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Three new percid fishes (Percidae: *Percina*) from the Mobile Basin drainage of Alabama, Georgia, and Tennessee

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Abstract

Three new species of *Percina* are described from upland drainages of the Mobile Basin. Two of the three species are narrowly distributed: *P. kusha*, the Bridled Darter, is currently known only from the Conasauga River drainage in Georgia and Tennessee and Etowah River drainage in Georgia, both tributaries of the Coosa River, and *P. sipsi*, the Bankhead Darter, which is restricted to tributaries of Sipsey Fork of the Black Warrior River in northwestern Alabama. The third species, *P. smithvanizi*, the Muscadine Darter, occurs above the Fall Line in the Tallapoosa River drainage in eastern Alabama and western Georgia. In a molecular analysis using mitochondrial cytochrome *b* sequence data, *P. kusha* and *P. smithvanizi* were recovered as sister species, while *Percina sipsi* was recovered in a clade consisting of *P. aurolineata* (*P. sciera* + *P. sipsi)*. Two of the three species, *P. kusha* and *P. sipsi*, are considered to be imperiled species and are in need of conservation actions to prevent their extinction. Description of these three darters increases the number of described species of *Percina* to 44. Sixteen are known to occur in the Mobile Basin, including nine that are endemic.

Key words: Percidae, *Percina*, *Percina kusha*, *Percina sipsi*, *Percina smithvanizi*, darter, new species, taxonomy, conservation, Alabama, Georgia, Tennessee, Mobile Basin

Introduction

There are 41 described species in the genus *Percina* (Near & Benard 2004; Nelson *et al*. 2004), the second-most species rich of 10 genera currently recognized in the family Percidae (Song *et al*. 1998). Of the 41 named species, 13 are known from the Mobile Basin of Alabama, Georgia, Mississippi and Tennessee, and six are endemic. Our description of three new species brings the total number of described species in the Mobile Basin to 16, nine of which are endemic to the Mobile Basin, representing the highest level of endemism in the genus *Percina* within any drainage of North America.

The first of the three new species to be recognized as taxonomically distinct, *Percina smithvanizi*, Muscadine Darter, was discovered during a survey of fishes in the Tallapoosa River drainage of Alabama and Georgia (Williams 1965). In the late 1960's, *P. kusha*, Bridled Darter, was discovered in headwaters of the Coosa River in Georgia and Tennessee (Stiles & Etnier 1971). *Percina sipsi*, Bankhead Darter, endemic to a small area in the Sipsey Fork watershed of the Black Warrior River drainage in north-central Alabama, went undetected until 1971 (Dycus & Howell 1974). Following discovery of these species, their existence, distribution, and presumed placement within the subgenus *Alvordius* became general knowledge among darter systematists. However, their recognition as valid species or subspecies was not consistent. Knowledge of the existence of these taxa has led to numerous published references to them as bridled or muscadine darters and

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Percina sp., *Percina* (*Alvordius*) sp., or *Percina* sp. cf. *macrocephala*, in ichthyological and conservation literature during the past four decades (Page & Burr 1991; Etnier & Starnes 1994; Boschung & Mayden 2004). Most publications referring to the three *Percina* species described herein included river drainage distribution data which facilitated association of citations with each of the three new species.

Prior phylogenetic studies of the genus *Percina* included samples of two of the three taxa described herein. Page & Whitt (1973a, b) included *P. kusha* and Near (2002) included *P. smithvanizi* in molecular studies. Page & Whitt (1973a) used isozyme variation of lactate dehydrogenase (Ldh), malate dehydrogenase (Mdh), and tetrazolium oxidase (To) loci to assess the relationships within the Etheostomatini, and Page and Whitt (1973b) used isozyme variation of Ldh to assess the monophyly of *Percina*. None of these loci were variable enough to infer relationships within subgenera of *Percina*, or to unequivocally determine sister relationship of *P. kusha*. Near (2002) postulated *P. smithvanizi* as the sister to *P. palmaris* based on mitochondrial cytochrome *b* gene sequence, although support for this clade was weak and other possible relationships varied depending on method of analysis.

Material and methods

Institutional abbreviations follow Leviton *et al*. (1985) and Leviton & Gibbs (1988), except for Cornell University Museum of Vertebrates (CUMV), Georgia Museum of Natural History (GMNH) and St. Louis University (STL). Type material of the three species of *Percina* described herein is deposited in the following institutions: Academy of Natural Sciences of Philadelphia (ANSP); Auburn University Museum (AUM); Cornell University Museum of Vertebrates (CUMV); Georgia Museum of Natural History (GMNH); North Carolina State Museum of Natural Sciences (NCSM); Tulane University (TU); University of Alabama Ichthyological Collection (UAIC); Florida Museum of Natural History, University of Florida (UF); University of Michigan Museum of Zoology (UMMZ); National Museum of Natural History (USNM); and University of Tennessee (UT).

Scale and fin ray counts and proportional measurements were based on the methods of Hubbs & Lagler (1958) and Richards & Knapp (1964). Degree of nape squamation was scored on a scale of 0 to 5 with 0 indicating a naked nape along midline of body anterior to dorsal fin and 5 indicating a nape that was completely covered with exposed scales. Individuals with a completely scaled nape but scales on the anterior portion were embedded was scored as 4. A score of 1–3 represents a successive increase in squamation of the posterior portion of the nape. The posterior extent of development of pored lateral line scales was numerically scored. A complete lateral line was assigned a 0 value, unpored scales before the caudal base were recorded with a negative value and pored scales present on the base of the caudal fin were given a positive value. Body length measurements are standard lengths (SL).

Body measurements for a morphometric analysis were made from photographs of preserved adult specimens. Individual specimens were laterally positioned right side down on insect pins mounted to a large rubber stopper. Small minuet pins were inserted at the base of fins and other critical landmarks, and specimens were photographed with a Sony Digital Mavica MVC-FD91 camera. Images were then digitized with SigmaScan Pro 5.0 software to record a geometric truss for shape analysis (Bookstein *et al*. 1985), using straight-line measurements of the landmarks enumerated in Figure 1. To evaluate shape differences, we employed the covariance matrix of log-transformed measurements in a sheared, size-free shape comparison using principal component analysis (Humphries *et al*. 1981; D.L. Swofford's computer algorithm Appendix A.5.1.2 in Bookstein *et al*. 1985, using SAS Release 8.2). For median fin measurements, "origin" and "insertion" refer to anterior and posterior positions at the base of the fin (Cailliet *et al*. 1986).

The color illustrations of all three species were drawn by Joe Tomelleri and are based on color photographs and notes made in the field of live and freshly preserved specimens.

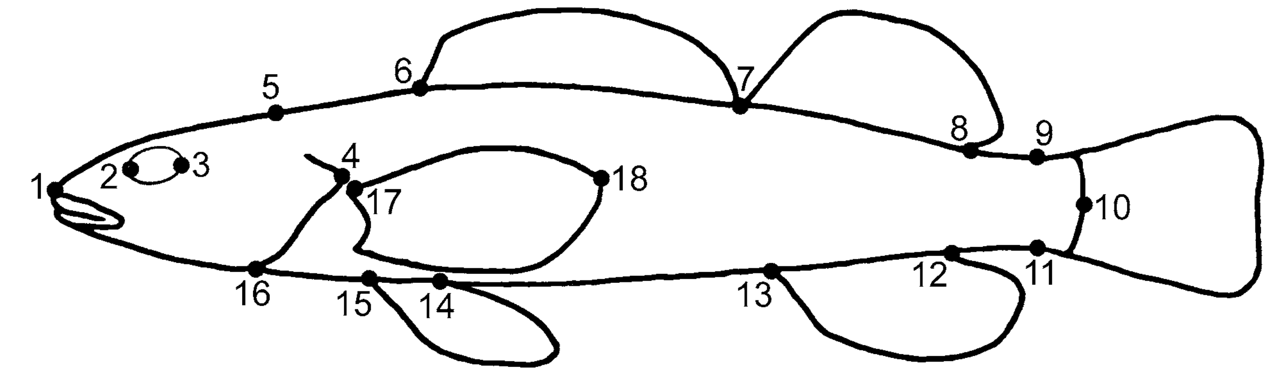

FIGURE 1. Landmark points used in reconstructing a geometric truss for morphometric shape analysis of three new *Percina* species from the Mobile Basin.

Genomic DNA was isolated from frozen or ethanol-fixed fin or muscle tissue using standard proteinase-K digestion, phenol-chloroform extraction, and ethanol precipitation (Hillis et al. 1996). This was used as template for double stranded reactions via PCR. The complete mitochondrial cytochrome b gene (cyt b) was amplified using primers in the flanking tRNAs (H15915 5'-AAC TGC AGT CAT CTC CGG TTT ACA AGA C-3', Irwin et al. 1991; Gludg-L, 5'-TGA CTT GAA RAA CCA YCG TT G-3', Palumbi et al. 1991). Each 25 uL reaction contained 1 uL genomic DNA, each primer at 1.0 uM, 4.0 uM $MgCl_2$, 2.5 uL 10x reaction buffer, and 1.25 units of Taq polymerase. Amplifications consisted of 35 cycles, each with 45 s denaturation at 94°C, 45 s annealing at 50°C, and 60 s extension at 70°C. PCR products were purified of unincorporated primers and nucleotides with QIAGEN Quick-Clean kits (QIAGEN, Valencia, California), sequenced using a dye-labeled dideoxy terminator sequencing kit (Big Dye, Applied Biosystems, Inc., Foster City, California) and visualized on an ABI 3100 automated sequencer (Auburn University Molecular Genetics Laboratory, Auburn, Alabama). Both light and heavy strands were sequenced for all samples.

Sequences were verified by consensus between the two strands, edited, and aligned by eye using BioEdit v5.0.9 (Hall 2001). Veracity of all mutations was assessed via comparative alignment and examination of the electropherograms. Individual sequences are deposited in GenBank (see materials examined for list of accession numbers). Arlequin v2.0 (Schneider et al. 2000) was used to examine nucleotide variation, substitution patterns, haplotype diversity, nucleotide diversity and mismatch distributions, and also to perform an Analysis of Molecular Variance (AMOVA).

We incorporated parts of the cyt b data sets of Song et al. (1998), Near et al. (2000), Near (2002), and Sloss et al. (2004) to test alternative hypotheses of relationships of the new species described herein. Outgroups included members of the Percinae and Luciopercinae (*Gymnocephalus*, *Perca*, *Romanichthys*, *Sander* and *Zingel*). Other etheostomine taxa (*Ammocrypta*, *Crystallaria*, and *Etheostoma*) served as additional tests of the monophyly of *Percina*.

Relationships between haplotypes were inferred under both parsimony and Bayesian criteria. Parsimony analysis (MP) utilized the heuristic search option in PAUP* v4.0 (Swofford 2002); starting trees were obtained with accelerated transformation and tree-bisection-reconnection branch swapping during 100 replicates of random sequence addition. Parsimony analyses were conducted with characters unweighted and unordered. All minimal-length trees were kept and zero-length branches collapsed. Support for individual nodes was assessed by performing 1000 jack-knife replicates with 37% data deletion in each replicate and JAC emulation selected (sensu Farris *et al*. 1996). Bayesian analysis utilized MrBayes 3.0 (Huelsenbeck & Ronquist 2001) under a GTR+G model as selected by the Akaike Information Criterion as implemented in ModelTest vers. 3.06 (Posada & Crandall 1998), a random starting tree, and uniform interval priors. Four-chain heated Markov chain Monte Carlo sampling was conducted for 3,000,000 generations, sampling trees every 1000 generations. We assessed stationarity by plotting likelihood scores against number of generations, and used a consensus tree of post-stationarity topologies to derive posterior probabilities. Posterior probabilities = to 0.95 were considered well-supported (Zander 2004).

***Percina kusha*, Williams & Burkhead, new species**
Bridled Darter
(Fig. 2a)

Holotype. UF 110303, male, 64 mm SL, Conasauga River at the mouth of Minnewauga Creek, 9.6 air km SSW of the center of Bueton (35°00'18"N; 34°41'28"W), Polk County, Tennessee, 3 April 1996.

Paratypes. Coosa River drainage—Conasauga River system

Georgia: Murray County: ANSP 187097 (1; 55 mm) Conasauga River at County Route 392 (Old Georgia Hwy 2), about 1.4 air km S of Tennessee state line (34°58'28"N; 84°38'43"W), 2 April 1994. GMNH 1463 (2; 50–53 mm) same locality, 9 July 1980. UF 110286 (1; 58 mm) same locality, 3 April 1996. UF 165704 (6; 38–60 mm) same locality, 28 April 1994. USNM 389726 (6; 38–60 mm) (out of NMB 1432) same locality, 28 April 1994. GMNH 1394F (1; 48 mm) Conasauga River at Gregorys Mill (34°57'10"N; 84°47'12"W), 4 November 1981. UF 110260 (2; 44–59 mm) Holly Creek at County Route 301, about 5.9 air km ESE of the center of Eton (34°48'55"N; 84°41'45"W), 2 April 1996.

Tennessee: Bradley County: INHS 76807 (1; 45 mm) Conasauga River at Tennessee Hwy 74 (Georgia Hwy 225), 4.8 km W of Conasauga (34°59'26"N; 84°46'32"W), 10 June 1970. TU 58937 (2; 42–46 mm) same locality, 17 October 1969. TU 58965 (3; 41–49 mm) same locality, 19 October 1969. TU 65939 (7; 44–49 mm) same locality, 29 June 1970. UAIC 8769.04 (1; 62 mm) same locality, 13 June 1977. UF 42736 (1; 57 mm) same locality, 14 June 1985. UF 42757 (2; 45–61 mm) same locality, 9 June 1985. UT 91.1524 (1; 53 mm) Conasauga River below Tennessee Hwy 74, 27 October 1977. **Polk County:** NCSM 44984 (3; 30–60 mm) Confluence of Jacks and Conasauga rivers, just N of the Georgia border (34°59'24"N; 84°38'10"W), 17 November 1967. UAIC 6768.07 (1; 40 mm) Ball Play Creek, about 1.8 air km NE of Conasauga community, 12 March 1983. NCSM 44983 (1; 54 mm) Minnewauga Creek at mouth (35°00'15"N; 84°41'26"W), 11 April 1989. UF 165703 (8; 44–63 mm) (out of UF 110303) same locality, 3 April 1996. UF 165734 (4; 43–52 mm) same locality, 20 January 2003. UT 91.4274 (5; 42–58 mm) Minnewauga Creek and tributary, 0.3 km above mouth and Conasauga River, 2 March 1992.

