

ETHEOSTOMA (NOTHONOTUS) WAPITI
(OSTEICHTHYES: PERCIDAE), A NEW DARTER FROM
THE SOUTHERN BEND OF THE TENNESSEE RIVER
SYSTEM IN ALABAMA AND TENNESSEE

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Abstract. — A new percid fish, *Etheostoma wapiti*, a member of the *E. maculatum* species group, is described from two tributaries to the Tennessee River in northwest Alabama and south central Tennessee. This rare darter, known from 55 specimens, is most closely related to *E. vulneratum* from which it differs in details of pigmentation and squamation. *Etheostoma vulneratum*, formerly treated as a subspecies of *E. maculatum* or *E. sanguifluum*, is elevated to species level based on phylogenetic analysis of the *maculatum* species group and subgenus *Nothonotus*. Comments on the former distribution and the remaining habitat of *E. wapiti* are presented.

In our (Williams & Etnier 1978) description of *Etheostoma aquali* we briefly considered the identity of three juvenile *Nothonotus*, one specimen collected in 1963 from Elk River at Fayetteville, Lincoln County, Tennessee, and two specimens collected in 1884 from Shoal Creek, Florence, Lauderdale County, Alabama. We suspected at that time that these specimens represented an undescribed species of the *E. maculatum* species group. No additional specimens were taken in a survey of the Elk River fishes by Jandebeur (1972) or in the several additional collections from the Elk River and Shoal Creek systems prior to 1980. Our hopes of eventually locating an extant population and seeing adults were renewed when Charles F. Saylor provided a juvenile from a Tennessee Valley Authority collection from Elk River Mile 41, Giles County, Tennessee, and another from Elk River Mile 40.8. A University of Tennessee Regional Faunas Class located a population in lower Richland Creek, a major Elk River tributary, in May 1981 where an adult female and a juvenile were collected. We revisited the Richland Creek locality in June 1982,

in anticipation of finally capturing an adult male in or near breeding condition. We were most interested in whether the red pigment patterns of adult males would be drastically different from those of other members of the *E. maculatum* species group. We were able to collect five adult males which to our great surprise completely lacked the bright red body spots and red fin markings typical of other members of the species group. Subsequent to discovery of the Richland Creek population, main channel Elk River populations have been located at one site in Lincoln County and two sites in Giles County, Tennessee, associated with anthropogenic limestone rubble, and at one site in Lincoln County, Tennessee and two sites in Limestone County, Alabama, where natural limestone bedrock formations abut or cross the river. At present there are only 55 known specimens of this rare but distinctive darter.

Phylogenetic analysis of subgenus *Nothonotus*, particularly the *Etheostoma maculatum* species group, indicates that both *E. sanguifluum* (Cope) and *E. vulneratum* (Cope) should be treated as species rather than as subspecies.



Fig. 1. *Etheostoma wapiti*, new species, holotype, USNM 288069, male, 71 mm SL (upper specimen) and allotype, USNM 288070, female, 55 mm SL (lower specimen).

Type material of *Etheostoma wapiti* is deposited in the collections of the American Museum of Natural History (AMNH), Academy of Natural Sciences of Philadelphia (ANSP), California Academy of Sciences (CAS), Cornell University (CU), Illinois Natural History Survey (INHS), University of Kansas (KU), Tulane University (TU), University of Alabama (UAIC), Florida State Museum (UF), University of Michigan (UMMZ), National Museum of Natural History, Smithsonian Institution (USNM), and the University of Tennessee (UT). Comparative material of other species of *Nothonotus* from the collections at USNM and UT were utilized in the preparation of this description. Methods described by Hubbs & Lagler (1958) were used in obtaining counts and measurements

except diagonal scale counts were made according to the techniques of Raney & Sutt-kus (1964). Vertebral counts were made using the methods of Bailey & Gosline (1955). Swofford's (1984) PAUP program, version 2.3, was used for phylogenetic analysis. Outgroups utilized include genus *Percina* and *Etheostoma* subgenera *Allohistium* and *Litocara* for polarizing characters within genus *Etheostoma*, with subgenus *Oligocephalus*, the hypothesized sister group of *Nothonotus*, used as outgroup for assessing polarity of additional characters within *Nothonotus*. As our primary objective was to assess relationships within the *E. maculatum* species group (*aquali*, *maculatum*, *microlepidum*, *moorei*, *rubrum*, *sanguifluum*, *vulneratum*, *wapiti*), we treated each outgroup as a single taxon, utilizing the most

Table 1.—Standard length (mm), and proportional measurements (in thousandths of SL) of the holotype (male) and four other males and five females of *Etheostoma wapiti*, new species. \bar{x} = mean.

