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Geographic Variation in the Blackside Darter, *Percina maculata* (Teleostei, Percidae), in the Ohio River Drainage of Kentucky

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ABSTRACT

Geographic variation in the blackside darter, *Percina* (*Alvordius*) *maculata*, in the Ohio River Basin of Kentucky was investigated by gathering meristic and morphometric data on 486 individuals from 16 drainages (13 Ohio River drainages). Character data were analyzed using frequency distribution tables and principal components analysis to identify trends in geographic variation and to recognize taxonomically distinct populations. Results did not indicate the need to diagnose new taxa, but populations show considerable variation. Among the most unusual populations are those in the Cumberland and Kentucky rivers, two drainages known for endemism and unusual biological communities.

INTRODUCTION

The blackside darter, *Percina maculata* (Figure 1), is the most widespread of the eight described species of the subgenus *Alvordius* (Page 1974). Its range extends from southeastern Saskatchewan and North Dakota east to southern Ontario and New York and south to northeastern Texas and Gulf Coast drainages as far east as the Mobile Bay drainage of Alabama (Page 1983). The species is distributed over four major basins, the Mobile Bay, Mississippi River, Great Lakes (excluding Lake Superior), and Hudson Bay; and three minor drainages of the Gulf Slope west of the Mobile Bay: the Calcasieu River, Lake Pontchartrain, and Pearl River (Beckham 1983, 1986). *Percina maculata* occurs in small to moderate-sized, clear streams with sand and gravel bottoms and typically is taken from the margins of large pools with some current or small pools associated with riffles (Trautman 1957). Less often the species is found over mud and among accumulations of brush (Page 1983).

Beckham (1983) studied geographic variation in *P. maculata* and found that meristic data exhibited pronounced clinal variation with relatively high interpopulational variability. The major trend was for a south-to-north decrease in counts for lateral line, transverse, caudal peduncle, and modified midventral scales and for lateral and dorsal blotches. Dorsal spine counts also exhibited a south-to-north decrease but to a lesser degree than other characters. Dorsal and anal ray counts showed the reverse trend, a south-to-north increase.

Beckham tested these trends within and between six major basins occupied by *P. maculata*: Hudson Bay, Great Lakes, Ohio River, Upper Mississippi, Lower Mississippi, and Gulf Slope. An analysis of variance (ANOVA) indicated a significant difference between at least two sample means for the majority of meristic characters examined. However, an ANOVA table was not presented in the analysis, and there was no indication of any significant or non-significant differences when more than two sample means were considered.

Beckham also conducted a stepwise discriminant functions analysis of nine meristic characters exhibiting the most variation to determine where differences in sample means were occurring and whether differences were the result of breaks between interior drainages or due primarily to geographic extremes. Transverse scale count was the most reliable character in discriminating populations. Successive steps in the analysis added dorsal blotches, caudal peduncle scales, lateral blotches, lateral line scales, dorsal spines, dorsal rays, midventral scales, and anal rays. Samples varied from a high of 82.4% being correctly identified for Hudson Bay to a low of 15.7% for Ohio River.

According to Beckham, the inability to demarcate populations in the Ohio River drainage resulted from the high variability of meristic characters. Only 132 specimens were examined from all Ohio river tributaries in Ken-

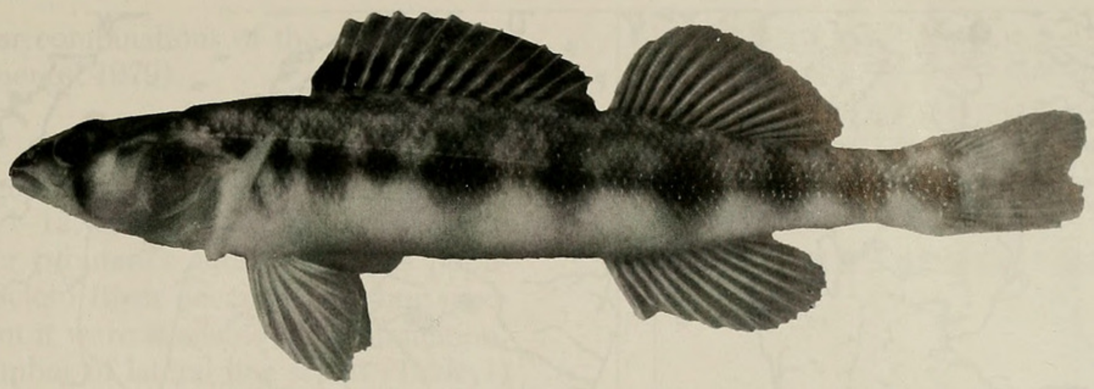

Figure 1. *Percina maculata.* INHS 43425 (60.1 mm SL, male); Eagle Creek, Carroll Co., Kentucky. Photo by K. S. Cummings.

tucky, and it is possible that distinct taxa from the Ohio river system were not detected. Specimens from above Cumberland Falls were not included in Beckham's study. Hubbs and Raney (1939) examined variation in the blackside darter over its entire range and described the species as "probably a complex of subspecies." Burr and Warren (1986) noted that this species exhibits considerable geographic variation in Kentucky. Our study was undertaken to examine geographic variation in *P. maculata* in the north and west-flowing tributaries of the Ohio River in Kentucky and to determine whether distinct taxonomic units exist.

Percina maculata is variably distributed in southern tributaries of the Ohio River (Beckham 1983; Burr and Warren 1986). It is widespread and common in the Tradewater, Green, Salt, Kentucky, Licking, Little Sandy, Big Sandy, and Kanawha rivers but is more rare in the Tennessee River system, with most records being from the Clarks River in western Kentucky, the last tributary of the Tennessee River before its confluence with the lower Ohio River. *Percina maculata* is present in the lower and upper portions of the Cumberland River but is absent from the middle portion (Etnier and Starnes 1993).

METHODS AND MATERIALS

Four hundred eighty-six specimens of *P. maculata* were examined meristically; morphometric data were collected on 149 specimens. Specimens examined were from 16 drainages (see "Material Examined"); 13 of the drainages are major tributaries of the Ohio River, and three drainages (Lake Huron, Lake Michigan, and Mississippi River) were examined for comparison to Ohio River populations (Figure 2). Standard length (SL) was used throughout. Only specimens greater than 45 mm SL were used for morphological analysis in order to reduce allometric bias. Counts were made only on specimens greater than 38 mm SL.

Counts and measurements were made as described by Hubbs and Lagler (1964), except for the number of transverse scales, which was counted from the origin of the second dorsal fin down and back to the anal fin, as proposed by Raney and Suttkus (1964). Counts of bilateral features were made on the left side.