Additional material (nontypes).

Coosa River drainage—Conasauga River system

Georgia: Murray County: AUM 10570 (1) Conasauga River at County Route 392 (Old Georgia Hwy 2), about 1.4 air km S of Tennessee state line (34°58'28"N; 84°38'43"W), 25 June 1975. UT 91.1690 (2) same locality, 1 October 1978. UT 91.149 (1) Conasauga River, about 1.6 km above junction with Jack’s River, 4 August 1966. **Murray/Whitfield counties:** GMNH 1394E (2) Conasauga River, below Gregory’s Mill, 10 October 1981. UT 91.1647 (3) Conasauga River, about 4 river km N of Beaver Lake Bridge (Old Georgia Hwy 2), Murray/Whitfield county line, 29 August 1978.

Tennessee: Bradley County: AUM 11720 (2) Conasauga River at Tennessee Hwy 74 (Georgia Hwy 225), 4.8 km W of Conasauga (34°59'26"N; 84°46'32"W), 19 July 1975. GMNH 1582 (2) same locality, 5 February 1982. UF 22590 (1) same locality, 25 June 1976. UF 26460 (4) same locality, 9 July 1977. UT 91.160 (1) Conasauga River, second riffle below Tennessee Hwy 74 bridge, 22 October 1969. UT 91.351 (2) same locality, 29 November 1969. UF 43969 (1) Conasauga River from Tennessee Hwy 74 bridge to 0.8 km downstream, 16 May 1970**. Polk County:** UF 22793 (2) Conasauga River, about 0.4 km below mouth of Minnewauga Creek (35°00'18"N; 84°41'41"W), 25 June 1976. UT 91.252 (1) Conasauga River at Boanerges Church Bridge (35°00'03"N; 84°45'13"W), 3–4 November 1968. UT 91.298 (2) same locality, 27-28 March

1969. UT 91.501 (11) Minnewauga Creek at mouth (35°00'15"N; 84°41'26"W), 3 March 1968. UT 91.159 (1) Minnewauga Creek, 17 March 1965.

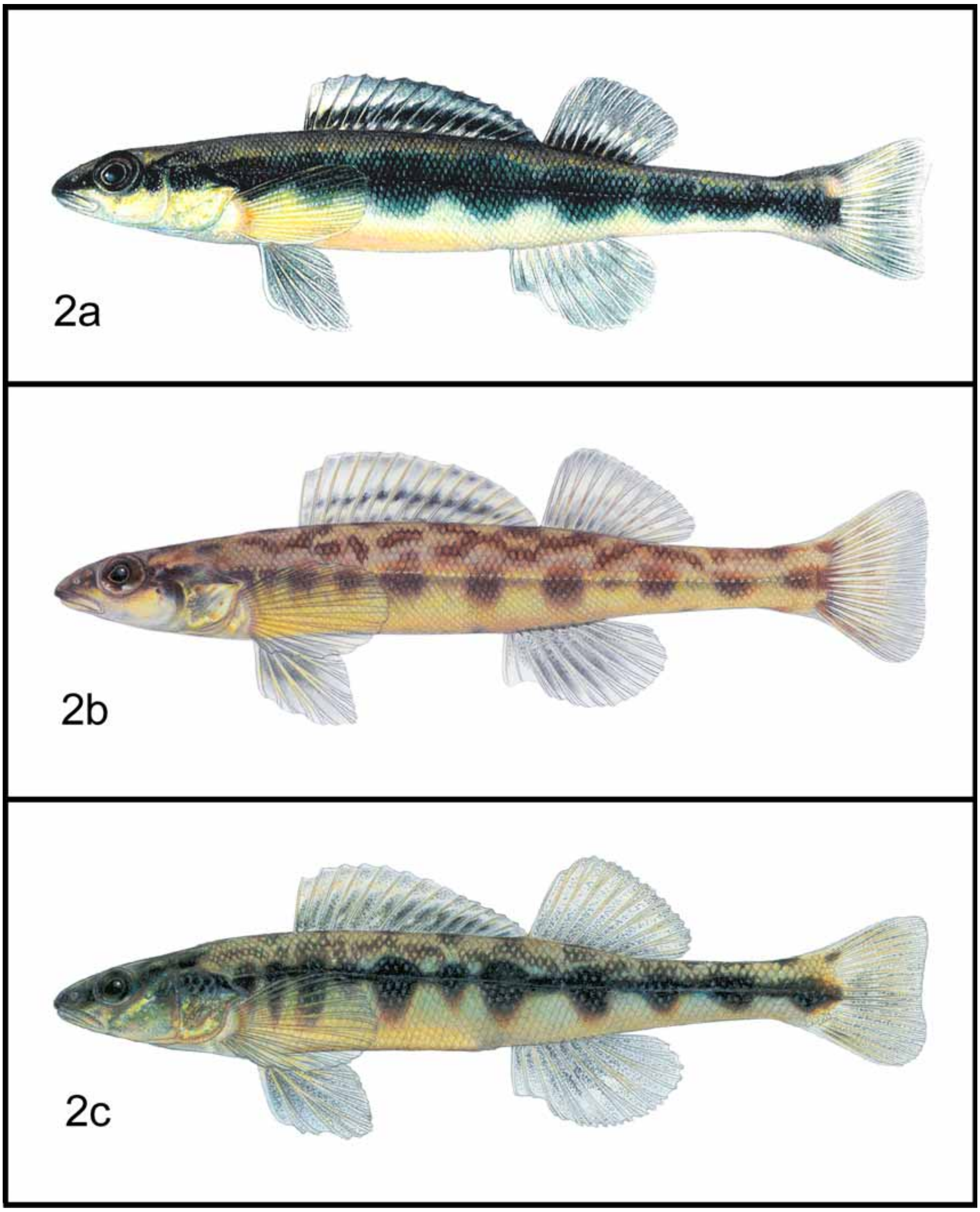

FIGURE 2. Three new species of *Percina* from the Mobile Basin of Alabama, Georgia and Tennessee. *Percina kusha* (2a) male 60 mm, paratype UF 165704, Conasauga River at County Route 392 bridge, 9.2 km NE of Cisco, Coosa River system, Murray County, Georgia, 28 April 1994; *P. sipsi* (2b) male 48 mm, UAIC 10274.02, Sipsey Fork River at Forest Service Road 234, 8.8 km NNE of Double Springs, Black Warrior River system, Winston County, Alabama, 2 March 1992; and *P. smithvanizi* (2c) male 58 mm, UAIC 10661.05, Rocky Branch, along US Hwy 78, 2.4 km W of Heflin, Tallapoosa River system, Cleburne County, Alabama, 4 April 1993.

Coosa River drainage—Etowah River system

Georgia: Dawson County: GMNH 74 (1) Etowah River, 8 July 1948. GMNH 2059 (1) Amicalola Creek at County Route 25, about 14.5 air km NNW of Dawsonville (34°29'59"N; 84°14'51"W), 8 May 1990. UF 165649 (4) same locality, 2 May 1990. UF 165647 (1) same locality, 3 April 1994. UAIC 10471.09 (1) same locality, 20 July 1992. NMB 1446 (1) Little Amicalola Creek at County Route 25 (34°30'04"N; 84°14'04"W), 17 June 1994. UF 165646 (1) Cochran Creek at County Route 45, about 2.1 km W of junction with State Route 342, 3 April 1994. UF 90079 (3) Amicalola Creek, off County Route 28, 2.2 air km SW of junction of County Route 28 and State Route 136, at Fausett Lake (34°31'42"N; 84°16'48"W), 19 November 1991. **Lumpkin County:** GMNH 2052 (1) Etowah River at Georgia Hwy 52 (34°32'05"N; 84°03'48"W), 13 May 1990. UF 165648 (3) Etowah River at County Route 72 (34°33'37"N; 84°04'27"W), 28 April 1994. UAIC 10621.14 (1) Etowah River, 10.6 km NW of Dahlonega, 1.6 km W of Whissenhunt Mountain on unpaved Forest Service road, 29 June 1990.

Material used in molecular analysis.

Coosa River drainage—Conasauga River system

Tennessee: Polk County: STL 1405.01 (3) Minnewauga Creek, just upstream of mouth (35°00'15"N; 84°41'26"W), 20 January 2003, EF613216.

Coosa River drainage—Etowah River system

Georgia: Dawson County: UAIC 13560.02 (2) Amicalola Creek, along Tate Hwy, 3.2 km NW of Afton (34°31'05"N 84°16'53"W), 24 March 2002, EF613217, EF613218.

Diagnosis. *Percina kusha* is distinguished from all other described species of *Percina* by a combination of the following characteristics: absence of bright colors on body and fins of adults; no orange band in spinous dorsal fin; no broad vertical bands on body extending dorsally across the back joining those of the other side; 7–11 lateral blotches connected to form a continuous dark brown to black lateral stripe with undulating margins; lateral stripe continuous with large, quadrate basicaudal blotch that extends onto base of caudal fin rays; small, dark blotch on upper and lower portion of caudal fin base, dorsal blotch typically darker; body below lateral stripe white to cream colored, without dark blotches, dusky in breeding males; suborbital bar absent or very poorly developed; lateral line complete, typically no pored scales on base of caudal fin; males with row of modified scales on midline of belly and one or two modified scales between base of pelvic fins; modified breast scale absent; nuptial tubercles absent; anal fin of breeding males not excessively elongate; males without caudal keel as a ventral extension of the caudal peduncle; snout not projecting beyond anterior margin of upper jaw; well-developed premaxillary frenum; serrae on margin of preopercle absent; branchiostegal membranes overlapping or very narrowly joined.

Percina kusha is distinguished from the other two species described herein by a combination of the following characters: dorsum above dark brown to black lateral stripe tan to light brown, uniformly pigmented, typically without dark reticulations; midline of dorsum without dark saddles or if present confined to midline of dorsum; scales present on nape, cheeks, opercles, and breast.

Description. *Percina kusha* is a moderately small species of *Percina*; the largest specimen examined is a 65 mm SL male. Typical shape of the head and body illustrated in Figure 2a. Frequency distribution of scale, fin ray and vertebral counts given in Tables 1–8. Degree of nape squamation presented in Table 9 and the posterior extent of development of pored lateral line scales given in Table 10. Proportional measurements presented in Table 11. Body moderately elongate, slender, snout moderately long, about equal in length to the orbit, and frenum well-developed. Preopercular margin entire and branchiostegal membranes separate or very narrowly joined. Total lateral line scales 58–73, usually 65–70; transverse scale rows 14–18, usually 17 in the Conasauga River population and 15 in the Etowah River population; caudal peduncle scales 18–25, usually 22–24 in the Conasauga River population and 19–21 in the Etowah River population; dorsal spines 11–15, usually 12–14; dorsal soft rays 9–11, usually 10; anal soft rays 6–9, usually 8; pectoral rays 13–14, usually 14; vertebrae 41–43, usually 42.

Lateral line usually complete but some individuals with 1–2 unpored scales anterior to posterior edge of hypural plate or a pored scale on the caudal fin base (Table 10). Scales present on the opercles and upper three quarters of the cheek. Nape completely scaled, occasionally with some embedded scales anteriorly. Scales on the anterior portion of breast and prepectoral area usually embedded. Belly typically scaled with the exception of the area immediately posterior of the base of the pelvic fins. Males with a row of enlarged, modified ctenoid scales present on midline of belly, but usually less well-developed or absent just posterior to pelvic fin base. There are usually 1–2 modified scales present between the base of pelvic fins. Occasionally an individual will have up to four modified scales but only one or two are large and well-developed. The large, modified breast scale at the anterior junction of the pelvic girdle of some *Percina* is absent in *P. kusha*. In females the row of scales along the midline of the belly is greatly reduced or absent but there are usually one or two modified scales present between the base of the pelvic fins. Breeding tubercles are absent but some males have thickened ridges along margin of anal fin rays.

TABLE 1. Lateral line scale counts for *Percina kusha*, *P. sipsi*, and *P. smithvanizi*.

	Lateral line scales																			
	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	N	
P. kusha																				
Conasauga										3	3	2	3	3	6	2	1	1	24	68.5
Etowah			2	1			2	1		4	3	1	2	2				1	19	64.9
P. sipsi	1	2	2	1	4	4	2	5	2	4	8	12	6	7	1	1	2		64	65.1
P. smithvanizi		3	2	3	5	14	9	17	22	11	9	11	6	2	3	1			118	63.9

TABLE 2. Transverse scale rows from soft dorsal fin origin to anal fin base for *Percina kusha*, *P. sipsi*, and *P. smithvanizi*.

	Scale rows									
	12	13	14	15	16	17	18	19	N	
P. kusha										
Conasauga	–	–	–	–	5	14	3	–	22	16.9
Etowah	–	–	6	10	3	–	–	–	19	14.8
P. sipsi	–	–	1	9	19	15	8	1	53	16.4
P. smithvanizi	2	11	35	53	18	1	1	–	121	14.7

TABLE 3. Least scale rows around caudal peduncle for *Percina kusha*, *P. sipsi*, and *P. smithvanizi*.

Species	Scale rows									
	17	18	19	20	21	22	23	24	25	N	
P. kusha											
Conasauga River	–	–	–	–	3	7	7	4	1	22	22.7
Etowah River	–	1	5	6	7	–	–	–	–	19	20.0
P. sipsi	–	4	13	17	8	2	–	–	–	44	19.8
P. smithvanizi	1	11	35	53	18	1	1	–	–	121	19.5

Live coloration of adult females and males is similar but females typically lack the dusky ground color present in males. Sides of the body with 8–11 elongate oval blotches which are connected forming a uniformly dark lateral stripe with undulating margins. In some individuals the dark blotches are discrete but connected by lighter brown pigment. Lateral blotches are lighter in color and less connected in juveniles. Anteriorly the lateral stripe is continuous with the postorbital and preorbital bars. Posteriorly the lateral stripe terminates on the base of the caudal fin in a somewhat quadrate-shaped blotch that is equal or slightly lighter in color to the lateral stripe. It is usually centered just below the midline of the caudal fin. The blotches on the upper and lower caudal fin base vary in size and intensity. In most individuals the upper blotch is larger and more intense. The lower blotch is often indistinct or merged with the basicaudal blotch. Above the dark, undulating lateral stripe, the dorsum is typically tan to light brown without any blotches, reticulations, bars or saddles. In some individuals thin, elongate blotches may be present along the midline of the dorsum and an adjacent scale row on each side, usually under the dorsal fins. Occasionally an individual may have a dusky, thin line, one or two scale rows wide, just above the lateral stripe. This line is often interrupted forming a series of long dashes above the lateral stripe. Intensity of the thin line of dark pigment varies but is always darker than the adjacent dorsal pigmentation but lighter than the lateral stripe. Any dark pigment present above the lateral blotches is most prevalent in juveniles. Below the lateral stripe the body is uniformly pigmented and lacks dark spots, blotches or reticulations. It is typically dusky on breeding males but always uniformly pigmented. Breast and lower side of head are white to cream colored but may be dusky in breeding males. Some individuals have a few melanophores on the anterior base of the pectoral fin. Suborbital bar is typically absent, but some breeding males have an irregular shaped cluster of melanophores on the midventral margin of the orbit.