	USNM 288069 holotype	Males		Females	
		\bar{x}	Range	\bar{x}	Range
Standard length	70.8	62.6	57.2–70.8	52.2	46.0–57.7
Body depth at dorsal-fin origin	215	218	213–223	232	217–251
Caudal peduncle depth	138	138	133–145	129	126–135
Caudal peduncle length	220	220	213–228	217	213–222
Pelvic fin length	168	179	168–189	191	185–200
Pectoral fin length	201	205	199–215	220	212–231
Head length	266	266	253–278	272	262–276
Snout length	71	70	67–74	72	68–75
Orbit length	66	67	66–69	72	69–74
Upper jaw length	71	76	71–83	74	73–76
Longest dorsal-fin spine	130	127	120–134	126	120–132
Longest dorsal-fin ray	145	151	145–156	146	142–150
1st anal-fin spine	95	98	95–105	101	97–105
Longest anal-fin ray	144	151	144–156	150	137–167

widespread character state as typical for the taxon. For instance, in *Oligocephalus* only *E. radiosum* has dark margins on median fins and only *E. pottsi* and *E. swaini* have caudal peduncle depth approximating that of *Nothonotus*. In these cases, the character coded for *Oligocephalus* was, respectively, median fins lacking dark margins, and caudal peduncle slender (see Phylogenetic Analysis, characters 2, 8).

Etheostoma wapiti, new species

Boulder Darter

Fig. 1, Tables 1–3

Etheostoma rufilineatum Gilbert, 1891:151.

Two of five specimens from Shoal Creek, Florence, Alabama.

Etheostoma microlepidum Raney & Zorach, 1967:93. Specimens from Shoal Creek, Florence, Alabama.

Etheostoma (Nothonotus) sp. Starnes & Etnier, 1986. Endemic in Tennessee River drainage.—Biggins, 1987, 1988. Endangered status proposed and finalized, respectively, under U.S. Endangered Species Act.

Holotype.—Adult male, USNM 288069, 70.8 mm standard length (SL), Richland

Creek at County Road 4209 crossing, 11.2 air miles south-southeast of Pulaski, Giles Co., Tennessee, 7 Jun 1982, W. C. Dickinson, D. A. Etnier, M. A. Etnier, C. E. Louton, J. A. Louton, W. C. Pennington.

Allotype.—Adult female, USNM 288070, 55 mm SL, taken with holotype.

Paratopotypes.—Paratypes taken with primary type are TU 148010 (2), UMMZ 213950 (2), and UT 91.3469 (1). Additional paratypes taken at the type locality are UT 91.2203 (2), 22 May 1981.

Other paratypes.—Elk River system, Tennessee: TU 30271 (1), 11 Apr 1963, and UT 91.3459 (1), 13 Sep 1988, Elk River Mile 89.7, Fayetteville, Lincoln Co., 0.25 miles below U.S. Highway 231 bridge. AMNH 58257 (2), ANSP 162645 (2), CAS 64178 (2), CU 71707 (2), and KU 22122 (5), Elk River Mile 61.0, Hamilton Mill, Lincoln Co., 13 Sep 1988. INHS 68229 (3), 14 Apr 1985, and UT 91.3075 (1), 25 Jun 1986, mouth of Indian Creek at Elk River Mile 52.5, Giles Co. UT 91.80 (1), Elk River Mile 41.0, Giles Co., 7 Oct 1980. UT 91.2628 (1), Elk River Mile 40.8, Giles Co., 2 Aug 1983. UT 91.3072 (4) and UF 44921 (4), Elk River Mile 52.5, at mouth of Indian Creek, Giles Co., 25 Jun 1986. UT 91.3084

Table 2.—Frequency distribution, sample size, and means of selected scale counts in *Etheostoma wapiti*, *E. aquali*, *E. vulneratum*, and Elk River system *E. camurum*. Counts for *E. aquali* from Williams & Etnier (1978) and *E. vulneratum* from Zorach & Raney (1967).

