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Endemic to the Cahaba River
of the Mobile Basin**

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ABSTRACT: Mayden, Richard L. and Bernard R. Kuhajda, 1989. Systematics of *Notropis cahabae*, A New Cyprinid Fish Endemic To The Cahaba River Of The Mobile Basin. Bulletin Alabama Museum of Natural History, Number 9:1-16, 10 tables, 7 figures. *Notropis cahabae*, known for many years as the Cahaba shiner, is herein described and compared with the morphologically similar and closely related *N. volucellus* (Cope) and *N. wickliffi* Trautman. The known range of *N. cahabae* is extremely limited, historically encompassing only about 140 river kilometers of the Cahaba River, but is limited today to about 28 kilometers. The species is restricted to the main channel of the Cahaba River in the Ridge and Valley Province between Helena, Alabama and the Fall Line at Centreville, Alabama. The status of this environmentally sensitive species has declined in recent years as a result of increased effluent from mining and development in the Cahaba River watershed. The extremely limited range and sensitive nature of *N. cahabae* has led the Alabama Department of Conservation and Natural Resources to recognize it as an endangered species. *Notropis cahabae* is a member of the *Notropis volucellus* species group and is sympatric with a form of *N. volucellus* found in the Mobile Basin. Based on morphological and biochemical analyses, *N. volucellus* as presently recognized is a complex of more than one taxon and *N. wickliffi* is a distinctive species. The Cahaba shiner differs from other members of the *N. volucellus* group in overall body shape, features of the cephalic lateralis system, meristic characteristics, four unique and derived alleles, as well as distinctive coloration and pigmentation patterns. Morphological and biochemical features support the hypothesis that *N. cahabae* is more closely related to *N. wickliffi* than to *N. volucellus*. The sister group relationship between these two large-river species provides further support for the Appalachian River connecting the Tennessee and Mobile drainages prior to the Pleistocene.

Introduction

Riverways of southeastern North America are characterized by a number of endemic fish species and represent one of the most diverse areas of the continent. The Mobile Basin of Mississippi, Alabama, Georgia, and Tennessee is prominent in this species rich zoogeographic region, ranking as the third most diverse drainage basin in North America and containing 157 species (Swift et al., 1986), about 40 of which are endemic. Within the Mobile Basin is the Cahaba River, its headwaters draining the Ridge and Valley Province and its lower reaches traversing the Gulf Coastal Plain. The Cahaba is of particular interest among North American rivers in that it is the most ichthyologically diverse, free-flowing river for its size within the continent. The Cahaba River flows for 354 river kilometers and presently is known

to contain 132 species. For some of these species this system represents their only remaining stronghold (Pierson et al., 1989).

Among the many native species in the Mobile Basin is the previously undescribed Cahaba shiner. This species is endemic to only a small portion of the Cahaba River, and has one of the smallest ranges for any North American fish species. The declining status of the Cahaba shiner has been recognized by researchers and the potential danger of its extinction has been of growing concern. Investigations by Stiles (1978) and Howell et al. (1982) indicate that the species is declining in numbers and special protection is warranted. The Cahaba shiner was listed as rare by Miller (1972) in the *Threatened Freshwater Fishes of the United States* and as endangered in the *IUCN Red Data Book* (Miller, 1977).

Deacon et al. (1979) listed the species as endangered for the American Fisheries Society Committee for Endangered Species. Likewise, Ramsey et al. (1972) and Ramsey (1976, 1986) listed the species as endangered. Herein, we describe the rare Cahaba shiner and distinguish it from two similar species: *Notropis volucellus* (Cope), the mimic shiner, from the Mobile Basin and elsewhere; and the channel shiner, *N. wickliffi* Trautman.

Methods

The following abbreviations are used throughout: Standard length (SL), predorsal length (PRD), postdorsal length (PSD), tip of snout to posterior bony margin of opercle (HL), snout length (SNL), eye diameter (ED), upper jaw length (UJL), distance between bony margins of orbits (IOD), depth of head at occiput (HD), width of head at

opercles (HW), posterior extent of mandible to occiput (MOC), pectoral fin insertion to occiput (PCOC), pelvic fin insertion to occiput (PVOC), body width at dorsal fin origin (BW), caudal peduncle depth (CPD), caudal peduncle width (CPW), tip of snout to insertion of pelvic fin (PRPV), pelvic fin insertion to dorsal fin origin (PVDO), pelvic fin insertion to insertion of last dorsal fin ray (PVDR), snout to anal fin origin (PRA), anal fin origin to insertion of last dorsal fin ray (ADR), anal fin origin to dorsal fin origin (ADO), pectoral fin insertion to dorsal fin origin (PCDO), insertion of last dorsal fin ray to ventral leading procurrent ray of caudal fin (DRVC), anal fin origin to dorsal leading procurrent ray of caudal fin (AODC), dorsal fin length (DF),

Table 1. Enzyme systems examined and electrophoretic conditions.

Enzyme (EC Number)	Locus	Tissue	Electrophoretic Conditions*
Acid phosphatase (EC 3.1.3.2)	Acp-A	Brain	D
Adenosine deaminase (EC 3.5.4.4)	Ada-A	Muscle	A
Adenylate kinase (EC 2.7.4.3)	Ak-A	Muscle	A
Aspartate aminotransferase (EC 2.6.1.1)	M-Aat-A S-Aat-A	Muscle Muscle	B B
Calcium-binding proteins (non-specific)	Cbp-1 Cbp-2	Muscle Muscle	C C
Creatine kinase (EC 2.7.3.2)	Ck-A Ck-B	Muscle Brain	C F
Cytosol aminopeptidase (EC 3.4.11.1)	S-Ap-A	Muscle	C
Dipeptidase (EC 3.4.13.11)	Pep-A Pep-S	Muscle Muscle	E E
Esterase (non-specific)	Est-1 Est-2	Brain Brain	E E
Fructose-bisphosphate aldolase (EC 4.1.2.13)	Ald-A	Muscle	D
Fumarate hydratase (EC 4.2.1.2)	Fum-A	Brain	D
General protein (non-specific)	Gp-I	Muscle	C
Glucose-6-phosphate dehydrogenase (EC 1.1.1.49)	G6pdh-A	Brain	D
Glucose-6-phosphate isomerase (EC 5.3.1.9)	Gpi-A Gpi-B	Brain Muscle	E E
Glycerol-3-phosphate dehydrogenase (EC 1.1.1.8)	G3pdh-A	Muscle	D
Isocitrate dehydrogenase (EC 1.1.1.42)	M-Icdh-A S-Icdh-A	Brain Brain	D D
L-Lactate dehydrogenase (EC 1.1.1.27)	Ldh-A Ldh-B	Brain Brain	A A
Malate dehydrogenase (EC 1.1.1.37)	M-Mdh-A S-Mdh-A S-Mdh-B	Brain Brain Muscle	D C C
Malic enzyme (EC 1.1.1.40)	M-Me-A S-Me-A	Muscle Muscle	D D
Mannose-6-phosphate isomerase (EC 5.3.1.88)	Mpi-A	Brain	C
α -Mannosidase (EC 3.2.1.24)	α -Man-I	Muscle	E
Phosphoglucomutase (EC 5.4.2.2)	Pgm-A	Muscle	C
Phosphogluconate dehydrogenase (EC 1.1.1.44)	Pgdh-A	Brain	A
Pyruvate kinase (EC 2.7.1.40)	Pk-A	Muscle	D
Superoxide dismutase (EC 1.15.1.1)	S-Sod-A	Brain	A
Triosephosphate isomerase (EC 5.3.1.1)	Tpi-A Tpi-B	Brain Brain	A A

* A: Tris-citrate pH 8.0 (Selander et al., 1971); B: Phosphate-citrate pH 8.0 (Selander et al., 1971); C: Histidine-HCl pH 8.0 (Brewer, 1970); D: Tris-citrate pH 7.0 (Whitt, 1970); E: "Poulik" system (Selander et al., 1971); F: EBT system of Page and Whitt (1973).

anal fin length (AF), pelvic fin length (PVF), pectoral fin length (PCF), dorsal fin rays (DR), anal fin rays (AR), pelvic fin rays (PVR), pectoral fin rays (PCR), lateral-line scale rows (LLS), body circumferential scale rows (CRS) above (CRSA) and below (CRSB) the lateral line, predorsal scales (PDS), and breast squamation (BRTS).

Methods employed for meristic variables follow Mayden (1988a). Color notes were taken from freshly captured as well as museum specimens. Multivariate analyses of morphometric and meristic data were performed using principal components analysis as described by Mayden (1988a) and the SAS statistical package. Components for morphometric variables were calculated from a covariance matrix; those for meristic variables from a correlation matrix. Meristic variation between species was tested using the SAS package for MANOVA ($P < 0.05$). Multiple range tests were performed with the Student-Newmans-Keuls Test ($P < 0.05$). Sexes were differentiated by examination of gonads. Tests of sexual dimorphism for meristic and morphometric variables were performed for each species using Student's *t*-test ($P < 0.05$).

For the electrophoretic analysis, specimens were captured by seine, frozen, and stored at -70°C prior to dissection. Voucher materials for electrophoretic samples are deposited in the University of Alabama Ichthyological Collection (UAIC). Skeletal muscle and eye/brain were dissected from each individual, mechanically homogenized, and centrifuged at 16,000 g at 4°C for 10 min to obtain the separate supernatant fractions. Extracts were subjected to horizontal starch gel electrophoresis at 5°C using 12% gels (Connaught Laboratories, Toronto). The products of 38 presumptive structural gene loci were resolved using standard histochemical staining methods and electrophoretic conditions (Table 1). Locus designations follow vertebrate homology, except where homology is uncertain and then they are numbered. Allelic products were lettered (lower case) to reflect differing mobilities within a locus and are relative to this study only. Population statistics of individual genotypes were produced using BIOSYS-1 (Swofford and Selander, 1981). Loci were considered polymorphic if more than one allele was detected. To determine relationships within the *Notropis volucellus* species group, a phylogenetic analysis was employed for allozyme data. Modified Rogers and Prevosti distances (Swofford and Selander, 1981) were employed in the distance Wagner analysis, where the multiple addition criterion was employed. FREQPARS (Swofford and Berlocher, 1987) was used to evaluate alternative topologies for shortest evolutionary trees using allelic frequencies of polymorphic loci and maximum parsimony. In determining synapomorphic features for supporting each node the FREQPARS reconstruction was employed. Herein, the locus was considered the character and allelic combinations as the character state in a transformation series. For all analyses *N. sp. cf. spectrunculus* represented the outgroup, following Mayden (1989).