Meristic characters included the number of total lateral line scales, pored lateral line scales, transverse scales, scales above the lateral line, scales below the lateral line, caudal peduncle scale rows, dorsal rays, dorsal spines, anal rays, anal spines, pectoral fin rays, and lateral blotches. Cheek, nape, and opercular squamation were analyzed as meristic variables. Only large lateral blotches were counted from the first full blotch posterior to the pectoral fin base back to, and including, the blotch ending at the hypural plate (Beckham 1983). Data were arranged in frequency distribution tables, and sample means and modes from each drainage were compared for geographic variation.

Morphometric characters included head length, head depth, head width, snout length, predorsal length, eye diameter, gape width, pectoral fin length, pelvic fin length, spinous dorsal fin base length, soft dorsal fin base length, anal fin base length, caudal fin length, caudal peduncle width, caudal peduncle depth, spinous dorsal fin origin to pelvic fin origin, spinous dorsal fin origin to anal fin or-

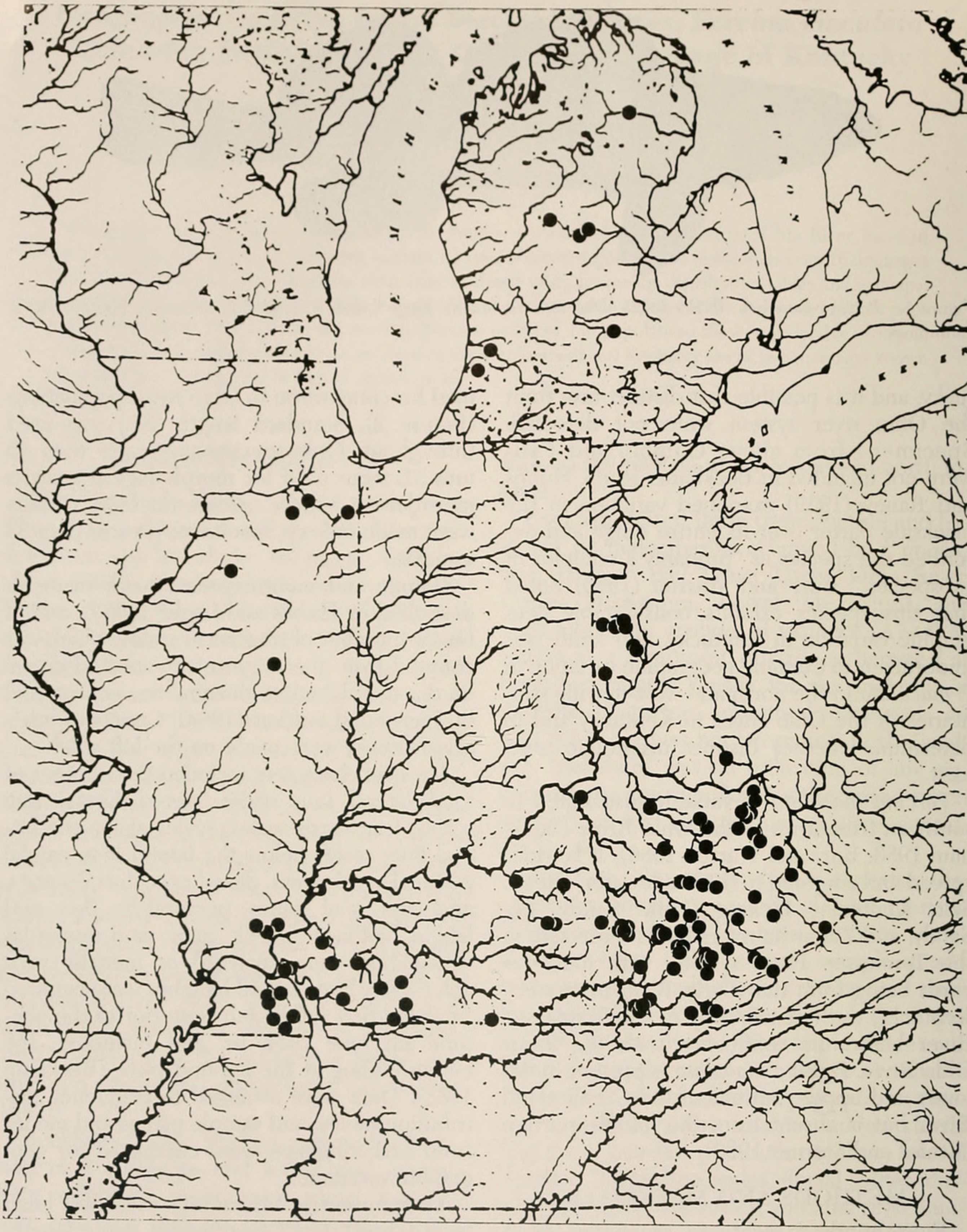

Figure 2. Collection localities for specimens of *P. maculata* examined.

igin, soft dorsal fin origin to anal fin insertion, soft dorsal fin origin to pelvic fin origin, spinous dorsal fin insertion to anal fin origin, and anal fin origin to soft dorsal fin insertion. The data were analyzed with the use of principal components analysis whereby the original set of variables was used to generate a new set of variables, uncorrelated with each other, that were linear combinations of the original variables (Pimentel 1979).

RESULTS

Although data for all populations are shown in Tables 1–12, comparisons are restricted to Ohio River tributaries and exclude the population in Scioto River because only four specimens from it were available for examination.

The number of lateral line scales (Table 1) varied from a low mean of 61.1 and a mode of 59 in Little Sandy River to a high mean of 70.2 and mode of 71 in Cumberland River above Cumberland Falls. In general, populations in extreme eastern Kentucky (e.g., Tygarts Creek, Little Sandy, and Big Sandy rivers) had the lowest counts, and those in the southeast and north (e.g., Cumberland, Kentucky, and Great Miami rivers) had the highest. The Kentucky River population had a bimodal count with a concentration of individuals around 67 scales and another around 71 scales.

The number of pored lateral line scales (Table 2) varied from a low mean of 59.7 and a mode of 57 in Little Sandy River to a high mean of 68.9 and mode of 70 in Cumberland River above the Falls. As for the lateral line scale count, populations in extreme eastern Kentucky (e.g., Tygarts Creek, Little Sandy, and Big Sandy rivers) had the lowest count, and populations in the southeast and north (e.g., Cumberland River above the Falls and Kentucky and Great Miami rivers) had the highest. The population in Cumberland River below the Falls had a mean of 65.9 and a mode of 67 scales; that above the Falls had a mean of 68.9 and a mode of 70 scales.

The number of transverse scales (Table 3) varied from a low mean of 16 and a mode of 16 in Tygarts Creek to a high mean of 18.3 in Cumberland River below the Falls (mode = 18–19), Tradewater River (mode = 19), and Green River (mode = 18). Populations in the north and the east (e.g., Tygarts Creek and Great Miami River) generally had the lowest counts, and those in western Kentucky (e.g., Tradewater and Green rivers) had the highest.