	Lateral line scales																			n	\bar{x}	
	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68			69
<i>E. wapiti</i>						1	3	1	2	5	7	3	7	7	12	—	2	—	1	1	52	61.65
<i>E. aquali</i>								1	1	3	7	17	6	6	4	6	3	3			57	62.21
<i>E. vulneratum</i>		1	2	3	2	7	9	14	9	9	7	5	3	—	2	1	2				76	57.87
<i>E. camurum</i>	2	—	—	3	2	5	2	5	2	1	1	1	1								25	55.88

	Anal-fin origin to first dorsal fin									n	\bar{x}
	13	14	15	16	17	18	19	20			
<i>E. wapiti</i>				1	1	8	18	18	7	53	18.36
<i>E. aquali</i>					5	13	23	13	3	57	17.93
<i>E. vulneratum</i>	1		3	14	23	16	10	6	3	76	16.57
<i>E. camurum</i>				3	13	5	3			24	16.33

	Second dorsal-fin origin to anal fin							n	\bar{x}
	13	14	15	16	17	18	19		
<i>E. wapiti</i>		4	9	23	7	8	1	52	16.17
<i>E. aquali</i>	1	16	26	13	1			57	14.95
<i>E. vulneratum</i>	8	11	30	23	4			74	15.19
<i>E. camurum</i>		8	7	8	1			24	15.08

	Caudal peduncle scales								n	\bar{x}
	18	19	20	21	22	23	24	25		
<i>E. wapiti</i>				6	14	20	10	3	53	22.81
<i>E. aquali</i>					2	28	13	10	56	22.71
<i>E. vulneratum</i>		3	6	15	26	18	8		76	21.97
<i>E. camurum</i>	2	9	3	8	2				24	19.96

(7), Elk River Mile 36.7, Giles Co., 17 Oct 1986.

Elk River system, Limestone Co., Alabama: UAIC 7851.01 (4), Elk River Mile 30.7, about 3 miles above Smith Hollow Road (Alabama highway 127) bridge, 24 Oct 1986. UT 91.3097 (1), Elk River Mile 29.7, 24 Oct 1986.

Other material not designated as types.—USNM 36670 (2) Shoal Creek, Florence [Lauderdale Co.], Alabama, 1884. A male taken with the holotype was frozen at UT for electrophoretic analysis; counts for this specimen are included in the tables. Two additional specimens, Elk River Mile 52.5,

Giles Co., Tennessee, 14 Sep 1988, were frozen for electrophoretic analysis at UAIC, and are not included in the tables.

Diagnosis.—*Etheostoma wapiti* is a species of subgenus *Nothonotus* as defined by Page (1981). Within *Nothonotus*, *E. wapiti* belongs to the *E. maculatum* species group (Williams & Etnier, 1978), all of which have a few scales associated with the post-orbital spot on the upper cheek (cheek completely naked in other *Nothonotus*). Within *Nothonotus*, *E. wapiti* differs from *acuticeps*, *aquali*, *jordani*, *juliae*, *maculatum*, *moorei*, *rubrum*, *sanguifluum*, and *tippecanoe* in having the combination of dark marginal

Table 3.—Frequency distribution, sample size, and means of selected fin-ray counts and vertebral counts in *Etheostoma wapiti*, *E. aquali*, *E. vulneratum*, and Elk River system *E. camurum*. Counts for *E. aquali* from Williams & Etnier (1978) and *E. vulneratum* from Zorach & Raney (1967). Vertebral counts for *E. camurum* not available.

