.117	0.278	3.748	2.946	0.111	24.244	9.763	1.729
Rhamphichthys marmoratus													
24	0.481	0.227	1.410	0.129	0.303	0.190	0	0.226	0	0.001	0	0	0
Sternopygus macrurus													
5	0.250	0	0.001	0.001	0.010	0	0	0.460	0.140	0	0	0.070	0
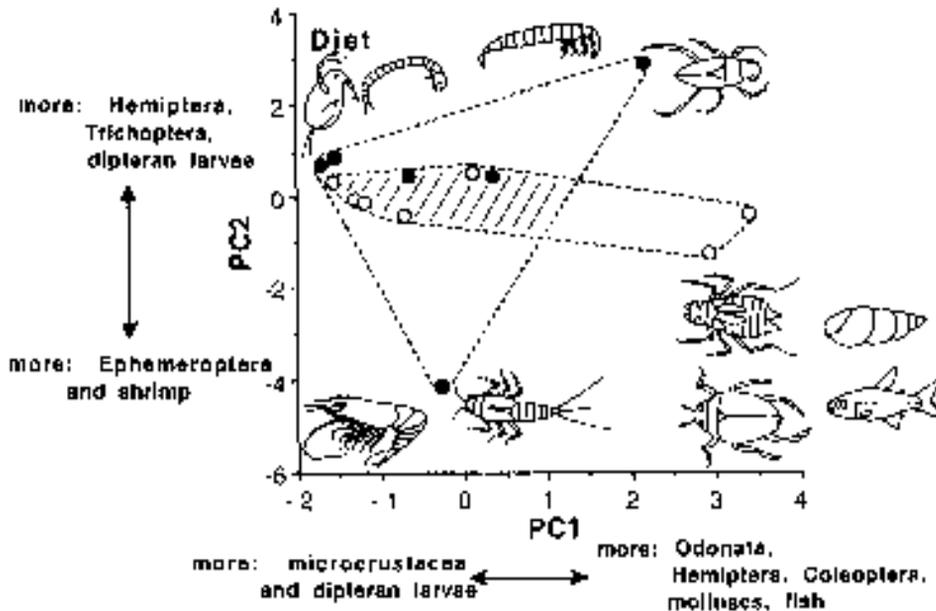
Figure 3. Plot of species scores on the first two PC axes from dietary data. Solid symbols are mormyriforms and open symbols are gymnotiforms.

da and Ostracoda). Because the three species that lacked records for mayflies, beetles, and zooplankton had very small sample sizes, these groups are probably consumed to varying degrees by all weakly electric fishes in these assemblages. Gymnotiforms consumed more terrestrial arthropods than mormyriforms, but terrestrial prey were not major diet components of either assemblage. Fishes were relatively unimportant prey for electric fishes, except for *Gymnotus carapo* which is strongly piscivorous at larger sizes (Winemiller 1989). Correlations between individual diet items and morphological attributes tended to be moderate-low, and only the correlation between mouth height and fish prey was statistically significant ($r = 0.64$, $p < 0.025$).

Species ordination with dietary data (Figure 3) showed a larger area of inter-assemblage overlap on the first two PC axes compared with morphological data. Higher scores on the first PC axis were associated with more Odonata, Hemiptera, Coleoptera, Mollusca and fishes, and less zooplankton/microcrustacea and aquatic Diptera (Table 2). The second PC axis described a continuum of more Hemip-

Table 2. PCA statistics from analysis of mormyriform and gymnotiform diet data.