TABLE 4. Dorsal fin spine counts for *Percina kusha*, *P. sipsi*, and *P. smithvanizi*.

Species	Dorsal fin spines						
	11	12	13	14	15	N	
P. kusha							
Conasauga	1	1	17	4	1	4	12.6
Etowah	–	5	11	3	–	19	12.9
P. sipsi	–	4	33	20	1	58	13.3
P. smithvanizi	6	31	75	17	–	129	12.8

TABLE 5. Dorsal fin ray counts for *Percina kusha*, *P. sipsi*, and *P. smithvanizi*.

Species	Dorsal fin rays				
	9	10	11	N	
P. kusha					
Conasauga	5	14	5	24	10.0
Etowah	–	17	2	19	10.1
P. sipsi	26	33	1	59	9.6
P. smithvanizi	34	88	7	128	9.8

TABLE 6. Anal fin ray counts for *Percina kusha*, *P. sipsi*, and *P. smithvanizi*.

Species	Anal fin rays					
	6	7	8	9	N	
P. kusha						
Conasauga	–	1	20	3	24	8.1
Etowah	–	3	16	–	19	7.8
P. sipsi	1	24	34	–	59	7.6
P. smithvanizi	–	24	93	5	122	7.8

TABLE 7. Pectoral fin ray counts for *Percina kusha*, *P. sipsi*, and *P. smithvanizi*.

Species	Pectoral rays					
	11	12	13	14	N	
P. kusha						
Conasauga	–	–	6	18	24	13.8
Etowah	–	–	5	14	19	13.7
P. sipsi	–	–	35	15	50	13.3
P. smithvanizi	1	7	87	21	116	13.1

TABLE 8. Vertebral counts in *Percina kusha*, *P. sipsi* and *P. smithvanizi*.

Species	Number of vertebrae					
	40	41	42	43	N	
P. kusha	–	14	20	2	36	41.7
P. sipsi	7	35	4	–	46	40.9
P. smithvanizi	6	39	12	–	57	41.1

Pigmentation of the spinous dorsal fin of males consists of a broad, dusky basal band, almost black in breeding males, an unpigmented submarginal band, and a thin, dusky marginal band. Dusky pigment in dorsal fin is usually darker posteriorly. Pigmentation of the soft dorsal and caudal fins is variable but typically there are dusky marginal and basal bands with an unpigmented band in between. The pelvic, pectoral, and anal fins are usually clear except dusky in breeding males.

Coloration of non-spawning males and females is yellowish above and below the dark bluish-black lateral stripe. Breast and belly are white to cream color. Top of head and snout variously mottled with yellowish-orange color. Dorsal, pectoral, and caudal fins pale yellowish and the pelvic and anal fins colorless.

Variation in the scale counts (Tables 1–3) between the Conasauga and Etowah River populations of *Percina kusha* was unexpected considering the proximity of the two drainages (Fig. 3). There is almost no overlap in number of scale rows from the soft dorsal origin to the anal fin base and the caudal peduncle scale rows. There is also a modal difference in the degree of nape squamation between the two drainages (Table 9). Analysis of mitochondrial DNA revealed very little differentiation between these populations, although they were recovered as reciprocally monophyletic groups (discussed below). A higher number of lateral line scales and vertebrae were reported for *P. lenticula* populations in the Etowah River drainage compared to the Coosa and Cahaba River populations (Richards & Knapp 1964; Suttkus & Ramsey 1967). This variation may be the result of habitat differences between the Etowah and Conasauga River drainages. Most of the Etowah drainage is in the Piedmont physiographic province, and most of the Conasauga is in the Valley and Ridge province (Fig. 3). The presence and distribution of other endemic species in the Etowah drainage (e.g. *Etheostoma etowahae*, *E. scotti*, and *Cambarus fasciatus*) suggests that the divide between the physiographic provinces has been an effective barrier to gene flow in some taxa, and may be responsible for speciation within the Piedmont portion of the Etowah River system.

Distribution. *Percina kusha* is restricted to the headwaters of the Coosa River in Georgia and Tennessee (Fig. 3). It occurs in the main channel of the upper reaches of the Conasauga River in Murray and Whitfield counties, Georgia, and Bradley and Polk counties, Tennessee. It is also known from short reaches of three tributaries to the Conasauga River: Holly Creek, Murray County, Georgia; and Ball Play and Minnewauga creeks, Polk County, Tennessee. In the Etowah River it occurs in the main channel in Dawson and Lumpkin counties, Georgia, and in several tributaries: Amicalola, Little Amicalola, Cochran and Shoal creeks, Dawson County, Georgia.

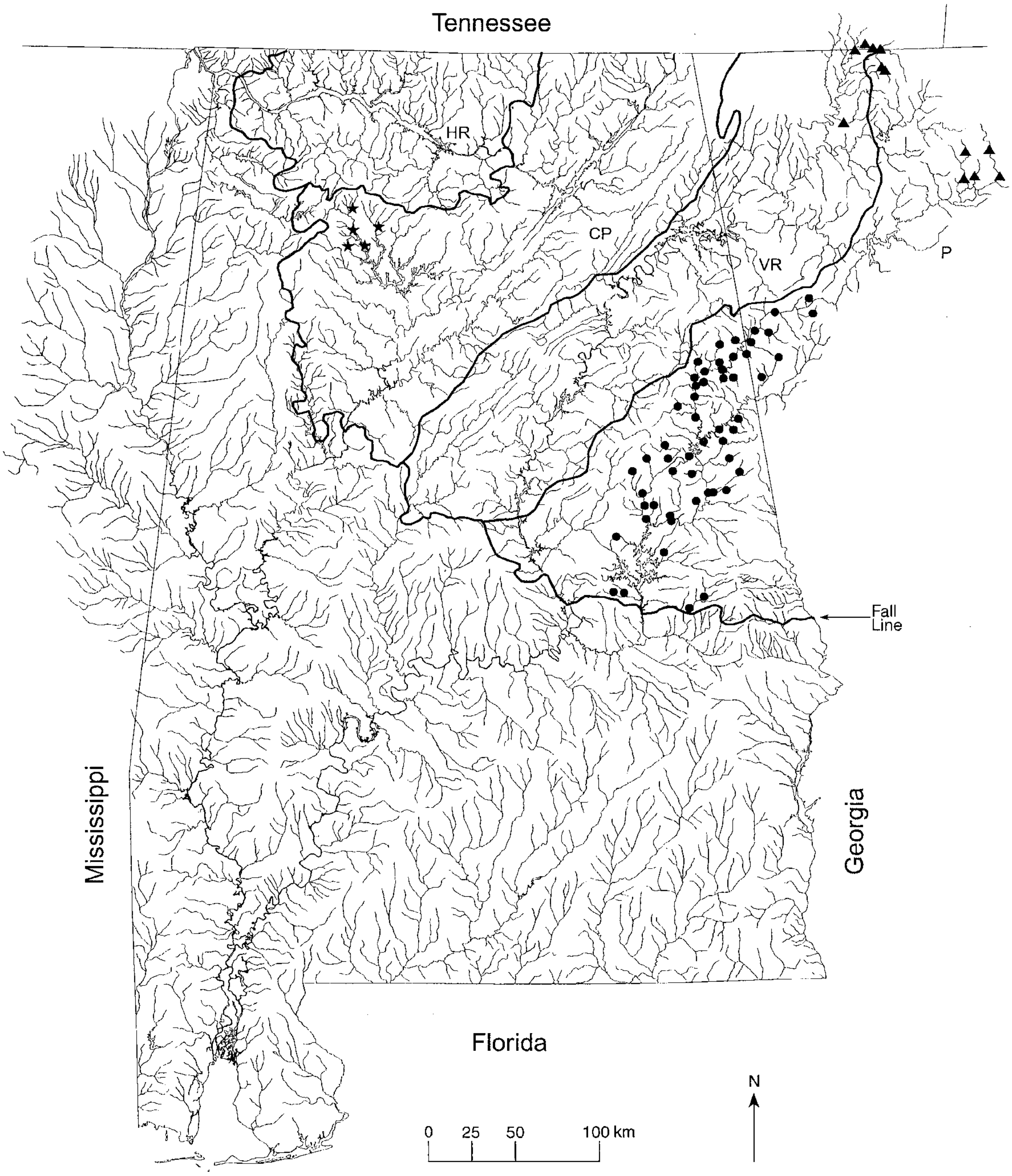

FIGURE 3. Distribution of three new species of *Percina* from the Mobile Basin of Alabama, Georgia and Tennessee. *Percina kusha* (triangles), *P. sipsi* (stars) and *P. smithvanizi* (circles). Upland physiographic provinces are outlined and identified by two letter abbreviations: HR = Highland Rim; CP = Cumberland Plateau; VR = Valley and Ridge; and P = Piedmont.

Ecology. *Percina kusha* inhabits small rivers and lower reaches of tributary creeks with good water quality. These streams are characterized by moderate gradient where the substrate consists of sand, gravel, cobble and bedrock. *Percina kusha* is usually found in flowing pools and backwaters adjacent to runs, where it has been observed hovering over or resting on submerged structures such woody debris, stems of *Justicia americana*, and large cobble. During winter we have observed *P. kusha* among leaf packs in pools. Frequent associates of *P. kusha* are *Campostoma oligolepis*, *Cyprinella trichroistia*, *C. venusta*, *Etheostoma stigmaeum*, *Hypentelium etowanum*, *Notropis xaenocephalus*, *P. kathae*, *P. nigrofasciata* and *P. palmaris*. Etnier & Starnes (1993) provide information on feeding and reproduction of the Conasauga River population. Johnson *et al*.

(2002) conducted a study of seasonal spawning habitat utilization in the Conasauga River in Murray County, Georgia, during 1999 and 2000. There is no information available on the ecology and biology of the Etowah River population of *P. kusha*.

TABLE 9. Degree of nape squamation in *Percina kusha*, *P. sipsi* and *P. smithvanizi*. Degree of nape squamation is based on a relative scale: 0 = nape naked along dorsal midline before spinous dorsal; 1–3 = successive increases in squamation of nape (posterior to anterior); 4 = nape wholly scaled but scales embedded at least anteriorly; and 5 = nape completely invested with exposed scales.

Species	Degree of nape squamation							
	0	1	2	3	4	5	N	
P. kusha								
Conasauga	–	–	–	2	19	2	23	4.0
Etowah	–	–	–	–	8	11	19	4.6
P. sipsi	56	5	6	–	–	–	67	0.3
P. smithvanizi	–	–	–	1	77	30	108	4.3

Conservation status. Etnier & Starnes (1991) considered the conservation status of *Percina kusha* to be endangered, like two other *Percina* species endemic to the upper Coosa River system, *P. antesella* and *P. jenkinsi*. In a review of conservation status of fishes in Georgia, Freeman (1999) assigned a status of rare (a species in need of protection because of its scarcity) to populations in Georgia. Warren *et al*. (2000) and Freeman *et al*. (2005) both regarded *P. kusha* as vulnerable (any taxon that may become endangered or threatened by relatively minor disturbance to its habitat). Based on our sampling and snorkeling observations, *P. kusha* appears to be a species that naturally occurs in low abundance, at least when compared to sympatric congeners such as *P. nigrofasciata* and *P. palmaris.* We do not know, however, what the actual range of the species was prior to European colonization. Its association with slow-flowing habitats suggests *P. kusha* could have occurred throughout the Conasauga and Etowah rivers, and possibly in the geographically intermediate Coosawattee River, below the gorge now impounded by Carters Dam and Reservoir (Fig. 3). Considering its very limited distribution in portions of two small rivers and threats to its habitat from municipal and industrial development and forestry and agriculture activities we consider *P. kusha* to be endangered.

Etymology. The specific name, *kusha*, is the Choctaw Indian name for cane or canebrake and is the origin of the name of the Coosa River (Foscue 1989). The common name, Bridled Darter, is in reference to the preorbital and postorbital bars that are continuous with the lateral stripe, thus resembling an equestrian bridle and reins.

Comparison with congeners. In the headwaters of the Coosa River in northwest Georgia, populations of *Percina kusha* are sympatric and occasionally syntopic with eight species of *Percina*: *P. antesella*, *P. aurolineata*, *P. jenkinsi*, *P. kathae*, *P. lenticula*, *P. nigrofasciata*, *P. palmaris* and *P. shumardi*. The dorsum of most individuals of *P. kusha* are uniformly pigmented above the dark brown to black lateral band which distinguishes it from all eight species of *Percina* which typically have well-developed saddles that extend across the back, mid-dorsal blotches, lateral and dorsolateral bars or a dorsolateral stripe (above dark lateral stripe). Morphologically, *P. kusha* is easily distinguished from the logperches, *P. jenkinsi* and *P. kathae*, which have a conical snout that projects beyond the anterior margin of the upper jaw. It differs from both *P. antesella* and *P. shumardi* in having a well-developed frenum and a row of modified scales along the midline of the belly of males. *Percina kusha* also lacks the elongate anal fin and breeding tubercles, which are well-developed on the anal, caudal, and pelvic fins, of breeding male *P. antesella* and *P. shumardi*. *Percina kusha* has very narrowly joined to overlapping gill membranes which differs from the more broadly joined membranes present in *P. lenticula* and *P. nigrofasciata*. The lateral blotches of *P. lenticula* and *P. nigrofasciata* are also more vertically elongate than those of *P. kusha*. The remaining species, *P. aurolineata*, differs in having a serrate preopercle and from 1–3 pored lateral line scales on the base of the caudal fin.