The number of scales above the lateral line varied from a low mean of 6.9 and a mode of 7 in Tygarts Creek to a high mean of 8.8 and mode of 9 in Tradewater River. Those populations in the east (e.g., Tygarts Creek and Lit-

Table 1. Frequency distribution of lateral line scale counts in *Percina maculata*.

Drainage	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	N	X	SD	CV
Lake Huron							1	3	1	5	9	2	6	5	2	1		2	2			1			40	67.6	3.31	0.05
Lake Michigan				1			3	2	1	1	1	1	1	1	1										13	64.6	3.23	0.05
Mississippi River					1	3	2	3	4	3	8	8	5		3	4			1						45	66.2	3.12	0.05
Direct tribs. lower Ohio R. (IL)				1				2				1	3		2	1		1		1					12	67.9	4.50	0.07
Tennessee River				1			3	1			1							1		1					7	63.9	4.53	0.07
Cumberland River (below falls)								1	1	1	2	3	2	4	2	2	2	1		1	1			2	25	69.8	4.19	0.06
Cumberland River (above falls)									1	1	1	3	1	4	4	5	1	2	2	3					28	70.2	3.01	0.04
Tradewater River									2	2	1	2	4	1		4	1	1	1						19	68.3	3.28	0.05
Green River			1				2	2	8	4	3	4	8	3	3	2	1	1							42	66.6	3.06	0.05
Salt River								1	1		1	2	3	3		2		1							12	68.8	1.99	0.03
Kentucky River	1					1	1	1	1	4	9	17	14	10	7	18	8	4	2	4	1	2	1		106	69.2	3.43	0.05
Licking River						1		4	3	3	4	1	4	2	4	3	1		1	1	1				33	67.6	3.73	0.06
Tygarts Creek			1	1		3	1	2	2	6	2				3										21	64.2	3.28	0.05
Little Sandy River				3	1		1		1	1															7	61.1	2.55	0.04
Big Sandy River					1	2	6	5		6	4	5	4	4	3		1								41	65.6	3.03	0.05
Great Miami River								1	1		1	2	3	4	5		3		1				1		22	69.3	3.21	0.05
Scioto River									1	1	1		1												4	65.8	1.71	0.03
Total	1		2	7	3	10	20	28	28	38	48	51	59	41	39	42	18	14	10	11	3	3	2	2	487			

Table 2. Frequency distribution of pored lateral line scale counts in *Percina maculata*.

Drainage	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	N	X	SD	CV
Lake Huron						1	3	2	6	4	6	7	2	1	2	1	2		1	1					40	66.2	3.71	0.06
Lake Michigan			1		1	3		3		1	2		1		1										13	63.5	3.41	0.05
Mississippi River			1		3	2	3	3	3	11	3	9	1	2	3				1						45	65.2	3.14	0.05
Direct tribs. lower Ohio R. (IL)	1					1	1			1	1	1	1	2	1		1			1					12	66.7	5.16	0.08
Tennessee River			1		2		2				1					1									7	62.7	4.42	0.07
Cumberland River (below falls)		1		1		1	2		2	2	2	4	1	1		1	1	1	1				1	1	25	65.9	6.36	0.10
Cumberland River (above falls)							2	1		1	2	3	3	2	6	1	2	2	3						28	68.9	3.43	0.05
Tradewater River					1		2		3	3	2	1		3	2		2								19	66.4	3.44	0.05
Green River			1	1		3	1	6	7	2	8	5	4	1	3		1								42	65.2	3.02	0.05
Salt River									1		3	3	1	2	2										12	67.4	1.83	0.03
Kentucky River	1	1			2	3	2	1	7	12	14	9	16	7	10	10	5	3		2	3	1			111	67.4	4.36	0.06
Licking River				2	2	3	2	3	2	4	2	4	3	1	2	2				1					33	65.2	3.89	0.06
Tygarts Creek	1	1	1		3	1	3	3	5				3												21	62.4	3.30	0.05
Little Sandy River		3		1		1		1	1																7	59.7	2.98	0.05
Big Sandy River			1		6	2	7	3	7	4	3	2	5	1	1										43	63.7	3.21	0.05
Great Miami River							1		1	1	2	6	3	3	1	2		1			1				22	68.1	3.00	0.04
Scioto River								1		2	1														4	64.8	1.26	0.02
Total	3	6	6	5	20	21	31	27	45	48	52	54	44	26	34	18	14	7	6	5	4	1	1	1	484			

tle Sandy River) had the lowest counts, and those in the west (e.g., Tradewater and Green rivers) had the highest.

The number of scales below the lateral line varied from a low mean of 9.9 and a mode of 9–10 in Tygarts Creek to a high mean of 12.2 and mode of 12 in Tradewater River. In general, populations in the north and east (e.g., Tygarts Creek and Great Miami River) had the lowest counts; those in western Kentucky (e.g., Tradewater and Green rivers) had the highest. The population in Cumberland River below the Falls had a mode of 12 scales; that above the Falls had a mode of 10.

The number of scale rows around the caudal peduncle (Table 4) varied from a low mean of 21.4 and a mode of 22 in Little Sandy River to a high mean of 24.4 and mode of 24 in Cumberland River below the Falls. As for scales below the lateral line and transverse scales, the populations in the north and east (e.g., Tygarts Creek, and Great Miami, Licking, and Little Sandy rivers) had the lowest counts, and those in western Kentucky (e.g., Tradewater and Green rivers) had among the highest.

Pectoral fin rays showed little variation (Table 5); 8 of 13 populations had a mode of 14 rays. Except for the Salt River population, which had a mode of 10 anal fin rays, little variation was found in the number of anal rays (Table 6); other Ohio River populations had modes of 8–9 rays.

The number of dorsal rays (Table 7) varied from a low mean of 11.7 and a mode of 12 in Kentucky River to a high mean of 12.5 and mode of 13 in Cumberland River below the Falls. Populations in eastern Kentucky (e.g., Cumberland River above the Falls, Kentucky River, and Tygarts Creek) generally had the lowest counts; those in western Kentucky (e.g., Tradewater, Green, and Salt rivers) had the highest. Most populations (9 of 13) had a mode of 14 dorsal spines (Table 8).

The number of lateral blotches (Table 9) varied from a low mean of 6.5 and a mode of 7 in Great Miami River, to a high mean of 7.7 and mode of 7 in Kentucky River. Populations in western Kentucky (e.g., Tradewater and Green rivers) generally had the lowest counts, while those populations in the east (e.g., Tygarts Creek, Kentucky, and Big Sandy rivers) had the highest.

Table 3. Frequency distribution of transverse scale counts in *Percina maculata*.