	First dorsal fin							Second dorsal fin						
	11	12	13	14	15	n	\bar{x}	11	12	13	14	n	\bar{x}	
<i>E. wapiti</i>		10	33	10		53	13.00	1	35	17		53	12.51	
<i>E. aquali</i>		9	49	3		60	12.90	1	21	33	3	58	12.66	
<i>E. vulneratum</i>	4	11	55	6	2	78	12.89	6	39	31		76	12.33	
<i>E. camurum</i>	3	18	3			24	12.00	1	12	11		24	12.42	

	Total dorsal-fin rays								Anal-fin soft rays						
	22	23	24	25	26	27	28	n	\bar{x}	7	8	9	10	n	\bar{x}
<i>E. wapiti</i>			8	27	16	2		53	25.23	8	35	8	1	52	8.04
<i>E. aquali</i>			4	24	25	5		58	25.54		2	42	15	59	9.22
<i>E. vulneratum</i>		1	7	43	21	3	1	76	25.28	16	50	9	1	76	7.93
<i>E. camurum</i>	1	2	9	10	2			24	24.42	8	15	1		24	7.71

	Pectoral-fin rays							Vertebrae					
	12	13	14	15	16	n	\bar{x}	38	39	40	41	n	\bar{x}
<i>E. wapiti</i>	2	23	28			53	13.49		4	5	1	10	39.70
<i>E. aquali</i>	1	25	31	2	1	60	13.63	2	27	1		30	38.97
<i>E. vulneratum</i>	2	23	47	4		76	13.70		6	25	1	32	39.84
<i>E. camurum</i>		6	16	2		24	13.83						

bands on median fins of both sexes, scales on the opercles, horizontal dark lines between scale rows on posterior half of body, a naked nape, and a completely scaled belly. Differs from *rufilineatum* in lacking large basicaudal pale spots, orange lips, and horizontal dark markings on the cheek. Differs from *bellum*, *camurum*, and *chlorobranchium* in lacking well defined pale submarginal bands on soft dorsal, caudal, and anal fins, and in having sexual dimorphism in soft dorsal and caudal fins throughout the year (pale yellow with small brown spots in female *wapiti*). Most similar to *E. vulneratum*, but differing from it (and all other *Nothonotus* except *acuticeps*, *chlorobranchium*, and occasional *maculatum*) in lacking red or orange on fins or body of nuptial males, and in having higher scale counts (Table 2). Other distinguishing characteristics of the species include moderately de-

veloped subocular bar, cheeks without wavy copper-colored lines.

In numerous adult and juvenile males a pale to yellowish submarginal band is present on the median fins that closely resembles that of male and female *E. camurum* and *E. chlorobranchium*. *Etheostoma camurum* and *E. wapiti* are sympatric in Elk River, and subadults and juveniles can be very difficult to separate. The former lacks any trace of a suborbital bar, never has scales associated with the postorbital dark spot, has a more blunt snout, and (Table 3) modally has 12 (vs. modally 13) dorsal spines.

Description. — *Etheostoma wapiti* is a moderately large species of the subgenus *Nothonotus*, the five adult (holotype and four paratopotypes) males from the type locality averaging 63.2 mm SL, the largest 70.8 mm SL. The three adult females from this collection are smaller, averaging 52.2 mm SL,

Table 4.—Characters useful in differentiating between five similar species in the *Etheostoma maculatum* species group.

Character	<i>E. wapiti</i>	<i>E. vulneratum</i>	<i>E. maculatum</i>	<i>E. sanguifluum</i>	<i>E. aquali</i>
Dark margins on anal, soft dorsal, and caudal fins	present	present	absent	absent	absent
Shape of caudal fin	truncate	truncate	rounded	rounded	rounded
Red on anal and pelvic fins, adult male	absent	absent	absent	present	present
Red on margin of spinous dorsal fin, adult male	absent	present	absent	present	present
Copper colored lines on cheek	absent	absent	absent	absent	present
Dark suborbital bar	present	present	often present	present	absent
Modal vertebral number	39 or 40	40	38	39	39
Mean lateral-line scales	61.65	57.87	60.91	56.53	62.21
Mean and (mode) of total dorsal-fin rays	25.23 (25)	25.28 (25)	24.65 (24–25)	24.97 (25)	25.53 (25–26)
Mean and (mode) of anal-fin soft rays	8.04 (8)	7.93 (8)	8.54 (8–9)	8.18 (8)	9.22 (9)

the largest 57.7 mm SL. Proportional measurements of the holotype and nine paratypes of *E. wapiti* are given in Table 1. The general body shape of *E. wapiti* is illustrated in Fig. 1.