***Percina sipsi*, Williams & Neely, new species**
Bankhead Darter
(Fig. 2b)

Holotype. UF 165737, 46 mm SL, Sipsey Fork at Alabama Hwy 33, 3 km NE of Rock Springs, Winston County, Alabama (34°13’05”N; 87°22’09”W), 20 January 2003.

Paratypes. Black Warrior River drainage—Sipsey Fork system

Alabama: Lawrence County: TU 163064 (1; 43 mm) Borden Creek, tributary to Sipsey Fork, 29 April 1992. TU 168262 (1; 50 mm) Borden Creek at Forest Road, Sipsey Wilderness, Section 12, 12 September 1993. UAIC 6427.03 (1; 39 mm) Borden Creek at Forest Service Route 224, Bankhead National Forest (34°18'34"N; 87°23'42"W), 19 April 1981. **Winston County:** AUM 18786 (6; 35–45 mm) West Fork Sipsey Fork at Forest Service Road 234, 8.8 km NNE of Double Springs (34°13'32"N; 87°22'37"W), 3 June 1979. UF 103304 (9; 37–49 mm) same locality, 17 April 1995. TU 83137 (7; 16–46 mm) same locality, 3 July 1971. UAIC 4329.21 (5; 39–46 mm) West Fork Sipsey Fork, 21.6 km ENE of Haleyville (34°17'03'N; 87°23'56"W), 2 November 1978. INHS 48682 (7; 29–47 mm) Sipsey Fork at Alabama Hwy 33, 3 km NE of Rock Springs (34°13’05”N; 87°22’09”W), 13 August 1998. UAIC 10390.08 (6; 31–40 mm) same locality, 20 August 1986. UF 165738 (5; 38–48 mm) same locality, 20 January 2003. UMMZ 194316 (9; 36–40 mm) Sipsey River at Low Pressure Bridge, about 6.4 km E of Alabama Hwy 195, about 8.8 km NNE of Double Springs (T9S, R8W, S23), 15 October 1971. USNM 211256 (35; 32–44 mm) Sipsey River, about 4 km W of Grayson and about 16 km NNE of Double Springs, (T9S, R8W, S10), 29 October 1971.

Additional material (nontypes).

Black Warrior River drainage—Sipsey Fork system

Alabama: Lawrence County: AUM 27232 (1) Borden Creek at gravel road, Sipsey Wilderness, 22.2 air km SW of Moulton, 30 August 1991. **Winston County:** AUM 27043 (4) Sipsey Fork at Alabama Hwy 33 (34°13’05”N; 87°22’09”W), 27 November 1990. TU 83136 (1) Sipsey Fork, 8.5 km E of Ashridge, 1 km above Lake Lewis Smith (T9S, R8W, S33), 3 July 1971. UAIC 1695.21 (8) West Fork Sipsey Fork, 22.5 km ENE of Haleyville (34°16'24"N; 87°22'28"W), 12 July 1978. UAIC 4323.18 (1) West Fork Sipsey Fork, 20.6 km ENE of Haleyville (34°17'56"N; 87°24'55"W), 2 November 1978. UAIC 10274.02 (3; 39–48 mm) West Fork Sipsey Fork at Forest Service Road 234, 8.8 km NNE of Double Springs (34°13'32"N; 87°22'37"W), 2 March 1992.

Material used in molecular analysis.

Black Warrior River drainage

Alabama: Winston County: STL 1406.01 (4) Sipsey Fork at Alabama Hwy 33, 3 km NE of Rock Creek (34°13'05"N; 87°22'09"W), 20 January 2003, EF613207, EF613208, EF613209, EF613210

Diagnosis. *Percina sipsi* is distinguished from all other described species of *Percina* by a combination of the following characteristics: absence of bright colors on body and fins of adults; no orange band in spinous dorsal fin; no broad vertical bands on body extending dorsally across the back joining those of the other side; 7–11 lateral blotches fused into continuous dark brown to black lateral stripe with undulating margins; lateral stripe continuous with large, somewhat quadrate basicaudal blotch that extends onto base of caudal fin rays; small, dark blotch on upper and lower portion of caudal fin base, dorsal blotch typically darker; body below lateral stripe white to cream colored, without dark blotches, becoming dusky in breeding males; suborbital bar absent or very poorly developed; lateral line complete, typically no pored scales on base of caudal fin; males with row of modified scales on midline of belly and one or two modified scales between base of pelvic fins;

modified breast scale absent; nuptial tubercles absent; anal fin of breeding males not excessively elongate; males without caudal keel as a ventral extension of the caudal peduncle; snout does not project beyond anterior margin of upper jaw; broad premaxillary frenum present; serrae on margin of preopercle absent; branchiostegal membranes very narrowly joined to overlapping.

Percina sipsi is distinguished from the other two species described herein by a combination of the following characters: dorsal saddles usually present but may be poorly developed, typically consisting of quadrate blotches on the posterior portion of nape, under posterior end of spinous dorsal fin, and the soft dorsal fin; dorsum with dusky brown reticulations above lateral stripe; cheeks and opercles scaled; nape typically naked, occasionally partially scaled; breast naked, occasionally with a few embedded cycloid scales.

Description. *Percina sipsi* is one of the two smallest species in the genus *Percina*, rarely exceeding 50 mm SL (*P. brevicauda*, maximum SL is 50 mm, see Suttkus *et al*. 1994). Shape of the head and body are illustrated in Figure 2b. Frequency distribution of scale, fin ray and vertebral counts given in Tables 1–8. Degree of nape squamation presented in Table 9 and posterior extent of development of pored lateral line scales given in Table 10. Proportional measurements presented in Table 11. Body terete, moderately elongate, snout moderately long, about equal to orbit in length, with a well-developed frenum. Preopercular margin entire and branchiostegal membranes separate or very narrowly joined. Total lateral line scales 56–72, usually 60–69; transverse scale rows 14–19, usually 16 or 17; caudal peduncle scales 18–22, usually 19–21; dorsal spines 12–15, usually 13 or 14; dorsal soft rays 9–11, usually 9 or 10; anal soft rays 6–8, usually 8; pectoral rays 13–14, usually 13; vertebrae 40–42, usually 41.

TABLE 10. Posterior extent of development of the pored lateral line scales in *Percina kusha*, *P. sipsi* and *P. smithvanizi*. Negative value indicates unpored scales before caudal fin base, positive value indicates pored scales on caudal fin base.

Species	Posterior extent of pored lateral line scales						
	–3	–2	–1	0	+1	N	
P. kusha							
Conasauga	–	2	7	14	2	23	–0.5
Etowah	–	–	1	13	5	19	0.2
P. sipsi	1	4	17	33	2	57	–0.5
P. smithvanizi	1	1	28	68	10	108	–0.2

Lateral line complete but occasionally an individual will have 1–3, usually one or two, unpored scales before the posterior edge of the hypural plate or a pored scale on the base of the caudal fin (Table 10). Embedded scales present on the upper three quarters of the cheek and opercle. Nape usually naked, occasionally with some embedded scales (Table 9). Breast and prepectoral area naked, rarely individuals with a few embedded scales. Belly typically scaled with the exception of the area immediately posterior of pelvic fin base. A row of enlarged, modified ctenoid scales present on midline of belly but ends a few scale rows posterior to pelvic fin base. Typically one or two modified scales present between the bases of pelvic fins. The large modified breast scale at the anterior margin of the pelvic girdle of some *Percina* is absent in *P. sipsi*. In females the scales along the midline of the belly and laterally one to two rows are often embedded. Midventral row of modified scales on the belly of females is greatly reduced in development and number compared to males and is absent in some individuals. There are usually one or two modified scales present between the bases of the pelvic fins. Breeding tubercles and the thickened ridges along margin of anal fin rays of some males are absent in females.

The general pattern of pigmentation in life is similar in males and females but females usually lack the dusky ground color present in males, most pronounced in breeding males. Sides of the body with 7–10 round to slightly oval, dark brown blotches which are typically connected by a lighter brown lateral stripe two or three scale rows wide. Some individuals appear to have smaller blotches between larger blotches but are obscured by the underlying lateral stripe. Lateral blotches are usually lighter in color and less connected in small individuals and females. Anteriorly the lateral stripe merges with the postorbital and preorbital bars. The lateral stripe terminates on the base of the caudal fin in a quadrate basicaudal blotch. There are also dark blotches on the caudal fin base above and below the basicaudal blotch. These blotches vary in size and intensity but the upper blotch is usually more distinct than the lower. Above the lateral stripe the dorsum is variously marked with tan to light brown reticulations and blotches, varying in size and intensity. Most reticulations are formed by darkly pigmented scales and are 1–3 scale rows wide. Some individuals have reticulations that are aligned in a pattern two or three scale rows above the lateral stripe while others have no discernible pattern. Along the midline of the dorsum there are up to nine tan to light brown poorly developed saddles and when present typically consist of quadrate blotches. These blotches are often irregular in shape and vary in their placement and development. Their alignment usually consists of one blotch on the nape just anterior to the dorsal fin origin and if a second is present it is located anteriorly on the nape, three blotches under the spinous dorsal, one near the junction of the spinous and soft dorsal fin, two under the soft dorsal fin, and two on the caudal peduncle. Below the lateral stripe the body is usually devoid of blotches, spots, or reticulations but may be dusky on breeding males. On the head, the cheeks and opercles below the postorbital stripe lack dark pigment but may be dusky on breeding males. A well-developed suborbital bar is absent but a cluster of large melanophores may be present on the midventral margin of the orbit. The breast is without any dark pigment but there is typically a cluster of melanophores present on the anterior prepectoral region.

The spinous dorsal fin of males has a thin, dusky margin, a clear submarginal band, and a dark basal band which is usually darker posteriorly. The soft dorsal, anal, and caudal fins are usually clear but may be dusky in breeding males, with a slight intensification of pigment towards the margin. The pelvic and pectoral fins are usually clear but are dusky in breeding males.

Distribution. *Percina sipsi* is known only from the Sipsey Fork of the Black Warrior River in the Bankhead National Forest in northwestern Alabama (Fig. 3). It occurs in Borden Creek in Lawrence County, and Brushy Creek, Caney Creek, and Sipsey Fork (recorded as West Fork Sipsey River on some maps) in Winston County. While the current known range of *P. sipsi* is very limited and confined downstream by Lewis Smith Reservoir, historically it is possible that the species ranged farther downstream in the Sipsey Fork and conceivably in the Locust and Mulberry forks of the Black Warrior River, which are all located in the Cumberland Plateau physiographic province (Fig. 3). Riverine habitat in the lower reaches of the Sipsey Fork was destroyed in 1960 by the Alabama Power Company impoundment behind Lewis Smith Dam. The current distribution of *P. sipsi* represents the most restricted range of any known species of *Percina*.

Ecology. *Percina sipsi* inhabits creeks and small rivers ranging in size from 5–40 m in width and 0.25 to 2 m in depth. The species occurs in clear water over sand and fine gravel, usually in association with leaf packs and/or woody debris, but occasionally over the broad expanses of open bedrock which are abundant in parts of the mainstem Sipsey Fork.

Conservation status. Ramsey (1976) published the first conservation status review of *Percina sipsi* and reported it to be a threatened species. Although the assigned conservation status category has varied in subsequent evaluations (Deacon *et al*. 1979; Ramsey 1984; Williams *et al*. 1989; Warren *et al*. 2000), all authors considered the Bankhead Darter's continued existence to be in a precarious situation. In the most recent assessment of conservation status of Alabama wildlife, Kuhajda (2004) reported it as a species of highest conservation concern. The entire range of this species is in the Bankhead National Forest, providing some level of protection. We consider *P. sipsi* to be highly endangered based on its restricted distribution, rarity within the occupied range, habitat vulnerability, and absence of downstream habitat for future recovery. *Percina sipsi* is extremely vulnerable and needs continuous monitoring and proactive management actions to prevent extinction.

Etymology. The specific name, *sipsi*, is the Chickasaw-Choctaw Indian name for poplar or cottonwood tree, and is the origin of "Sipsey" in the stream name, Sipsey Fork of the Black Warrior River (Foscue 1989), to which this species is endemic. The common name, Bankhead Darter, is in reference to the William B. Bankhead National Forest which encompasses the range of the species.

Comparison with congeners. In the Sipsey Fork, a tributary to the Black Warrior River, *Percina sipsi* occurs with five species of *Percina*: *P. kathae*, *P. maculata*, *P. nigrofasciata*, *P. sciera* and *P. shumardi*. Prior to construction of the impoundments on the Black Warrior River it may have occurred sympatrically with a sixth species, *P. brevicauda*. *Percina sipsi* is distinguished from *P. kathae* which has the snout projecting beyond the anterior margin of the upper jaw, numerous narrow vertical bars on the dorsum and a well-developed basicaudal spot. It differs from *P. maculata* which has a well-developed subocular bar and basicaudal spot and a dark blotch on the base of the anterior 3–4 membranes of the spinous dorsal fin. Males of *P. maculata* typically have a well-developed modified breast scale. *Percina sipsi* can be distinguished from *P. nigrofasciata* which has vertically elongate lateral blotches and moderately joined gill membranes. *Percina sipsi* differs from *P. shumardi* in having a well-developed frenum and a row of modified scales along the midline of the belly of males. Breeding males of *P. sipsi* also lack the elongation of the anal fin and breeding tubercles on the anal, caudal, and pelvic fins that are characteristic of *P. shumardi*. *Percina sciera* is superficially very similar to *P. sipsi* and the two are difficult to distinguish in the field. The most reliable characters to distinguish the two species are the more moderately joined gill membranes and typically serrate preopercle margin in *P. sciera* compared to the narrowly joined gill membranes and smooth preopercle margin of *P. sipsi*. Nape squamation is also a helpful character to distinguish the two species, with *P. sciera* having exposed and/or embedded scales over the entire nape while *P. sipsi* is typically naked or only has a few embedded scales. *Percina sipsi* is a small species, 50 mm maximum known SL, while *P. sciera* often exceeds 50 mm SL. The standard length of 58 mm for *P. sipsi* (UAIC 10274.02) reported in Boschung and Mayden (2004) should read 48 mm. If *P. sipsi* and *P. brevicauda* were found to occur sympatrically they could be distinguished by the presence of a frenum in *P. sipsi* and a black basicaudal spot in *P. brevicauda*.