Drainage	14	15	16	17	18	19	20	21	N	X	SD	CV
Lake Huron	1	10	18	9	1				39	16.0	0.84	0.05
Lake Michigan			6	6	1				13	16.6	0.65	0.04
Mississippi River		2	12	17	9	4			44	17.0	1.02	0.06
Direct tribs. lower Ohio R. (IL)			2	3	3	4			12	17.8	1.14	0.06
Tennessee River				2	4		1		7	18.0	1.00	0.06
Cumberland River (below falls)		1		5	8	8	2	1	25	18.3	1.24	0.07
Cumberland River (above falls)			8	8	11		1		28	17.1	1.01	0.06
Tradewater River			1	5	4	6	3		19	18.3	1.19	0.07
Green River			2	4	21	9	5	1	42	18.3	1.05	0.06
Salt River			2	2	5	2		1	12	17.9	1.38	0.08
Kentucky River		1	9	32	43	18	7	1	111	17.8	1.08	0.06
Licking River		4	7	9	12	1			33	17.0	1.10	0.07
Tygarts Creek	2	4	9	5	1				21	16.0	1.02	0.06
Little Sandy River		1	3	2	1				7	16.4	0.98	0.06
Big Sandy River		3	13	18	7	2	1		44	16.9	1.06	0.06
Great Miami River		2	9	4	6		1		22	16.8	1.22	0.07
Scioto River			1	3					4	16.8	0.50	0.03
Total	3	28	102	134	137	54	21	4	483			

The percentage of the opercle covered with scales (Table 10) varied little among populations (most means were 94–99 and 100) with the exception of the population in Cumberland River above the Falls which had a mean of 51 and a mode of 50–75. The population in Cumberland River below the Falls and those populations to the east and north (e.g., Tygarts Creek, and Kentucky, Licking, Little Sandy, and Big Sandy rivers) had a few individuals with reduced squamation on the opercle.

The percentage of the nape covered with scales (Table 11) varied from a low mean of 28 and a mode of 10 in Cumberland River above the Falls to a high mean of 97 and a mode of 100 in Tennessee River. In general, populations in eastern Kentucky (e.g., Tygarts Creek and Kentucky, Licking, Little Sandy, and Big Sandy rivers) had the lowest percentages, and those in the west (e.g., Tennessee, Tradewater, and Green rivers) had the highest. With a mean of 87 and a mode of 100, the population in Cumberland River below the Falls differed substantially from that above the Falls with a mean of 28 and a mode of 10.

The percentage of the cheek covered with

Table 4. Frequency distribution of counts of scales around the caudal peduncle in *Percina maculata*.

Drainage	18	19	20	21	22	23	24	25	26	27	28	N	X	SD	CV
Lake Huron			6	16	13	4						39	21.4	0.88	0.04
Lake Michigan				1	4	5	3					13	22.8	0.93	0.04
Mississippi River			1	10	21	12	1					45	22.0	0.82	0.04
Direct tribs. lower Ohio R. (IL)					1	3	7	1				12	23.7	0.78	0.03
Tennessee River				1	1	3	2					7	22.9	1.07	0.05
Cumberland River (below falls)				1		3	10	7	3		1	25	24.4	1.33	0.05
Cumberland River (above falls)				1	11	10	5	1				28	22.8	0.92	0.04
Tradewater River					2	1	7	7	2			19	24.3	1.11	0.05
Green River					1	5	23	13				42	24.1	0.72	0.03
Salt River					2	3	4	3				12	23.7	1.07	0.05
Kentucky River	1			2	9	22	57	16	2		1	111	23.7	1.15	0.05
Licking River				4	14	6	8	1				33	22.6	1.08	0.05
Tygarts Creek			1	7	7	4	2					21	22.0	1.07	0.05
Little Sandy River			2	2	3	1						8	21.4	1.06	0.05
Big Sandy River			2	3	17	13	8	1				44	22.6	1.09	0.05
Great Miami River				4	9	4	4	1				22	22.5	1.14	0.05
Scioto River			1		3							4	21.5	1.00	0.05
Total	1		13	52	117	99	141	51	7		2	483			

Table 5. Frequency distribution of pectoral ray counts in *Percina maculata*.

Drainage	12	13	14	15	N	X	SD	CV
Lake Huron		7	24	8	39	14.0	0.63	0.04
Lake Michigan	1	5	5	2	13	13.6	0.87	0.06
Mississippi River	3	31	11		45	13.2	0.53	0.04
Direct tribs. lower Ohio R. (IL)		10	2		12	13.2	0.39	0.03
Tennessee River		3	3	1	7	13.7	0.76	0.06
Cumberland River (below falls)	1	7	17		25	13.6	0.57	0.04
Cumberland River (above falls)		7	17	4	28	13.9	0.63	0.05
Tradewater River	1	9	9		19	13.4	0.61	0.05
Green River	1	21	18	2	42	13.5	0.63	0.05
Salt River		3	7	2	12	13.9	0.67	0.05
Kentucky River	1	23	68	19	111	13.9	0.64	0.05
Licking River		8	21	4	33	13.9	0.60	0.04
Tygarts Creek		8	10	3	21	13.8	0.70	0.05
Little Sandy River			6	2	8	14.3	0.46	0.03
Big Sandy River		14	29	1	44	13.7	0.51	0.04
Great Miami River		11	10	1	22	13.5	0.60	0.04
Scioto River		2	2		4	13.5	0.58	0.04
Total	8	169	259	49	485			

scales (Table 12) varied from a low mean of 33 and mode of 15 in Cumberland River above the Falls to a high mean of 95 and mode of 100 in Great Miami River. Populations in northeastern Kentucky (e.g., Licking River and Tygarts Creek) had the lowest percentages, and those in the west (e.g., Tennessee and Tradewater rivers) had the highest. As for nape squamation, a large difference in mean and mode occurred between populations below (mean = 84, mode = 90–100) and above (mean = 33, mode = 15) the Falls in the Cumberland River.

A principal components analysis of meristic characteristics of Ohio River populations in Kentucky failed to show any clear separations. In contrast, when morphometric data for these same populations were analyzed, populations in the Kentucky, Big Sandy, and Tradewater rivers emerged from one another. The best separation was shown by the plot of PCII against PCIII (Figure 3). A MANOVA indicated that all three populations differed significantly from one another (Kentucky River vs. Big Sandy River, $P < 0.0001$; Kentucky River vs. Tradewater River, $P = 0.0007$; Big

Table 6. Frequency distribution of anal ray counts in *Percina maculata*.