Frequency distributions of scale, fin-ray, and vertebral counts for *E. wapiti* are given in Tables 2, 3. Body scaled except for the breast, prepectoral, and nape areas. Cheeks naked except for the typical presence of 2–5 embedded to partially exposed cycloid and/or ctenoid scales behind eye. Opercles scaled. Lateral-line complete with 55–69 (\bar{x} = 61.6) scales. Transverse scales, anal-fin origin to first dorsal fin 15–20 (\bar{x} = 18.4) and origin of second dorsal fin to anal fin 14–19 (\bar{x} = 16.2). Caudal peduncle scale rows 21–25 (\bar{x} = 22.8). Dorsal fin with 12–14 (\bar{x} = 13.0) spines and 11–13 (\bar{x} = 12.5) soft rays. Total dorsal fin elements 24–27 (\bar{x} = 25.2). Anal fin with 2 spines and 7–9 (\bar{x} = 8.0) soft rays. Pectoral-fin rays 12–14 (\bar{x} = 13.5). Vertebrae 39–41 (\bar{x} = 39.7). Branchiostegal rays 6–6, branchiostegal membranes separate. Frenum broad. Table 4 contains a summary of characters useful in differentiating between *Etheostoma*

aquali, *E. maculatum*, *E. sanguifluum*, *E. vulneratum*, and *E. wapiti*.

Cephalic sensory canal pores are as follows: lateral canal pores 5–6, usually 5; preoperculummandibular canal pores 10–11, usually 10; infraorbital canal pores 7–9, usually 8; supraorbital canal pores 3; supratemporal canal pores 3; coronal pore single.

Coloration. — Following color description is based on the series collected at type locality on 7 Jun 1982. Body of males olive to grayish without red spots. Posterior half of body with 10–14 dark horizontal stripes between scale rows. Stripes are absent on belly and become pale dorsally and ventrally along caudal peduncle. Humeral scale black. Belly, breast, and prepectoral area grayish. Head grayish with distinct dark gray to black suborbital bar and postorbital spot. Iris dark with some yellow pigment. Cheeks uniform gray without chromatic markings. Gular area pale blue. Spinous dorsal fin dark gray with thin black marginal band and narrow pale yellow submarginal (marginal anteriorly) band. Soft dorsal fin gray with black marginal band and pale yellow submarginal

band. Black marginal band on spinous and soft dorsal fins is wider and darker posteriad. Anal fin gray with narrow dark gray to black marginal band on posterior third of fin. Membrane between anal spines pale bluegreen. Caudal fin grayish with faint bluegreen base, pale yellow submarginal band, and black marginal band. Pelvic fins grayish with faint bluegreen membranes near base. Pectoral fins grayish with dusky margin posteriorly. Subadult males and unsexed juveniles collected during June and October 1986 had orange to red on caudal fin, narrow red margin and occasional red anterior interradiation membranes of spinous dorsal fin, and occasional dirty red spots on posterior sides. Larger males from these collections lacked red or orange colors, except one October adult male had about ten obscure dirty red spots along posterior sides and reddish caudal fin. In the 13 adults (all males 43–62 mm SL) collected on 13 Sep 1988 and examined on 7 Oct, 1 of the smaller specimens had marginal red-orange on interradiation membranes 1, 2, 4, and 6 of the spinous dorsal fin, and an additional 3 had marginal red-orange on membrane 1. Five of these had a few dirty red spots on the sides and five had orange on dorsal and ventral principal caudal fin rays in contrast to the pale yellow middle rays. The five largest males in this series (55–62 mm SL) were noticeably less colorful—none had red in the spinous dorsal fin, one had the red-orange caudal fin color described above, and four had pale yellow rays in either the soft dorsal or anal fin.

In females, coloration of head and body similar to that of males except paler. Spinous dorsal fin dusky gray, margin of first interradiation membrane red. Soft dorsal and caudal fin pale yellow with dark brown speckles. Anal fin dusky gray, not speckled with brown. Median fins with narrow black marginal band. Pectoral and pelvic fins were colorless.