***Percina smithvanizi*, Williams & Walsh, new species**

Muscadine Darter
(Fig. 2c)

Holotype. UF 165735, 47 mm SL, Turkey Creek at unnumbered county road, about 2.9 km W of Burwell, Carroll County, Georgia (33°35’45”N; 85°13’36”W), 19 January 2003.

Paratypes. Tallapoosa River drainage

Alabama: Chambers County: AUM 23918 (7; 38–51 mm) Tallapoosa River, 2.4 km SSE of Wadley(33°06'07"N; 85°33'25"W), 1 November 1982. UAIC 8525.07 (4; 35–51 mm) same locality, 14 May 1986. UAIC 8526.09 (6; 43–53 mm) same locality, 14 May 1986. **Clay County:** TU 157782 (3; 44–48 mm) Enitachopco [Enitochope] Creek at Alabama Hwy 9, 4.5 km SSW of Ashland (33°14'24"N; 85°51'34"W), 12 April 1990. UMMZ 185373 (5; 45–54 mm) same locality, 21 September 1963. **Cleburne County:** UF 98484 (5; 38–47 mm) Snake Creek at County Route 13, about 5.6 km SW of the center of Heflin (33°35'49"N; 85°37'21"W), 16 July 1992. **Elmore County:** TU 157794 (6; 29–50 mm) Gold Branch, 2.9 km E of Alabama Hwy 63 (32°41'35"N; 86°00'26"W), 12 April 1990. **Randolph County:** AUM 23824 (19; 32–49 mm) Crooked Creek, 7.4 km NW of Malone (33°14'36"N; 85°38'36"W), 27 September 1982. NCSM 44986 (6; 45–55 mm) Tallapoosa River, 6.4 km NNW of Wadley (33°10'27"N; 85°35'04"W), 26 March 1991. NCSM 44987 (7; 36–54 mm) same locality, 4 September 1996. UAIC 8508.14 (2; 38–53 mm) same locality, 4 September 1996. UAIC 10830.20 (5; 40–44 mm) same locality, 26 March 1991. USNM 218508 (6; 34–54 mm) Jones Creek at US Hwy 431, approximately 0.6 km N of Roanoke (33°10'32"N; 85°23'21"W), 17 April 1978. USNM 322736 (5; 43–53 mm) Cornhouse Creek at Alabama Hwy 431 (33°14'20"N; 85°26'31"W), 23 March 1970. UT 91.2143 (16; 30–50 mm) Little Tallapoosa River at US Hwy 431 about 6.4 km N of Wedowee

(33°22'03"N; 85°28'36"W), 16 May 1981. **Tallapoosa County:** INHS 57809 (5; 40–51 mm) Josie Leg Creek at Alabama Hwy 22, 6.1 km SW of Perryville (33°00'07"N; 85°49'58"W), 12 March 1989. NCSM 44985 (4; 39–43 mm) Hillabee Creek, at Alabama Hwy 22, about 9.7 km NE of Alexander City (32°59'07"N; 85°51'41"W), 22 March 1995. UF 91625 (14; 35–53 mm) same locality, 6 April 1992. TU 168037 (4; 44–52 mm) Emuckfaw Creek, 4.8 km W of Daviston (33°03'18"N; 85°41'41"W), 10 July 1993. TU 168051 (1; 51 mm) same locality, 10 July 1993. UAIC 6787.14 (3; 38–54 mm) Emuckfaw Creek 5.3 km SSE of New Site (32°59'43"N; 85°44'58"W), 3 June 1985. UAIC 8518.09 (5; 40–51 mm) same locality, 11 March 1985. UAIC 8476.20 (16; 37–51 mm) Tallapoosa River, 10.8 km SSW of Daviston (32°57'52"N; 85°41'52"W), 22 October 1986. UAIC 8510.10 (3; 35–51 mm) Tallapoosa River, 5.6 km SSE of New Site (32°59'06"N; 85°45'09"W), 11 March 1985. UF 165730 (3; 44–49 mm) Wind Creek at second bridge on Alabama Hwy 50 upstream of mouth (32°40'42"N 85°52'34"W), 18 January 2003. UF 165733 (5; 35–40 mm) Emuckfaw Creek at Alabama Hwy 49, just upstream of Horseshoe Bend NHP (32°59'40"N 85°44'59"W), 18 January 2003. USNM 199818 (14; 35–48 mm) Unnamed tributary of Sougahatchee Creek at Alabama Hwy 49, 19 km N of Tallassee (32°38'04"N; 85°47'48"W), 10 April 1965.

Georgia: Carroll County: UF 165736 (6; 43–48 mm) Turkey Creek at unnumbered county road, about 2.9 km W of Burwell (33°35'45"N 85°13'36"W), 19 January 2003. **Haralson County:** GMNH 1548 (3; 45–57 mm) Tallapoosa River at County Road 130, 23 May 1981. UF 15856 (5; 35–53 mm) North Fork of Walkers Creek at Georgia Hwy 120, 6.1 km SW of Buchanan, 23 April 1968. UF 165731 (8; 43–51 mm) Beech Creek at Georgia Hwy 120, 5.2 km SW of Buchanan (33°45'46"N 85°13'22"W), 19 January 2003. **Paulding County:** UF 165732 (3; 51–58 mm) McClendon Creek at Georgia Hwy 101, 5 km SSE of Beulah (33°51'45"N 84°59'35"W), 19 January 2003. USNM 218470 (10; 38–50 mm) same locality, 17 April 1978.

Additional material (nontype).

Tallapoosa River drainage

Alabama: Chambers County: AUM 22087 (4) Tallapoosa River, 2.7 km SSE of Wadley (33°06'05"N; 85°33'23"W), 8 December 1981. **Clay County:** AUM 15034 (7) White Oak Creek, 1.9 km S of Cragford (33°14'05"N; 85°40'20"W), 26 July 1977. UAIC 2153 (7) Ketchepedrakee Creek, 0.5 km S of Dempsey (33°26'29"N; 85°46'15"W), 6 July 1966. UF 15444 (5) Little Hillabee Creek, 17.7 km NE of Goodwater, 12 September 1963. UF 93917 (1) Creek formed by confluence of Horse Creek and Cave Creek, 2 km SE of Union (33°26'01"N; 85°47'12"W), 16 July 1992. **Cleburne County:** UAIC 6625.08 (3) Cahulga Creek at Alabama Hwy 9 (33°36'19"N; 85°36'09"W), 11 April 1982. **Lee County:** AUM 8677 (2) Sougahatchee Creek, about 3.4 km NW of Loachapoka (32°37'10"N; 85°38'01"W), 17 October 1950. **Randolph County:** AUM 23298 (6) Cornhouse Creek, 4.2 km NE of Malone (33°13'26"N; 85°32'54"W), 8 June 1982. UAIC 6793.22 (9) same locality, 21 July 1983. AUM 23794 (22) Crooked Creek, 7.4 km NW of Malone (33°14'36"N; 85°38'36"W), 18 August 1982. AUM 23962 (29) same locality, 8 November 1982. UAIC 8483.10 (12) same locality, 20 February 1985. UAIC 8487.15 (20) same locality, 7 November 1985. UAIC 8496.12 (5) same locality, 3 April 1986. UAIC 8512.12 (20) same locality, 21 January 1986. UF 99383 (2) Hurricane Creek at County Route 26, about 9.6 km NNW of Wadley (33°10'31"N; 85°35'54"W), 25 May 1995 . UF 104096 (1) same locality, 2 March 1996. **Tallapoosa County:** JDW 95-15 (4) Hillabee Creek at Alabama Hwy 22, 10 km NE of Alexander City (32°59'07"N; 85°51'41"W), 22 March 1995. UAIC 6418.11 (5) same locality, 16 November 1980. UAIC 8494.09 (4) Tallapoosa River, 6 km SSE of New Site (32°59'06"N; 85°45"09"W), 11 March 1985. UAIC 8522.12 (6) same locality, 8 May 1986. UAIC 8495.21 (3) Emuckfaw Creek, 5.3 km SSE of New Site (32°59'43"N; 85°44'58"W), 20 February 1986.

Georgia: Paulding County: UF 165650 (1) Thomasson Creek at Georgia Route 136, 3 km WSW of Yorkville (33°55'01"N; 85°01'44"W), 1 May 1990.

Materials used in molecular analysis.

Tallapoosa River drainage

Alabama: Tallapoosa County: STL 731.02 (1) Wind Creek at second bridge on Alabama Hwy 50 upstream of mouth, below old mill dam (32°40'42"N; 85°52'34"W), 18 January 2003, EF613213. STL 732.01 (1) Emuckfaw Creek at Alabama Hwy 19 just NW of Horseshoe Bend (32°59'40"N; 85°44'59"W), 18 January 2003, EF613214.

Georgia: Carroll County: STL 1383.01 (1) Turkey Creek at unnumbered county road 3 km NW of Burwell (33°35'45"N; 85°13'36"W), 19 January 2003, EF613211. **Haralson County:** STL 1384.01 (1) Beech Creek at Georgia Hwy 120, 5.2 km SW of Buchanan (33°45'46"N; 85°13'22"W), 19 January 2003, EF613215. **Paulding County:** STL 1385.01 (1) McClendon Creek at Georgia Hwy 101, 5 km SSE of Beulah (33°51'45"N; 84°59'35"W), 19 January 2003, EF613212.

Diagnosis. *Percina smithvanizi* is distinguished from all other described species of *Percina* by a combination of the following characteristics: absence of bright colors on body and fins of adults; no orange band in spinous dorsal fin; no broad vertical bands on body extending dorsally across the back joining those of the other side; 7–11 lateral blotches connected to form a continuous dark brown to black lateral stripe with undulating margins; lateral stripe continuous with large, somewhat quadrate basicaudal blotch, which extends onto base of caudal fin rays; a small dark blotch on upper and lower portion of caudal fin base, dorsal blotch typically darker; suborbital bar absent or very poorly developed; lateral line complete, typically no pored scales on base of caudal fin; males with row of modified scales on midline of belly and one or two modified scale between base of pelvic fins; modified breast scale absent; nuptial tubercles absent; anal fin of breeding males not excessively elongate; males without caudal keel as a ventral extension of the caudal peduncle; snout does not extend beyond anterior margin of upper jaw; broad premaxillary frenum present; serrae on margin of preopercle absent; branchiostegal membranes very narrowly joined to overlapping.

Percina smithvanizi is distinguished from the other two species described herein by a combination of the following characters: dorsal saddles usually present, typically consist of quadrate blotches on the posterior portion of nape, under posterior end of spinous dorsal fin, and anterior portion of soft dorsal fin; dorsum with dusky brown reticulations above lateral stripe; scales present on nape, cheeks, opercles and breast. Body depth variable among all three species, but average body depth relative to SL is deeper in *P. smithvanizi* than congeners described herein (see Morphometric comparisons).

Description. A moderately small species of *Percina*, the largest specimen examined is a male 63 mm SL. Frequency distribution of scale, fin ray and vertebral counts given in Tables 1–8. Lateral line usually complete, but often has an unpored scale before the posterior edge of the hypural plate. Less frequently, a single pored lateral line scale present on the caudal fin base. Anteriormost portion of belly often naked, but midventral row of belly scales usually present and composed of modified ctenoid scales in both sexes, but usually more enlarged in males. Prepectoral region invested with exposed scales, as are the opercles and upper three-fourths of the cheeks. Nape fully covered with scales, usually embedded anteriorly, but often exposed (Table 9). Posterior portion of breast with embedded or exposed scales, but naked anteriorly. Enlarged ctenoid scales present between pelvic fin bases, but usually absent on breast on the anterior margin of the pelvic bones. Total lateral line scales 57–71, usually 60–68; transverse scale rows 12–18, usually 14–16; caudal peduncle scales 17–23, usually 19–21; dorsal spines 11–14, usually 12 or 13; dorsal soft rays 9–11, usually 9 or10; anal soft rays 7–9, usually 8; pectoral rays 11–14, usually 13; vertebrae 40–42, usually 41.

The most prominent feature of pigmentation in adults is the blue-black, undulating lateral stripe, formed by the coalescence of 8–11 elongate-oval lateral blotches, and contrasting sharply with the light areas above and below. The lateral blotches are usually brownish and more separated in juveniles. A large, well-defined quadrate basicaudal spot is present as a continuation or slightly interrupted continuation of the lateral band, and extends onto the base of the central caudal fin rays. Smaller, usually less obvious, blotches are present at the bases of the upper and lower principal caudal rays, although the lowermost blotch is frequently absent or obsolescent. The dorsum above the lateral stripe is tan to yellowish, and is variously marked with alternating brownish saddles and intermediate blotches, which are rarely continuous across both sides of the dorsum.

There is usually a dark brown saddle present on the nape. Males possess dusky marginal and basal bands in the spinous dorsal fin but the pigment in the basal band is darker and more concentrated posteriorly. The caudal fin is vaguely marked with three or four light bars. Other fins in the male are dusky, without pronounced banding. The breast and belly are dusky. A cluster of melanophores is usually present on the anterior base of the pectoral fin. Preorbital and postorbital bars are well-developed, and appear continuous with the lateral stripe. The suborbital bar is usually absent, or is very faintly developed in males as a scattering of melanophores and extending directly downward and slightly forward from the ventral margin of the orbit. The upper lip is pigmented above to about half its length posteriorly. The lower surface of the head is usually white to cream color.

Females are similar in color to males, but lack the dusky ground color on the body and fins and dark bands in the spinous dorsal. The cheek, breast, and belly are white to cream colored, often with a scattering of dark-edged scales present around the anal fin. The dorsal fin rays are irregularly marked with faint blotches. The pelvic, pectoral, and anal fins are clear to dusky.

Spawning coloration of males and females collected in early June was yellowish above the lateral stripe, which was blue-black in males but slightly less intense in females, and some yellowish color was present immediately below the lateral stripe. A very pale greenish sheen was present on the lower sides in females. The rays of the dorsal, pectoral, and caudal fins were pale yellowish, the pelvic and anal rays colorless. The top of the snout and head were variously mottled or sprinkled with dusky, brown, orange, or yellow color. A brassy patch was present on the anterior portion of the opercles in adults, diminished in size in juveniles, and all specimens possessed some light blue iridescent pigment on the lower jaw and ventral surface of the head.