Notropis cahabae, new species
Cahaba Shiner
Figure 1

HOLOTYPE.—University of Alabama Ichthyological Collection, UAIC 9119.01, breeding male, 39.8 mm, Cahaba River, 7.2 km NNE Centreville, Sec. 32, T 24 N, R 10 E, Bibb Co., Alabama, 22 June 1986, J. M. Pierson and S. G. Puleo.

PARATYPES.—A total of 420 specimens deposited as follows: 8—UAIC 8471.06 (36.4–44.6 mm, same data as holotype); 7—UAIC 9121.01 (38.3–48.1 mm, Cahaba River at Co. Rd. 27, Sec. 33, T 24 N, R 10 E, Bibb Co., Alabama, 12 October 1984); 1—UAIC 9120.01 (41.7 mm, same locality as 9121.01, 23 April 1986); 5—UAIC 8358.08 (34.7–40.8 mm, same locality as 9121.01, 20 May 1988); 14—UAIC 8339.05 (17.1–32.5 mm, same locality as 9121.01, 2 April 1989); 3—UAIC 7703.05 (34.3–46.4 mm, same locality as 9121.01, 12 October 1984); 3—UAIC 7702.07 (36.1–46.6 mm, same locality as 9121.01, 12 October 1984); 358—UAIC 8578.02 (14.8–42.3 mm, mouth of unnamed tributary to Cahaba River, 1.1 km downstream from mouth of Little Ugly Creek, Sec. 3, T 24 N, R 10 E, Bibb Co., Alabama, 7 February 1985); 1—Auburn University, AUM 17153 (50.4 mm, same locality as 9121.01, 10 June 1978); 1—AUM 17355 (57.8 mm, Cahaba River, 1.1 km SSE confluence with Little Cahaba River, Sec. 28, T 24 N, R 10 E, Bibb Co., Alabama, 26 June 1978); 1—AUM 18627 (39.7 mm, same locality as 9121.01, 6 December 1978); 3—Illinois Natural History Survey, INHS 65086 (37.7–42.6 mm, same data as 8358.08); 3—Southern Illinois University at Carbondale, SIUC 17081 (35.7–37.8 mm, same data as 8358.08); 3—Tulane University, TU 156263 (36.4–38.5 mm, same data as 8578.02); 3—University of Florida, UF 79940 (35.8–44.0 mm, same data as 8358.08); 3—University of Michigan, Museum of Zoology, UMMZ 215338 (34.3–39.9 mm, same data as 8578.02); 3—United States National Museum, USNM 305204 (38.0–38.7 mm, same data as 8578.02).

DIAGNOSIS.—A species of the *Notropis volucellus* species group as diagnosed by Mayden (1989). Distinguished from other members of the species group by a lateral stripe on the caudal peduncle with straight dorsal and ventral margins, not expanded ventrally; dorsum without a well-defined predorsal stripe or dark predorsal spot; dorsal caudal peduncle scales uniformly pigmented and dark; margins of predorsal scales broadly outlined and diffuse; cephalic tubercles fine; preoperculomandibular and infraorbital-posttemporal canals complete; lateral-line scale rows usually 34; predorsal scale rows usually 13 or 14; gill rakers usually 7 to 9; breast usually with embedded and/or exposed scales; unique and derived alleles at Acp-A, Gpi-A, M-Aat-A, and Tpi-A loci.

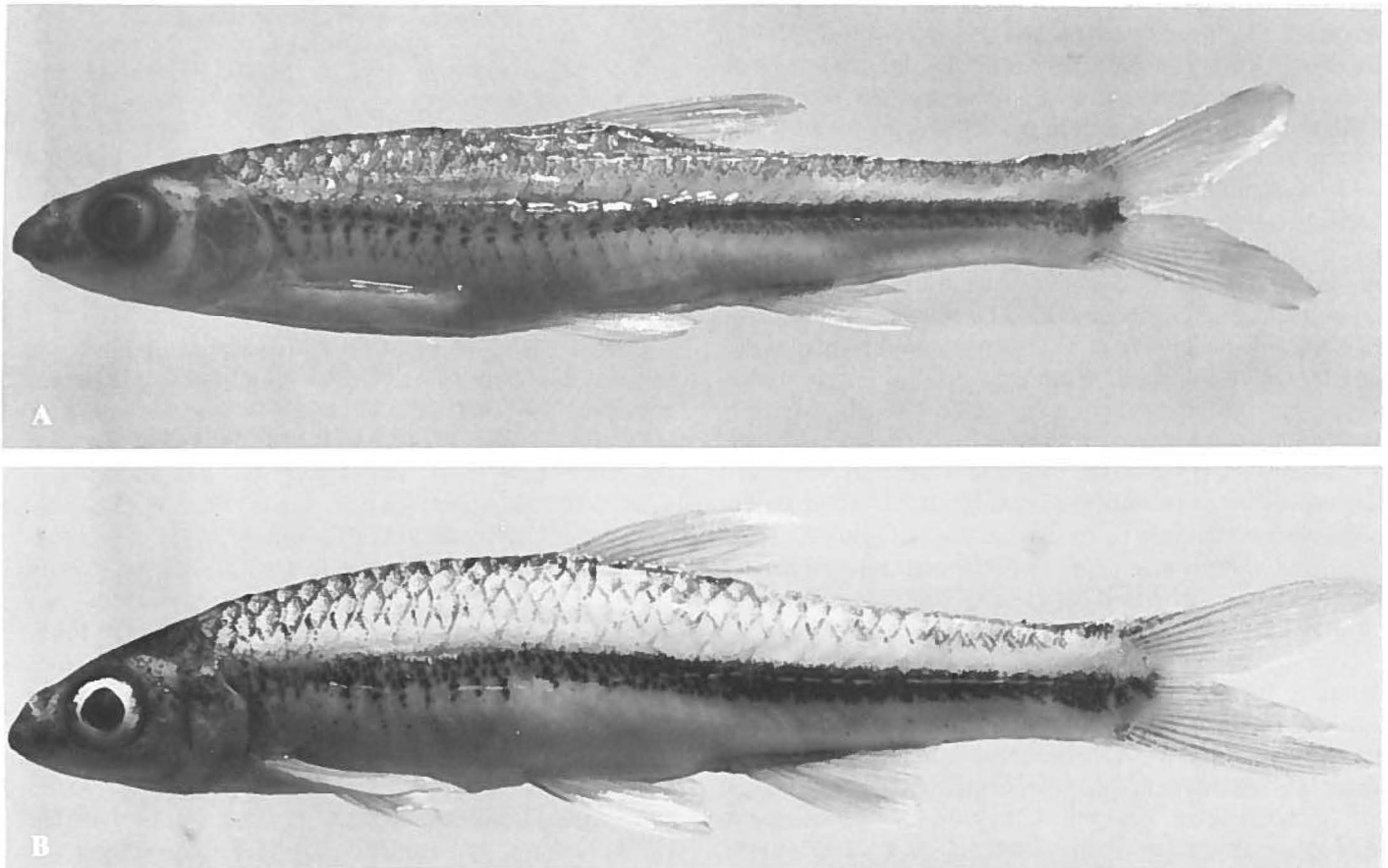


Figure 1. A) *Notropis cahabae*, new species. Holotype, breeding male, 39.8 mm SL, UAIC 9119.01; B) *N. volucellus*. Breeding male, 42.0 mm SL, UAIC 8358.05.

DESCRIPTION.—Proportional measurements and significant meristic variation (pectoral fin rays, lateral-line scale rows, body-circumferential scale rows, body-circumferential scale rows above and below lateral line, predorsal scale rows, breast squamation, and gill rakers) for *N. cahabae* are listed in Tables 2 to 5. General body shape and pigmentation are illustrated in Figures 1 and 2.

Dorsal fin rays 7 (1 individual), 8 (78), 9 (1); \bar{x} = 8.00, SD = 0.159. Anal fin rays 7 (4), 8 (75), 9 (1); \bar{x} = 7.96, SD = 0.249. Pelvic fin rays 8 (74), 9 (6); \bar{x} = 8.08, SD = 0.265. Principal caudal fin rays 19 (80). Caudal peduncle scale rows 12 (80). Caudal peduncle scale rows above lateral line 5 (80). Caudal peduncle scale rows below lateral line 5 (80).

Lateral line on body complete to hypural plate. Supratemporal canal interrupted; pores per side number 0 (2), 2 (7), 3 (24), 4 (7); \bar{x} = 2.85. Supraorbital canal complete and not joining infraorbital or posttemporal canals posterior to orbit; pores 8 (6), 9 (5), 10 (7), 11 (1), 12 (1); \bar{x} = 9.30. Infraorbital canal complete and continuous with posttemporal canal in most specimens (incomplete in 2 specimens); pores 10 (4), 11 (9), 12 (4), 13 (3); \bar{x} = 11.30. Preoperculo-mandibular canal complete in most specimens (incomplete in 4 specimens); pores 10 (1), 11 (3), 12 (13), 13 (2), 14 (1); \bar{x} = 11.95.

Peritoneum silver with numerous large melanophores. Intestine short and S-shaped, Type I of Kafuku (1958). Pharyngeal teeth 0,4-4,0 (20).

PIGMENTATION.—Breeding and non-breeding adults and juveniles plain, not brightly colored (Fig. 1). Dorsum, ventrally to one or two scale rows above lateral stripe, light olivaceous. Pre- and postdorsal stripes generally not developed; if present, stripe narrow and weakly developed. Wedge-shaped spot at origin of dorsal fin not developed. Dorsolateral scales lightly outlined with melanophores. Most scales with melanophores lightly distributed centrally; posterior edges of scales with two broadly indistinct lines; scales silver or white basally and between posterior lines. Distinct, silver/iridescent green stripe extending entire length of body separating olivaceous dorsum from distinct, darkly pigmented lateral stripe. Lateral stripe narrow, less than one scale deep, most intense posterior to dorsal fin origin, and with distinctly straight dorsal and ventral margins (Fig. 2); stripe terminating on caudal base in caudal spot no wider than caudal stripe. Lateral stripe on caudal peduncle with straight ventral margin, not expanded into lobe (Fig. 2). Anteriorly, lateral stripe more diffusely pigmented; melanophores most prominently distributed above lateral

Table 2. Morphological characters for *Notropis cahabae*, *N. volucellus* from Mobile Basin (M) and Tennessee/Cumberland (T) drainages, and *N. wickliffi*. Means and ranges of proportions in thousandths of a millimeter.

