



Systematics of *Aphredoderus sayanus* (Teleostei: Aphredoderidae)

Author(s): Jeffrey M. Boltz and Jay R. Stauffer, Jr.

Source: *Copeia*, Feb. 11, 1993, Vol. 1993, No. 1 (Feb. 11, 1993), pp. 81-98

Published by: American Society of Ichthyologists and Herpetologists (ASIH)

Stable URL: <https://www.jstor.org/stable/1446298>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

American Society of Ichthyologists and Herpetologists (ASIH) is collaborating with JSTOR to digitize, preserve and extend access to *Copeia*

Systematics of *Aphredoderus sayanus* (Teleostei: Aphredoderidae)

JEFFREY M. BOLTZ AND JAY R. STAUFFER, JR.

The pirate perch, *Aphredoderus sayanus* (Gilliams), occurs in rivers of the Atlantic and Gulf slopes, the Mississippi Valley, and scattered parts of the eastern Great Lakes Basin in the United States. Populations on the Atlantic Slope have been considered subspecifically distinct from populations in the Mississippi Valley; those from the Gulf of Mexico drainage have been considered intermediate. The subspecies' distributions are believed to be similar to the distributions of subspecies of *Esox americanus* Gmelin (Esocidae). The purpose of this study was to assess geographic variation and the taxonomic status of populations from the three geographic areas.

Twenty-seven characters were examined on 1211 individuals. Many of the characters, when examined separately, exhibited clinal or discordant geographic trends. For the serial elements, the Mississippi Valley populations generally had highest mean values. A lack of correlation with environmental data indicated that most of the clinal patterns were not attributable to environmental conditions. Principal components analysis of meristic data yielded two geographic groups, Atlantic Slope populations and Mississippi Valley populations; Gulf Slope populations were intermediate. For mensural data, analyzed by sheared principal components analysis, there was also no overlap between the Atlantic Slope and Mississippi Valley populations, but the amount that each of these overlapped with the Gulf of Mexico Slope populations increased. *Aphredoderus sayanus*, thus, encompasses two valid subspecies, *Aphredoderus sayanus sayanus* and *Aphredoderus sayanus gibbosus*. *Aphredoderus s. sayanus* occurs on the Atlantic Slope south to the Satilla River, and *A. s. gibbosus* occurs on the Gulf of Mexico Slope west of the Mississippi River, in the Mississippi Valley, and in the Great Lakes. Populations from the Saint Marys River of the Atlantic Slope west to the Pearl River of the Gulf Slope are considered intergrades.

THE pirate perch, *Aphredoderus sayanus*, of the monotypic family Aphredoderidae, inhabits lowland areas of the Atlantic Slope, the Gulf of Mexico Slope (hereafter termed Gulf Slope), the Mississippi Valley, and the Great Lakes (Lee, 1980). Aphredoderidae is one of eight families of freshwater fishes endemic to North America (Berra, 1981).

The cloacal vent of *A. sayanus* moves from the "normal" (i.e., abdominal) position in juveniles to the jugular region in adults (Jordan and Evermann, 1896; Mansueti, 1963). Confusion generated by this ontogenetic migration led systematists to describe the fish as a new species three different times and as a new genus two different times (Jordan, 1877). The original description as *Scolopsis sayanus* was based on three adult specimens collected from a pond near Philadelphia, Pennsylvania, but the unusual position of the vent was not mentioned (Gilliams, 1824).

Original inclusion of the pirate perch in the genus *Scolopsis* was based on presence of a spiny interorbital bone. *Scolopsis* is now known to be-

long to an unrelated family of fishes, Nemipteridae. The pirate perch was removed from *Scolopsis* and placed in *Aphredoderus* by LeSueur (1833), who concurrently described another new species, *Aphredoderus gibbosus*, from Lake Pontchartrain, Louisiana. LeSueur noted that *A. sayanus* and *A. gibbosus* differed with respect to scale size and vent position. Although he recognized the similarities between the two, he did not consider them to be subspecies. Jordan (1877) recognized that the two taxa were probably phylogenetically related, and Jordan and Evermann (1896) demonstrated (1) how close this relationship was, (2) that differences previously observed in the position of the anus were, in fact, correlated with growth, and (3) that the various nominal genera and species were assigned based on these ontogenetic changes. As a result, Jordan and Evermann (1896) considered the groups to belong to a single species, *A. sayanus*.

Despite Jordan and Evermann's (1896) recognition of a single species, *Aphredoderus* has been hypothesized to encompass two distinct

taxonomic units. These have usually been considered subspecies in the literature, despite the recommendation of Bailey et al. (1954) that subspecies not be recognized until complete assessment of geographic variation was performed. Lee (1980) observed that the taxonomic and distributional relationships of the two forms were similar to those of the subspecies of *Esox americanus* (Crossman, 1966). The purpose of this study was to determine the level of geographic variation within *A. sayanus* and to assess subspecies validities and distributions.

MATERIALS AND METHODS

The 1211 specimens examined were obtained from 160 collections distributed among 45 major river drainages or geographic areas (Fig. 1). Museum abbreviations follow Leviton et al. (1985). Analyses included both mature and immature individuals varying in standard length (SL) from 26–86 mm. Mansueti (1963) reported that there is an ontogenetic transformation of the first soft ray to the last spine in the anal fin of the pirate perch; however, because this transformation is completed by the time the fish is approximately 20 mm SL, it should not affect the results of this study.

Twenty-seven meristic and morphometric characters were examined for each individual. In addition, the presence or absence of a lateral pigment band was noted. Radiographs were taken of 12 fishes from each of eight different rivers or geographic areas to determine the number of vertebrae. Measurements were made to the nearest 0.1 mm with dial calipers. Counts and measurements follow Hubbs and Lagler (1964), with the exception of those noted below. Scales above the lateral-line series were counted from the first complete scale row anterior to the dorsal fin to the first scale above the lateral-line series. Caudal-peduncle scales were counted from the first scale row above the lateral-line series to the scale adjacent to the lateral-line series on the opposite side. Dorsal-fin base length was measured from the insertion of the first spine to the insertion of the last ray. Head length and postorbital head length did not include the soft opercular membrane; both were measured to the tip of the spine located on the opercle. Number of scale rows on the caudal fin was taken to be the greatest number of scale rows posterior to the hypural plate. Distance from snout to vent was measured from the tip of the snout to the front of the vent. Distance from the vent to the anal fin was measured from the insertion of the first anal-fin spine to the front of the vent. All measurements

were made point-to-point except caudal peduncle length, for which the plane was measured.

The first portion of the analysis included general descriptive statistics. Mean, range, standard deviation, and coefficient of variation were computed for each variable for each of the 45 river groupings. The morphometric variables were transformed to ratios of either standard length or head length for this part of the analysis. Frequency distributions of each meristic character were also computed for each river grouping. These data are available on request from JMB.

Principal components analysis (PCA) with the correlation matrix factored was used to examine the meristic data. PCA is a valuable and widely used multivariate tool for examining meristic variables for geographic trends (Strauss, 1980; Chernoff et al., 1982; Matthews, 1987).

Sheared PCA with the covariance matrix factored was used to analyze morphometric data. Sheared PCA removes much of the effect of the individual size from the sheared components, reducing problems normally associated with comparing different-sized individuals (Humphries et al., 1981; Bookstein et al., 1985). All statistical analyses were performed using the Statistical Analysis System statistical package (SAS Institute, 1985).

Spatial autocorrelation analysis was performed to identify significant patterns of variation across geographic distance. Distances were computed from the mean latitude and longitude of samples from a given river using a spatial autocorrelation analysis program supplied by Wartenberg (unpubl.).

RESULTS

Overview.—The populations of *A. sayanus* could be divided into three morphological groups: (1) north- and mid-Atlantic Slope; (2) southern Atlantic Slope and eastern Gulf Slope; and (3) western Gulf Slope, Great Lakes, and Mississippi Valley populations. Populations from the north- and mid-Atlantic Slope usually could be identified by having three anal-fin spines, four dorsal-fin spines, 11 pectoral-fin rays, and 36–47 (usually <42) lateral-line scales. Populations from the western Gulf Slope, Great Lakes, and Mississippi Valley were characterized by usually having two anal-fin spines, three dorsal-fin spines, 12 pectoral-fin rays, and 42–56 (usually >45) lateral-line scales. In addition, specimens from the north- and mid-Atlantic Slope had a lateral pigment stripe, whereas those from the Mississippi Valley and Gulf Slope did not. The southern Atlantic Slope and eastern Gulf Slope



Fig. 1. Localities from which specimens of *Aphredoderus sayanus* were examined. The distribution of *Aphredoderus sayanus gibbosus* in the Mississippi River and Great Lakes drainages and of *Aphredoderus sayanus* along the Atlantic Slope are shown. Populations occurring between these distributions are considered intergrades.

populations were intermediate; they usually had two or three anal-fin spines, three dorsal-fin spines, 11 or 12 pectoral-fin spines, and 37–56 (usually 43–48) lateral-line scales.

Meristics.—The specimens exhibited noticeable geographic variation with respect to the following meristic characters: (1) lateral-line scales, (2) scale rows above the lateral line, (3) scale rows

below the lateral line, (4) scale rows on the cheek, (5) caudal-peduncle scales, (6) anal-fin spines, (7) dorsal-fin spines, (8) dorsal-fin rays, and (9) pectoral-fin rays. All of these scale-related characters exhibited similar geographic trends (Table 1), with values for the Atlantic Slope populations typically lower than values for the Gulf Slope or Mississippi Valley populations. On the Atlantic Slope, the lowest values were as-

TABLE 1. DESCRIPTIVE STATISTICS FOR THE SCALE CHARACTERS WHICH EXHIBITED NOTICEABLE GEOGRAPHIC VARIATION.