Nuptial tubercles were absent, but males in spawning condition had ridged, white epidermal thickenings on the anal rays, which may function as reproductive contact structures.

Distribution. *Percina smithvanizi* is restricted to streams draining the region above the Fall Line in the Tallapoosa River system (Fig. 3). It is widely distributed above the Fall Line except it is absent in upper reaches of the Little Tallapoosa River in Georgia (see Conservation status).

Ecology. *Percina smithvanizi* is common in the Tallapoosa drainage in the Tallapoosa River proper (width 75–125 m, depth 0.5–1 m) as well as tributaries (width 4–5 m, depth 0.2–1 m and larger). Individuals occur in clear water flowing over sand, gravel, rubble, and bedrock, in pools below riffles as well as riffles with moderate current, occasionally from margins of large rocks in the areas of fast flowing water. Areas of swift current yielded the larger specimens, while the smaller individuals were found in habitats with more moderate flow. Species most frequently captured with *P. smithvanizi* were *Cottus* sp. Tallapoosa Sculpin (Neely et al. in press), *Etheostoma tallapoosae*, *Hypentelium etowanum*, and *P. palmaris*. Other species commonly captured with *P. smithvanizi* included *Campostoma oligolepis*, *Phenacobius catostomus*, *Cyprinella gibbsi*, *Noturus funebris*, and *N. leptacanthus*. A detailed account of the ecology and biology of *P. smithvanizi* was reported by Wieland & Ramsey (1987).

Conservation status. *Percina smithvanizi* is a relatively common darter in undisturbed streams above the Fall Line in the Tallapoosa River. However, it has disappeared in disturbed streams and impoundments associated with mainstream dams on the Tallapoosa River. It has also disappeared from most of the headwaters of the Little Tallapoosa River in Georgia. The species was regarded as vulnerable by Freeman *et al*. (2005).

The upper two-thirds of the Tallapoosa River drainage was historically isolated from the lower one-third by a series of falls located at the Fall Line, near the present day town of Tallassee, Alabama. In the early 1900's three dams were constructed on the Tallapoosa River in the vicinity of the Fall Line further isolating the upper and lower portions of the river system. The falls appear to have represented a barrier to upstream dispersal for many fishes, including *Percina nigrofasciata*. In a survey of fishes in the Tallapoosa River system (Williams 1965) *P. nigrofasciata* was absent from most of the upper Tallapoosa River with the exception of the upper reaches of the Little Tallapoosa River in Georgia. Based on comparison of meristic and pigmentation characters with data from Crawford (1965), it appears that this population of *P. nigrofasciata* was introduced from the adjacent Chattahoochee River system where the species is common (Williams 1965). Crawford (1965) reported a collection of *P. nigrofasciata* in the upper Tallapoosa River drainage, near the junction of the Tallapoosa and Little Tallapoosa rivers, but this record is based on specimens of *P. smithvanizi*. In the upper reaches of the Little Tallapoosa River system, the absence of *P. smithvanizi* in the presence of an introduced population of *P. nigrofasciata* suggests possible competitive displacement. If competitive displacement is occurring in the Little Tallapoosa River, the population of *P. smithvanizi* above the backwaters of R.L. Harris Reservoir may be at risk. Additional populations of *P. nigrofasciata* have been reported from tributaries of Lake Martin (Boschung & Mayden 2004). These populations should be monitored to evaluate their movement and possible impact on *P. smithvanizi* and other darters.

TABLE 11. Proportional measurements of *Percina kusha*, *P. sipsi* and *P. smithvanizi*, expressed in thousandths of standard length.

	P. kusha (n = 23)			*P. sipsi* (n = 18)			*P. smithvanizi* (n = 21)		
	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
standard length (mm)	43–65	—	—	37–50	—	—	43–57	—	—
snout length	41–58	50	4.4	41–54	46	3.9	38–52	46	4.4
eye diameter	47–73	64	6.3	56–70	63	3.3	57–71	65	3.9
head length	219–258	235	9.2	206–243	229	10.0	212–257	231	11.7
head depth	124–147	133	5.6	119–149	135	7.8	135–157	142	5.6
occiput - pelvic fin origin	132–172	144	8.2	120–150	140	9.7	143–169	153	7.5
snout - pelvic fin origin	262–293	275	7.5	247–285	271	11.1	254–304	278	15.7
predorsal length	329–355	339	7.2	314–339	328	6.6	311–344	326	8.6
pelvic fin origin - first dorsal fin origin	142–185	158	9.6	137–175	156	11.7	150–188	166	10.2
body depth	124–169	141	12.8	112–167	141	15.4	134–181	155	12.1
pectoral fin length	114–205	167	23.1	141–215	185	20.0	133–216	182	17.0
first dorsal fin origin - anal fin origin	308–359	333	11.1	309–353	328	9.7	328–357	342	7.2
pelvic fin origin - second dorsal fin origin	317–434	393	21.7	382–412	399	8.1	378–416	396	12.0
first dorsal fin base length	219–317	260	22.8	219–331	266	25.5	210–321	272	27.7
pelvic fin origin - anal fin origin	320–398	354	17.2	323–371	343	12.5	330–367	347	9.3
second dorsal fin base length	115–153	134	9.2	93–159	134	15.4	128–160	143	7.9
second dorsal fin origin - anal fin origin	117–147	134	7.5	121–149	134	8.2	135–159	145	5.9
second dorsal fin origin - anal fin insertion	139–177	155	8.9	136–171	158	7.6	154–189	168	9.2
anal fin origin - second dorsal fin insertion	168–214	183	10.2	155–220	189	15.7	180–213	195	9.8
anal fin base length	101–139	119	9.4	103–149	125	12.0	117–154	133	11.1
second dorsal fin insertion - anal fin insertion	87–103	97	4.6	94–119	101	6.3	91–108	98	3.6
second dorsal fin insertion - caudal fin	197–251	231	13.6	203–270	236	16.2	205–239	228	8.2
anal fin insertion - caudal fin	236–291	262	13.5	245–292	269	10.3	239–288	258	11.8
caudal peduncle depth	65–79	72	3.4	72–84	76	3.5	70–79	74	2.6

Etymology. We take great pleasure in naming this species for our good friend and colleague, Dr. William F. Smith-Vaniz, in recognition of his outstanding contributions to ichthyology in general and specifically for his authorship of the first book on the Freshwater Fishes of Alabama (Smith-Vaniz 1968).

The common name, Muscadine Darter, is based on the dark purplish color of the lateral stripe in live individuals that is similar to the color of ripe Muscadine (*Vitis rotundifolia*) fruit in early fall. Muscadine vines occur along many of the more pristine streams inhabited by the Muscadine Darter.

TABLE 12. Sheared principal component loadings for morphometric variables for three new *Percina* species from the Mobile Basin. Measurements represent linear distances between landmarks as enumerated in Figure 1.

Landmarks	Measurement	Size	Sheared PC II	Sheared PC III
1 - 10	standard length	0.194	0.134	-0.031
1 - 2	snout length	0.240	0.514	0.028
2 - 3	eye diameter	0.153	0.110	0.207
1 - 4	head length	0.198	0.254	0.087
5 - 16	head depth	0.217	-0.071	0.061
5 - 15	occiput - pelvic fin origin	0.235	-0.125	0.272
1 - 15	snout - pelvic fin origin	0.197	0.191	0.135
1 - 6	predorsal length	0.200	0.215	0.096
6 - 15	pelvic fin origin - first dorsal fin origin	0.214	-0.147	0.333
6 - 14	body depth	0.224	-0.280	0.459
17 - 18	pectoral fin length	0.141	-0.138	0.324
6 - 13	first dorsal fin origin - anal fin origin	0.210	0.040	0.083
7 - 15	pelvic fin origin - second dorsal fin origin	0.185	0.061	0.053
6 - 7	first dorsal fin base length	0.219	-0.141	-0.192
13 - 15	pelvic fin origin - anal fin origin	0.195	0.130	0.105
7 - 8	second dorsal fin base length	0.233	-0.169	-0.276
7 - 13	second dorsal fin origin - anal fin origin	0.237	-0.144	-0.015
7 - 12	second dorsal fin origin - anal fin insertion	0.209	-0.192	-0.156
8 - 13	anal fin origin - second dorsal fin insertion	0.216	-0.153	-0.243
12 - 13	anal fin base length	0.200	-0.355	-0.287
8 - 12	second dorsal fin insertion - anal fin insertion	0.200	0.084	-0.169
8 - 10	second dorsal fin insertion - caudal fin	0.181	0.252	-0.173
10 - 12	anal fin insertion - caudal fin	0.190	0.261	-0.180
9 - 11	caudal peduncle depth	0.178	-0.007	-0.155
	% Variance	83.5	4.6	2.8
	Cumulative %		87.9	90.6

Comparison with congeners. In the Tallapoosa River drainage above the Fall Line, *Percina smithvanizi* occurs with three other species of *Percina*: *P. kathae*, *P. nigrofasciata* and *P. palmaris*. The pigmentation pattern of *P. smithvanizi* differs from *P. kathae* which has numerous narrow, vertical bars on the side and a well-developed basicaudal spot. Also the cone-shaped snout of *P. kathae* projects beyond the anterior margin of the upper jaw. *Percina smithvanizi* can be distinguished from *P. nigrofasciata* which has moderately joined gill membranes, vertically elongate lateral blotches and often has irregular shaped blotches on the belly. The broad saddles that extend across the back and bright colors of the fins and body of *P. palmaris* readily distinguish it from *P. smithvanizi*.

Morphometric comparisons

Proportional measurements for the three species of *Percina* are provided in Table 11. Results of the sheared principal component analysis (PCA) are presented in Table 12 and Figures 4–5. In the PCA of all species, the first three components accounted for 91% of the morphometric variance. Variable loadings on the first principal component were positive and indicative of PC I as a general size factor (Bookstein *et al*. 1985), and this component accounted for 83.5% of the total variance in the complete covariance matrix; values for PC II and PC III were 4.6% and 2.8%, respectively. The scatter of component scores on sheared PC II and sheared PC III revealed little differentiation among all three species (Fig. 4), with greatest overlap on both component axes between *P. sipsi* and *P. smithvanizi*. Heaviest loadings on sheared PC II were snout length and head length (both positive) and anal fin base length and body depth (both negative). Heaviest loadings on sheared PC III were body depth, pectoral fin length, pelvic fin origin to spinous dorsal fin origin (all positive), and anal and soft dorsal fin base lengths (both negative) (Table 12).

To further compare shape differences between *Percina kusha* and *P. smithvanizi*, a second principal component analysis was done with the removal of measurements for *P. sipsi* from the data matrix. In this analysis, the first three components accounted for 88% of the morphometric variance, with loadings on PC I through PC III of 76.8%, 5.3%, and 2.6%, respectively. A scatter plot of component scores revealed moderate separation between the two species along PC II (Fig. 5). Variables that loaded most heavily on sheared PC II were anal fin base length and body depth (both positive) and snout length and head length (both negative); proportional differences between *P. kusha* and *P. smithvanizi* in these measurements were accompanied by substantial overlap in range values (Table 11).

Based on results of the morphometric analysis, the combination of mensural data were of limited use in distinguishing specimens among the three *Percina* species. In spite of broad overlap for all morphometric characters among species, a slight difference in body depth between *P. smithvanizi* and the other two species was evident in a bivariate plot of log body depth versus log SL (Fig. 6). Analysis of covariance (ANCOVA; SPSS ver. 12.0) confirmed homogeneity of variance in the regression lines (Table 13). Using the Bonferroni procedure to control for type I error across three comparisons ($p < 0.0167$), post hoc contrasts indicated that *P. smithvanizi* differed significantly in adjusted mean log body depth from specimens of both *P. kusha* ($F = 10.99$; $p = 0.002$) and *P. sipsi* ($F = 7.75$; $p = 0.007$), but that the latter two did not differ from each other.

TABLE 13. Analysis of covariance (ANCOVA) results for differences in log body depth between three new species of *Percina* from the Mobile Basin. Differences between species and the covariate (log SL) are significant; the interaction term tests for differences in slopes of the regression lines indicated in Figure 6 and is not significant. Sums of squares (SS) are Type III.

Source	df	SS	F	P
species	2	0.024	7.563	0.001
log SL	1	0.120	74.427	<0.001
species*log SL	2	0.002	0.538	0.587
Error	58	0.093		

TABLE 14. Estimates of genetic diversity in the three new species described herein.

	N	Gene diversity	Nucleotide diversity	Mean pairwise difference	Theta_{st}
Percina sipsi	4	1.0 +/- 0.18	0.002	2.33 +/- 1.59%	2.18
Percina smithvanizi	6	1.0 +/- 0.09	0.003	3.53 +/- 2.09%	4.38
Percina kusha	5	0.7 +/- 0.22	0.003	4.00 +/- 2.40%	3.36

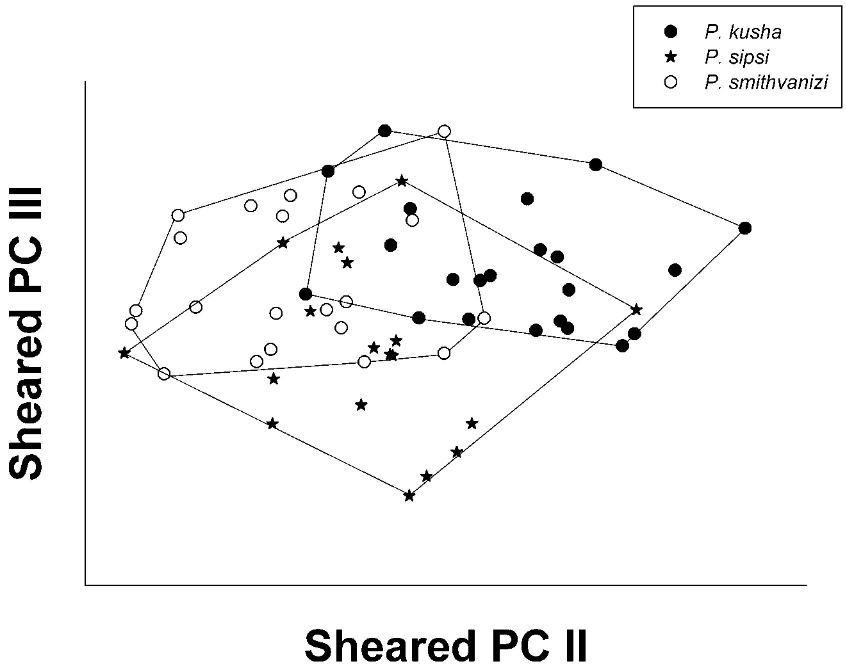

FIGURE 4. Scatter plot of scores on second and third sheared principal components for 24 morphometric characters of three new *Percina* species from the Mobile Basin.