Trait	<i>N. cahabae</i> (N = 80)			<i>N. volucellus</i> (M; N = 20)			<i>N. volucellus</i> (T; N = 20)			<i>N. wickliffi</i> (N = 20)		
	Range	\bar{x}	SD	Range	\bar{x}	SD	Range	\bar{x}	SD	Range	\bar{x}	SD
SL	33.3-50.5	39.0	3.84	37.2-48.6	41.3	2.84	35.2-54.7	43.0	5.37	37.9-49.8	44.5	3.41
PRD/SL	504-561	529	0.012	505-549	531	0.011	497-549	518	0.013	472-548	518	0.018
PSD/SL	467-545	510	0.015	476-509	491	0.009	474-538	512	0.016	508-550	528	0.014
HL/SL	219-259	238	0.009	214-236	224	0.007	221-251	239	0.008	238-262	250	0.007
SNL/HL	461-587	521	0.029	555-628	595	0.022	498-582	544	0.022	501-580	548	0.024
ED/HL	276-384	322	0.022	277-375	322	0.027	247-354	304	0.023	310-388	353	0.022
UJL/HL	170-310	237	0.030	117-312	181	0.044	132-305	207	0.044	191-306	257	0.030
IOD/HL	191-281	231	0.018	213-366	252	0.041	189-247	214	0.019	186-256	226	0.018
HD/SL	50-88	67	0.008	55-111	66	0.012	48-84	64	0.008	54-79	64	0.007
HW/SL	134-164	144	0.005	138-162	149	0.006	145-166	154	0.007	159-177	166	0.005
MOC/HL	584-769	679	0.043	617-779	697	0.040	597-771	673	0.041	653-764	707	0.032
PCOC/SL	113-162	134	0.010	125-159	139	0.010	107-161	139	0.012	136-164	151	0.007
PVOC/SL	283-376	331	0.016	291-369	341	0.017	286-347	316	0.016	313-376	348	0.018
BW/SL	87-135	108	0.011	113-134	126	0.006	85-118	110	0.009	106-147	124	0.010
CPD/SL	77-105	93	0.006	79-108	95	0.006	74-101	88	0.006	92-109	100	0.004
CPW/SL	22-49	35	0.005	33-59	44	0.007	26-46	35	0.005	28-46	37	0.006
PRPV/SL	454-520	489	0.013	437-516	486	0.017	459-505	481	0.014	482-521	507	0.010
PVDO/SL	143-238	187	0.018	180-227	204	0.014	166-224	188	0.013	196-254	214	0.012
PVDR/SL	135-235	201	0.019	189-239	218	0.015	129-225	197	0.024	207-258	224	0.011
PRA/SL	622-734	673	0.018	645-701	678	0.017	638-715	674	0.019	632-738	689	0.022
ADR/SL	132-185	159	0.011	145-182	168	0.010	124-176	157	0.013	181-216	196	0.010
ADO/SL	212-280	240	0.012	179-261	238	0.018	220-271	242	0.015	256-316	286	0.014
PCDO/SL	274-350	317	0.013	285-341	318	0.015	192-335	297	0.030	277-354	312	0.016
DRVC/SL	384-536	421	0.023	377-433	403	0.017	388-454	416	0.016	387-447	416	0.013
AODC/SL	295-404	369	0.017	345-395	362	0.014	354-394	375	0.011	336-371	354	0.011
DF/SL	199-263	230	0.012	182-235	211	0.011	215-263	232	0.012	233-260	243	0.008
AF/SL	153-214	177	0.012	153-175	161	0.007	159-206	182	0.012	160-201	178	0.011
PVF/SL	129-186	157	0.009	140-171	153	0.009	147-179	162	0.008	139-173	160	0.010
PCF/SL	148-218	184	0.015	163-202	179	0.011	166-229	199	0.016	150-225	186	0.021

line. Anteriorly, below diffuse lateral stripe, melanophores concentrated at lateral line pores, providing punctuated pattern; posteroventral and anteroventral arcs extending full

height of elevated lateral-line scales from each pore, providing a herring-bone pattern. Venter silver/white except for weakly developed stripe from anal fin base to ventral pro-

Table 3. Counts of total circumferential scale rows and those above and below the lateral line in *Notropis cahabae*, *N. volucellus*, and *N. wickliffi*.

	Total body-circumferential scales										N	\bar{x}	SD
	17	18	19	20	21	22	23	24					
<i>Notropis cahabae</i>		2	3	75							80	19.91	0.363
<i>Notropis volucellus</i>													
Mobile Dr.	1			18	1						20	19.90	0.718
Tennessee/Cumberland Drs.			1	17	1	1					20	20.10	0.553
<i>Notropis wickliffi</i>					1	2	2	15			20	23.55	0.887

	Above lateral line						Below lateral line						N	\bar{x}	SD
	8	9	10	11	\bar{x}	SD	7	8	9	10	11				
<i>Notropis cahabae</i>		80			9.00	0.0	2	3	75				80	8.91	0.363
<i>Notropis volucellus</i>															
Mobile Dr.	1	18	1		9.00	0.324	1		19				20	8.90	0.447
Tennessee/Cumberland Drs.		18	1	1	9.15	0.489		1	19				20	8.95	0.224
<i>Notropis wickliffi</i>			1	19	10.95	0.224			3	2	15		20	10.60	0.754

Table 4. Counts of lateral-line and predorsal scale rows in *Notropis cahabae*, *N. volucellus*, and *N. wickliffi*.

	Lateral-line scales						N	\bar{x}	SD
	32	33	34	35	36	37			
<i>Notropis cahabae</i>		11	47	22			80	34.14	0.631
<i>Notropis volucellus</i>									
Mobile Dr.			3	14	3		20	35.00	0.562
Tennessee/Cumberland Drs.			3	13	3	1	20	35.10	0.718
<i>Notropis wickliffi</i>	2	17	1				20	32.95	0.394

	Predorsal scales					N	\bar{x}	SD
	12	13	14	15	16			
<i>Notropis cahabae</i>	1	29	36	13	1	80	13.80	0.770
<i>Notropis volucellus</i>								
Mobile Dr.		1	7	11	1	20	14.60	0.681
Tennessee/Cumberland Drs.		8	7	4	1	20	13.90	0.912
<i>Notropis wickliffi</i>	3	7	8	2		20	13.45	0.887

current rays of caudal fin. Dorsum of head, snout, and dorsum of opercle and preopercle olivaceous. Lateral stripe extends anteriorly along dorsal half of opercle, through orbit, and across lacrymal on snout, but not around tip of snout. Venter of head below orbit silver/white.

All fins clear, except for light development of melanophores along rays. Caudal, pectoral, and dorsal fins

Table 5. Variation in numbers of pectoral fin rays, gill rakers, and percent breast squamation in *Notropis cahabae*, *N. volucellus*, and *N. wickliffi*.

	Pectoral rays					N	\bar{x}	SD
	13	14	15	16	17			
<i>Notropis cahabae</i>	19	42	18	1		80	14.01	0.720
<i>Notropis volucellus</i>								
Mobile Dr.	1	14	4	1		20	14.25	0.639
Tennessee/Cumberland Drs.	3	13	4			20	14.05	0.605
<i>Notropis wickliffi</i>		2	15	2	1	20	15.10	0.641

	Gill rakers					N	\bar{x}	SD	
	5	6	7	8	9				10
<i>Notropis cahabae</i>		2	7	6	4	1	20	7.75	1.070
<i>Notropis volucellus</i>									
Mobile Dr.	3	5	11	1		20	6.50	0.827	
Tennessee/Cumberland Drs.	2	2	10	6		20	7.00	0.918	
<i>Notropis wickliffi</i>	1	5	11	3		20	6.80	0.768	

	Breast squamation					N	\bar{x}	SD
	0	0.25	0.50	0.75	1.00			
<i>Notropis cahabae</i>	7	14	12	36	11	80	0.59	0.296
<i>Notropis volucellus</i>								
Mobile Dr.	16	3		1		20	0.08	0.183
Tennessee/Cumberland Drs.	16	2	2			20	0.08	0.164
<i>Notropis wickliffi</i>	20					20	0.0	0.0

with all rays outlined by melanophores, best developed anteriorly; anal and pelvic fin rays with less intense development of melanophores.

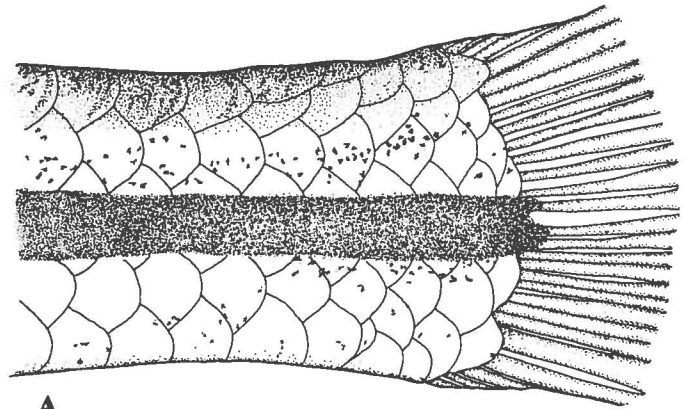
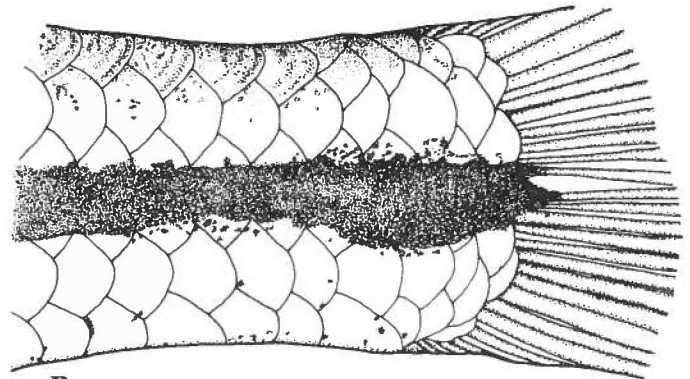
**A****B**

Figure 2. Caudal peduncle pigmentation. A) *Notropis cahabae*, with lateral stripe straight on dorsal and ventral margins; B) *N. volucellus*, with lateral stripe expanded into a ventrally deflected lobe.