	PCA axis						
	1	2	3	4	5	6	7
Eigenvalue	3.09	2.45	1.9	1.58	1.31	1.23	0.82
Proportion of variation	0.24	0.19	0.15	0.12	0.10	0.09	0.06
Cumulative variation	0.24	0.43	0.58	0.70	0.80	0.89	0.95

Eigenvectos 1 & 2:

Vegetation	0.19	0.11
Zooplankton	−0.32	0.09
Diptera	−0.35	0.34
Ephemeroptera	−0.14	−0.44
Odonata	0.32	0.06
Trichoptera	0.08	0.45
Hemiptera	0.28	0.31
Coleoptera	0.37	−0.02
Molluscs	0.49	0.14
Worms	−0.24	0.15
Fishes	0.29	−0.15
Shrimp	0.12	−0.55
Terr. arthropods	−0.06	−0.06
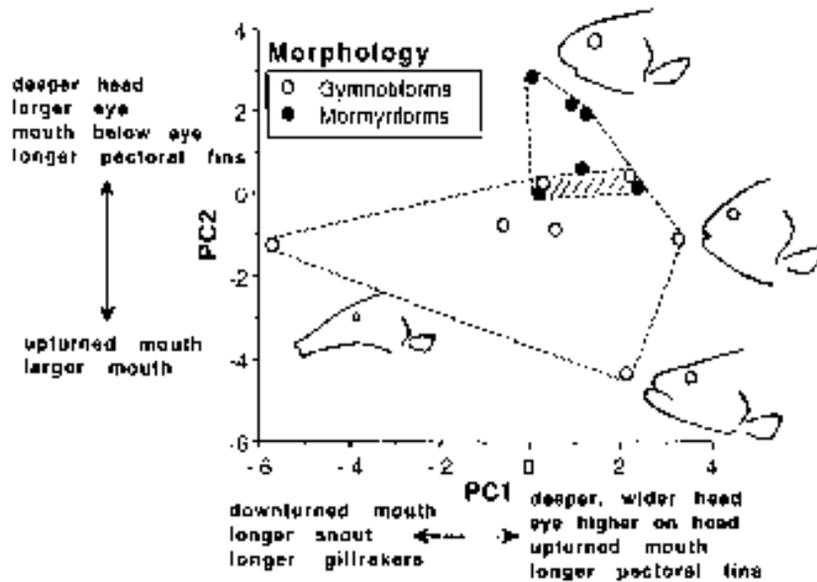
Figure 4. Plot of species scores on the first two PC axes from morphological data (solid symbols = mormyriforms, open symbols = gymnotiforms).

tera, Trichoptera and Diptera, and less Ephemeroptera and shrimp. Two mormyrids (*Petrocephalus, Pollimyrus*) and three gymnotiforms (*Adontosternarchus, Brachyhypopomus, Eigenmannia*) clustered in the region of low scores on axis 1 and intermediate scores on axis 2. *Gymnotus* and *Sternopygus* had highset scores on axis 1. The highest score on diet axis 2 was *Hippopotamyrus discorhynchus*, and *H. ansorgii* was lowest on axis 2. The degree of dietary variation was roughly comparable between the two assemblages, with gymnotiforms varying more along axis 1, and mormyriforms varying more along axis 2 (Figure 3). Based on the mean nearest neighbor Euclidean distances computed from species scores on the first six PC axes, the mormyriform assemblage had a more varied diet (mormyriform = 3.10, gymnotiform mean = 2.33). Based on the standard deviation of nearest neighbor Euclidean distances, the degree of dispersion within diet space was approximately the same (mormyriform = 1.71, gymnotiform = 1.61).

Species ordination by the first two principal components (PC1 and 2) from the morphological analysis showed a relatively small region of overlap between the two assemblages (Figure 4). The first PC axis described a gradient of increasing head depth and width, eyes positioned higher on the head, more upturned mouth, longer pectoral fins, shorter snout, and shorter gill rakers (Table 3). High species

Table 3. PCA statistics from analysis of mormyriform and gymnotiform morphological data.