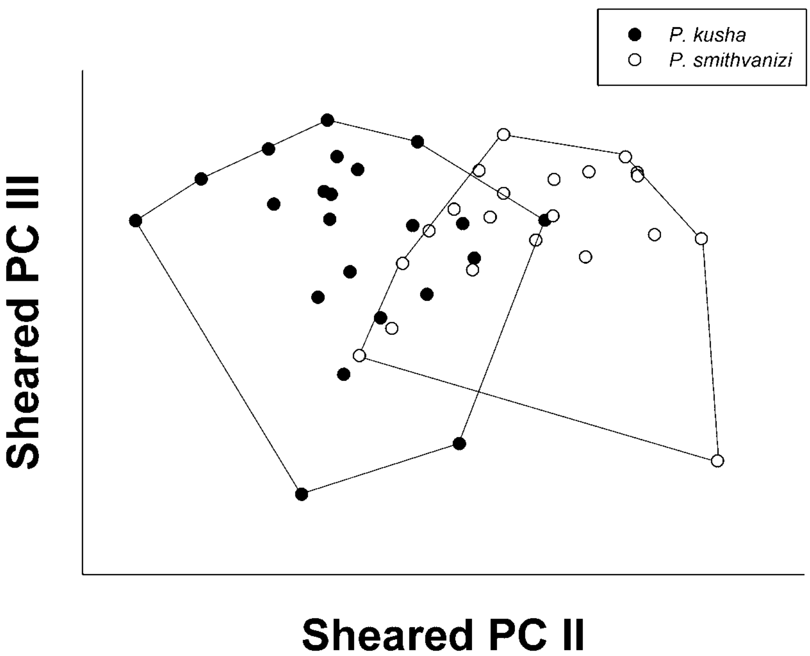

FIGURE 5. Scatter plot of scores on second and third sheared principal components for 24 morphometric characters of *Percina kusha* and *P. smithvanizi*.

Molecular analyses

Our mtDNA data set consisted of 83 OTUs, including seven outgroup taxa. Thirty-three most-parsimonious topologies (L = 3972, CI = 0.22, RC = 0.13) were recovered in the unweighted MP analysis. The Bayesian topology (Fig. 7) was nearly identical to the consensus tree of the MP topologies, differing primarily in the degree of resolution of basal branches. Several features of these trees are worthy of note. While support for many terminal nodes was generally high, the basal relationships of the genus *Percina* are poorly resolved, consistent with the analyses of Near (2002) and Sloss et al. (2004). The subgenera *Cottogaster*, *Imostoma*, *Percina* and *Swainia* were all resolved as monophyletic groups, with strong support. Sufficient structure was resolved, however, to clearly support a sister-taxon relationship between *P. kusha* and *P. smithvanizi*, as well as a strongly supported clade consisting of *P. aurolineata* + (*P. sciera* + *P. sipsi*). The three taxa described herein were never recovered as a monophyletic group in any analyses. There was no consistent geographic structure observed in populations of either *P. sipsi* or *P. smithvanizi*, however, populations of *P. kusha* from the Conasauga and Etowah River were always recovered as reciprocally monophyletic groups.

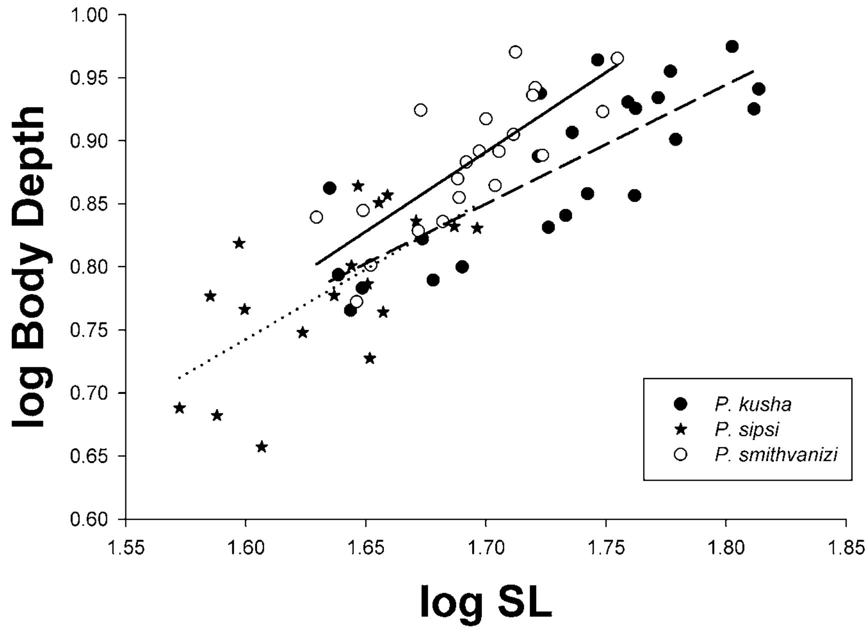

FIGURE 6. Relationship of log-transformed body depth and standard length of three new *Percina* species from the Mobile Basin. Regression lines: solid, *P. smithvanizi*; dashed, *P. kusha*; dotted, *P. sipsi*.

Populations of *Percina sipsi*, *P. smithvanizi*, and *P. kusha* displayed relatively low levels of variation (Table 14). The five sampled specimens of *P. kusha* possessed three haplotypes; there were seven substitutions (four transitions and three transversions) and no indels. All sampled individuals from the Conasauga River shared a single haplotype, which differed from the two haplotypes sampled from the Etowah River by 0.53-0.64% pairwise sequence divergence. The two Etowah haplotypes were 0.09% divergent from each other. The six sampled specimens of *P. smithvanizi* (representing the entire geographic range of the taxon) possessed four haplotypes; there were ten substitutions (five transitions and five transversions) and no indels. The haplotypes had pairwise sequence divergence values between <0.01% and 0.26%.

The four sampled specimens of *Percina sipsi* each had unique haplotypes; there were five substitutions (two transitions and three transversions) and no indels. Haplotypes had pairwise sequence divergence values between 0.18% and 0.35%. One specimen from the Sipsey Fork identified as *P. sciera* on the basis of lateral blotching, fully scaled nape and a well-developed suborbital bar, had a haplotype that was very similar to that of *P. sipsi* (and which only differed from *P. sipsi* by between 0.26% and 0.44%). This specimen was resolved with *P. sipsi* in all analyses.

Although *P. sipsi* and *P. sciera* are morphologically similar (see Comparison with congeners, above), recovery of a sister-taxon relationship between them was unexpected.

The specimens used in the molecular analysis were adult, morphologically "good" *P. sipsi* and *P. sciera*. Our data do not allow us to determine whether this represents a natural relationship or an artifact of the mito-chondrial locus examined. Considerable evidence exists for occasional mitochondrial introgression in darters

(Page *et al.* 2003, Mendelson & Simons 2006, N.J. Lang & J.M. Ray unpublished data), and we suspect that our recovery of *P. sipsi* stems from introgression with *P. sciera*, but require additional nuclear data to test this hypothesis. Minimally, the haplotypic variation observed within *P. sipsi* suggests that if the mitochondrial genome is introgressed with *P. sciera*, it is not the result of a recent event.

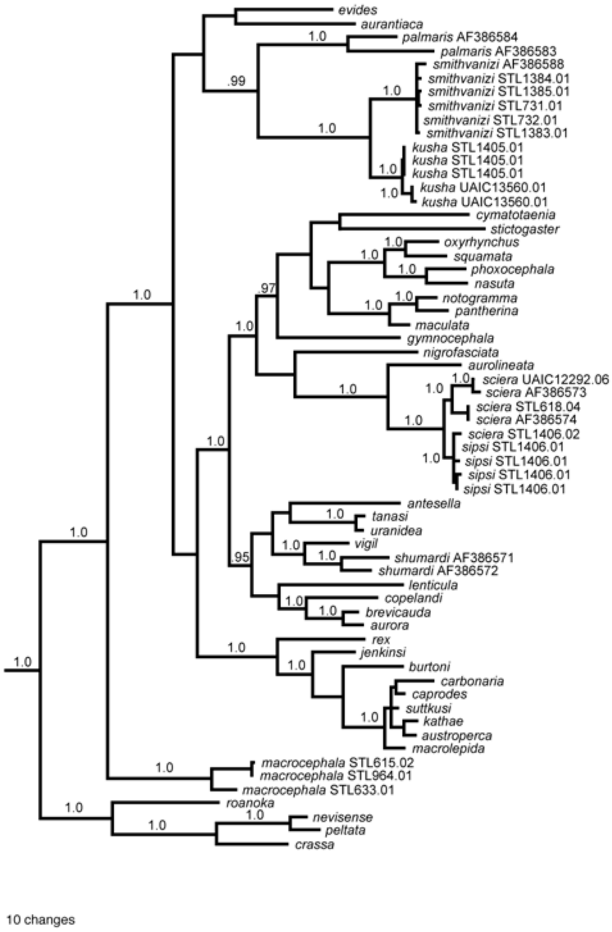

FIGURE 7. Phylogram from Bayesian analysis. Outgroup taxa not shown for clarity. Posterior probability (when above 95%) is indicated above that node.

Discussion

Relationships among species of *Percina* have been the subject of considerable attention during the past 50 years beginning with a proposed alignment of the recognized species into eight subgenera by Bailey & Gosline (1955). Using a variety of characters, Page (1974) employed a numerical taxonomic approach to reexamine the subgeneric alignment of the 32 species of *Percina* known at that time and recognized nine subgenera. Only one of the three species described herein, *P. kusha,* was included in the analysis by Page (1974) and it was assigned to the subgenus *Alvordius*. Based on color and morphological characters all three species were subsequently considered to belong to the subgenus *Alvordius*. More recently Near (2002) examined the phylogenetic relationships among 40 species of the genus *Percina* using mitochondrial cytochrome *b* gene sequences. This analysis did not result in the recovery of a monophyletic *Alvordius*, although many taxa formerly allocated to this subgenus were resolved in a large polytomy. Based on the results of his analysis, Near (2002) recognized eight clades with a group of eight species, including *P. smithvanizi*, that were not classified (placed) in one of the monophyletic clades. Near (2002) recovered *P. smithvanizi* as sister to *P. palmaris* although support for this clade was low. Five of the clades recognized by Near (2002) were in agreement with subgenera delineated by Page (1974).

The additional taxon sampling in the current study supports a close relationship between *P. kusha* and *P. smithvanizi*, but do not provide a robust hypothesis of the relationships of this clade.

Additional analyses based on different markers will be required to produce a robust phylogeny of the group and in particular the three taxa described herein, as well as to resolve the discord between morphologically diagnosed subgenera (Page 1974) and clades inferred from mitochondrial data (e.g., Near 2002).

Percina kusha superficially resembles *P. macrocephala* in having a dark, boldly contrasting, undulating lateral stripe, but the latter species differs in having the snout longer than the orbit length; cheeks, opercles and breast typically naked; it has smaller scales (70–90 lateral line scales, 8 or 9 scales above and 11 or 12 scales below the lateral line, 20–28 transverse scales), more fin rays (dorsal spines 11–14, dorsal rays 12–13), and more vertebrae (44–45, data from Bailey & Gosline 1955). It also differs in details of pigmentation, particularly in having a well-developed subocular bar, dark saddles along the midline of the dorsum, dark vermiculations above the lateral stripe and a dusky bar connected to and extending downward from the rounded basicaudal spot. Based on color and morphology, *P. kusha* and *P. macrocephala* do not appear to be closely related.

Percina sipsi and *P. smithvanizi* superficially resemble *P. aurolineata* and *P. sciera* in having a series of dark blotches connected to form a dark lateral stripe along the side of the body. However, both *P. aurolineata* and *P. sciera* usually have one or more pored lateral line scales on the caudal fin base. The majority of individuals of the three species described herein have a complete lateral line but typically lack pored scales on the base of the caudal fin beyond the hypural flexure. *Percina aurolineata* and *P. sciera* also have moderately joined branchiostegal membranes and serrate preopercular margins. In addition, *P. kusha*, *P. sipsi*, and *P. smithvanizi* are unusual among species of the genus in possessing a modal count of 10 dorsal soft rays and 8 anal rays.

Based on morphological characters, *Percina smithvanizi* was originally aligned with the subgenus *Alvordius* and was thought to represent an upland species isolated from related taxa in drainages below the Fall Line in the Mobile Basin. Based on this assumption, *P. smithvanizi* was often compared to *P. maculata*, the only other species in the subgenus *Alvordius* in the Mobile Basin. In the eastern Mobile Basin, *P. maculata* is confined to the Alabama, Cahaba, and Tallapoosa River drainages below the Fall Line. Based on color and morphology *P. smithvanizi* and *P. maculata* are probably not closely related. *Percina maculata* has a black blotch on the base of the first 3 to 4 membranes of the spinous dorsal fin, a well-defined black basicaudal spot, and 1 or more modified ctenoid scales on the center of the breast near the anterior ends of the pelvic girdle—a character it shares in common with *P. gymnocephala*, *P. notogramma*, *P. pantherina* and *P. peltata*.

While the broader relationships of the new species are equivocal, our mitochondrial data does not support recognizing them as a monophyletic group, as prior investigators have hypothesized. Additional sequence data from a different gene or genes are required to further resolve relationships within *Percina* and, in particular, of the three new species described herein.

Additional materials used in molecular analyses

***Percina macrocephala*: Kentucky: Allen County:** STL 964.01 (1) Trammel Fork, at Kentucky Hwy 240, 1.6 km SW of Allen Springs (36°49'40"N; 86°19'54"W), 22 June 2003, EF613202. **Pennsylvania: Warren County:** STL 615.02 (1) Brokenstraw Creek, at mouth of Little Brokenstraw Creek in Pittsfield (41°49'59"N; 79°23'03"W), 24 December 2002, EF613201. **Virginia: Smyth County:** STL 633.03 (1) North Fork Holston River, at USGS gauging station 2.4 km NE of Saltville (36°53'50"N; 81°44'47"W), 25 October 2003, EF613203.