Drainage	6	7	8	9	10	11	N	X	SD	CV
Lake Huron			1	24	13	2	40	9.4	0.63	0.07
Lake Michigan			1	6	6		13	9.4	0.65	0.07
Mississippi River			10	31	4		45	8.9	0.55	0.06
Direct tribs. lower Ohio R. (IL)			2	10			12	8.8	0.39	0.04
Tennessee River			3	3	1		7	8.7	0.76	0.09
Cumberland River (below falls)			10	12	3		25	8.7	0.68	0.08
Cumberland River (above falls)			7	18	3		28	8.9	0.59	0.07
Tradewater River		1	2	12	4		19	9.0	0.75	0.08
Green River	1		7	31	3		42	8.8	0.66	0.07
Salt River			2	2	7	1	12	9.6	0.90	0.09
Kentucky River			42	66	3		111	8.6	0.53	0.06
Licking River			10	21	2		33	8.8	0.56	0.06
Tygarts Creek			11	10			21	8.5	0.51	0.06
Little Sandy River			4	4			8	8.5	0.53	0.06
Big Sandy River		2	15	25	2		44	8.6	0.65	0.08
Great Miami River			1	16	5		22	9.2	0.50	0.05
Scioto River	1		2	1			4	7.8	1.26	0.16
Total	2	3	140	282	56	3	486			

Table 7. Frequency distribution of dorsal ray counts in *Percina maculata*.

Drainage	9	10	11	12	13	14	15	N	$\bar{X}$	SD	CV
Lake Huron			2	15	23			40	12.5	0.60	0.05
Lake Michigan				5	8			13	12.6	0.51	0.04
Mississippi River			8	26	11			45	12.1	0.65	0.05
Direct tribs. lower Ohio R. (IL)			1	10	1			12	12.0	0.43	0.04
Tennessee River			1	3	2	1		7	12.4	0.98	0.08
Cumberland River (below falls)		1	4	7	9	3	1	25	12.5	1.16	0.09
Cumberland River (above falls)		1	9	14	4			28	11.8	0.75	0.06
Tradewater River			1	11	7			19	12.3	0.58	0.05
Green River	1		3	20	16	2		42	12.3	0.87	0.07
Salt River		1	1	4	6			12	12.3	0.97	0.08
Kentucky River		5	38	58	10			111	11.7	0.71	0.06
Licking River			4	23	6			33	12.1	0.56	0.05
Tygarts Creek		1	3	16	1			21	11.8	0.60	0.05
Little Sandy River			1	4	3			8	12.3	0.71	0.06
Big Sandy River			5	29	9	1		44	12.1	0.63	0.05
Great Miami River			2	14	4	2		22	12.3	0.77	0.06
Scioto River			1	2	1			4	12.0	0.82	0.07
Total	1	9	84	261	121	9	1	486			

Sandy River vs. Tradewater River, $P <$ 0.0001). Additionally, the plot of PCII against PCIII indicated that three other populations overlapped with Kentucky, Big Sandy, or Tradewater river populations but were separate from the remaining two. Tygarts Creek overlapped with Kentucky River but was separate from Big Sandy and Tradewater rivers (Figure 3). Both the Tennessee and Green rivers overlapped with the Tradewater River population but were separate from the Kentucky and Big Sandy rivers (Figure 3).

For morphometric data, the first principal component (PCI) explained 90.1% of the variance (Table 13); however, PCI is primarily a size component strongly influenced by variation in size of the specimens and provides little taxonomic information (Pimentel 1979). Loading most heavily on PCII (2.4% of the variance) were eye diameter, pectoral fin length, gape width, snout length, and caudal peduncle width; on PCIII (1.5%) were gape width, snout length, eye diameter, anal fin base length, and the length from the spinous dorsal fin origin to the anal fin insertion; on PCIV (1.2%) were caudal peduncle width, soft

Table 8. Frequency distribution of dorsal spine counts in *Percina maculata*.

Drainage	12	13	14	15	16	N	$\bar{X}$	SD	CV
Lake Huron		2	28	10		40	14.2	0.52	0.04
Lake Michigan		2	8	3		13	14.1	0.64	0.05
Mississippi River	3	27	9	6		45	13.4	0.81	0.06
Direct tribs. lower Ohio R. (IL)	3	8			1	12	13.9	0.79	0.06
Tennessee River	1	1	5			7	13.6	0.79	0.06
Cumberland River (below falls)	2	9	12	2		25	13.6	0.77	0.06
Cumberland River (above falls)		4	13	9	2	28	14.3	0.82	0.06
Tradewater River		7	7	5		19	13.9	0.81	0.06
Green River	1	18	17	6		42	13.7	0.75	0.06
Salt River		3	5	4		12	14.1	0.79	0.06
Kentucky River	2	27	63	16		109	13.8	0.70	0.05
Licking River		15	16	2		33	13.6	0.61	0.04
Tygarts Creek		6	11	3	1	21	14.0	0.80	0.06
Little Sandy River		4	4			8	13.5	0.53	0.04
Big Sandy River	1	4	28	11		44	14.1	0.65	0.05
Great Miami River	2	1	10	7	1	21	14.2	0.98	0.07
Scioto River		1	2			3	13.7	0.58	0.04
Total	15	139	238	84	5	482			

Table 9. Frequency distribution of counts of lateral blotches in *Percina maculata*.

Drainage	5	6	7	8	9	10	N	X	SD	CV
Lake Huron	8	26	4	1			39	6.0	0.65	0.11
Lake Michigan	4	8	1				13	5.8	0.60	0.10
Mississippi River	5	24	10	4	1		44	6.4	0.89	0.14
Direct tribs. lower Ohio R. (IL)			11				11	7.0	0.00	0.00
Tennessee River		2	4		1		7	7.0	1.00	0.14
Cumberland River (below falls)	1	5	15	3			24	6.8	0.70	0.10
Cumberland River (above falls)		2	21	5			28	7.1	0.50	0.07
Tradewater River	2	2	15				19	6.7	0.67	0.10
Green River		7	33	1	1		42	6.9	0.53	0.08
Salt River			10	2			12	7.2	0.39	0.05
Kentucky River		1	51	46	12	1	111	7.7	0.72	0.09
Licking River		3	23	7			33	7.1	0.55	0.08
Tygarts Creek		1	11	8	1		21	7.4	0.68	0.09
Little Sandy River		1	5	2			8	7.1	0.64	0.09
Big Sandy River		1	27	15	1		44	7.4	0.57	0.08
Great Miami River	4	6	9	3			22	6.5	0.93	0.15
Scioto River			2	2			4	7.5	0.58	0.08
Total	24	89	252	99	17	1	482			

dorsal fin base length, anal fin base length, and eye diameter; and on PCV (0.9%) were anal fin base length, soft dorsal fin base length, length between spinous dorsal fin origin and pelvic fin origin, pectoral fin length, and the length from the spinous dorsal fin origin to the anal fin insertion.