TUBERCULATION.—Few specimens in reproductive condition were available. However, breeding materials indicate that from May to July males are tuberculate and females contain mature and maturing oocytes. No tuberculate females are known. The description below is based on breeding males from UAIC 8471.06 and 9119.01.

Dorsum of head sparsely covered with small, erect tubercles; more heavily concentrated posteriolaterally and anteriorly. Between nares and above orbits tubercles more heavily concentrated and arranged in small patches, especially between nares. Snout with broad band of erect tubercles, extending from and included on both lacrymals. Lower jaws,

branchiostegals, suborbital regions, and dorsal half of opercle with sparsely scattered, fine, and erect tubercles. Pectoral fin with rays one to seven tuberculate, with a single row per ray and one to four tubercles per segment. Dorsal, anal, caudal, and pelvic fins without tubercles.

SEXUAL DIMORPHISM.—Males and females of *N. cahabae* are very similar, differing in minor color characteristics during the breeding season. Based on available samples, melanophores are more heavily concentrated and intense along anterior rays of the pectoral and dorsal fins of males than in females.

No significant sexual variation was noted in meristic characters. Sexes differed significantly, however, in nine morphometric variables (Table 6; Student's t-test, $P < 0.05$). Males typically possess longer pectoral fins, heads, and upper jaws. Females generally have longer snouts, wider bodies, and more posteriorly placed pelvic and anal fins. The displacement of the anal and pelvic fins posteriorly is evidenced by the increased percentage of the pelvic fin to occiput, pelvic fin to dorsal fin origin, and anal fin origin to dorsal fin origin distances, relative to standard length (Table 6).

Table 6. Morphometric characters exhibiting sexual dimorphism in *Notropis cahabae*. Means and ranges of proportions in thousandths of a millimeter.

Trait	Males (N = 40)			Females (N = 40)		
	Range	\bar{x}	SD	Range	\bar{x}	SD
SL	33.3-47.8	37.8	3.20	34.6-50.5	40.1	4.12
HL/SL	224-259	241	0.008	219-257	235	0.009
SNL/HL	461-571	513	0.027	461-587	528	0.029
UJL/HL	182-304	245	0.031	170-310	230	0.028
PVOC/SL	286-361	326	0.014	283-376	335	0.016
BW/SL	87-132	107	0.010	90-135	111	0.010
PVDO/SL	143-232	183	0.016	151-238	192	0.019
ADO/SL	212-259	236	0.012	221-280	245	0.012
PCF/SL	158-218	188	0.014	148-215	181	0.014

VARIATION.—No geographic variation was noted in meristic and morphometric traits or coloration within the limited range of the Cahaba shiner.

ETYMOLOGY.—The name *cahabae* is a noun in a genitive case referring to the Cahaba River, to which the new species is endemic. The common name, Cahaba shiner, also refers to the observation that this shiner is restricted to this river and has been used by ichthyologists for this species for many years.

Distribution

Notropis cahabae is restricted to the main channel of a short portion of the Cahaba River, predominately in the Ridge and Valley Province of Alabama (Fig. 3). Prior to

1984, the Cahaba shiner was not known to occur below the Fall Line. Since then, collecting efforts have discovered this species at four locations in the Gulf Coastal Plain (Fig. 3) (Pierson et al., 1989). These collections are represented by only a few individuals and are probably the result of waif dispersal below Cahaba Falls at Centreville from preferred habitats in the Ridge and Valley Province.

Historically, the range of this shiner included about 140 river kilometers (76 mi), from Helena, Shelby Co., to Centreville, Bibb Co., Alabama, but has since declined significantly both in range and population size, primarily as a result of the detrimental effects of development and mining on the Cahaba watershed (Stiles, 1978; Howell et al., 1982; Ramsey, 1982). Few individuals of the shiner have been recorded in recent years above Piper bridge (Co. Rd. 24), and the stronghold for the species is now limited to only about 28 river kilometers (15 mi) between the Fall Line and Piper bridge (Fig. 3). Given the habitat of this species and the distribution patterns of other Mobile Basin endemics, it is probable that *N. cahabae* had a more widespread distribution in the basin, including the Coosa River System, prior to extensive habitat modifications.

Habitat and Ecology

The principal habitat of the Cahaba shiner includes the main channel of the Cahaba River, primarily in areas where shallow shoal macrohabitats predominate. *Notropis cahabae* is not associated with smaller tributary creeks and streams like the mimic shiner, *N. volucellus*, except during times of flooding. During high water, the Cahaba shiner has been observed to move into the lower sections of major tributaries and to reside temporarily in backwater habitats with the mimic shiner (Stiles, 1978; R. A. Stiles, pers. comm.). This pattern of seasonal variation in habitat preference is similar to the seasonal cycles observed in Ohio River populations of the closely related channel shiner, *N. wickliffi*. This species occurs primarily in larger rivers and the lower portions of large river tributaries (Trautman, 1981).

Studies by Ramsey (1982), Howell et al. (1982), and Stiles (1978), and our personal observations indicate that *N. cahabae* occurs primarily over a clean sand or sand-gravel substrate in water 0.25 to 1.5 meters in depth. Ramsey (1982) did find the species occasionally over a strictly gravel substrate. Howell et al. (1982) reported the shiner from a large (0.8 km) shoal area below Piper Bridge, where it was typically associated with sand, sand-gravel, or mollusk-shell fragment substrate in quieter water just below swift riffles traversing an extensive solid bedrock base. These authors also found the species to be common in two to three centimeters of water over a sand substrate in *Justicia* beds adjacent to swift riffles. Ramsey (1982) noted pre-spawning individuals in May 1970 and 1981 near the substrate and congregated at the end of long pools, just above riffles. Spawning and post-spawning habitats are unknown, but are probably associated with clean, broad, rocky riffles, as has been

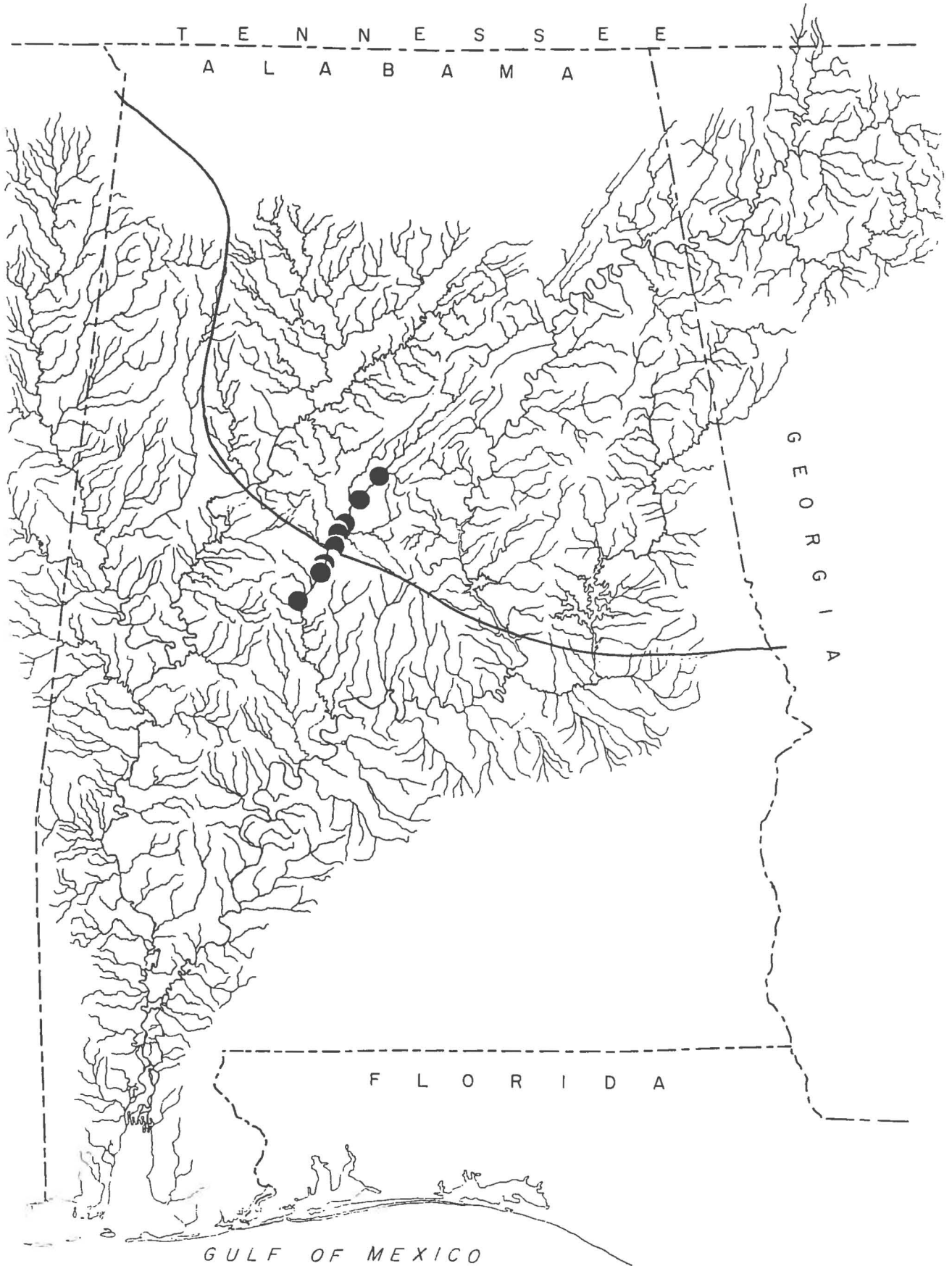


Figure 3. Distribution of *Notropis cahabae*. Solid line represents Fall Line.

suggested for the related mimic shiner, *N. volucellus* (Cross, 1967).