***Percina sciera*: Alabama: Colbert County:** STL 618.04 (1) Rock Creek, at Sally Burns Road SSW of Mynot (34°36'33"N; 88°03'49"W), 29 March 2003, EF613206. **Winston County:** STL 1406.02 (1) Sipsey Fork, at Alabama Hwy 33 3 km NE of Rock Creek (34°13'05"N; 87°22'09"W), 20 January 2003, EF613205. **Mississippi: Simpson County:** UAIC 12992.06 (1) Strong River, at Mississippi Hwy 28 3.2 km W of Pinola (31°53'11"N; 89°59'37"W), 6 December 1986, EF613204.

From GenBank: *Ammocrypta beanii*, AF386535; *Ammocrypta clara*, AF183941; *Ammocrypta meridiana*, AF183942; *Ammocrypta pellucida*, AF183943; *Crystallaria asprella*, AF099881; *Etheostoma aquali*, AF386537; *Etheostoma blennioides*, AF386539; *Etheostoma camurum*, AF386536; *Etheostoma cinereum*, AF386545; *Etheostoma exile*, AF386541; *Etheostoma flabellare*, AF386544; *Etheostoma gracile*, AF386538; *Etheostoma kennicotti*, AF386543; *Etheostoma sagitta*, AF386542; *Etheostoma vitreum*, AF386540; *Gymnocephalus cernuus*, AF386598; *Perca flavescens*, AF386600; *Perca fluviatilis*, AF386599; *Percina antesella*, AF386587; *Percina aurantiaca*, AF386579; *Percina aurolineata*, AF386575; *Percina aurora*, AF386566; *Percina austroperca*, AF386546; *Percina brevicauda*, AF386567; *Percina burtoni*, AF386554; *Percina carbonaria*, AF386553; *Percina caprodes*, AF386550; *Percina copelandi*, AF386568; *Percina crassa*, AF386593; *Percina cymatotaenia*, AF386589; *Percina evides*, AF375947; *Percina gymnocephala*, AF386581; *Percina jenkinsi*, AF386555; *Percina kathae*, AF386549; *Percina lenticula*, AF386586; *Percina macrocephala*, AF386591, AF386592; *Percina macrolepida*, AF386552; *Percina maculata*, AF386557; *Percina nasuta*, AF386561; *Percina nevisense*, AF386596; *Percina notogramma*, AF386559; *Percina nigrofasciata*, AF386590; *Percina oxyrhynchus*, AF386565; *Percina palmaris*, AF386583, AF386584; *Percina pantherina*, AF386558; *Percina peltata*, AF386595; *Percina phoxocephala*, AF386563; *Percina rex*, AF386556; *Percina roanoka*, AF386597; *Percina sciera*, AF386573, AF386574; *Percina shumardi*, AF386571; *Percina smithvanizi*, AF386588; *Percina squamata*, AF386564; *Percina stictogaster*, AF045355; *Percina suttkusi*, AF386551; *Percina tanasi*, AF386578; *Percina uranidea*, AF386576; *Percina vigil*, AF386569; *Romanichthys valsanicola*, AF045361; *Sander canadense*, AF386603; *Sander vitreus*, AF386602; *Zingel streber*, AF386601.

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References

Bailey, R.M. & Gosline, W.A. (1955) Variation and systematic significance of vertebral counts in the American fishes of the family Percidae. *Miscellaneous Publications Museum Zoology University Michigan*, 93, 1–44.

Bookstein, F.L., Chernoff, B., Elder, R.L., Humphries, Jr., J.M., Smith, G.R. & Strauss, R.E. (1985) *Morphometrics in Evolutionary Biology.* Academy of Natural Sciences Special Publication 15, Philadelphia, Pennsylvania, 277 pp.

Boschung, H.T. & Mayden, R.L. (2004) *Fishes of Alabama*. Smithsonian Books, Washington, DC, 736 pp.

Cailliet, G.M., Love, M.S. & Ebeling, A.W. (1986) *Fishes: a Field and Laboratory Manual on their Structure, Identification, and Natural History.* Wadsworth Publishing Company, Belmont, California, 194 pp. (reissued 1996 by Waveland Press, Inc.).

Crawford, R.W. (1956) A study of the distribution and taxonomy of the percid fish *Percina nigrofasciata* (Agassiz). *Tulane Studies Zoology*, 4, 1–55.

Deacon, J.E., Kobetich, G., Williams, J.D. & Contreras, S. (1979) Fishes of North America: endangered, threatened, or of special concern: 1979. *Fisheries*, 4, 30–44.

Dycus, D.L. & Howell, W.M. (1974) Fishes of the Bankhead National Forest of Alabama. Final report to the Alabama Department of Conservation and Natural Resources, Montgomery, Alabama, 51 pp.

Etnier, D.A. & Starnes, W.C. (1991) An analysis of Tennessee's jeopardized fish taxa. *Journal of the Tennessee Academy of Science*, 66, 129–133.

Etnier, D.A. & Starnes, W.C. (1994) *The Fishes of Tennessee*. The University of Tennessee Press, Knoxville, Tennessee, 681 pp.

Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D. & Kluge, A.G. (1996) Parsimony jackknifing outperforms neighbor-joining. *Cladistics*, 12, 99–124.

Foscue, V.O. (1989) *Place Names in Alabama*. University of Alabama Press, Tuscaloosa, Alabama, 175 pp.

Freeman, B.J. (1999) Muscadine Darter, *Percina* sp. cf. *macrocephala*. *In*: *Protected Animals of Georgia*. Georgia Department of Natural Resources, Nongame Wildlife and Natural Heritage Section, State of Georgia, pp. 191–192.

Freeman, M.C., Irwin, E.R., Burkhead, N.M., Freeman, B.J. & Bart, Jr., H.L. (2005) *Status and conservation of the fish fauna of the Alabama River system*. American Fisheries Society Symposium, 45, 557–585.

Hall, T. (2001) BioEdit v5.0.9. North Carolina State University, Raleigh, North Carolina.

Hillis, D.M., Mable, B.K., Larson, A., Davis, S.K. & Zimmer, E.A. (1996) Nucleic acids: sequencing and cloning. *In*: Hillis, D.M., Moritz, C. & Mable, B.K. (Eds.), *Molecular systematics*. 2nd edition. Sinauer Associates, Sunderland, Massachusetts, pp. 321–381.

Hubbs, C.L. & Lagler, K.F. (1958) Fishes of the Great Lakes region. 2nd edition. *Cranbrook Institute Science Bulletin*, 26, 1–213.

Huelsenbeck, J.P. & Ronquist, F. (2001) Mr. Bayes: Bayesian inference of phylogeny. *Bioinformatics*, 17, 754–755.

Humphries, Jr., J.M., Bookstein, F.L., Chernoff, B., Smith, G.R., Elder, R.L. & Potts, S.L. (1981) Multivariate discrimination by shape in relation to size. *Systematic Zoology*, 30, 291–308.

Irwin, D.M., Kocher, T.D. & Wilson, A.C. (1991) Evolution of cytochrome *b* gene of mammals. *Journal of Molecular Evolution*, 32, 128–144.

Johnson, C.E., Kleiner, K.J. & Herrington, S.J. (2002) Seasonal, diel and spawning habitat of the rare Muscadine Darter (*Percina* sp.) in the Conasauga River, Georgia. *Southeastern Fishes Council Proceedings*, 44, 1–11.

Kuhajda, B.R. (2004) Warrior bridled darter, *Percina* sp. cf. *macrocephala*. In: Mirarchi, R.E., Garner, J.T., Mettee, M.F. & O'Neil, P.E. (Eds.), Alabama Wildlife, Vol. 2, Imperiled Aquatic Mollusks and Fishes. University of Alabama Press, Tuscaloosa, Alabama, pp. 200–201.

Leviton, A.E. & Gibbs, Jr., R.H. (1988) Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Supplement No. 1: additions and corrections. *Copeia*, 1988, 280–282.

Leviton, A.E., Gibbs, Jr., R.H., Heal, E. & Dawson, C.E. (1985) Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia*, 1985, 802–832.

Mendelson, T.C. & Simons, J.N. (2006) AFLPs resolve cytonuclear discordance and increase resolution among barcheek darters (Percidae: *Etheostoma*: *Catonotus*). *Molecular Phylogeny and Evolution*, 41, 445–453

Near, T.J. (2002) Phylogenetic relationships of *Percina* (Percidae: Etheostomatinae). *Copeia*, 2002, 1–14.

Near, T.J. & Benard, M.F. (2004) Rapid allopatric speciation in logperch darters (Percidae: *Percina*). *Evolution*, 58, 2798–2808.

Near, T.J., Porterfield, J.C. & Page, L.M. (2000) Evolution of cytochrome *b* and the molecular systematics of *Ammocrypta*. *Copeia*, 2000, 701–711.

Neely, D.A., Williams, J.D. & Mayden, R.L. In press. Two new species of *Cottus* (Teleostei: Cottidae) from the Tallapoosa and Chattahoochee river drainages in Alabama and Georgia. *Copeia*.

Nelson, J.S., Crossman, E.J., Espinosa-Pérez, H., Findley, L.T., Gilbert, C.R., Lea, R.N. & Williams, J.D. (2004) *Com-*

mon and Scientific Names of Fishes from the United States, Canada, and Mexico. American Fisheries Society, Special Publication 29, Bethesda, Maryland, 386 pp.
Page, L.M. (1974) The subgenera of *Percina* (Percidae: Etheostomatini). *Copeia*, 1974, 66–86.
Page, L.M. & Burr, B.M. (1991) *A Field Guide to Freshwater Fishes of North America North of Mexico*. The Peterson Field Guide Series, Houghton Mifflin Company, Boston, Massachusetts, 432 pp.
Page, L.M., Hardman, M., & Near, T.J. (2003) Phylogenetic relationships of barcheek darters (Percidae: *Etheostoma*, subgenus *Catonotus*) with descriptions of two new species. *Copeia*, 512–530.
Page, L.M. & Whitt, G.S. (1973a) Lactate dehydrogenase isozymes, malate dehydrogenase isozymes and tetrazolium oxidase mobilities of darters (Etheostomatini). *Comparative Biochemistry Physiology*, 44B, 611–623.
Page, L.M. & Whitt, G.S. (1973b) Lactate dehydrogenase isozymes of darters and the inclusiveness of the genus *Percina*. *Biological Notes*, 82, 1–7.
Palumbi, S.R., Martin, A., Romano, S., McMillan, W.O., Stice, L. & Grabowski, G. (1991) The simple fool's guide to PCR: a collection of PCR protocols. Department of Zoology and Kewalo Marine Laboratory, University of Hawaii, Honolulu, Hawaii, 46 pp.
Posada, D. & Crandall, K.A. (1998) MODELTEST: testing the model of DNA substitution. Bioinformatics, 14, 817–818.
Ramsey, J.S. (1976) Freshwater fishes. *In*: Endangered and threatened plants and animals of Alabama. *Bulletin Alabama Museum of Natural History*, 2, pp. 53–65.
Ramsey, J.S. (1984) Freshwater fishes. *In*: Vertebrate wildlife of Alabama. Alabama Agricultural Experiment Station, Auburn University, Alabama, pp. 1–14.
Richards, W.J. & Knapp, L.W. (1964) *Percina lenticula*, a new percid fish, with a redescription of the subgenus *Hadropterus*. *Copeia*, 1964, 690–701.
Schneider, S., Roessli, D. & Excoffier, L. (2000) ARLEQUIN: a software for population genetics data analysis, v2.0. University of Geneva, Switzerland.
Sloss, B.L., Billington, N. & Burr, B.M. (2004) A molecular phylogeny of the Percidae (Teleostei, Perciformes) based on mitochondrial DNA sequence. *Molecular Phylogenetics and Evolution*, 32, 545–562.
Smith-Vaniz, W.F. (1968) *Freshwater Fishes of Alabama*. Agricultural Experiment Station, Auburn University, Alabama, 211 pp.
Song, C.B., Near, T.J. & Page, L.M. (1998) Phylogenetic relations among percid fishes as inferred from mitochondrial cytochrome *b* DNA sequence data. *Molecular Phylogenetics and Evolution*, 10, 343–353.
Stiles, R.A. & Etnier, D.A. (1971) Fishes of the Conasauga River drainage, Polk and Bradley counties, Tennessee. *Journal of the Tennessee Academy of Science*, 46, 12–16.
Suttkus, R.D. & Ramsey, J.S. (1967) *Percina aurolineata*, a new percid fish from the Alabama River system and a discussion of ecology, distribution and hybridization of darters of the subgenus *Hadropterus*. *Tulane Studies in Zoology*, 13, 129–145.
Suttkus, R.D., Thompson, B.A. & Bart, Jr., H.L. (1994) Two new darters, *Percina* (*Cottogaster*), from the southeastern United States, with a review of the subgenus. *Occasional Papers Tulane University Museum of Natural History*, 4, 1–46.
Swofford, D.L. (2002) PAUP* v4.0 PPC. Phylogenetic analysis using parsimony (*and other methods). Sinauer Associates, Sunderland, Massachusetts.
Warren, M.L., Burr, B.M., Walsh, S.J., Bart, H.L., Cashner, R.C., Etnier, D.A., Freeman, B.J., Kuhajda, B.R., Mayden, R.L. & Robison, H.W. (2000) Diversity, distribution, and conservation status of the native freshwater fishes of the southern United States. *Fisheries*, 25, 7–31.
Wieland, W. & Ramsey, J.S. (1987) Ecology of the Muscadine Darter, *Percina* sp. cf. *macrocephala*, in the Tallapoosa River, Alabama, with comments on related species. *Southeastern Fishes Council Proceedings*, 17, 5–17.
Williams, J.D. (1965) *Studies on the fishes of the Tallapoosa River system in Alabama and Georgia*. Master of Science thesis, University of Alabama, University, Alabama, 135 pp.
Williams, J.E., Johnson, J.E., Hendrickson, D.A., Contreras-Balderas, S., Williams, J.D., Navarro-Mendoza, M., McAllister, D.E. & Deacon, J.E. (1989) Fishes of North America endangered, threatened, or of special concern: 1989. *Fisheries*, 14, 2–20.
Zander, R.H. (2004) Minimal values for reliability of bootstrap and jackknife proportions, decay index, and Bayesian posterior probability. *Phyloinformatics*, 2, 1–13.