	PCA axis				
	1	2	3	4	5
Eigenvalue	5.25	3.37	1.22	1.13	0.89
Proportion of variation	0.40	0.26	0.10	0.09	0.07
Cumulative variation	0.40	0.66	0.76	0.85	0.92
Eigenvectors 1 & 2:					
head depth	0.36	0.26			
head width	0.40	−0.09			
eye position	0.31	0.17			
eye diameter	0.25	0.40			
mouth orientation	0.20	−0.39			
aperture orientation	−0.25	0.39			
mouth width	0.30	−0.30			
mouth height	0.33	−0.15			
snouth length	−0.30	−0.15			
pectoral fin length	0.25	0.37			
gill raker length	−0.26	0.01			
number of gill rakers	−0.17	0.19			
gut length	0.01	−0.35			

Figure 5. The distributions of within-fauna and between-fauna species pairings for the first three nearest neighbors based on Euclidean distances with dietary and morphological data.

gradient (lowest score on PC2). Based on the mean nearest neighbor Euclidean distances computed from species scores on the first four PC axes, the gymnotiform assemblage had greater morphological diversity than the mormyriform assemblage (gymnotiform = 3.37, mormyriform = 2.55). Based on the standard deviation of nearest neighbor Euclidean distances, gymnotiforms were more dispersed in morphological space (gymnotiform = 1.00, mormyriform = 0.60).

Despite the fact that virtually no correlation was observed between morphological Euclidean distance and dietary distance (r = 0.045, p < 0.001, based on 156 species pairings), evidence of inter-assemblage convergent evolution was uncovered. Forty six percent of the first nearest neighbors based on diet were inter-assemblage pairings (Figure 5). Inter-assemblage pairings comprised 46% of the second and 54% of the third dietary nearest neighbors. For morphology, 38%, 23% and 38% of the pairings were between assemblages for the first, second, and third nearest neighbors, respectively. Mean (with standard deviation) Euclidean distances for inter-assemblage morphological pairings were 2.67 (1.05), 2.74 (0.52), and 3.89 (1.06) for the first, second, and third nearest neighbors respectively. Mean (SD) distances for intra-assemblage morphological pairings for nearest neighbors one through three were 2.75 (0.67), 3.42 (0.95), and 3.44 (0.73). Mean (SD) Euclidean distances for inter-assemblage dietary pairings were 2.13 (1.47), 3.76 (1.66), and 2.56 (1.32) for the first, second, and third nearest neighbors, respectively. Mean (SD) distances for intra-assemblage dietary pairings for nearest neighbors one through three were 2.69 (1.91), 1.88 (0.80), and 3.89 (1.39).

The mean convergence index was approximately 0.5 for the first dietary neighbor and 0.4 for the nearest morphological neighbor (Figure 6). The mean convergence index ranged between 0.25 and 0.5 for the second and third dietary and morphological neighbors. The following inter-assemblage convergences were identified based on the criterion of having lowest Euclidean distance for the first nearest neighbor based on morphology: *Apternotus* with *H. ansorgii*, *Eigenmannia* with *Marcusenius*, *Rhamphichthys* with *Mormyrus*, and *Sternopygus* with *H.*
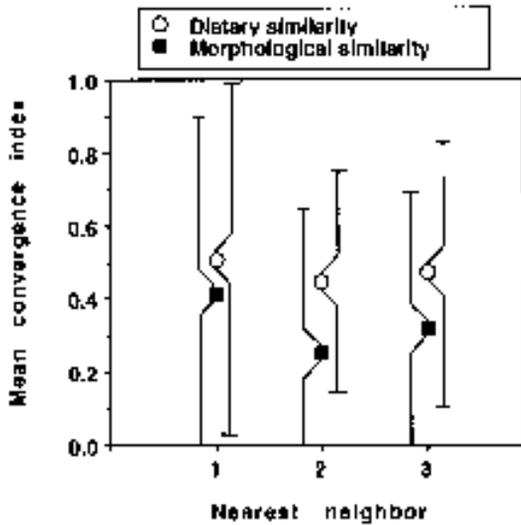
scores on the second axis were associated with a deeper head, larger eyes, a mouth positioned lower on the head, a more downturned mouth aperture, and a smaller mouth. Four extreme morphotypes are illustrated in Figure 4. *Adontosternarchus devananzii* has a deep head, eyes positioned high on the head, an upturned mouth, relatively long pectoral fins, a short snout, and short gill rakers (highest score on PC1); the long snouted *Rhamphichthys marmoratus* is at the opposite end of this morphological gradient (lowest score on PC1). *Petrocephalus catastoma* has a deep head, large eyes, a small mouth low on the head, and relatively long pectoral fins (highest score on PC2); *Gymnotus carapo* has a large mouth, a dorsoventrally compressed head, and lies at the opposite end of this