DISCUSSION

Populations examined in our study exhibit considerable geographic variation, with the most extreme character states in individuals from the Cumberland and Kentucky rivers. However, it appears that gene flow is occurring even among the most divergent populations, and no population is taxonomically diagnosable.

Percina maculata in the Cumberland River above Cumberland Falls has several characteristics that distinguish it from the Cumberland River population below the Falls. Lateral line and pored lateral line scale counts were higher above the Falls than below (Tables 1, 2); transverse scales, scales above the lateral line, scales below the lateral line, caudal peduncle scales, and dorsal rays were much low-

Table 10. Frequency distribution of percentages of opercle covered with scales in *Percina maculata*.

Drainage	10	25	50	75	100	N	X	SD	CV
Lake Huron					40	40	100	0.00	0.00
Lake Michigan					13	13	100	0.00	0.00
Mississippi River					45	45	100	0.00	0.00
Direct tribs. lower Ohio R. (IL)					12	12	100	0.00	0.00
Tennessee River					7	7	100	0.00	0.00
Cumberland River (below falls)		1	1	1	22	25	94	0.18	0.19
Cumberland River (above falls)	4	5	8	9	2	28	51	0.27	0.53
Tradewater River					19	19	100	0.00	0.00
Green River					42	42	100	0.00	0.00
Salt River					12	12	100	0.00	0.00
Kentucky River			1	3	107	111	99	0.06	0.06
Licking River				2	31	33	98	0.06	0.06
Tygarts Creek				1	19	20	99	0.06	0.06
Little Sandy River				1	7	8	97	0.09	0.09
Big Sandy River			1	2	39	42	98	0.09	0.09
Great Miami River					22	22	100	0.00	0.00
Scioto River					4	4	100	0.00	0.00
Total	4	6	11	19	453	483			

Table 11. Frequency distribution of percentages of nape covered with scales in *Percina maculata*.

Drainage	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	N	X	SD	CV
Lake Huron	2		4	2	2	5	2	1	4	1	2		1		3	7	2	1	2			40	44	0.27	0.62
Lake Michigan			1				2				1		1			1		2	2	3		13	68	0.29	0.43
Mississippi River	1		3	2	1	1	1	2	4	1	3		4			3	7	1	5	4	2	45	60	0.30	0.50
Direct tribs. lower Ohio R. (IL)											1					1	2		3	1	4	12	88	0.15	0.17
Tennessee River																			1	2	4	7	97	0.04	0.04
Cumberland River (below falls)									1		2			1		2	2	1	3	1	12	25	87	0.18	0.21
Cumberland River (above falls)		2	7	2	4	3	1	2	3		1					1	1				1	28	28	0.24	0.84
Tradewater River																2	1		2	1	13	19	95	0.09	0.09
Green River						1							1			5		6	3	5	21	42	91	0.15	0.16
Salt River				1	2		1		1		2					2			1	2		12	55	0.30	0.56
Kentucky River	6		16	2	2	5	4	3	10		5		10		5	2	5	6	11	12	5	109	54	0.33	0.62
Licking River	2	2	1	2	4	1	1	4	6		1		2		3	2			1	1		33	39	0.26	0.67
Tygarts Creek			1				1	1	4		6		1		1			4		2		21	57	0.24	0.41
Little Sandy River						2		3		1	1							1				8	42	0.19	0.46
Big Sandy River				7	1		4	1	3		6		4		1	3	3	1	6	4		44	56	0.28	0.50
Great Miami River						1				1	3		1	1		2		2	7	3	1	22	76	0.21	0.27
Scioto River					1	1			1								1					4	41	0.27	0.66
Total	11	4	33	18	17	20	17	17	47	4	34	0	25	2	13	33	24	25	47	41	63	484			

Table 12. Frequency distribution of percentages of cheek covered with scales in *Percina maculata*.

Drainage	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	N	X	SD	CV
Lake Huron											2				1	1	1	6	13	2	14	40	90	0.12	0.13
Lake Michigan																	1		1		11	13	98	0.06	0.06
Mississippi River									1		2		2		2	2	6		7	5	18	45	87	0.16	0.18
Direct tribs. lower Ohio R. (IL)					1				1		1				1		1		3		4	12	78	0.27	0.35
Tennessee River																	1	1	1		4	7	94	0.09	0.09
Cumberland River (below falls)						1							2		1	3	2	1	7	1	7	25	84	0.17	0.21
Cumberland River (above falls)		4	3	5	2		1	3	1	1	2		1	1		4						28	33	0.25	0.76
Tradewater River													3				3		2	4	7	19	88	0.14	0.16
Green River							2				3		2			1	6	1	15	9	2	42	80	0.22	0.27
Salt River													2		1				3	1	5	12	88	0.16	0.18
Kentucky River	3		2		4		3		4		9		5		5	3	16	7	23	2	25	111	75	0.27	0.36
Licking River					1					1	2	1	1	1	3	2	3	7	7		4	33	78	0.18	0.23
Tygarts Creek			1	2	2				1		4						1		3		7	21	65	0.35	0.53
Little Sandy River																1	1	1	3	2		8	88	0.07	0.08
Big Sandy River			2		1		1		1		2		3	1		3	2	1	7	1	19	44	81	0.26	0.32
Great Miami River																1	1	1	5		14	22	95	0.08	0.08
Scioto River																			1		3	4	98	0.05	0.05
Total	3	4	8	7	11	1	7	3	9	2	27	1	22	3	14	21	45	26	101	27	144	484			

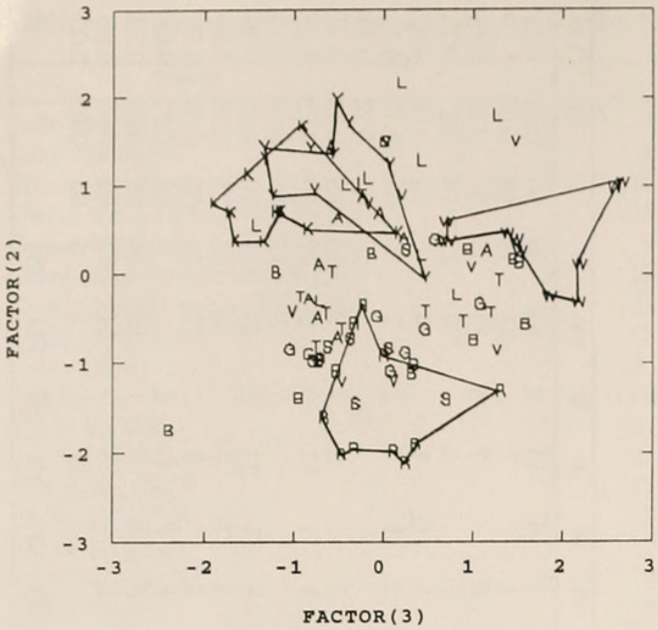

Figure 3. Principal component analysis of morphometric variables for *P. maculata*. T = Tennessee River, K = Kentucky River, W = Big Sandy River, V = Little Sandy River, G = Green River, R = Tradewater River, L = Licking River, S = Salt River, Y = Tygarts Creek, A = Cumberland River (above Falls), B = Cumberland River (below Falls). Outlined populations are ones with extreme values.

er above the Falls than below (Tables 3, 4, 7). The population above the Falls exhibited much reduced opercle, nape, and cheek squamation. *Percina maculata* was described by Beckham (1983) as having a fully scaled opercle; however, the majority of specimens examined from above the Falls had percentages of squamation at 75% and below (Table 10). Mean percentages of scales covering the nape and cheek (28% and 33%, respectively) fall well below the means for other Ohio River populations (Tables 11, 12).