River code	River or geographic area	Number of coll.	Number of invd.	Lateral row scale			Scale rows above LS			Scale rows below LS			Scale rows cheek			Caudal peduncle scales		
				Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
1	North of Potomac River	6	29	39-49	42.6	2.6	8-11	9.3	0.7	10-15	11.0	1.1	3-4	3.4	0.5	15-19	16.2	0.9
2	Potomac River	4	26	39-47	43.9	2.0	8-10	9.3	0.6	12-16	13.6	1.0	4-6	4.6	0.6	15-17	16.2	0.6
3	York River	2	16	42-46	44.3	1.5	9-12	10.3	0.8	13-16	14.4	1.0	4-5	4.5	0.5	14-18	16.2	1.1
4	James River	1	12	37-44	40.1	2.2	9-10	9.5	0.5	9-12	10.8	1.0	3-4	3.9	0.3	14-16	14.8	0.7
5	Chowan River	3	17	36-46	42.0	2.8	9-12	9.7	0.8	10-14	11.8	1.1	4-5	4.2	0.4	13-16	14.4	0.7
6	Roanoke River	5	21	36-45	40.8	2.2	7-12	9.3	1.2	8-15	11.3	1.4	3-5	3.8	0.5	12-17	14.4	1.3
7	Tar River	4	33	36-48	43.3	2.5	9-12	10.2	0.9	10-14	12.4	1.1	4-5	4.5	0.5	13-16	15.1	0.8
8	Neuse River	3	25	36-47	41.2	2.4	8-12	9.7	1.0	10-15	11.4	1.2	3-5	4.1	0.5	13-17	15.1	0.9
9	Cape Fear River	6	41	36-45	41.7	1.8	7-12	9.7	1.1	8-15	11.6	1.6	3-6	4.2	0.5	12-17	14.8	1.3
10	Peedee River	7	36	37-46	42.2	2.2	7-12	9.1	1.2	8-15	11.4	1.8	3-5	4.2	0.6	13-17	14.4	1.1
11	Santee River	2	14	37-46	40.7	2.8	7-11	8.5	1.4	9-13	10.1	1.4	4-5	4.3	0.5	14-16	14.9	0.9
12	Edisto River	3	19	37-43	40.4	1.7	8-11	9.4	0.7	10-13	10.9	0.9	4-5	4.1	0.3	13-16	14.5	0.7
13	Combahee River	4	32	36-44	40.5	2.2	9-12	9.7	0.8	8-13	10.4	1.1	4-5	4.4	0.5	13-15	14.3	0.8
14	Savannah River	2	18	37-45	42.2	2.7	9-12	10.1	0.9	10-13	10.7	0.8	4-5	4.4	0.5	14-16	14.8	0.8
15	Ogeechee River	3	35	37-47	42.7	2.5	9-13	10.6	1.0	10-15	12.5	1.5	4-5	4.6	0.5	13-17	14.9	1.1
16	Altamaha River	3	17	41-48	44.5	2.1	8-12	10.5	1.1	11-15	13.5	1.3	4-5	4.8	0.4	14-17	15.8	1.0
17	Satilla River	4	26	38-47	41.8	2.6	9-12	10.2	1.0	10-17	12.2	1.6	4-6	4.5	2.0	13-17	14.5	1.1
18	Saint Marys River	3	36	38-48	44.6	2.1	9-14	11.0	1.0	10-15	12.5	1.3	4-6	5.0	0.5	14-17	16.1	0.8
19	Saint Johns River	3	30	42-51	46.2	1.6	8-14	11.0	1.4	9-15	12.1	1.3	3-6	4.9	0.8	14-19	16.9	1.0
20	Withlacoochee River	1	6	45-49	46.8	1.7	10-11	10.7	0.5	12-14	13.2	0.8	4-6	5.3	0.8	16-18	17.3	0.8
21	Suwannee River	7	60	37-49	45.0	2.9	7-13	10.7	1.4	8-16	12.5	2.0	4-6	4.7	0.6	13-18	16.0	1.4
22	Aucilla River	1	8	40-47	43.6	2.7	9-11	10.0	0.5	11-14	12.9	1.0	4-5	4.9	0.4	15-17	16.3	0.7
23	Ochlochonee River	3	27	39-53	46.4	3.6	9-14	11.7	1.3	11-15	13.1	1.1	4-6	5.0	0.4	14-18	16.7	1.0
24	Apalachicola River	7	56	41-54	47.6	3.0	7-14	11.0	1.6	9-16	13.0	1.6	3-7	5.5	0.8	14-18	16.0	0.9
25	Choctawatchie River	1	10	45-53	47.6	2.5	10-13	11.5	1.0	11-14	12.7	1.0	5-6	5.3	0.5	15-17	16.1	0.7
26	Pensacola Bay	5	35	38-52	46.5	4.4	8-14	11.1	1.7	9-17	12.3	2.2	4-7	5.0	0.9	13-19	16.1	1.7
27	Mobile Bay	4	23	42-51	46.0	2.4	10-13	11.4	0.8	10-15	13.0	1.4	4-6	5.0	0.8	14-17	15.7	1.0
28	Pascagula River	3	20	35-50	44.3	2.7	9-13	10.9	1.2	9-14	12.5	1.4	4-6	4.7	0.6	14-18	16.2	1.2
29	Wolf River	1	6	42-47	45.3	2.0	10-12	10.5	0.8	10-13	11.5	1.1	4-5	4.5	0.6	15-17	15.5	0.8
30	Pearl River	1	10	40-46	43.8	1.7	9-11	9.8	0.9	9-14	11.4	1.7	4-5	4.4	0.5	14-17	15.7	0.8
31	Sabine River	1	6	45-52	50.2	3.0	11-13	12.0	0.9	14-17	15.5	1.1	5-6	5.2	0.4	17-19	18.2	0.8
32	Gulf Coast of Texas	5	52	46-56	50.8	2.3	10-14	11.6	1.0	10-16	13.5	1.2	4-6	5.2	0.6	16-20	18.2	1.0
33	Red River	5	58	43-55	48.8	2.3	9-14	11.5	1.1	11-16	13.4	1.2	4-6	5.1	0.5	14-19	17.3	1.1

TABLE 1. CONTINUED.

River code	River or geographic area	Number of coll.	Number of invd.	Lateral row scale			Scale rows above LS			Scale rows below LS			Scale rows cheek			Caudal peduncle scales		
				Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
34	Oachita River	2	20	45-52	49.2	2.0	10-13	11.9	1.0	10-18	14.4	2.2	4-6	5.3	0.8	16-19	17.9	0.9
35	White River	4	15	45-51	48.5	1.9	9-13	11.5	1.1	12-16	13.6	1.0	4-6	4.9	0.5	16-19	17.3	0.9
36	Green River	3	15	43-51	48.0	2.0	11-12	11.7	0.5	11-15	12.9	1.1	4-5	4.2	0.4	15-19	16.9	1.2
37	Ohio River	3	30	45-52	48.8	1.8	10-14	11.8	0.9	12-16	13.1	1.0	3-6	4.8	0.5	16-18	17.3	0.7
38	Middle Mississippi River	13	87	42-54	48.7	2.4	9-14	11.2	1.2	10-15	12.6	1.1	3-6	4.6	0.6	13-19	16.8	1.0
39	Tennessee River	1	14	47-53	49.0	1.8	10-13	11.6	0.9	11-15	13.9	1.4	5-6	5.4	0.5	16-18	17.2	0.7
40	Cumberland River	2	9	47-53	49.8	2.2	10-14	11.2	1.5	10-14	12.2	1.2	4-4	4.0	0	17-21	18.0	1.2
41	Wabash River	4	31	43-53	48.7	2.3	9-14	11.7	1.1	11-15	13.2	1.1	4-5	4.7	0.5	15-18	17.1	0.8
42	Muddy River	3	34	46-55	50.0	2.0	10-14	12.0	0.8	12-16	13.8	1.1	4-6	5.2	0.5	16-19	17.4	0.9
43	Kashaskia River	1	12	45-52	49.5	2.3	10-14	10.9	1.1	11-14	12.3	0.8	4-5	4.4	0.5	15-17	16.4	0.8
44	Illinois River	6	30	45-52	47.9	2.0	10-13	11.3	0.8	11-15	13.2	1.1	4-6	4.9	0.5	16-18	17.4	0.7
45	Great Lakes	6	54	45-54	49.4	2.1	9-13	10.9	1.1	10-16	13.6	1.6	4-6	4.7	0.7	15-18	16.8	0.8

sociated with specimens from the Combahee River of South Carolina (caudal-peduncle scales), the Santee River of South Carolina (scales above and below the lateral line), the James River of Virginia (lateral-line scales), and the area north of the Potomac River (cheek-scale rows). The populations south of the Combahee River on the Atlantic Slope typically yielded higher values than the more northern populations on the Atlantic Slope. Specimens from the Saint Marys and Saint Johns rivers of Florida had particularly high values for the Atlantic Slope (Table 1). Values for the scale counts from the Gulf Slope populations were intermediate to those of the Atlantic Slope and Mississippi Valley populations; however, an east-west cline was evident in this area, the more western populations having the higher values (Table 1). The Sabine River (Texas) and the Texas Gulf Slope populations had the highest values for scale rows above and below the lateral line, lateral-line scales, and caudal-peduncle scales, but the Apalachicola River population (Florida, Georgia, Alabama) had the highest mean number of scale rows on the cheek. In general, the Mississippi Valley populations exhibited consistently higher values for the scale characters.

Two basic patterns of geographic variation were evident in the fin element characters. There was a reduction in number of anal-fin spines from the Atlantic Slope to the Mississippi Valley (Table 2). There were three anal-fin spines in 95.9% of the individuals from the Atlantic Slope, two in 4%, and four in one individual. Compared to the remainder of the Atlantic Slope, the Saint Marys River in Florida had a high proportion (30.6%) of individuals with two anal-fin spines. Eighty-four percent of the individuals from the Gulf Slope had three anal-fin spines, 15.9% had two, and one individual had four. In the Mississippi Valley, only 33.4% of the individuals had three anal-fin spines, 66% had two, and one individual had four. North of the Red River, there was a sharp break in the number of anal-fin spines; populations north of the Red River drainages had a low mean number of anal-fin spines compared to those from the rest of the distribution (Table 2). The number of dorsal-fin spines followed a pattern similar to that for anal-fin spines (Table 2). There were four dorsal-fin spines in 68.1% of the individuals on the Atlantic Slope and three in the remaining 31.9%. Within the Atlantic Slope, all the individuals from the James River and north had four dorsal-fin spines. At the Satilla River, there was a sharp break in the mean number of dorsal-fin spines; individuals to the north typically had four spines, whereas

TABLE 2. DESCRIPTIVE STATISTICS FOR THE FIN ELEMENT CHARACTERS WHICH EXHIBITED GEOGRAPHIC VARIATION.