Figure 6. The mean convergence index (with SD) for the first three nearest neighbors based on dietary and morphological data.

ansorgii. Based on diets, the following inter-assemblage pairings had the lowest distances for the first nearest neighbor: *Brachyhypopomus* with *H. ansorgii, Adontosternarchus* with *Marcusenius, Rhamphichthys* with *Mormyrus, Eigenmannia* with *Petrocephalus,* and *Rhamphichthys* with *Pollimyrus.*

Discussion

The two groups of weakly electric fishes have similar arrays of ecological niches within the broader ecological classification of nocturnal invertebrate foragers. Macrophagous benthic foragers were represented by a single *H. ansorgii* from the Zambian samples and a few individuals of *Apteronotus* and *Sternopygus* from the Venezuelan samples. These fishes were highly convergent in morphology but weakly convergent based on diets. Diet information was based on very small sample sizes for these three species, and larger samples probably would reinforce the hypothesis of convergent evolution. Marrero and Taphorn (1991) listed *Apteronotus albifrons* as feeding on benthic insects, shrimp, and fish. Marrero (1987) found that *Apteronotus bonapartii,* an apternotid with morphology similar to *A. albi-*

frons, ate mostly large benthic mayfly nymphs. At other sites, *Sternopygus* feed on mayflies, odonata and other benthic insects, and very large individuals sometimes eat small fish (Winemiller personal observation; Marrero & Taphorn 1991). Skelton (1993) listed *H. ansorgii* as a benthic insect feeder.

Long-snouted electric fishes probe the substrate (e.g., crevices, leaf litter, vegetation mats) for aquatic invertebrates. One long-snouted fish occurred in each assemblage; *Mormyrus* (mormyriform) and *Rhamphichthys* (gymnotiform) were highly convergent in both morphology and diet. The two long-snouted fishes were also the largest weakly electric species captured from their respective assemblages. Species with more extreme long-snouted ecomorphologies exist in each continental fauna (Marrero & Winemiller 1993), but these species tend to inhabit deeper river channels of the Amazon/Orinoco Rivers and central/west Africa.

Several fishes in each assemblage fed heavily on microcrustaceans and micro-insects, chironomid larvae in particular. Among mormyriforms, *Petrocephalus* tends to be a midwater zooplanktivore (frequently captured by castnet in open water habitats at night), *Pollimyrus* is strictly a microphagus vegetation-dweller, and *Marcusenius* forages for aquatic invertebrates over soft bottom sediments and in dense vegetation. Among gymnotiforms, *Eigenmannia* is the midwater zooplanktivore, *Brachyhypopomus* is the microphagus vegetation-dweller, and *Adontosternarchus devananzii* captures invertebrates from the benthos and vegetation. The coloration of these fishes also shows convergence: *Petrocephalus* and *Eigenmannia* are light (transparent, white, or silvery) and the other four are mottled brown.

Hippopotamyrus discorhynchus was not strongly convergent with any gymnotiform based on morphology, but *Rhamphichthys* was its second dietary nearest neighbor based largely on the common heavy use of aquatic diptera larvae (chironomids). Whereas *Rhamphichthys* probes soft substrates and crevices with its long snout, the bulbous-snouted *H. discorhynchus* apparently forages for chironomid larvae buried in soft sediments (Skelton 1993). *Gymnotus,* the piscivore, was the other species in the dataset that did not show a strong pattern of in-