Although spawning habitats are unknown for the Cahaba shiner, this species is known to be in reproductive condition from May to July. Tuberculate males and gravid females with mature oocytes have been observed during these months, but actively spawning individuals (as indicated by running eggs and milt) have been collected only in mid- and late June (Ramsey, 1982; Oliver, 1986). Reproductively spent males and females have been collected in late June, further supporting a mid- to late June spawning period. Ramsey (1982) also presented data for young-of-the-year individuals, ranging in length from 17 to 19 mm SL, in late July, which also supports May to June spawning. Ramsey (1978) further suggested that this shiner may be an annual species, surviving for only one year and dying after a spring-summer spawning.

Little is known about the biology of *Notropis wickliffi* except for preferred habitats (Trautman, 1981). *Notropis volucellus* is known to live 2 to 3 years (Black, 1945; Moyle, 1973) and presumably spawns from June to August, depending upon geographic location (Black, 1945; Cross, 1967; Pflieger, 1975). Based on tuberculate males and gravid females, our observations and those of Oliver (1986) indicate that periods of active reproduction overlap considerably for populations of *N. cahabae* and *N. volucellus*, ranging from mid-May to early July. Oliver (1986) also found both species to mature in the first year of life, between 35 and 37 mm SL, but to differ in the number and size of mature oocytes produced. Cahaba shiners produced significantly fewer and smaller oocytes than the mimic shiner, and averaged a significantly smaller ovarian weight-somatic weight ratio.

Allozyme Variation

Of the 38 presumptive gene loci examined for species of the *N. volucellus* species group, 18 were determined to be monomorphic for all taxa (Cbp-1, Cbp-2, Ck-A, Ck-B, S-Ap-A, Ald-A, Gp-1, G3pdh-A, M-Icdh-A, S-Icdh-A, Ldh-B, M-Mdh-A, S-Mdh-A, α -Man-1, Pgm-A, Pk-A, S-Sod-A, Tpi-B). The remaining loci were polymorphic in one or more population or species (Table 7). The sample of *N. cahabae* was polymorphic for only four of the 38 systems, M-Aat-A, Est-1, Est-2, and Gpi-A. Other members of the species group expressed more genetic variability and were polymorphic for six to nine loci (Table 7). Summaries of overall variability within the Cahaba shiner include a mean of 1.2 alleles per locus, a mean heterozygosity of 0.063, and only 20% polymorphic loci. Sympatric mimic shiners possessed a mean of 1.4 alleles per locus, a mean heterozygosity of 0.049, and 35% polymorphic loci.

A comparison of genotype arrays for *N. cahabae* and presumed relatives within the *N. volucellus* group (Table 7) supports the distinctiveness of this species. Of the 20 polymorphic loci, the Cahaba shiner is distinctive from sympatric *N. volucellus* at ten enzyme systems. These include

fixed differences or unique alleles in either *N. cahabae* or *N. volucellus* from the Mobile Basin at the loci Acp-A, Ada-A, M-Aat-A, Pep-A, Est-1, Est-2, Gpi-A, Ldh-A, S-Mdh-B, and Tpi-A. Unique alleles present in *N. cahabae* at four loci, Acp-A (allele *a*), Gpi-A (*a*, *b*), M-Aat-A (*b*), and Tpi-A (*a*), separate this species from all populations of *N. volucellus* and *N. wickliffi* (Table 7). Further support for genetic independence of the Cahaba shiner from the more widespread *N. volucellus* complex and *N. wickliffi* is the frequent occurrence of distinctive alleles in *N. cahabae*, found only rarely in single populations of *N. volucellus*. Presumptive homologous allelic products of Ada-A (*b*) and S-Mdh-B (*b*) are fixed in *N. cahabae*, while the former is absent in *N. volucellus* and *N. wickliffi* and the latter is not present in *N. volucellus* (Table 7). Likewise, Est-1 (*b*) is rarely expressed in *N. cahabae*, but commonly expressed in *N. volucellus* and *N. wickliffi*.

Preliminary evidence from patterns of allozyme variation within the *N. volucellus* species group corroborate observed patterns of morphological variation and support a polytypic *N. volucellus* complex. Within *N. volucellus*, at least three different forms can be identified on the basis of fixed and/or disproportionately distributed unique allelic products (Table 7). All *N. volucellus* share a fixed Acp-A (*c*) product, distinctive from other members of the species group, and also share a polymorphic and derived Pep-A (*a*) product. Mimic shiners from the Kiamichi River are distinctive and possess unique, derived alleles for Est-1 (*a*), G6pdh-A (*b*), and Mpi-A (*a*) (Table 7). *Notropis volucellus* from the Tennessee and Ohio rivers are distinctive from all other populations and species at the M-Aat-A locus through expression of the more anodally migrating and primitive *a* allele. Although the sample size is limited, the single specimen of *N. wickliffi* is distinctive from other members of the species group for the derived Acp-A (*d*) and Tpi-A (*c*) alleles and in expressing a primitive Ldh-A (*b*) allele, characteristic of the outgroup *N. sp. cf. spectrunculus*.

Although a more intensive investigation is warranted to evaluate these loci in differentiating members of the *N. volucellus* complex, patterns of variation in *N. volucellus* indicate that it is not a single, panmictic population as implied by present taxonomy. Three or more forms may presently be masquerading under *N. volucellus*, although evaluation of this hypothesis must await additional samples from throughout the range of the species. Further, allozymic patterns of variation at several loci support genetic isolation of *N. cahabae* and perhaps *N. wickliffi* from their previously presumed close relative, *N. volucellus*.

Comparisons

Notropis cahabae, *N. volucellus*, and *N. wickliffi* may be distinguished from one another on the basis of meristic, morphometric, coloration, and allozyme characters, as well as characteristics of the lateralis system and tuberculation. These features are summarized in Tables 8 to 10, illustrated

Table 7. Genotypic composition for species of the *Notropis volucellus* species group. Genotypes are listed first, followed by number of individuals in parentheses.

Species	Locus									
	Acp-A	Ada-A	Ak-A	M-Aat-A	S-Aat-A	Pep-A	Pep-S	Est-1	Est-2	Fum
<i>Notropis cahabae</i>	aa(8)	bb(8)	aa(8)	bb(6) bc(1) cc(1)	aa(8)	bb(8)	bb(8)	bd(3) dd(5)	cc(4) cd(3) dd(1)	bb(8)
<i>Notropis volucellus</i> Mobile Dr.	cc(8)	aa(4) ac(2) cc(2)	aa(8)	cc(8)	aa(8)	aa(3) ab(2) bb(3)	bb(8)	bb(8)	cb(7) cc(1)	bb(8)
Tennessee/Ohio Drs.	cc(9)	aa(5) bb(4)	aa(8) bb(1)	aa(9)	aa(8) ab(1)	aa(8) ab(1)	bb(9)	bb(9)	aa(1) ac(2) cc(2) bb(4)	bb(9)
Kiamichi Dr.	cc(5)	aa(5)	aa(5)	cc(5)	aa(5)	aa(2) ab(2) bb(1)	aa(2) bb(3)	aa(1) ab(1) bb(3)	cc(4) cd(1)	bb(5)
<i>Notropis wickliffi</i>	dd(1)	aa(1)	aa(1)	cc(1)	aa(1)	bb(1)	bb(1)	bb(1)	bb(1)	bb(1)
<i>Notropis</i> sp. cf. <i>spectrunculus</i>	bb(5)	aa(1) ab(1) bb(3)	aa(5)	aa(5)	aa(5)	bb(5)	bb(5)	bb(3) bc(1) cc(1)	aa(1) ad(1) bb(2) bc(1)	ab(2) bb(3)

Species	Locus									
	G-6pdh-A	Gpi-A	Gpi-B	Ldh-A	S-Mdh-B	M-Me-A	S-Me-A	Mpi-A	Pgdh-A	Tpi-A
<i>Notropis cahabae</i>	aa(8)	aa(1) ab(3) bb(4)	aa(8)	cc(8)	bb(8)	bb(3)	aa(8)	bb(8)	bb(8)	aa(8)
<i>Notropis volucellus</i> Mobile Dr.	aa(8)	cd(1) dd(7)	aa(8)	ac(1) cc(6) cd(1)	aa(8)	bb(5)	aa(7) bb(1)	bb(8)	bb(7) bc(1)	bb(8)
Tennessee/Ohio Drs.	aa(9)	cc(2) cd(2) dd(5)	aa(7) ab(2)	cc(9)	aa(9)	aa(1) ab(1) bb(6)	aa(9)	bb(9)	aa(1) bb(8)	bb(9)
Kiamichi Dr.	bb(5)	dd(5)	aa(5)	cc(5)	aa(5)	aa(2) ab(1)	aa(5)	aa(3) ab(2)	bb(5)	bb(5)
<i>Notropis wickliffi</i>	aa(1)	dd(1)	aa(1)	bb(1)	bb(1)	aa(1)	aa(1)	bb(1)	bb(1)	cc(1)
<i>Notropis</i> sp. cf. <i>spectrunculus</i>	aa(1)	ee(5)	aa(4) ab(1)	bb(5)	aa(5)	aa(5)	aa(5)	bb(5)	bb(5)	bb(5)

in Figures 1 and 2, and are discussed below.

With regard to meristic features, all of the species are generally similar. *Notropis wickliffi* is distinguished from other species on the basis of a greater number of body-circumferential scales, both above and below the lateral line (Table 3). This species also has significantly more pectoral fin rays (Table 5) and fewer lateral-line scale rows (Table 4) than the other two species. *Notropis cahabae* can be distinguished from *N. volucellus* occurring both in the Mobile Basin and Tennessee/Cumberland drainages by significantly fewer lateral-line scale rows, from Mobile Basin

N. volucellus by significantly fewer predorsal scale rows, and from both *N. volucellus* and *N. wickliffi* in possessing a scaled breast region and in having significantly more gill rakers on the first arch (Table 5).