River* code	Anal-fin spines			Dorsal-fin spines			Dorsal-fin rays			Pectoral-fin rays		
	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
1	3-3	3.0	0	4-4	4.0	0	10-12	11.3	0.6	10-13	11.2	0.7
2	2-3	3.0	0.2	4-4	4.0	0	11-12	11.6	0.5	10-11	10.7	0.5
3	3-3	3.0	0	4-4	4.0	0	11-14	12.1	0.6	10-12	10.7	0.6
4	3-3	3.0	0	4-4	4.0	0	10-12	11.3	0.8	10-12	11.2	0.6
5	3-3	3.0	0	3-4	3.9	0.3	11-12	11.2	0.4	10-11	10.8	0.4
6	3-4	3.1	0.2	3-5	3.9	0.5	8-12	11.3	1.0	10-12	10.9	0.4
7	2-3	3.0	0.2	3-4	3.6	0.5	10-12	11.6	0.6	10-12	11.1	0.6
8	2-3	3.0	0.2	3-4	3.9	0.3	11-12	11.5	0.5	10-11	10.9	0.3
9	3-3	3.0	0	3-4	3.9	0.3	11-13	11.5	0.6	10-12	10.9	0.4
10	3-3	3.0	0	3-4	3.8	0.4	11-13	11.5	0.6	10-13	11.3	0.7
11	3-3	3.0	0	4-4	4.0	0	10-12	10.9	0.6	10-11	10.3	0.5
12	3-3	3.0	0	3-4	3.7	0.5	11-12	11.7	0.5	10-12	10.9	0.4
13	3-3	3.0	0	3-4	3.8	0.4	11-12	11.6	0.5	10-12	11.3	0.6
14	2-3	2.9	0.2	3-4	3.7	0.5	11-12	11.4	0.5	11-13	11.7	0.7
15	2-3	2.9	0.3	3-4	3.4	0.5	11-12	11.6	0.5	10-12	11.1	0.5
16	3-3	3.0	0	3-4	3.4	0.5	11-13	11.6	0.6	10-12	11.3	0.6
17	3-3	3.0	0	3-4	3.7	0.5	11-13	11.8	0.5	10-12	11.2	0.7
18	2-3	2.7	0.5	3-4	3.1	0.3	10-13	11.7	0.7	10-12	11.3	0.5
19	2-3	3.0	0.2	3-3	3.0	0	11-12	11.8	0.4	10-12	11.1	0.5
20	2-3	2.3	0.5	3-4	3.2	0.4	11-11	11.0	0	11-12	11.2	0.4
21	3-4	3.0	0.1	3-4	3.3	0.5	10-13	11.8	0.6	10-12	11.2	0.6
22	2-3	2.6	0.5	3-4	3.1	0.4	11-12	11.5	0.5	10-12	11.1	0.8
23	2-3	2.9	0.4	3-3	3.0	0	11-13	11.9	0.5	10-13	11.6	0.7
24	2-3	3.0	0.2	3-4	3.0	0.2	11-13	11.7	0.5	11-13	11.8	0.7
25	3-3	3.0	0	3-4	3.2	0.4	11-12	11.9	0.3	11-12	11.4	0.5
26	2-3	2.8	0.4	3-3	3.0	0	11-13	12.0	0.5	10-12	11.3	0.6
27	2-3	2.5	0.5	3-4	3.0	0.2	11-14	12.0	0.8	10-13	12.0	0.8
28	2-3	2.8	0.4	3-4	3.1	0.2	10-14	12.0	0.8	11-13	11.0	0.6
29	2-3	2.5	0.6	3-3	3.0	0	12-12	12.0	0	11-12	11.8	0.4
30	2-3	2.7	0.5	3-3	3.0	0	11-12	11.8	0.4	11-12	11.5	0.5
31	2-3	2.5	0.6	3-4	3.2	0.4	12-13	12.3	0.5	11-13	12.2	0.8
32	2-3	2.9	0.3	3-4	3.1	0.3	10-14	12.2	0.7	10-13	11.8	0.6
33	2-3	2.6	0.5	3-4	3.0	0.1	11-14	12.1	0.7	11-13	11.8	0.7
34	2-3	2.1	0.3	3-3	3.0	0	11-13	12.1	0.6	10-13	11.8	0.7
35	2-3	2.3	0.5	3-3	3.0	0	10-13	11.7	0.7	11-13	11.7	0.8
36	2-3	2.1	0.3	3-3	3.0	0	11-13	12.1	0.6	11-13	12.1	0.6
37	2-3	2.2	0.4	3-4	3.0	0.2	11-13	12.2	0.5	9-13	11.8	0.8
38	2-3	2.4	0.5	3-4	3.0	0.1	11-13	12.0	0.5	9-14	11.8	0.7
39	2-3	2.4	0.5	3-3	3.0	0	11-13	11.9	0.6	11-12	11.8	0.4
40	2-3	2.3	0.5	3-3	3.0	0	12-13	12.1	0.3	11-12	11.7	0.5
41	2-3	2.5	0.5	3-4	3.0	0.2	11-13	12.0	0.6	11-13	11.8	0.6
42	2-3	2.6	0.5	3-4	3.1	0.3	12-13	12.4	0.5	11-13	12.2	0.6
43	2-3	2.3	0.5	3-3	3.0	0	11-13	12.2	0.6	11-12	11.6	0.5
44	1-3	2.2	0.5	3-3	3.0	0	11-13	11.9	0.5	11-13	11.9	0.6
45	2-3	2.1	0.3	3-4	3.1	0.3	11-13	12.2	0.6	11-13	12.2	0.7

* See Table 1 for definition of river codes.

individuals to the south primarily had three spines (Table 2). On the Gulf Slope, 89.3% of the individuals had three dorsal-fin spines; the remaining 10.7% had four. In the Mississippi Valley, 97.3% of the individuals had three dorsal-fin spines; the remaining 2.7% had four spines. From these data, it is evident that the

populations from the Satilla River and north had a much higher proportion of individuals with four dorsal-fin spines than did the other populations.

Another cline is distinguished by an increase in the number of dorsal-fin and pectoral-fin rays from the Atlantic Slope to the Mississippi Valley

(Table 2). Within the Atlantic Slope, there was a slight north-south increase in the numbers of both dorsal-fin and pectoral-fin rays, with the lowest mean count for each occurring in the Santee River population. Values for the Gulf Slope populations were intermediate to those for the Atlantic Slope and Mississippi Valley populations. Within the Gulf Slope populations, there was an east-west increase in the mean number of dorsal-fin and pectoral-fin rays. The highest mean dorsal-fin ray number occurred in the Muddy River (Illinois) population; the highest mean pectoral-fin ray number occurred in the Great Lakes population. Within the Mississippi Valley populations, the mean values for both characters were consistently high. When dorsal-fin rays and dorsal-fin spines are added to give total dorsal-fin elements, the patterns observed when they were viewed separately collapse. In the case of total elements, the mean values for the Atlantic Slope and Mississippi Valley were similar. The addition of a ray in the Mississippi Valley made up for the corresponding loss of a spine. The mean values for dorsal-fin elements for the Gulf Slope were slightly lower than those for the other regions.

With such a large data set ($n = 1211$), it is very difficult to interpret multivariate ordination when the data from all individuals are included in the analysis. Therefore, the following meristic analysis was conducted using character means for the 45 major river groupings.

For many of the rivers, the sample consisted of specimens from more than one collection made at various times. Several authors have discussed the importance of including a temporal component in geographic variation studies (Gould and Johnston, 1972; Endler, 1977). The stability of morphometric and meristic data is a function of the amount of plasticity of a character and the ease with which a character is influenced by the environment (Chernoff, 1982). Several studies have indicated that differences among populations are not stable (Vogt and Jameson, 1970; Sokal et al., 1971). Although this idea is difficult to test directly when specimens are difficult to obtain, as in the case of the pirate perch, inferences can still be made. Several of the collections examined in this study are separated by 40 years. Nevertheless, specimens from these rivers cluster together; differences observed among the geographic areas are, thus, apparently stable (Boltz, 1988).

Chernoff et al. (1982) indicated that before using the character means in PCA for the a priori groups (rivers, in this case), it is desirable to know whether individuals from at least some of the a priori groups can be distinguished from

each other. Adopting the approach of Chernoff et al. (1982) and Matthews (1987), two sets of five river systems each were randomly selected from the 45 river systems, the only constraint being that each of the three major geographic groups be represented in each set. For both sets, PCA completely separated all individuals of at least some river systems from those of other systems (Figs. 2–3). On the scatterplot of the first and second PCA scores for all individuals from the first set of rivers (Fig. 2), the following river pairs were completely separated: White-York, White-Neuse, White-Savannah, Choctawatchie-Savannah, and Choctawatchie-Neuse; almost complete separation existed for the Choctawatchie-York and Savannah-York pairs. In the second set of rivers (Fig. 3), complete separation occurred between the following river pairs: Potomac-Cumberland, Potomac-Ouachita; almost complete separation was found for Cumberland-Satilla, and Ouachita-Satilla. Within river groups, there was character variation (e.g., Satilla, Mobile Bay), but these randomly selected rivers illustrated that most individuals from some rivers can be separated from each other by PCA of meristic characters.

A plot of PC-I versus PC-II of character means for individual river groupings was prepared (Fig. 4). Characters that loaded strongly (>0.80) on PC-I were pectoral-fin rays, scales along lateral-line series, scale rows above lateral-line series, scale rows below lateral-line series, caudal-peduncle scales, dorsal-fin spines, and dorsal-fin rays (Table 3). The Atlantic Slope and Mississippi Valley populations were completely separated in multivariate space; the Gulf Slope populations were intermediate in position.