terfaunal morphological convergence. *Gymnotus*'s second dietary nearest neighbor was *Mormyrus*, and this was largely a function of their large diet breadths. For example, *Gymnotus* fed on every food category, mostly in substantial volumes, and *Mormyrus* fed on every category except aquatic Hemiptera. *Gymnotus* has no piscivorous equivalent among upper Zambezi (i.e., above Victoria Falls) mormyriforms, however *Mormyrops deliciousus* (Mormyridae) is a piscivore that occurs in the middle and lower Zambezi as well as throughout central and western Africa. The head morphologies of *Mormyrops* and *Gymnotus* are very similar (e.g., wide head, large supraterminal mouth), and both species show shifts from juvenile diets that are invertebrate dominated to piscivory as adults (Winemiller 1989, Skelton 1993).

Convergent evolution of ecological attributes is not a dichotomous all-or-none phenomenon, rather it can be identified along a continuum by a variety of methods (Winemiller 1991b, Winemiller et al. 1995). The choice of attributes and quantitative analytical methods can influence results. For example, if measurements of detailed osteological attributes provide the basis for comparisons, then it would be very difficult to identify convergent patterns. In some cases, phylogenetically distant taxa might not even share certain osteological components. We chose to use relatively macro-scale morphological attributes that have inferred relationships to ecological performance, in this instance foraging. Given our methods, the identification of a certain amount of weak or intermediate convergence is to be expected. However, the extent of strong interfaunal convergences observed in this dataset is very significant, and indicates that the two groups of weakly electric fishes somehow have been selected to fill a similar array of ecological niches in their respective floodplain faunas.

Given the evidence for convergent ecomorphology between the two assemblages, the lack of correspondence between morphological distances and dietary distances appears problematic. The missing piece to this ecological puzzle is microhabitat use. Anterior morphology determines not only what can be efficiently eaten by a fish, but also how efficiently it forages in different kinds of microhabitats. We did not have information on foraging frequency in different microhabitats, and this factor might have explained some of the scatter around the regression of morphological and dietary distances. We have already noted how some of the morphologically convergent species pairs forage in similar ways in the same habitats (e.g., substrate probing by long-snouted forms).

Despite the fact that mormyriforms are members of an older lineage, phylogenetic divergence is greater in gymnotiforms (6 families, sensu Mago 1994) than mormyriforms (2 families). The Venezuelan floodplain contained more families (5) and genera (7) of weakly electric fishes than the Zambian floodplain (1 family, 5 genera). Even so, the extent of ecomorphological divergence was similar within the two local fish assemblages, with gymnotiforms having slightly more morphological variation, and mormyriforms having slightly more diet variation. On a continental faunal basis, the two groups probably contain about the same number of species [ca. 200 mormyriforms (Daget et al. 1984); ca. 100 gymnotiforms are described (Mago-Leccia 1994), but new gymnotiforms are being discovered at a much faster rate than new mormyriforms] and show similar ranges of ecomorphological variation associated with a variety of aquatic habitats, including tube-snouted and other benthos-probing insectivores, planktivores, and piscivores. Notable differences do exist; mormyriforms are unique in having species with long lower lip protuberances used for benthic probing (e.g., *Gnathonemus petersi*), and a few large-mouthed, deep-water gymnotiforms seem to have no mormyriform equivalent (e.g. *Apteronotus anas, A. bonapartii*). The South American ichthyofauna contains more species than African fauna, but the resultant potential for more interspecific interactions in the Neotropics seems not to have greatly skewed ecomorphological radiation in the two groups of weakly electric fishes. Likewise, the much smaller Caño Maraca floodplain has more fish species (82) than the upper Zambezi floodplain (68 species, see also Winemiller 1996), yet weakly electric fish species richness and ecomorphological variation are similar. While provocative, the results of this study constitute a sample size of one. To test the generality of the find-

ings and perhaps illuminate factors influencing ecological divergence, convergence, and the formation of local species assemblages, comparisons should be performed for weakly electric fish assemblages from other kinds of aquatic habitats and from floodplain habitats in other areas of Africa and South America.

Acknowledgements

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