Overall variance of all meristic traits (number of gill rakers not included) with respect to the three species is best summarized in principal components analysis (PCA). The first PC served as the best axis for separation of *N. wickliffi* from the other two species (Fig. 4). Characters loading most significantly along this axis included those discussed above identifying *N. wickliffi* as a distinct taxon, including pec-

toral fin rays, lateral-line scale rows, and body-circumferential scale rows (Table 8). The second PC axis served primarily to distinguish between *N. cahabae* and *N. volucellus* from the Mobile Drainage (Fig. 4). *Notropis volucellus* from the Tennessee/Cumberland drainages expressed the complete range of variation displayed by both *N. cahabae* and *N. volucellus* from the Mobile Basin. Characters predominately loading along PCII included numbers of predorsal and lateral-line scale rows and breast squamation (Table 8).

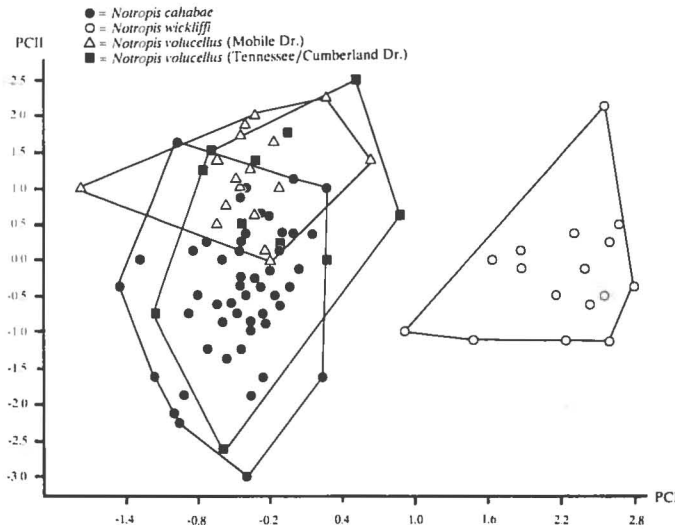


Figure 4. Plot of scores on first and second principal components for 10 meristic characters of species in the *Notropis volucellus* species group.

Notropis cahabae may be distinguished from the sympatric *N. volucellus* and allopatric populations of *N. volucellus* and *N. wickliffi* by characters relating to coloration and pigmentation. The lateral stripe on the caudal peduncle of *N. cahabae* is not expanded ventrally into an obvious lobe, but has a straight dorsal and ventral margin (Fig. 2). In *N. volucellus* and *N. wickliffi* the lateral stripe on the caudal peduncle is expanded into a ventrally deflected lobe (Fig. 2). *Notropis cahabae* also differs from *N.*

Table 8. Variance loadings for the principle components in the analysis of meristic variables for *Notropis cahabae*, *N. volucellus*, and *N. wickliffi*.

Variable	PCI	PCII
DR	0.277	-0.060
AR	0.211	0.536
PVR	-0.025	0.242
PCR	0.586	0.389
LLS	-0.584	0.472
CRS	0.965	-0.054
CRSA	0.943	-0.074
CRSB	0.896	-0.028
PDS	-0.186	0.589
BRTS	-0.483	-0.442

volucellus in the intensity of coloration and pigmentation. In the Cahaba and channel shiners the dorsal coloration is fairly uniform, with melanophores evenly distributed, and the predorsal stripe and spot is nonexistent to very lightly pigmented. The dorsal caudal peduncle scales in these two species are also uniformly pigmented from the dorsal fin to the caudal fin, and the margins of dorsolateral scales are only lightly pigmented and not well defined. In *N. volucellus* the predorsal stripe and spot are both evident, the dorsolateral scales have sharply outlined margins, and the dorsal caudal peduncle scales are more heavily pigmented posteriorly.

Notropis cahabae, *N. volucellus*, and *N. wickliffi* may also be distinguished on the basis of features in the cephalic lateralis system and breeding tuberculation. In *N. cahabae*, *N. wickliffi*, and the Tennessee and Cumberland populations of *N. volucellus*, the preoperculo-mandibular canal is complete in nearly all specimens (interrupted in 3, 0, and 2 specimens, respectively, of 20 specimens from each). In *N. volucellus* from the Mobile Basin the preoperculo-mandibular canal is interrupted between the mandible and preopercular bone (N = 20). The connection of the infraorbital with the posttemporal canal, posterior to the orbit, also varies to some degree among the species. The connection is complete in all *N. wickliffi* (N = 20), 75% of *N. cahabae* (15 of 20), 85% of *N. volucellus* from the Tennessee/Cumberland drainages (17 of 20), and 50% of *N. volucellus* from the Mobile Basin (10 of 20). The differential variation in the cephalic lateralis system is further indication of divergence between these three taxa and provides additional support that, as presently recognized, *N. volucellus* is not a single species. *Notropis cahabae* and *N. volucellus* also differ from one another in the relative sizes of cephalic breeding tubercles. Although the distribution of cephalic tubercles in both taxa appears to be similar, tubercle size in *N. cahabae* is smaller than those observed on similar-sized *N. volucellus*. Breeding males of *N. wickliffi* have not been observed.

Members of the *N. volucellus* species group differ from one another in overall shape, estimated through body measurements and PCA. Because the sexes of *N. cahabae* and other species differ significantly in some body measurements (Table 6), the PCAs were examined separately for each sex. Although some overlap was observed, PCII and PCIII served as the best overall components for differentiation of the species. *Notropis cahabae* is morphologically distinguishable nearly 100% of the time from *N. wickliffi* and the sympatric form of *N. volucellus* from the Mobile Basin. Allopatric *N. volucellus* from the Tennessee and Cumberland drainages, however, exhibit considerably more spatial overlap with *N. cahabae* in both males and females.

For males, PCII served as the best overall component to separate *N. wickliffi* from other species (Fig. 5; Table 9). This component describes variation between the species in

eye diameter, upper jaw length, dorsal fin length, placement of the anal and pectoral fins, width of the caudal peduncle, and predorsal length. *Notropis wickliffi* typically has a larger eye, longer mouth, more posteriorly placed anal fin, a longer and more anteriorly placed dorsal fin, shorter predorsal length, and a narrower caudal peduncle than the other species. Separation of *N. cahabae* from the two distinct forms of *N. volucellus* is best accomplished along PCIII. This axis describes variation in body width, caudal peduncle length, width, and depth, placement of the pelvic and dorsal fins, predorsal length, and anal and pectoral fin length. For these traits, the variation in *N. cahabae* lies largely between the extremes displayed by the morphologically distinct and separable forms of *N. volucellus* (Fig. 5). Specimens of *N. volucellus* from the Mobile Basin have more robust bodies, and more posteriorly placed pelvic and dorsal fins than *N. volucellus* from the Tennessee and Cumberland drainages and most *N. cahabae* (Fig. 5; Table 9). Likewise, *N. volucellus* from the latter drainages typically have longer caudal peduncles, shorter predorsal lengths, and longer anal and pectoral fins.

For females, separation of all taxa is not as readily apparent using PCA (Fig. 6; Table 9). Like males, no overlap

Table 9. Variance loadings for the principle components in the analysis of morphometric variables for males and females of *Notropis cahabae*, *N. volucellus*, and *N. wickliffi*.

Variable	Males			Females		
	PCI	PCII	PCIII	PCI	PCII	PCIII
SL	0.989	-0.094	-0.013	0.992	-0.078	-0.066
PRD	0.932	-0.256	0.145	0.982	-0.057	-0.078
PSD	0.947	0.129	-0.233	0.977	-0.059	0.127
HL	0.917	0.137	-0.117	0.941	-0.027	0.228
SNL	0.928	0.081	0.104	0.952	0.113	-0.010
ED	0.718	0.418	0.110	0.801	0.099	0.378
UJL	0.373	0.398	-0.049	0.425	0.013	0.528
IOD	0.770	0.027	0.143	0.771	0.074	-0.120
HD	0.495	-0.153	0.001	0.519	-0.138	-0.049
HW	0.924	0.176	-0.002	0.951	0.118	0.109
MOC	0.836	0.211	-0.016	0.917	0.078	0.141
PCOC	0.839	0.177	0.112	0.911	0.110	0.107
PVOC	0.924	-0.036	0.265	0.947	0.088	0.002
BW	0.797	0.116	0.318	0.887	0.311	-0.118
CPD	0.828	0.126	0.325	0.913	0.235	0.102
CPW	0.567	-0.262	0.277	0.642	0.368	-0.304
PRPV	0.961	0.056	0.035	0.983	0.025	0.021
PVDO	0.872	0.208	0.115	0.851	0.395	-0.071
PVDR	0.824	0.172	0.262	0.857	0.307	-0.037
PRA	0.973	-0.038	-0.001	0.989	-0.008	-0.056
ADR	0.854	0.363	0.201	0.903	0.293	0.166
ADO	0.893	0.378	0.054	0.932	0.195	0.232
PCDO	0.875	-0.226	0.228	0.813	0.312	-0.228
DRVC	0.845	-0.093	-0.208	0.942	-0.145	0.079
AODC	0.858	-0.249	-0.253	0.921	-0.214	-0.089
DF	0.824	0.291	-0.173	0.897	-0.056	0.300
AF	0.757	0.089	-0.252	0.844	-0.233	0.214
PVF	0.867	0.033	-0.122	0.901	-0.148	0.061
PCF	0.722	0.169	-0.323	0.776	-0.274	-0.033

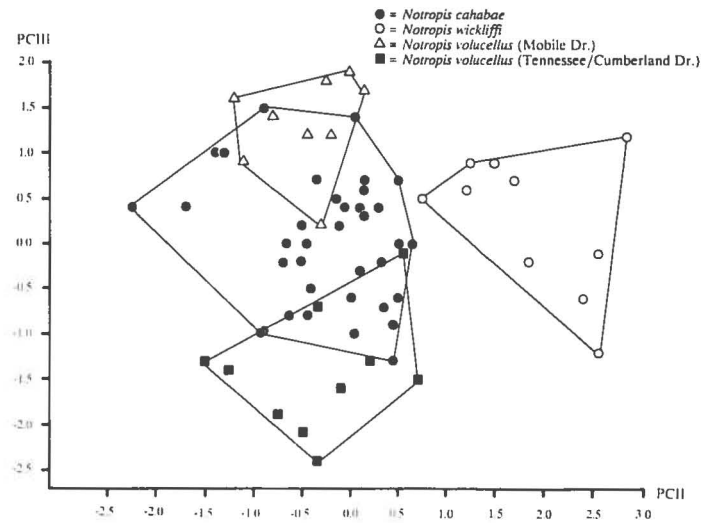


Figure 5. Plot of scores on second and third principal components for 29 morphometric characters for males of species in the *Notropis volucellus* species group.