Three fishes are endemic to the upper Cumberland River drainage: *Phoxinus cumberlandensis, Etheostoma sagitta sagitta,* and *E. nigrum susanae* (Starnes and Starnes 1978). The closest relatives of *P. cumberlandensis* are *P. tenneseensis* and *P. oreas* (Starnes and Jenkins 1988). *Phoxinus tenneseensis* occurs in the upper Tennessee River drainage, and *P. oreas* is found in the upper Tennessee, New, and Atlantic Slope drainages. The ancestor of these three species is thought to have lived in the preglacial Teays River drainage, and a population isolated in the Cumberland River drainage above the Falls differentiated into *P. cumberlandensis* (Starnes and Jenkins 1988).

The arrow darter, *E. sagitta,* includes two subspecies, *E. s. sagitta,* an endemic of the Cumberland River above the Falls, and *E. s. spilotum* of the upper Kentucky River basin (Kuehne and Bailey 1961). The two forms are readily distinguishable (Kuehne and Bailey 1961) and presumably differentiated after a stream capture event isolated them (discussed below).

Table 13. Variable loadings for principal component analysis of measurements of *Percina maculata*.

Variable	PCI	PCII	PCIII	PCIV	PCV
Head length	0.0598	−0.0067	0.0022	0.0045	0.0026
Head depth	0.0719	−0.0067	0.0032	−0.0001	−0.0081
Head width	0.0631	−0.0073	−0.0016	0.0077	0.0003
Snout length	0.0835	−0.0182	−0.0149	−0.0097	−0.0022
Predorsal length	0.0616	−0.0051	0.0039	0.0083	0.0004
Eye diameter	0.0497	−0.0126	−0.0023	0.0155	0.0093
Gape width	0.0859	−0.0332	−0.0186	−0.0188	−0.0061
Pectoral fin length	0.0645	−0.0164	−0.0021	0.0133	0.0121
Pelvic fin length	0.0631	−0.0061	0.0038	0.0064	0.0092
Spinous dorsal fin base length	0.0683	0.0023	0.0078	0.0057	−0.0033
Soft dorsal fin base length	0.0757	0.0105	0.0136	−0.0131	0.0146
Anal fin base length	0.0736	0.0085	0.0062	−0.0211	0.0115
Caudal fin length	0.0592	−0.0099	0.0041	0.0093	0.0052
Caudal peduncle width	0.1060	0.0389	−0.0344	0.0082	0.0013
Caudal peduncle depth	0.0672	0.0056	0.0027	−0.0019	−0.0045
Spinous dorsal fin origin to pelvic fin origin	0.0780	0.0034	0.0117	0.0003	−0.0147
Spinous dorsal fin origin to anal fin origin	0.0690	0.0008	0.0079	0.0101	−0.0079
Soft dorsal fin origin to anal fin insertion	0.0769	0.0098	0.0087	−0.0051	0.0004
Soft dorsal fin origin to pelvic fin origin	0.0649	0.0014	0.0063	0.0069	−0.0068
Spinous dorsal fin insertion to anal fin origin	0.0800	0.0094	0.0078	0.0002	−0.0062
Anal fin origin to soft dorsal fin insertion	0.0730	0.0096	0.0054	−0.0108	−0.0001

Studies by Kuehne and Bailey (1961) and Starnes and Starnes (1979) suggest that multiple faunal exchanges have occurred between the Cumberland and Kentucky rivers. *Etheostoma sagitta* and *E. baileyi* both occur only in the upper Cumberland and upper Kentucky river basins (Kuehne and Bailey 1961). The absence of close relatives of these two darters in the central Ohio River basin suggests that their presence in the upper Kentucky River is a result of transfer by stream capture. Kuehne and Bailey (1961) hypothesized that the transfer occurred when Little Richland Creek, an upper Cumberland tributary, was captured by Collins Fork, a small tributary of the upper Kentucky River. Alternatively, these darters entered the Cumberland from the Kentucky River. This latter hypothesis is based on the Pliocene connection of the Kentucky River to the Teays River (which flowed west to the Mississippi River) and the fact that the closest relative to *E. sagitta* is *E. nianguae,* an inhabitant of the Missouri River system in Missouri (Burr and Page 1986; Burr and Warren 1986).

Etheostoma nigrum susanae, endemic to the upper Cumberland River, appears to intergrade with *E. n. nigrum* in the headwaters of the adjacent Kentucky River system to the north (Starnes and Starnes 1979). Several populations from the upper Kentucky River system, particularly in the Middle Fork, have reduced head and belly squamation, closely approaching that of *E. n. susanae,* that probably results from gene flow between upper Cumberland and Kentucky river populations (Starnes and Starnes 1979). Strange (1998) interpreted mitochondrial DNA variation in the upper Cumberland and upper Kentucky River drainages to suggest that *E. n. susanae* had invaded the upper Cumberland system at least twice, the first time from an unknown source and the second time from the Kentucky River.

Percina maculata in the Kentucky River has several unusual characteristics. In particular, lateral line scales exhibit a bimodal distribution; a strong cluster of individuals centers around 67 scales and another around 71 scales (Table 1). Mean lateral line scale counts for the Licking River, which lies just northeast of the Kentucky River, and Cumberland River above the Falls (just to the south) were 67.6 and 70.2, respectively, suggesting that introgression into the Kentucky River population is occurring from the Licking and upper Cumberland river systems. Specimens from the Kentucky River also share with the Cumberland River population reduced squamation on the nape, cheek, and opercle, again suggesting intergradation.