Distribution and habitat.—*Etheostoma*

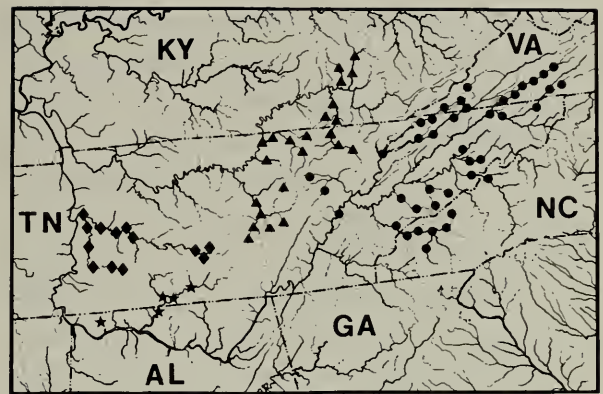


Fig. 2. Geographic distribution of *Etheostoma wapiti* (stars), *E. vulneratum* (dots), *E. aquali* (diamonds) and *E. sanguifluum* (triangles).

wapiti is known from the Elk River system in Tennessee and the Shoal Creek system in Alabama, both northern tributaries of the Tennessee River, along the southern portion of the Highland Rim physiographic province (Fig. 2). It was first collected in Shoal Creek in 1884 by C. H. Gilbert and J. Swain and subsequently reported (as *E. rufilineatum*) by Gilbert (1891). No habitat data were given and the only locality information was "Shoal Creek, Florence, Alabama." Shoal Creek, located east-northeast of Florence, Lauderdale Co., enters the Tennessee River about seven miles east of Florence. The lower portion is flooded by backwaters of Wilson Dam which extend upstream to the Lauderdale County Road 64 crossing. The two specimens of *E. wapiti* collected by Gilbert and Swain were most likely collected in the lower portion of Shoal Creek. While recent extensive efforts to collect *E. wapiti* in the unimpounded portion of Shoal Creek have been unsuccessful, it may still occur there since the remaining stream habitat appears to be in good condition and supports a large variety (50 species) of fishes.

The boulder darter is currently known from eight localities in the main channel of Elk River and from the lower reaches of two Elk River tributaries, Richland and Indian creeks. Adults have been found only in areas

of boulder substrate, and we consider this strong circumstantial evidence that it shares egg-clumping reproductive habits with other members of the *maculatum* species group. In Elk River proper the most upstream record (two specimens, River Mile 89.7, Fayetteville, 1963, 1988) is in an area strongly influenced by cold water releases from Tims Ford Reservoir, completed in 1970. The 12 adult males and 1 juvenile from Elk River Mile 61.0, 13 Sep 1988, were collected in a high energy bend of the river where boulders eroded from an adjacent bluff provide habitat. Single juveniles from River Miles 40.8 and 41.0 are likely waifs that dispersed downstream from the Richland Creek population (mouth at River Mile 42.6). Elsewhere in Elk River, Tennessee, the population at the mouth of Indian Creek (River Mile 52.5) is apparently utilizing limestone slabs from a collapsed mill dam for spawning substrate; juveniles from this population enter lower Indian Creek, but no adults have been taken there and suitable spawning habitat is virtually absent. At River Mile 36.7, adults were taken in association with boulders from a former stone bridge. In Elk River, Alabama, natural outcrops of limestone occur above and below the Smith Hollow Road (Alabama Highway 127) bridge, and boulder darter populations are presumably rather continuous from River Mile 30.7 (ca. 400 m above bridge) downstream to about River Mile 29. At River Mile 28.1 (upstream end of Gallus Island) Elk River is impounded when Wheeler Reservoir is at full pool, and boulder darters were not collected.

Historically the boulder darter probably occurred in the main channel of the Tennessee River between Muscle Shoals and the mouth of the Elk River, a distance of approximately 45 miles. It is likely that it also occurred upstream from the mouth of Elk River and in the lower portion of other northern tributaries of the southern bend of the Tennessee River such as the Flint and Paint Rock rivers.

Conservation.—There are presently 55 known specimens of *Etheostoma wapiti*. Its habitat is difficult to sample with standard kick-seining methods which may account, at least in part, for its rarity. However, most of its potential habitat of deep, rocky, flowing pools in rivers and lower portions of large tributaries has been altered by impoundment, pollution, and siltation. It is likely that additional reproducing populations could be established in Elk River by merely providing suitable spawning substrate in areas with adequate current and good water quality. The restricted distribution of *E. wapiti* and loss of potential habitat in other large rivers of the area prompted the U.S. Fish and Wildlife Service to list it as an Endangered species (Biggins, 1988).