is observed between the two forms of *N. volucellus* and either of these with *N. wickliffi*. Further, minimal overlap is observed between *N. cahabae* and samples of *N. wickliffi* and *N. volucellus* from the Mobile Basin. However, considerable spatial overlap is observed between *N. cahabae* and *N. volucellus* from the Tennessee and Cumberland drainages (Fig. 6). Variables describing most shape variation along PCII include body and caudal peduncle depth and width, placement of the dorsal fin, and anal and pectoral fin lengths. *Notropis wickliffi*, *N. volucellus* from the Mobile Basin, and some *N. cahabae* typically have more robust (deep and wide) bodies, smaller fins, and shorter caudal peduncles (Fig. 6; Table 9). Along PCIII, females vary in reference to head length, eye diameter, up-

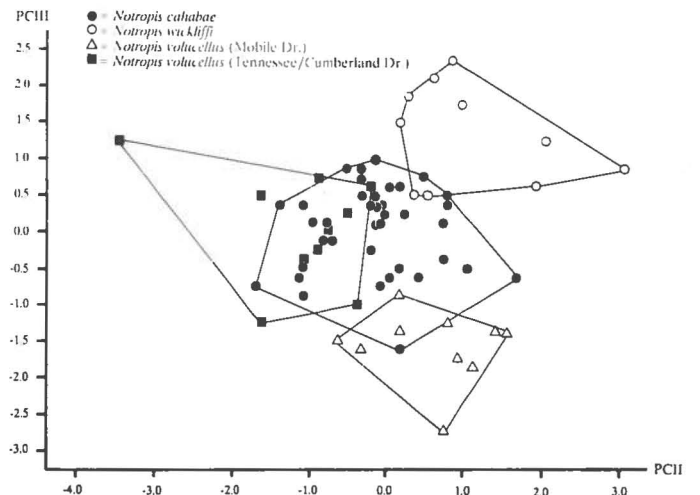


Figure 6. Plot of scores on second and third principal components for 29 morphometric characters for females of species in the *Notropis volucellus* species group.

per jaw length, body depth and width, and dorsal fin length. *Notropis wickliffi* and *N. volucellus* from the Mobile Basin represent two extremes along this axis, with *N. cahabae* and Tennessee/Cumberland *N. volucellus* occupying an intermediate spatial location. Females of *N. wickliffi* typically have longer heads and upper jaws, larger eyes, more anteriorly placed dorsal fins, more robust bodies, and longer dorsal fins (Fig. 6).

Notropis cahabae and forms within the *N. volucellus* complex (both in the Mobile Basin and Mississippi River Basin) differ allozymically (Tables 7 and 10). On the basis of 38

presumptive gene loci, *N. cahabae* can be distinguished from sympatric *N. volucellus* at ten enzyme systems, including Acp-A, Ada-A, M-Aat-A, Pep-A, Est-1, Est-2, Gpi-A, Ldh-A, S-Mdh-B, and Tpi-A (Table 7). From all forms of *N. volucellus*, *N. cahabae* also differs with fixed, unique alleles at Acp-A, S-Mdh-B, and Tpi-A, and possesses unique, derived alleles, but in a polymorphic condition at three loci, including M-Aat-A, Est-1, and Gpi-A. From *N. wickliffi*, the Cahaba shiner may be differentiated by diagnostic allelic products at Acp-A, Ada-A, M-Aat-A, Est-1, Est-2, Gpi-A, Ldh-A, M-Me-A, and Tpi-A (Table 7).

Table 10. Morphological and allozyme characters distinguishing *Notropis cahabae*, *N. volucellus* from Mobile Basin (M) and Tennessee/Cumberland/Ohio (T) drainages, and *N. wickliffi*.

Character	<i>N. cahabae</i>	<i>N. volucellus</i> (M)	<i>N. volucellus</i> (T)	<i>N. wickliffi</i>
Lateral stripe on caudal peduncle	Straight dorsal and ventral margin	Expanded into ventrally deflected lobe	Expanded into ventrally deflected lobe	Expanded into ventrally deflected lobe
Predorsal stripe and spot	Nonexistent to lightly pigmented	Heavily pigmented and evident	Heavily pigmented and evident	Nonexistent to lightly pigmented
Caudal peduncle scales	Uniformly pigmented	More heavily pigmented posteriorly than anteriorly	More heavily pigmented posteriorly than anteriorly	Uniformly pigmented
Circumferential scales above and below lateral line	Usually 9	Usually 9	Usually 9	Usually 11
Lateral-line scales	Usually 34-35	Usually 35	Usually 35	Usually 33
Breast squamation	Usually scaled	Usually naked	Usually naked	Naked
Pectoral rays	Usually 14	Usually 14	Usually 14	Usually 15
Preoperculo-mandibular canal	Usually complete	Interrupted	Usually complete	Complete
Acp-A	a	c	c	d
Pep-A	b	a/b	a/b	b
Est-1	b/d	b	b	b
Gpi-A	a/b	c/d	c/d	d
S-Mdh-B	b	a	a	b
Tpi-A	a	b	b	c

Relationships and Biogeography

Although sample sizes for some taxa are limited in biochemical comparisons, the number of loci examined in this analysis and derived characters from color pattern variation provide hypotheses of species relationships which can be subjected to further testing. In all analyses, the *N. volucellus* complex, including samples from the Mobile, Tennessee, Ohio, and Kiamichi drainages, formed a monophyletic group. The interrelationships of diagnosable forms within this complex differed, however, for distance analyses, but this clade was sister to a clade inclusive of *N. cahabae* and *N. wickliffi* (Fig. 7).

Distance Wagner analyses, using allozyme variation and two characters describing coloration of the dorsum, with

both modified Rogers and Prevosti distances produced two different tree topologies. In both topologies the *N. volucellus* complex was monophyletic and sister to a clade involving *N. cahabae* and *N. wickliffi*. Within *N. volucellus*, however, the Tennessee/Ohio drainage samples were either sister to Mobile drainage samples or Kiamichi River specimens. Of the two topologies, the shortest trees for both distances were those depicting the Mobile drainage and Tennessee/Ohio drainage samples as sister groups, sister to the Kiamichi River samples.

Evaluation of distance trees and additional, alternative topologies with FREQPARS for the maximally parsimonious hypotheses revealed a single minimum length tree describing speciation in the *N. volucellus* species group. The

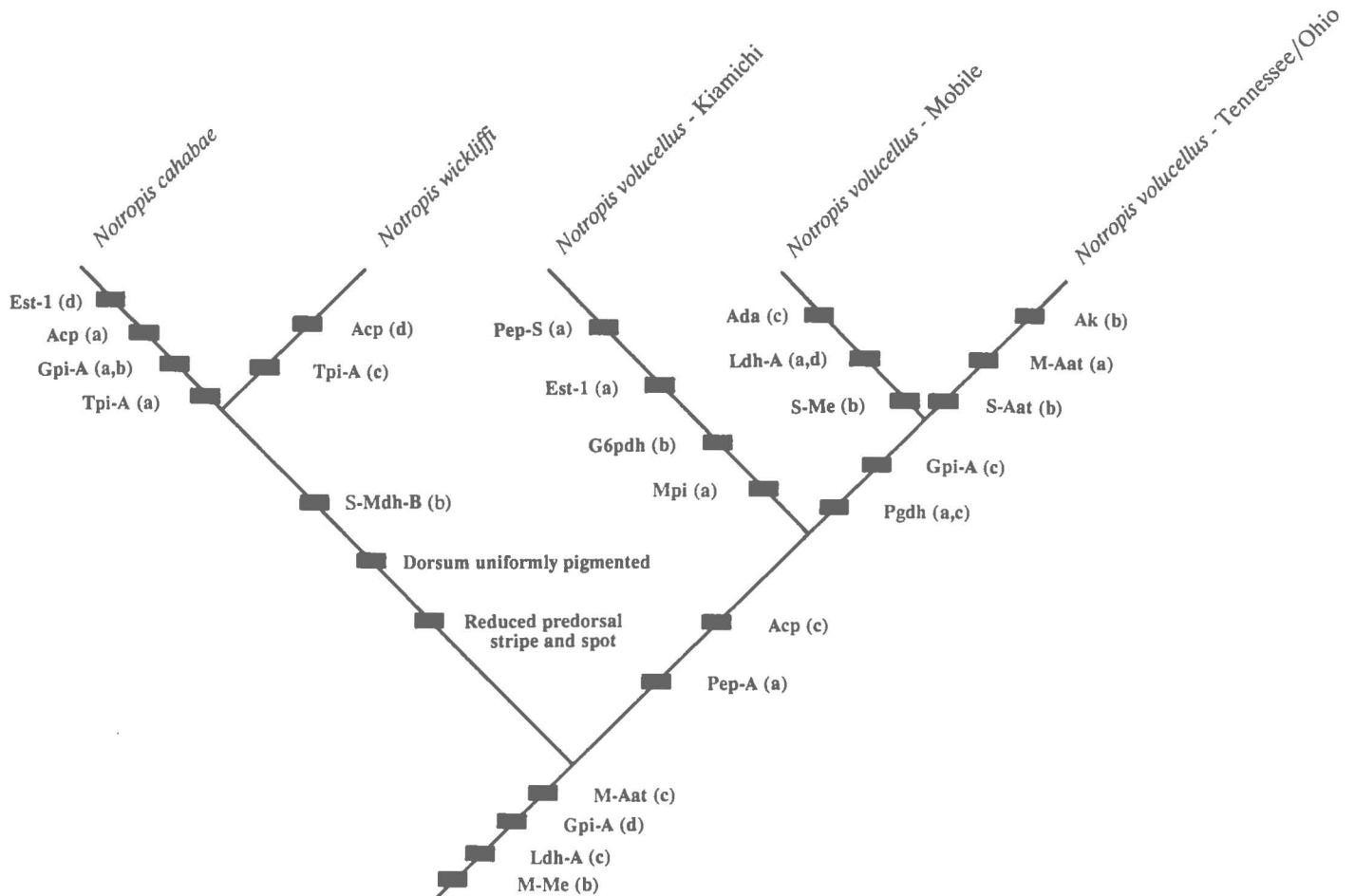


Figure 7. Hypothesized phylogenetic relationships among species in the *Notropis volucellus* species group. Solid bars on branches represent synapomorphic or autapomorphic characters. Allozyme characters depicted include derived alleles in a transformation series at each locus as part of a synapomorphic allelic combination and are discussed in text and presented in Table 7.

shortest topology (length = 54.2) depicted the *N. volucellus* complex with Mobile and Tennessee/Ohio river populations forming a monophyletic group sister to Kiamichi River samples, and this clade sister to *N. cahabae* plus *N. wickliffi* (Fig. 7). Alternative topologies, including the additional distance Wagner resolution with Mobile and Kiamichi samples as sister taxa, ranged in length from 55.5 to 58.4.