Morphometrics.—Five morphometric variables, expressed as percent head length or percent standard length, exhibited noticeable geographic variation: (1) head depth, (2) postorbital head length, (3) orbit length, (4) body depth, and (5) caudal-peduncle depth (Table 4). Head depth was consistently high for Atlantic Slope populations north of and including the Peedee River. Head depths for other Atlantic Slope populations were variable but similar to values for the Gulf Slope and Mississippi Valley populations. Values for postorbital head length were consistently greater for the Green River (Kentucky) population and for populations further north in the Mississippi Valley than for populations found elsewhere (Table 4). The Gulf Slope and Atlantic Slope populations had similar values for postorbital head length, but the values for the Gulf Slope populations were extremely variable. Orbit length was consistently

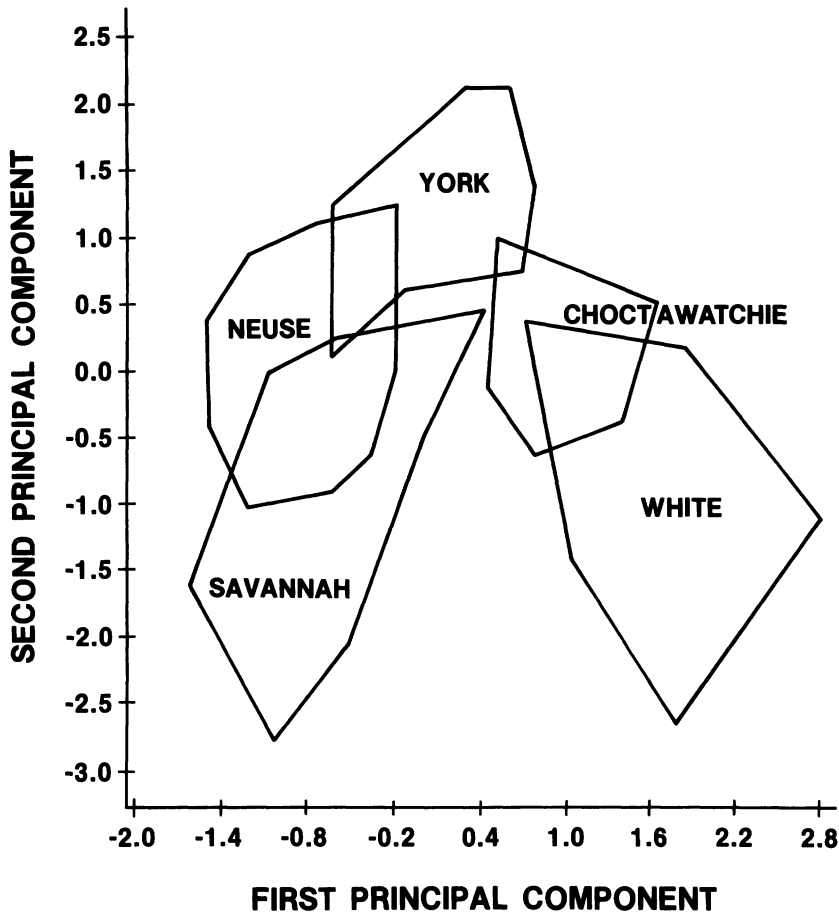


Fig. 2. Plot of the first and second principal components from five randomly selected populations of *Aphredoderus sayanus*, derived from principal components analysis of the meristic characters.

shorter in specimens from Mississippi Valley populations from the Green River and north than for other populations. The small eye size of populations from the upper Mississippi Valley probably accounted for the long postorbital head length (above) for the same populations. Body depth was greatest in populations from the Mississippi Valley and the northern parts of the Atlantic Slope. Mean body depths of the Gulf Slope populations were clearly smaller than those of the Mississippi Valley and Atlantic Slope populations. The Santee River population had a small caudal-peduncle depth when compared to populations in all other rivers; caudal-peduncle depths for populations throughout the remainder of the distribution were variable but similar to each other.

Mean values for the morphometric characters were not used for the computation of sheared PCA because the shearing procedure accounts for the difference in the sizes of individuals both within and among the a priori

groups (rivers). The factor patterns resulting from this analysis are listed in Table 5. Because all scatterplots of the sheared components with the meristic components were created using the mean sheared PCA score for each river group, it is possible to plot the first sheared component against the first meristic component (Fig. 5); such a plot should, and in this case does, best distinguish the groups (Humphries et al., 1981). The Atlantic Slope populations were completely separated from the Mississippi Valley populations; the Gulf Slope populations were intermediate.

Character variability.—The mean meristic and morphometric coefficients of variation (CV) were computed for each river system by adding the values of coefficients of variation for all meristic or mensural characters and dividing by the number of characters. The mean meristic CV does not include the value for scale rows on the caudal fin. These CV values were much

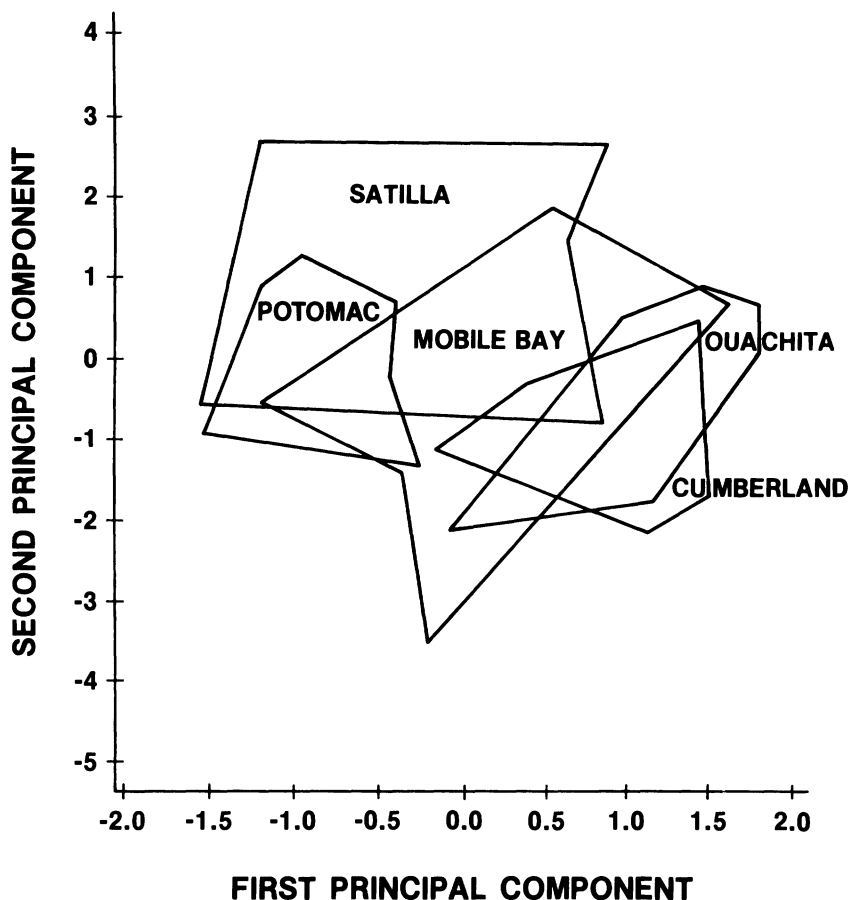


Fig. 3. Plot of the first and second principal components from five randomly selected populations of *Aphredoderus sayanus* derived from principal components analysis of the meristic characters.

higher than the values for the other characters and would greatly inflate the mean. The mean morphometric CV did not include vent-anal fin or snout-vent length because these characters were highly allometric. The only obvious trend in the values for the meristic CV was a tendency for Gulf Slope populations to have higher values than did populations from other areas (Boltz, 1988). Within each geographic region, however, there was a great deal of variation in the magnitudes of the CV. With two exceptions, the CV values for the mensural characters were consistent throughout the different geographic areas. Populations from the Saint Marys River on the Atlantic Slope to the Choctawatchie River (Florida) on the Gulf Slope and from the Wolf River (Mississippi) west to the Brazos River (Texas) on the Gulf Slope had consistently lower CV values than did populations from other geographic regions (Boltz, 1988).

Pigmentation.—Coloration and pigmentation patterns are important in recognizing and de-

lineating both species and subspecies in many groups of fishes (Behnke, 1972; Baltz and Moyle, 1981; Stauffer, 1988). In *A. sayanus*, individuals from the Atlantic Slope possessed a distinctive pigmentation pattern: they had a lateral pigment stripe extending from just anterior to the anal-fin origin to just anterior to the caudal fin (Fig. 6). This lateral pigment stripe was never present in Gulf Slope or Mississippi Valley populations. This lateral stripe had not been reported previously in the literature, although the specimen drawn in Eddy and Underhill (1974) bears one. The lateral stripe was most prominent in the mid-Atlantic Slope populations; its intensity lessened to the north and south, and it may have even become sufficiently faded as to be difficult to discern, particularly south of the Satilla River. This series of transitions from a prominent stripe to a diffuse stripe, to a total lack of stripe followed the pattern of sharp breaks in other characters such as lateral-line scales and dorsal-fin spines. The manifestation of the stripe appeared not to be associated with

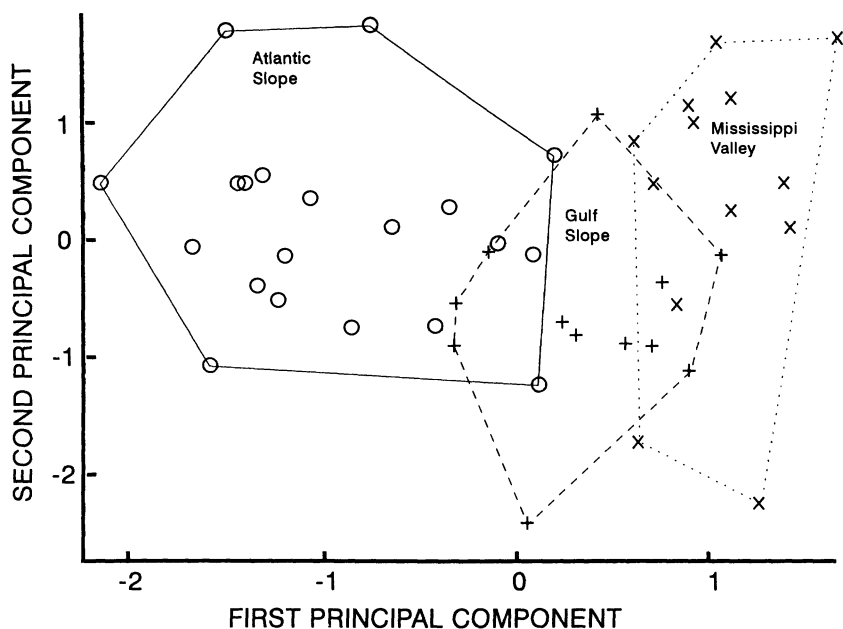


Fig. 4. Plot of the first and second principal components derived from principal components analysis of *Aphredoderus sayanus* using mean values for the meristic characters. 0 = Atlantic Slope; + = Gulf Slope; × = Mississippi Valley.

TABLE 3. CHARACTER LOADINGS FOR THE FIRST THREE PRINCIPAL COMPONENTS RESULTING FROM THE PRINCIPAL COMPONENT ANALYSES OF THE MERISTIC CHARACTERS OF *Aphredoderus sayanus*. Variance explained by each factor: factor 1–52.5%, factor 2–10.5%; factor 3–9.0%.