Etymology.—The species name, *wapiti*, is an American Indian name for the American elk and calls attention to the Elk River system, the only habitat presently known to support the species. The common name, boulder darter, is in reference to the habitat of adults.

We suggest the vernacular names of wounded darter for *E. vulneratum* and bloodfin darter for *E. sanguifluum*. These names are suggested by the meanings of the Latin *vulneratum* (=wounded) and *sanguifluum* (=flowing blood).

Phylogenetic analysis.—Following are characters utilized in assessing relationships within subgenus *Nothonotus*, with a brief survey of their distribution in outgroups and in *Nothonotus*. Our polarity judgements are included, but the PAUP program was run with polarity unfixd.

1. Horizontal dark lines on sides of body above and below lateral line. This character does not appear in any of the outgroups, and is essentially a subgeneric synapomorphy, secondarily lost only in *jordani* and *tippecanoe* as suspected autapomorphies.

2. The deep-bodied, slab-sided form of *Nothonotus* species (expressed as caudal peduncle depth divided by SL, data from Page

1981, and UT specimens) is a presumed synapomorphy for the subgenus. The caudal peduncle is slender in genus *Percina* (above ratio = 0.065–0.100) and in *Etheostoma* subgenera *Allohistium* (0.098) and *Litocara* (0.088–0.092). In subgenus *Oligocephalus* Page's (1981) values range from 0.089 to 0.116, with only *grahami* (0.115), *pottsi* (0.116), and *swaini* (0.112) having ratios higher than 0.108. Ten adults of both *grahami* and *swaini* from the UT collection were measured, and we get a value identical to Page's for *swaini*, but a value of 0.103 for *grahami*. In *Nothonotus*, Page's values range from 0.111 to 0.128. We rechecked three of Page's lower values with ten UT specimens, and get an identical value for *bellum* (0.114), but higher ratios for *jordani* (0.120 vs. 0.111) and *chlorobranchium* (0.133 vs. 0.118).

3. The darkened anterior interrational membranes of the spinous dorsal fin occur throughout subgenus *Nothonotus*, with similar pigment occurring in outgroups only in four of nine species of *Percina* subgenus *Alvordius* and in *Percina* (*Imostoma*) *shumardi*. We consider it to be a synapomorphy for *Nothonotus*.

4. Males with distinctive nuptial colors of blue, green, gray, or brown on breast. *Nothonotus* is often accorded the subgeneric vernacular of "bluebreast darters," and this presumed synapomorphy is consistent throughout the subgenus except in *juliae* (males darken on throat and breast, James & Taber 1986), and in *jordani* where green of the breast may extend to adjacent branchiostegal membranes and/or belly. In outgroups, nuptial breast color of this nature is absent (*Percina*, *Allohistium*, *Litocara*) or occasionally present only in *lepidum* (green branchiostegal membranes and breast) and *whipplei* (blue breast). In some other *Oligocephalus* (*caeruleum*, *radiosum*, *spectabile*) the orange-red of the branchiostegal membranes may extend onto the breast.

5. Naked nape. The consistent and excessive loss of nape squamation, typical of

all *Nothonotus* except *juliae*, does not occur in outgroups, and is considered a synapomorphy uniting *Nothonotus* other than *juliae*. We interpret the scaly nape of *juliae* as symplesiomorphic with outgroups.

6. United gill membranes, an autapomorphy occurring in *juliae*, are absent from outgroups and from other *Nothonotus*.

7. Naked opercles. Autapomorphy, *acuticeps*. Opercles are consistently scaled in outgroups and other *Nothonotus*.

8. Marginal dark bands on caudal, soft dorsal, and anal fins. A presumed synapomorphy for *Nothonotus* except *juliae*, *acuticeps*, and *tippecanoe*. The character is absent in outgroups except in *E. (Oligocephalus) radiosum*. Characters 9, 10, 11, and 14 support our assuming this to be a shared reversal in *aquali*, *maculatum*, and *sanguifluum*. Character 10 suggests a possible homoplasy in *tippecanoe*.

9. Red spots on body of nuptial males. A synapomorphy for all species of *Nothonotus* except *acuticeps*, *juliae*, *tippecanoe*, and *wapiti*. Character 10 suggests a possible reversal in *tippecanoe*. Presence of red spots in juvenile males plus characters 10, 11, 14, and 15 indicate an obvious reversal in nuptial male *wapiti*. In outgroups, similar pigment occurs only in *E. (Oligocephalus) whipplei*.