Populations of *P. maculata* in Tygarts Creek and Licking, Little Sandy, and Big Sandy rivers exhibit low values in several meristic characters compared to values for other Ohio River tributaries. The Little Sandy River population has the lowest mean values for lateral line scales, pored lateral line scales, scales around the caudal peduncle, anal rays (shared with Tygarts Creek), and dorsal spines (Tables 1, 2, 4, 6). The Tygarts Creek population has the lowest mean values for transverse scales, scales above the lateral line, scales below the lateral line, and anal rays (shared with Little Sandy River) (Tables 3, 6). *Percina maculata* in the Licking River groups with Little Sandy River and Tygarts Creek for scales around the caudal peduncle, percentage opercle squamation, percentage nape squamation, and percentage cheek squamation. *Percina maculata* in the Big Sandy River groups with Little Sandy River and Tygarts Creek for lateral line scales, pored lateral line scales, percentage opercle squamation, and percentage nape squamation. Geological evidence indicates that these and other eastern tributaries of the Ohio River were tributaries of the ancestral Teays River and were separated from the Kentucky River in the early Pleistocene (Hocutt et al. 1986). As a result, the Licking River fauna closely resembles the Big Sandy fauna, rather than that of the adjacent Kentucky River, which has faunal affinities with lower Ohio River tributaries (Hocutt et al. 1986).

Populations of *P. maculata* in the Tradewater, Green, and lower Cumberland rivers, tributaries of the lower Ohio River, exhibit high values in several meristic characters. The highest mean value for transverse scales in *P. maculata* is shared by the Tradewater, Green, and lower Cumberland rivers (Table 3). The Tradewater river population has the highest means and modes for scales above the lateral line, scales below the lateral line, and number of pectoral fin rays (Table 5). The population of *P. maculata* in the lower Cumberland River has the highest values for scale rows around the caudal peduncle and dorsal rays (Tables 4, 7). The extreme values for these populations can be attributed to the fact that they are geographically distant from drainages to the east (e.g., Kentucky and Big Sandy rivers). The Tradewater, Tennessee, and Green river populations overlap each other on the plot of PCII and PCIII but are separate from the Kentucky and Big Sandy river populations (Figure 3). The distance between eastern and western drainages effectively serves as a barrier to gene flow and has led to populational differences in meristic characters and body shape.

Although *P. maculata* shows considerable variation in tributaries of the Ohio River, new taxa cannot be diagnosed. The examination of large samples from Ohio River tributaries suggests that gene flow has prevented speciation, even in geologically distinct areas such as the upper Cumberland River.

MATERIAL EXAMINED

Numbers of specimens of *P. maculata* are in parentheses. Complete locality data may be obtained from the authors upon request. Institutional abbreviations are as listed in Leviton et al. (1985).

Lake Huron drainage. MICHIGAN: Oscoda Co., UMMZ 194283 (29); Isabella Co., INHS 57895 (8), 57913 (1), 57924 (2). Lake Michigan drainage. MICHIGAN: Ingham Co., INHS 79581 (1); Allegan Co., INHS 38819 (2), 41972 (10). Mississippi River drainage. ILLINOIS: Kankakee Co., INHS 5356 (6), 5630 (4); Woodford Co., INHS 10930 (14); Piatt Co., INHS 8541 (10); Will Co., INHS 4872 (11). Direct tributaries, Ohio River. ILLINOIS: Pope Co., INHS 1350 (6), 1468 (4), 41009 (2). Tennessee River drainage. KENTUCKY: Calloway Co., INHS 40872 (1); SIUC 7681 (1), 10405 (2); Graves Co., SIUC 8755 (1), 11866 (1); Marshall Co., INHS 77681 (1). Below Cumberland Falls, Cumberland River drainage. KENTUCKY: Trigg Co., INHS 41907 (1); SIUC 12274 (1); Livingston Co., INHS 75545 (1), 75546 (4); Laurel Co., EKU 536 (1); SIUC 8511 (2); Rockcastle Co., SIUC 15568 (2); Jackson Co., SIUC 14902 (1), 27174 (2); Logan Co., SIUC 11616 (6); Todd Co., SIUC 10333 (4). Above Cumberland Falls, Cumberland River drainage. KENTUCKY: McCreary Co., SIUC 6872 (9), 9466 (13), 23852 (1); Whitley Co., SIUC 2382 (1), 8451 (1); Bell Co., SIUC 186 (1), 16894 (1); Letcher Co., SIUC 23251 (1). Tradewater River drainage. KENTUCKY: Crittenden Co., INHS 78370 (1); Caldwell Co., SIUC 8913 (18). Green River drainage. KENTUCKY: Todd Co., INHS 58214 (4); SIUC 9241 (30); Christian Co. INHS 27502 (7); Allen Co., EKU 140 (1). Salt River drainage. KENTUCKY: Marion Co., SIUC 14257 (8); EKU 757 (1); Bullitt Co., SIUC 16987 (2); Washington Co., INHS 75543 (1). Kentucky River drainage. KENTUCKY: Clay Co., INHS 43044 (19), 64303 (3), 79026 (8), 79196 (4), 86873 (1), 88555 (3); EKU 593 (2); Lincoln Co., EKU 342 (7), 387 (1), 400 (1), 411 (2), 429 (2); Jackson Co., EKU 435 (2), 576 (3), 968 (1); Owsley Co., EKU 765 (1); INHS 79213 (1), 88536 (1); Letcher Co., EKU 1299 (8), 1303 (8); Carroll Co., EKU 485 (2); INHS 42992 (1); Wolfe Co., EKU 24 (2); INHS 39096 (3); Powell Co., EKU 1270 (8); INHS 87422 (3); Rockcastle Co., EKU 455 (2); Lee Co., EKU 1271 (2); Breathitt Co., INHS 64290 (6); Leslie Co., INHS 78497 (4). Licking River drainage. KENTUCKY: Montgomery Co., EKU 1304 (1); INHS 75544 (1); Bath Co., EKU 1272 (2); Nicholas Co., EKU 1315 (1); Fleming Co., SIUC 11375 (3), 16834 (1); Magoffin Co., SIUC 8243 (25). Tygarts Creek drainage. KENTUCKY: Carter Co., EKU 137 (4), 1061 (2), 1068 (5); SIUC 5660 (2), 9314 (1); INHS 88040 (7); Greenup Co., EKU 164 (1). Little Sandy River drainage. KENTUCKY: Elliott Co., EKU 1038 (1); SIUC 11225 (2); Carter Co., SIUC 7177 (7), 13387 (1). Big Sandy River drainage. KENTUCKY: Pike Co., EKU 59 (2); INHS 76999 (20); Lawrence Co., SIUC 8824 (7); Martin Co., SIUC 8864 (13); Floyd Co., SIUC 16587 (2). Great Miami River drainage. OHIO: Darke Co., OSM 63502 (2), 63538 (4), 63556 (4), 63562 (2), 63594 (1); Miami Co., OSM 63533 (3), 63572 (1), 63609 (1), 63902 (1); Preble Co., OSM 4836 (3). Scioto River drainage. OHIO: Scioto Co., OSM 62750 (4).

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