Character	Factor pattern		
	Factor 1	Factor 2	Factor 3
Anal-fin spines	-0.739	-0.042	0.416
Anal-fin rays	0.346	0.691	0.378
Pelvic-fin rays	0.030	0.710	0.113
Pectoral-fin rays	0.823	-0.003	-0.181
Caudal-fin rays	-0.086	-0.062	-0.392
Scales along lateral series	0.947	0.036	-0.169
Scale rows above lateral series	0.955	-0.021	0.042
Scale rows below lateral series	0.807	0.121	0.216
Scale rows on cheek	0.724	-0.166	0.283
Caudal-peduncle scales	0.861	0.079	-0.256
Scale rows on caudal fin	0.420	-0.512	0.643
Dorsal-fin spines	-0.877	0.234	0.094
Dorsal-fin rays	0.819	0.083	0.074

sex or season. Overall pigmentation of preserved specimens varied greatly within each geographic region with individuals varying from dark to light.

DISCUSSION

Environmental conditions have been shown to affect the phenotypes of many fishes. Barlow (1961) described trends that would be expected to result from temperature or other environmental gradients. Temperature during development has been shown to affect the phenotype of rainbow trout (Macgregor and MacCrimmon, 1977), cisco species (Todd et al., 1981), minnows and sunfishes (Hubbs, 1922), red wing blackbirds (James, 1983), Pacific tree frogs (Calhoun and Jameson, 1970), and a ceratopogonid fly species (Atchley, 1971), among others. It is important to determine whether the observed differences in pirate perch phenotype are potentially products of environmental conditions.

Fishes such as *A. sayanus* that have a “U-shaped” geographic distribution (Fig. 1) are potentially important in the study of the effect of environmental parameters (particularly temperature) on the morphology of a species. Both the Atlantic Slope and Mississippi Valley populations of *A. sayanus* have north-south distributions that span a wide temperature range. If

TABLE 4. DESCRIPTIVE STATISTICS FOR THE MENSURAL CHARACTERS WHICH EXHIBITED NOTICEABLE GEOGRAPHIC VARIATION.

River ^a code	Head ^b depth		Postorbital ^b head length		Orbit ^b length		Body ^c depth		Caudal ^c peduncle depth	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
1	49-87	65.7	40-48	45.1	24-34	28.9	31-40	34.8	16-21	18.8
2	56-73	65.0	42-49	45.5	23-31	28.0	29-35	32.8	17-22	20.7
3	57-67	62.6	44-49	46.6	22-31	26.5	30-35	33.0	18-22	20.1
4	56-71	63.7	41-46	44.5	25-29	27.5	27-30	29.1	21-24	21.7
5	48-75	57.6	29-47	43.7	21-31	28.2	27-32	30.3	18-26	21.3
6	55-76	66.6	42-49	45.9	23-31	26.5	28-33	31.5	13-23	20.4
7	51-70	61.5	40-56	43.7	24-32	27.3	26-32	29.5	17-23	20.9
8	54-72	61.4	42-50	44.7	25-31	28.1	29-33	31.0	18-24	21.3
9	45-98	61.5	41-50	44.9	23-33	26.7	28-34	31.4	16-24	21.3
10	51-83	64.7	42-48	44.9	21-30	25.8	26-36	31.0	17-24	20.7
11	47-66	53.9	40-45	42.9	25-33	28.1	29-34	32.4	12-23	15.6
12	50-70	62.1	41-47	44.0	28-31	29.1	28-32	30.4	18-23	20.8
13	50-65	58.0	42-48	45.1	23-30	27.2	27-35	31.1	17-24	20.9
14	48-64	55.4	39-45	42.9	24-37	30.5	29-34	31.1	18-22	20.0
15	50-67	59.8	38-92	45.3	22-30	25.7	27-35	30.5	17-23	20.1
16	50-64	56.3	39-48	44.9	24-32	28.7	27-31	30.0	17-22	20.2
17	53-68	60.1	40-47	43.6	24-34	29.3	26-30	28.3	17-24	21.3
18	50-66	57.7	42-49	45.8	24-33	28.4	26-33	29.5	16-22	19.5
19	42-60	53.8	42-49	46.4	23-30	27.1	26-31	28.4	16-22	19.2
20	54-60	58.2	45-49	47.7	24-28	26.2	27-31	29.3	18-21	19.8
21	45-71	57.3	41-48	44.6	24-32	29.4	26-34	28.8	17-24	20.4
22	57-67	61.4	41-43	42.8	30-33	31.6	29-32	30.5	19-21	19.8
23	51-69	59.6	40-50	43.9	27-37	30.9	27-31	29.1	10-23	20.2
24	49-78	60.0	37-46	42.1	25-36	30.0	24-34	29.7	16-24	21.1
25	54-64	59.4	36-45	41.1	28-35	32.8	26-30	28.0	17-22	20.2
26	50-77	60.5	38-48	42.4	25-36	29.9	25-34	29.7	17-24	21.0
27	51-69	62.7	43-97	50.1	22-50	25.6	30-35	32.8	16-22	20.4
28	48-78	57.1	40-62	44.7	24-38	28.1	27-36	30.7	18-23	20.2
29	51-48	55.8	42-46	44.0	26-30	28.7	29-31	30.5	17-20	19.2
30	51-61	56.8	44-46	45.7	23-27	25.6	27-31	29.8	16-21	19.6
31	55-56	60.0	44-48	46.3	25-30	28.6	28-32	30.1	19-22	21.7
32	49-61	57.6	42-50	45.8	22-31	26.3	25-31	28.0	17-23	20.7
33	47-60	53.7	40-49	45.5	22-31	26.4	21-33	29.2	17-23	20.3
34	40-69	53.3	42-48	44.6	26-31	28.1	26-31	29.5	17-22	21.1
35	50-69	56.2	43-48	45.7	24-32	28.1	28-34	30.4	17-22	20.4
36	50-62	56.0	43-52	47.6	21-30	24.9	28-32	30.1	18-23	20.6
37	47-80	58.8	44-63	48.2	22-38	25.2	29-33	31.3	18-23	20.9
38	43-64	54.8	42-52	46.5	21-30	26.2	27-35	30.4	15-24	20.4
39	51-60	58.8	45-50	48.2	22-29	25.3	30-34	31.6	18-23	20.6
40	52-71	61.1	41-46	45.5	21-25	23.7	29-34	31.6	17-21	19.4
41	49-70	61.4	44-50	47.0	21-30	25.4	28-33	31.1	18-24	21.0
42	46-66	58.4	44-50	47.0	21-28	24.7	28-34	31.2	17-23	20.3
43	43-57	52.9	45-48	47.0	23-27	25.4	28-31	29.7	18-22	20.4
44	42-69	62.2	43-49	46.3	22-31	26.5	30-35	33.0	17-24	20.6
45	43-70	58.4	43-49	46.8	20-29	23.7	23-36	32.5	19-26	22.0

^a See Table 1 for definition of river codes.

^b Expressed as percent head length.

^c Expressed as percent standard length.

the observed differences in morphology resulted from environmental factors alone, the patterns of morphological variation should follow north-south environmental gradients both in eastern and western areas. To determine whether or not environmental and physical pa-

rameters affected the observed phenotypes, Spearman's correlation coefficients were calculated for all characters examined in the analysis, as well as for the first meristic component and for several environmental and physical variables (latitude; longitude; mean air temperature

TABLE 5. CHARACTER LOADINGS OF THE MENSURAL CHARACTERS ON THE FIRST THREE COMPONENTS RESULTING FROM SHEARED PRINCIPAL COMPONENTS ANALYSIS OF *Aphredoderus sayanus*.

Character	Size	Sheared		Unsheared	
		PC-2	PC-3	PC-2	PC-3
Standard length	0.261	0.011	-0.072	0.013	-0.073
Head length	0.249	0.051	0.057	0.054	0.056
Head depth	0.258	-0.008	0.474	-0.006	0.473
Body depth	0.279	0.053	0.309	0.056	0.308
Anal fin to vent	0.412	-0.710	0.112	-0.706	0.111
Snout to vent	0.165	0.624	0.077	0.626	0.076
Orbit length	0.173	-0.109	-0.174	-0.108	-0.174
Caudal peduncle depth	0.306	0.197	0.238	0.200	0.237
Interorbital length	0.252	0.108	0.075	0.111	0.074
Caudal-peduncle length	0.250	0.095	-0.489	0.097	-0.490
Pelvic-fin length	0.256	-0.013	-0.342	-0.010	-0.342
Pectoral-fin length	0.271	0.036	-0.381	0.039	-0.382
Dorsal-fin base length	0.263	0.105	-0.193	0.108	-0.194
Postorbital head length	0.265	0.129	0.149	0.131	0.148

in Jan., April, July, and Oct.; mean annual temperature; mean annual precipitation; and elevation). For each locality from which fishes were examined, latitude and longitude were recorded to the nearest half degree, and values for the environmental and physical variables of interest were obtained from the nearest station listed in the Climatic Atlas of the United States (U.S. Department of Commerce, 1985).

We initially examined the correlations using all localities from which fishes were examined. No strong (>0.6) correlations resulted from any of the possible combinations, or from separate examinations of the Atlantic Slope, Gulf Slope, and Mississippi Valley populations. We then plotted the first meristic principal component against mean latitude and longitude (for all collection sites within a river) for the 45 river

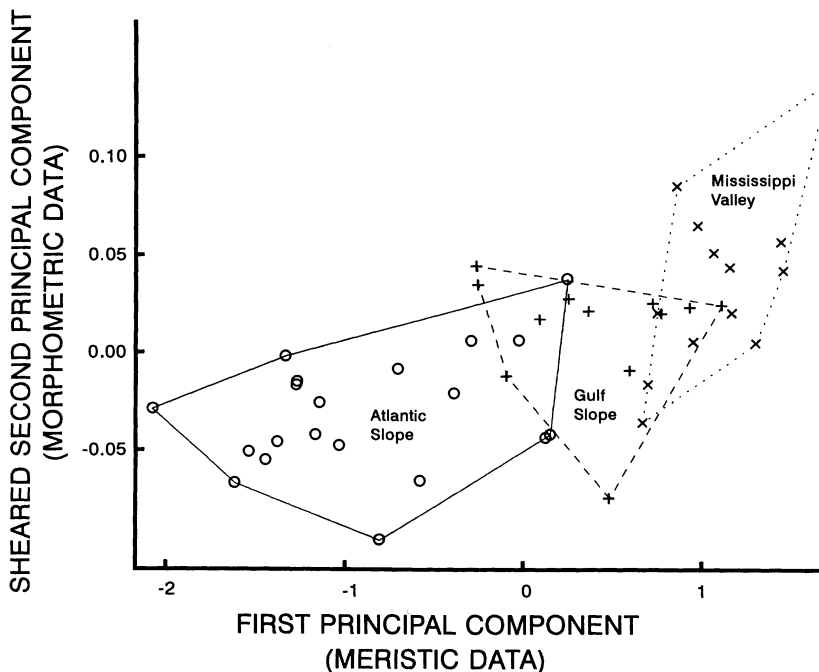


Fig. 5. Plot of the first sheared principal component and the first meristic component of *Aphredoderus sayanus* 0 = Atlantic Slope; + = Gulf Slope; x = Mississippi Valley.