Using FREQPARS to interpret character evolution of allozyme and morphological features, the monophyly of *N. volucellus* is supported by allelic combinations inclusive of two derived alleles, Acp-A (c) and Pep-A (a). Within *N. volucellus* the sister group relationship between forms from the Mobile and Tennessee/Ohio drainages is supported by a derived Gpi-A (c) and alleles *a* and *c* at Pgdh-A. All three forms of *N. volucellus* within this clade are also diagnosed by three to four derived traits, with the expression of M-Aat-A (a) in *N. volucellus* from the Tennessee/Ohio drainages representing a reversal to the primitive condition (Fig. 7). The sister group relationship between *N. cahabae* and *N. wickliffi* is supported by a derived allelic combina-

tion and two coloration features. Both species possess the apomorphic S-Mdh-B (b), unique to these two species. *Notropis volucellus* and *N. sp. cf. spectrunculus* both possess the primitive *a* allele at S-Mdh-B locus. Relative to *N. sp. cf. spectrunculus* and *N. volucellus* these species also possess a derived reduction and/or loss of the well-defined predorsal stripe and spot, and have a uniformly pigmented dorsum with poorly defined scale margins. *Notropis cahabae* and *N. wickliffi* are each diagnosed by four and two autapomorphic combinations of alleles, respectively. Hypothesized synapomorphic characters for the entire *N. volucellus* species group include allelic combinations inclusive of M-Aat-A (c), Gpi-A (d), Ldh-A (c), and M-Me-A (b). The absence of the derived Ldh and Me products in *N. wickliffi* is likely the result of both products being polymorphic and excluded from the limited sample size of this species. Both products are occasionally polymorphic and rare in samples of other species (Table 7).

Species relationships depicted in the *N. volucellus* species group (Fig. 7) are consistent with an ancestral Central Highlands fish fauna occurring prior to the Pleistocene as

discussed by Mayden (1985, 1987a, 1987b, 1988b). The sister group relationship hypothesized between *N. cahabae* from the Mobile Basin and *N. wickliffi* from the Mississippi Basin, as well as between Tennessee/Ohio and Mobile forms of *N. volucellus*, is concordant with and replicated by numerous other fishes and molluscs. As discussed by Mayden (1987a, 1987b, 1988b), this replicated biogeographic pattern between upper Mobile Basin and Tennessee Drainage fishes is largely the result of the breakup of the large Miocene Appalachian River. Although some disagreement exists over the occurrence of any major river connection between these drainages (Mayden, 1988b), the correlation of two additional speciation events within a single clade of *Notropis* provides additional support for the ancient nature of the fauna. The probable large size of this ancient Appalachian River as hypothesized by Mayden (1987a, 1987b) is also supported here by the sister group relationship between two large-river taxa, *N. cahabae* and *N. wickliffi*. Both species possess large-river ecological characteristics and life-history tactics presumably evolved in their common ancestor.

Status

Although members of the *Notropis volucellus* species group can be considered common representatives in some eastern North American rivers, the same is not true for *Notropis cahabae*. Given the extremely limited distribution of the Cahaba shiner and the observation that the species' range has become increasingly more restricted, this species has been listed as endangered by the Alabama Department of Conservation and Natural Resources. The disappearance of upper Cahaba River populations of this shiner are indicative of adverse modifications of habitats fundamental to the species in the Cahaba Drainage. Given that the stronghold of this rare fish encompasses only 28 river kilometers of the main channel of the Cahaba River, it is imperative that this species be monitored to prevent further deterioration of its status, that natural habitat of this species be maintained, and that any adverse modifications of any upstream portions of the Cahaba River be strictly monitored and prevented in the future. This species represents one of the most geographically restricted shiners in North America and its preservation and protection are extremely critical in light of present and planned deforestation, development, and mining in the upper Cahaba River watershed.

Acknowledgements

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Material Examined

Specimens in this study not designated as types and those used in comparative analyses are listed below. Vouchers for specimens used in biochemical analyses are identified by UAIC catalog numbers.

Morphological Comparisons: *Notropis cahabae*. Alabama: Bibb Co.: AUM 17243 (1), 17290 (1), 18013 (1), 18253 (1), 18588 (1), Cahaba R. at Co. Rd. 27, Sec. 33, T 24 N, R 10 E; UAIC 7196.12 (1), Cahaba R., 1 km downstream from Harrisburg bridge, Sec. 29, T 22 N, R 9 E; UAIC 7769.07 (6), Cahaba R. at Co. Rd. 27, Sec. 33, T 24 N, R 10 E; UAIC 8579.01 (14), Cahaba R., 1.6 river km downstream of Co. Rd. 24, Sec. 3, T 24 N, R 10 E; UAIC 9122.01 (1), mouth of Caffee Cr. at confluence with Cahaba R., Sec. 9, T 24 N, R 10 E; UAIC 9123.01 (8), 9124.01 (82), Cahaba R. at mouth of Little Ugly Cr., Sec. 3, T 24 N, R 10 E. **Perry Co.:** UAIC 7191.07 (1), Cahaba R., 4.8 km NE Heiberger, 3.2 km upstream from Jericho bridge, Sec. 15, T 21 N, R 8 E. **Shelby Co.:** AUM 2555 (1), Cahaba R., 4.2 km SW Helena at Co. Rd. 52, Sec. 20, T 20 S, R 3 W.

***N. volucellus*. Mobile Basin: Alabama: Bibb Co.:** UAIC 8358.05 (511), Cahaba R. at Co. Rd. 27, Sec. 33, T 24 N, R 10 E; UAIC 8578.01 (329), mouth of unnamed tributary to Cahaba R., 1.1 km downstream of Little Ugly Cr., Sec. 3, T 24 N, R 10 E. **Perry Co.:** UAIC 7195 (67), Cahaba R., 10.5 km NE of Marion and 2.1 km E of Marion Fish Hatchery, Sec. 23, T 20 N, R 8 E. **Tennessee River Drainage: Alabama: Lauderdale Co.:** UAIC 4981.03 (3), Blue Water Cr., E of Killen on US Hwy 72, Sec. 19, T 2 S, R 8 W. UAIC 8580.13 (63), Shoal Cr. at Goose Shoals bridge on Co. Rd. 94. **Tennessee: Hancock Co.:** UAIC 4898.07 (46), Clinch R. near Sneedville, 6.4 km upstream from Hwy 31. **Monroe Co.:** UAIC 4148.09 (4), Little Tennessee R., SW of Knoxville at US Hwy 411. **Moore Co.:** UAIC 4001.04 (1), Elk R. at Stiles Ford, 2.1 km SSE Champ and 1.3 km NNE of Shiloh bridge. **Morgan Co.:** UAIC 4897.08 (4), Emory R., 4 km SW of Wartburg. **Cumberland River Drainage: Tennessee: DeKalb Co.:** UAIC 3390.11 (26), Smith Fork Cr. at Hwy 53. **Wilson Co.:** UAIC 3394.09 (2), 3395.05 (15), Smith Fork Cr. at Co. Rd. 6161.

***N. wickliffi*. Alabama: Marshal Co.:** UT 44.3054, Flint R., river mile 5.5 to 8.2. **Wisconsin: Crawford Co.:** UMMZ 78255 (5), Mississippi R., 1.6 km N Prairie de Chien. **Buffalo Co.:** UMMZ 78090 (12), Mississippi R. at Buffalo. **Tennessee: Decatur Co.:** UT 44.1741 (25), Tennessee R. at head end of Eagle Nest Island. **Ohio: Lawrence Co.:** OSU 60201 (31), Ohio R., Rome Twp., river mile 301 ramp. **Meigs Co.:** OSU 59853 (30), E. Br. Shade R., Chester Twp., at Hwy 248 bridge, Sec. 1, T 4 N, R 12 W. **Pennsylvania: Armstrong Co.:** UT 44.4057 (20), Allegheny R. lock and dam no. 5 and 6.

Biochemical Comparisons: *N. cahabae*. Alabama: Bibb Co.: UAIC 9124.01 (8 frozen specimens), Cahaba R. at mouth of Little Ugly Cr., Sec. 3, T 24 N, R 10 E, 30 March 1989.

***N. volucellus*. Alabama: Bibb Co.:** UAIC 9124.02 (8), Cahaba R. at mouth of Little Ugly Cr., Sec. 3, T 24 N, R 10 E, 30 March 1989. **Kentucky: Allen Co.:** UAIC 8413.09 (3), Trammel Fk. at Old State Rd. ford, 1.6 km NNE of Red Hill, 21 June 1988. **Oklahoma: Pushmataha Co.:** UAIC 7963.05 (5), Kiamichi R. at first bridge N of Antler on Hwy 2, Sec. 36,

T 1 S, R 16 E, 16 October 1987. **Tennessee: Sevier Co.:** UAIC 7955 (1), Little Pigeon R. at Red Bank Rd., 8 km ESE of Sevierville, 24 September 1987. **Virginia: Lee Co.:** UAIC 7951 (3), Powell R. at Hwy 70, 1.6 km S of Bowling, 23 September 1987. **Scott Co.:** UAIC 7952 (2), Copper Cr., 2.4 km W Bellamy at Co. Rd. 643, 22 September 1987.

N. wickliffi. **Illinois: Jackson Co.:** UAIC 8415.10 (1), Mississippi R. at Grand Tower, Sec. 23, T 10 S, R 14 E, 22 June 1988.

N. sp. cf. spectrunculus. **Virginia: Scott Co.:** UAIC 7953.12 (5), Copper Cr. at Co. Rd. 643, 2.4 km W of Bellamy, 22 September 1987.

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