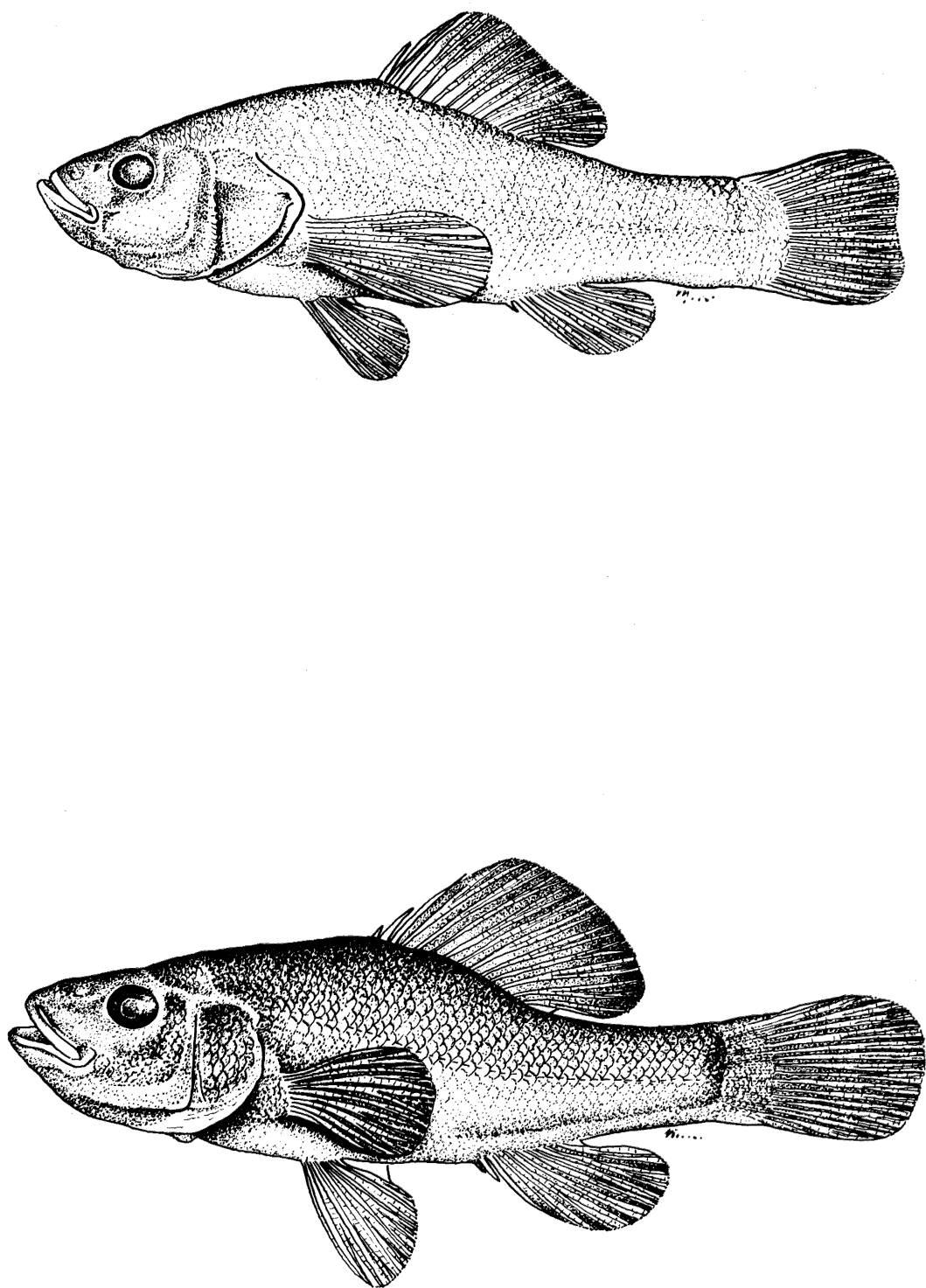


Fig. 6. Illustration of the difference in pigmentation patterns of Mississippi Valley (top) and Atlantic Slope (bottom) specimens.

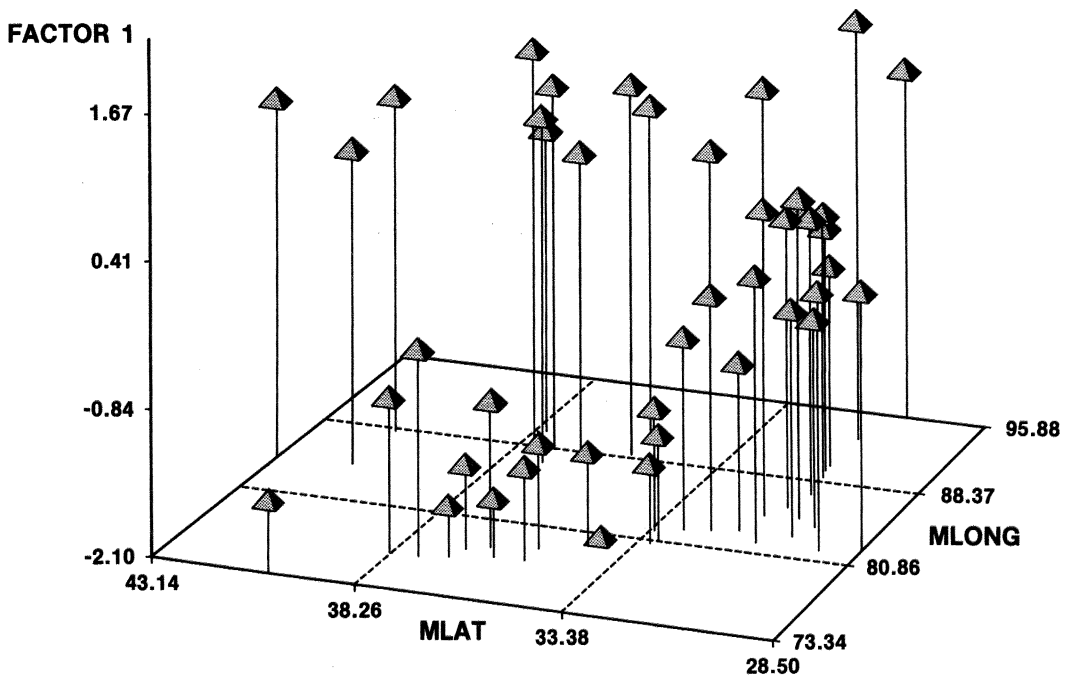


Fig. 7. Plot of the first meristic component by mean latitude and mean longitude for each of the 45 river groupings.

groupings (Fig. 7). From these data, it is apparent that there was a longitudinal trend in the first meristic component but not a latitudinal one. It is difficult to determine whether the longitudinal trend was a result of climatic differences or genetic differences; there were no strong correlations between longitude and any of the environmental or physical variables included in the analysis.

Spatial autocorrelation (Morna's I , at 100-km intervals) of the first meristic principal component scores across direct geographic distances were positive and significant ($P < 0.05$) up to 600 km (Fig. 8). The autocorrelations from 700–1900 km were negative and significant. These data again suggested that individuals are similar with respect to meristic characters within broad geographic areas but are extremely different across larger geographic areas. This means that populations are, not surprisingly, most similar overall to nearby populations.

The separation in time, by as much as 40 years, within an area did not appear to affect the trend of individuals from geographically close rivers being similar in morphology. Furthermore, within a given river drainage, the individual collections used in the analysis were often separated from each other by several years, with no apparent separation of individuals by different years. For example, the Neuse River

population depicted in Figure 2 consists of individuals collected in 1954, 1970, and 1986, and there was no segregation of the individuals collected in different years. The York River population portrayed in the same figure consists of individuals collected in 1951 and 1969. Again, there was no apparent segregation of individuals associated with the year in which they were collected. It is reasonable to conclude, therefore, that the observed differences in phenotype both within and among geographic areas are stable over time for this species. Thus, we rely solely on zoogeographic evidence to explain the observed morphological variation of *A. sayanus*.

The Mississippi River basin is probably the center of origin and dispersal of the majority of the freshwater fishes of North America (Robison, 1986); the region contains all eight families of fishes endemic to North America (Berra, 1981; Lee et al., 1980). The earliest known fossil relative of the pirate perch, *Trichophanes hanes*, was described from a Palogene lignite formation (Cavender, 1986); it is believed to have originated in the Eocene (Miller, 1959; Cavender, 1986). Two additional relatives, *Trichophanes foliarum* and *Trichophanes copei*, were described from fossils found in the Florissant Lake Beds of Colorado. These lake beds were formed during the early Oligocene (Rosen and Patterson, 1969). There is little doubt, therefore, that

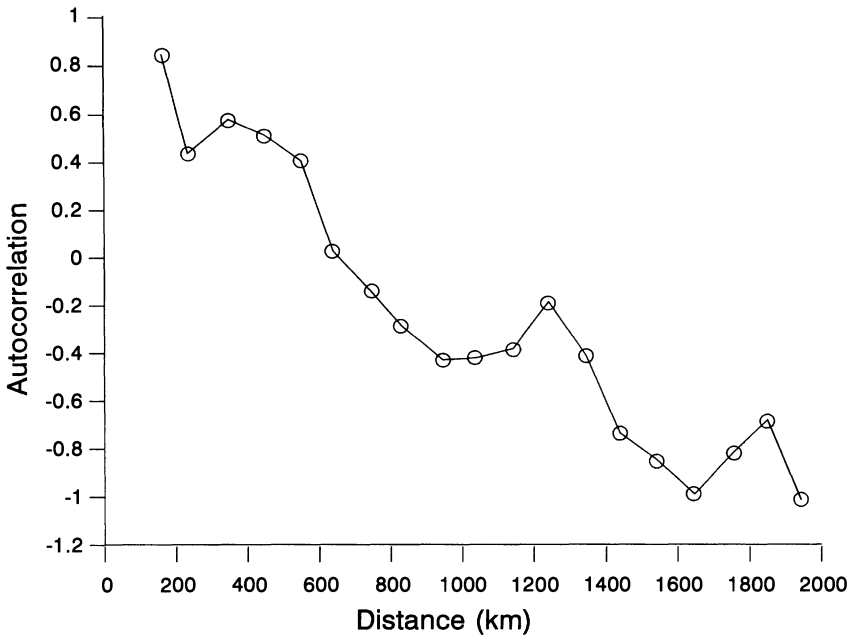


Fig. 8. Spatial autocorrelation of meristic principal component scores, by 100 km of distance, all points are significantly different (<0.05).

the Aphredoderidae had their origins in the Teays-Mississippi River system. The pirate perch is a primary freshwater species (Myers, 1938); its dispersal occurred only via freshwater routes.

Thus, areas of the southern Atlantic Slope and eastern Gulf Slope are of particular interest relative to their role as an avenue of dispersal, and, in fact, their *A. sayanus* populations are intermediate in morphology. These regions have been alternately separated and broadly connected several times during the Cenozoic era (Swift et al., 1986). During the latter half of the Miocene, sea levels were low enough that the shore line would have extended down, or nearly down, to the continental shelf (Gilbert, 1987). The newly exposed coastal plain habitat would have been much less continuous than today, with much of the surface water draining into the underlying porous limestone (C. R. Gilbert, pers. comm.). This fragmentation could have eliminated many coastal plain inhabitants in this area, thus isolating the Atlantic Coastal populations of *A. sayanus* from the remainder of their populations. This separation could have lasted as long as 5 million years (Gilbert, 1987). Reamalgamation could have occurred during the Pliocene, when sea levels were higher than they are at present. During the Pliocene, a similar sequence of events may have taken place but with effects of a much smaller magnitude. In light of these occurrences, eastern Gulf Slope populations should theoretically have originat-

ed from a combination of individuals from the Mississippi Valley and individuals from the Atlantic Slope. The data from this study support this hypothesis, because individuals from the eastern Gulf Slope were morphologically intermediate to individuals from the Atlantic Slope and the Mississippi Valley (Fig. 8).

Throughout this study, "Gulf Slope" referred to rivers draining into the Gulf of Mexico east of the Mississippi River. Populations in this area had the potential of having a dual origin, whereas those populations west of the Mississippi River likely were formed from individuals of the Mississippi Valley form.

Although the major split of the Atlantic Slope populations from the Mississippi Valley populations was primarily a Miocene-Pliocene event, occurrences in the Pleistocene could have played an important role in the evolution of *A. sayanus* within the Atlantic Slope and Mississippi Valley. On the Atlantic Slope, many areas north of the Delaware River were glaciated at some point during the Pleistocene; southern Virginia and northern North Carolina served as a refugium for freshwater fishes during this time (Schmidt, 1986). Within this refugium, there may have been intermixing of previously distinct populations of individual fish species; the result may have been that these populations were the founders of new populations after the glacier receded (Crossman, 1966; Cole, 1967; Jenkins and Zorach, 1970).

The morphological data herein tend to support the idea that such a refugium existed and that there was mixing of different populations. Figure 5 shows that there is a tight grouping of the populations of *A. sayanus* from many of these rivers when meristic and morphological data are plotted in multivariate space. Also, many of the mensural and meristic characters, when examined individually, have a high degree of uniformity throughout this area (see Boltz, 1988).

Burr and Page (1986) proposed that during the Pleistocene there was a second refugium located in the middle Mississippi Valley. This refugium would have served as the source of individuals colonizing the remainder of the distribution of the pirate perch. The data in Figure 5 support this notion; individuals from middle Mississippi Valley populations are morphologically similar to each other. The populations from the Great Lakes and Gulf Slope populations west of the Mississippi River are also morphologically similar to the individuals from the Mississippi Valley, suggesting that these populations originated from individuals in this refugium.

From the results of the multivariate analyses and descriptive statistics, it is evident that populations of the pirate perch from the Atlantic Slope and Mississippi Valley are morphologically distinct and warrant subspecific status. For the subspecies of the Atlantic Slope, *A. s. sayanus*, we suggest the Satilla River as the southern boundary. Although the Satilla River is more closely associated geographically with the Saint Marys and Suwannee rivers (all three originating in the Okefenokee Swamp), and has more species in common with the Saint Marys and Saint Johns rivers to the south (Swift et al., 1986), the morphologies of its pirate perch are more similar to those of populations to the north. The Satilla River was the location of a sharp break in number of dorsal-fin spines, scale rows along the lateral-line series, and pigmentation patterns. In addition, the Satilla River population is closer in multivariate space to the northern rivers than to the southern ones. Several rivers on the Atlantic Slope north of the Satilla River, however, are closer to the Saint Marys and Saint Johns rivers than to the Satilla River in multivariate space; therefore, the subspecific boundary does not denote a sharp break in all the characters examined but, instead, reflects general trends. The Mississippi Valley subspecies, *A. s. gibbosus*, occurs from the Mississippi River west along the Gulf Slope and throughout the entire Mississippi Valley and Great Lakes basins. Determining the boundary for this subspecies in the southern portion of its distribu-

tion is problematic. Individuals from the Gulf Slope populations have intermediate values for most characters when compared to fishes from the other two geographic regions; therefore, no sharp breaks clearly distinguish one area from another. The Gulf Slope populations of the pirate perch from west of the Mississippi River were much more similar to the Mississippi Valley forms than to the eastern Gulf Slope forms. This is not surprising because the rivers of the Gulf Slope west of the Mississippi River have had much different geologic histories than the more eastern Gulf Slope rivers (Hocutt and Wiley, 1986). Again, these boundaries are in part arbitrary, and there may be a few populations that do not fit the overall trend. Individuals in the populations from the Saint Marys River of the southern Atlantic Slope to the Pearl River of the mid-Gulf Slope are termed intergrades.

These subspecies distributions are similar to those reported by Crossman (1966) for *E. americanus*; they differ, however, in that the southern boundary for the Atlantic Slope form of *A. sayanus* is the Satilla River, whereas the southern boundary for the Atlantic Slope form of *E. americanus* was the Saint Marys River. All of the other taxonomic breaks for these two species occur at the same locations.

MATERIALS EXAMINED

Institutional abbreviations follow Leviton et al. (1985), except those noted below. Atlantic Slope drainages north of the Potomac River—USNM 68293, USNM 35970, CU 31179, CU 30292, CU 31742, CU 34943. Potomac River—AEL (Appalachian Environmental Laboratory) 1022, AEL 1012, USNM 238466. York River—VIMS 1269, VIMS 00031. James River—CU 29188. Chowan River—VIMS 2453, VIMS 2453B, CU 67667. Roanoke River—CU 29925, CU 34538, CU 30158. Tar River—CU 19449, CU 11712, CU 25911, NCSM 9498. Neuse River—CU 25871, NCSM 13008, NCSM 10920. Cape Fear River—CU 30169, CU 25901, CU 26038, NCSM 3005, NCSM 10261, NCSM 10349. Pee Dee River—CU 15194, CU 11092, CU 15224, CU 15187, CU 11903, CU 14293, NCSM 12097. Santee River—USNM 238428, USNM 238419. Edisto River—USNM 238422, CU 43680, UT 80.6. Combahee River—CU 15240, CU 44120, CU 44125, CU 44119. Savannah River—USNM 238438, USNM 238449. Ogeechee River—CU 15578, CU 11846, UGAMNH 553. Altamaha River—UGAMNH 1465, UGAMNH 1020, UMMZ 88393, Satilla River—UGAMNH 1022, UGAMNH 1574, UGAMNH 1573, CU 28198. Saint Marys River—CU 35177, CU 43343, UF 6545, UF 6722. Saint Johns River—UMMZ 210097, USNM 133269, PSU 2211. Withlacooche River—UT 80.11. Suwannee River—USNM 162423, UGAMNH 608, CU 54849, CU 47120, UF 58262, UF 34033, UF 8412. Aucilla River—UF 52389. Ochlocknee River—UGAMNH 405, UF 54457, UF 53616. Apalachicola River—UF 52770, UF 54030, UGAMNH 699, UGAMNH 699A, CU 17173, UMMZ 163468, UAIC 1134.06. Choctawatchie River—UF 72546. Pensacola Bay—UF 57646, UF 55893, UAIC 3553.14, UAIC 2708.11, CU 16153. Mobile Bay—USNM 167972, UAIC 3603.01, UAIC 3602.04, UAIC 3598.03. Pascagoula River—UMMZ 155457, UMNZ 163721, UAIC 2489.03. Wolf River—UMMZ 163701. Pearl River—UMMZ 170670. Brazos River and Goose Creek—UMMZ 129862, UMMZ 129937, UMMZ 129806, UF 29535. Sabine River—USNM 44431. Red River—UMMZ 184034, UMMZ 170823, UMMZ 170867, NLU 48821, UOMZ 30756, Ouachita River—NLU 42983, USNM 173146. White River—UMMZ 128498 and 2065, UMOG 2065, UMOG 2064, UMOG 2058. Green River—SIUC 9008, SIUC 9566, SIUC 1897. Ohio River—INHS 1343, INHS 7013, INHS 1261. Middle Mississippi River—UMMZ 153255, UMMZ 153290, UMMZ 154791,

UMMZ 153115, UMMZ 149881, UMMZ 161033, UMMZ 153200, USNM 230732, USNM 230945, SIUC 10016, SIUC 629, UT 80.15. Tennessee River—UT 80.9. Cumberland River—SIUC 1498, CU 47397. Wabash River—INHS 10039, INHS 11545, INHS 8635, UOMZ 43203. Muddy River—INHS 15128, INHS 13103, UMMZ 130320. Kaskaskia River—UMMZ 163077. Illinois River—INHS 5722, INHS 5702, INHS 13873, UMMZ 81367, UMMZ 78471. Great Lakes—UMMZ 136995, UMMZ 163113, UMMZ 137424, UMMZ 136975, UMMZ 137014, USNM 64173.

ACKNOWLEDGMENTS

This manuscript is based on a portion of a dissertation submitted by JMB in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Pennsylvania State University. We thank the following individuals for the loan of specimens: J. Humphries, CU; Bruce Collette, USNM; Carole Olmi, VIMS; W. Palmer, NCSM; D. Etnier, UT; E. McGhee, UGAMNH; D. Nelson, UMMZ; G. Burgess, UF; B. Kuhajada, UAIC; N. Douglas, NLU; T. Coon, UMOG; B. Burr, SIUC; L. Page, INHS; F. McCormick, UOMZ.

We also thank C. Gilbert for his review of an earlier draft of this manuscript. D. Swofford provided the SAS program to compute sheared PCA. The art work was prepared by M. Katz, and M. Tangedal helped in the preparation of figures.

LITERATURE CITED

- ATCHLEY, W. R. 1971. A comparative study of the cause and significance of morphological variation in adults and pupae of *Culicoides*: a factor analysis and multiple regression study. *Evolution* 25:563–583.
- BAILEY, R. M., H. E. WINN, AND C. L. SMITH. 1954. Fishes from the Escambia River. Alabama and Florida, with ecological and taxonomic notes. *Proc. Acad. Nat. Sci. Philadelphia* Vol. CBI: 109–164.
- BALTZ, D. M., AND P. B. MOYLE. 1981. Morphometric analysis of the tule perch (*Hysterothorax traski*) populations in three isolated drainages. *Copeia* 1981:305–311.
- BARLOW, G. W. 1961. Causes and significance of morphological variation in fishes. *Syst. Zool.* 10: 105–117.
- BEHNKE, R. J. 1972. The systematics of salmonid fishes of recently glaciated lakes. *J. Fish. Res. Bd. Canada* 29:639–671.
- BERRA, T. M. 1981. An atlas of distribution of the freshwater fish families of the world. Univ. of Nebraska Press, Lincoln.
- BOLTZ, J. M. 1988. Geographic variation in morphology of the pirate perch, *Aphredoderus sayanus*. Unpubl. Ph.D. diss., Pennsylvania State Univ., University Park.
- BOOKSTEIN, F., B. CHERNOFF, R. ELDER, J. HUMPHRIES, G. SMITH, AND R. STRAUSS. 1985. Morphometrics in evolutionary biology. *Acad. Nat. Sci. Philadelphia Spec. Publ.* 15.
- BURR, B. M., AND L. M. PAGE. 1986. Zoogeography of fishes of the lower Ohio-upper Mississippi basin, p. 287–324. The zoogeography of North American freshwater fishes. C. H. Hocutt and E. O. Wiley (eds.). John Wiley and Sons, New York, New York.
- CALHOUN, R. E., AND D. L. JAMESON. 1970. Canonical correlation between variation in weather and variation in size of the Pacific tree frog *Hyla regilla* in southern California. *Copeia* 1970:124–134.
- CAVENDER, T. M. 1986. Review of the fossil history of North American freshwater fishes, p. 699–724. *In: The zoogeography of North American freshwater fishes.* C. H. Hocutt and E. O. Wiley (eds.). John Wiley and Sons, New York, New York.
- CHERNOFF, B. 1982. Character variation among populations and the analysis of biogeography. *Amer. Zool.* 22:425–439.
- , R. R. MILLER, AND C. R. GILBERT. 1982. *Notropis orca* and *Notropis simus*, cyprinid fishes from the American southwest, with description of a new subspecies. *Occ. Papers Mus. Zool. Univ. Michigan* 698:1–49.
- COLE, C. F. 1967. A study of the eastern johnny darter, *Etheostoma olmstedi* Storer (Teleostei: Percidae). *Ches. Sci.* 8:29–51.
- CROSSMAN, E. J. 1966. A taxonomic study of *Esox americanus* and its subspecies in eastern North America. *Copeia* 1966:1–20.
- EDDY, S., AND J. C. UNDERHILL. 1974. Northern fishes. Univ. of Minnesota Press, Minneapolis.
- ENDLER, J. A. 1977. Geographic variation, speciation, and clines. *Monographs in population biology*, Vol. 10. Princeton Univ. Press, Princeton, New Jersey.
- GILBERT, C. R. 1987. Zoogeography of the freshwater fish fauna of southern Georgia and peninsular Florida. *Brimleyana* 13:25–54.
- GILLIAMS, J. 1824. Description of a new species of fish of the Linnean genus *Perca*. *J. Acad. Nat. Sci. Philadelphia* 4:80–82.
- GOULD, S. J., AND R. F. JOHNSTON. 1972. Geographic variation. *Ann. Rev. Syst. Ecol.* 3:457–498.
- HOCUTT, C. H., AND E. O. WILEY. 1986. The zoogeography of North American freshwater fishes. John Wiley and Sons, New York, New York.
- HUBBS, C. L. 1922. Variations in the number of vertebrae and other meristic characters of fishes correlated with the temperature of the water during development. *Amer. Nat.* 66:360–372.
- , AND K. L. LAGLER. 1964. Fishes of the Great Lakes region (2d ed.). Cranbrook Inst. Sci. Bull. 26: 1–213.
- HUMPHRIES, J. M., F. L. BOOKSTEIN, B. CHERNOFF, G. R. SMITH, R. L. ELDER, AND S. G. POSS. 1981. Multivariate discrimination by shape in relation to size. *Syst. Zool.* 30:291–308.
- JAMES, F. C. 1983. Environmental component of morphological differentiation in birds. *Science* 221: 184–186.
- JENKINS, R. E., AND T. ZORACH. 1970. Zoogeography and characters of the American cyprinid fish *Notropis bifrenatus*. *Chesapeake Sci.* 11:174–182.
- JORDAN, D. S. 1877. Contributions to North American ichthyology. A. Notes on Cottidae, Etheostom-

- idae, Percidae, Centrarchidae, Aphredoderidae, Dorysomatidae, and Cyprinidae; B. Synopsis of the Siluridae. *Bull. U.S. Natl. Mus.* 10:1-120.
- , AND B. W. EVERMANN. 1896. The fishes of north and middle America: a descriptive catalogue of the species of fishlike vertebrates found in the waters of North America, north of the Isthmus of Panama. *Ibid.* No. 47, Pt. I: 785-787.
- LEE, D. S. 1980. *Aphredoderus sayanus* (Gilliams), p. 484. *In: Atlas of North American freshwater fishes.* D. S. Lee, C. R. Gilbert, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. (eds.). North Carolina State Museum of Natural History, Raleigh.
- , C. R. GILBERT, R. E. JENKINS, D. E. MCALLISTER, AND J. R. STAUFFER, JR. 1980. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh.
- LESUEUR. 1833. *Aphredoderus*, p. IX, 445. *In: Histoire naturelle des poissons.* Cuvier and Valenciennes (eds.). F. G. Levrault, Paris, France.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802-832.
- MACGREGOR, B., AND H. R. MACCRIMMON. 1977. Evidence of genetic and environmental influences on meristic variation in the rainbow trout, *Salmo gairdneri* Richardson. *Env. Biol. Fish.* 2:25-33.
- MANSUETI, A. J. 1963. Some changes in morphology during ontogeny of the pirate perch, *Aphredoderus s. sayanus*. *Copeia* 1963:546-557.
- MATTHEWS, W. J. 1987. Geographic variation in *Cyprinella lutrensis* (Pisces: Cyprinidae) in the United States, with notes on *Cyprinella lepida*. *Copeia* 1987: 616-637.
- MILLER, R. R. 1959. Origin and affinities of the freshwater fish fauna of western North America, p. 187-222. *In: Zoogeography.* C. L. Hubbs (ed.). Am. Assn. Advan. Sci. Publ. 51. Stanford, California.
- MYERS, G. S. 1938. Fresh-water fishes and West Indian zoogeography. *Smithson. Rpt.* 1937:339-364.
- ROBISON, H. W. 1986. Zoogeographic implications of the Mississippi River Basin, p. 267-286. *In: The zoology of North American freshwater fishes.* C. H. Hocutt and E. O. Wiley (eds.). John Wiley and Sons, New York, New York.
- ROSEN, D. E., AND C. PATTERSON. 1969. A new fish of the genus *Xiphophorus* from Guatemala, with remarks on the taxonomy of endemic forms. *Am. Mus. Novit.* 2379:1-29.
- SAS INSTITUTE INC. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute, Inc., Cary, North Carolina.
- SCHMIDT, R. E. 1986. Zoogeography of the northern Appalachians, p. 137-160. *In: The zoogeography of North American freshwater fishes.* C. H. Hocutt and E. O. Wiley (eds.). John Wiley and Sons, New York, New York.
- SOKAL, R. R., N. H. HEYFORD, AND J. R. L. KISHPAUGH. 1971. Changes in microgeographic variation patterns of *Pemphigus populitransversus* over a six-year span. *Evolution* 25:584-590.
- STAUFFER, J. R., JR. 1988. Three new rock-dwelling cichlids (Teleostei: Cichlidae) from Lake Malawi, Africa. *Copeia* 1988:663-668.
- STRAUSS, R. E. 1980. Genetic and morphometric variation and the systematic relationships of eastern North American sculpin (Pisces: Cottidae). Unpubl. Ph.D. diss., Pennsylvania State Univ., University Park.
- SWIFT, C. C., C. R. GILBERT, S. A. BORTONE, G. H. BURGESS, AND R. W. YERGER. 1986. Zoogeography of the freshwater fishes of the southeastern United States: Savannah River to Lake Pontchartrain, p. 213-266. *In: The zoogeography of North American freshwater fishes.* C. H. Hocutt and E. O. Wiley (eds.). John Wiley and Sons, New York, New York.
- TODD, T. N., G. R. SMITH, AND L. E. CABLE. 1981. Environmental and genetic contributions to morphological differentiation in ciscoes (Coregonidae) of the Great Lakes. *Canadian J. Fish. Aquat. Sci.* 38:59-67.
- U. S. DEPARTMENT OF COMMERCE. 1985. Climatic atlas of the United States. Environmental Sciences Services Administration, Environmental Data Service, Washington, D.C.
- VOGT, T., AND D. L. JAMESON. 1970. Chronological correlation between change in weather and change in morphology of the Pacific tree frog in southern California. *Copeia* 1970:135-144.
- SCHOOL OF FOREST RESOURCES, PENNSYLVANIA STATE UNIVERSITY, UNIVERSITY PARK, PENNSYLVANIA 16802. PRESENT ADDRESS (JMB): HARZA ENGINEERING COMPANY, 150 SOUTH WACKER DRIVE, CHICAGO, ILLINOIS 60606. Submitted 4 Jan. 1991. Accepted 11 Jan. 1992. Section editor: W. J. Matthews.