10. Sexual dimorphism of fin pigment pattern throughout the year. The darkly speckled median fins of females of *rufilineatum*, *jordani*, *tippecanoe*, and the *maculatum* species group are markedly different from the pattern in males and persist throughout the year and in preservative. Except for *tippecanoe*, where it is tentatively treated as an autapomorphy, we consider it a synapomorphy for these species. In *Percina*, sexual pattern dimorphism in median fins is essentially absent (cannot be sexed in preservative) and sexual dichromatism is absent or weakly expressed during the breeding season except in subgenera *Ericosma*, *Hypohomus*, and *P. (Alvordius) crassa* and *roanoka*. In genus *Etheostoma* out-

groups and other *Nothonotus*, sexual dichromatism may be spectacular, especially during the breeding season, but these are alcohol-soluble pigments that are lost in preservative, again making accurate pattern-based sexing of museum specimens difficult or impossible.

11. Presence of scales on upper cheek, near postorbital spot. Although scaly cheeks are widespread in outgroups, and naked cheeks are routinely and, we suspect, correctly considered the derived condition in percids, we note that these scales, absent from *Nothonotus* except the *maculatum* species group (*aquali*, *maculatum*, *microlepidum*, *moorei*, *rubrum*, *sanguifluum*, *vulneratum*, *wapiti*) must be considered derived under the most parsimonious phylogenetic hypothesis.

12. Reduced belly squamation. A synapomorphy for *moorei* and *rubrum*. In other *Nothonotus* and in *Etheostoma* outgroups the belly is fully scaled or occasionally and variably with a small naked area anteriorly. In genus *Percina*, a small portion of the anterior belly may be naked, or there may be seasonally or sexually variable naked areas corresponding to the position of the modified midventral scales.

13. Reduced vertebral number. A synapomorphy for *rubrum* and *moorei* and homoplastic in *juliae*. Modal vertebral counts as low as 36 also occur commonly in subgenus *Oligocephalus*, but not in other outgroups or in other *Nothonotus*.

14. Egg clumping. A synapomorphy known or inferred to be shared by six species of the *maculatum* species group, absent in outgroups, and absent in other *Nothonotus*. Voirs (1988) confirms that *E. moorei* buries its eggs in the gravel as is typical of other *Nothonotus*. It seems likely that *E. rubrum* will also be an egg-burier given the presence of adult males in gravel riffle areas throughout the breeding season.

15. Anal fin lacking bright colors in males, lacking spots in females. In genus *Percina*, anal fins of males lack bright colors except

in nuptial *P. (Ericosma) evides* and *P. (Hypohomus) aurantiaca* where it is or may be iridescent blue. In genus *Etheostoma* outgroups, the anal fin of males is blue, green, or red, or combinations of these colors. In *Nothonotus*, the anal fin of males is orange, red, or green except in *vulneratum* and *wapiti*. In *wapiti*, a trace of iridescent blue was noted between the anal spines in nuptial males, but the remainder of the fin was gray, while in *vulneratum* the entire fin is gray. Failure of *vulneratum* and *wapiti* males to develop brightly colored anal fins during the breeding season (a presumed synapomorphy) implies significantly different courtship behavior. Correlated with this, the anal fin of female *vulneratum* and *wapiti* is unspotted, whereas in the remainder of the *maculatum* species group plus *jordani*, *rufilineatum*, and *tippecanoe*, females have the anal fin spotted (see character 10). While we do not feel justified in considering these as separate characters (anal fin pigmentation of males and females is likely to have the same genetic basis), our confidence in this character's validity as an indicator of the sister-species relationship between *vulneratum* and *wapiti* is certainly enhanced by its deviation from the *maculatum* species group norm in both sexes.

16. Absence (loss) of dark margins on soft-rayed median fins. In genus *Percina* and in *Etheostoma* subgenera *Allohistium* and *Litocara*, median fins other than the spinous dorsal lack dark margins. In *Oligocephalus*, a dark margin on the soft dorsal is frequently present, but only in *radiosum* do all three soft-rayed median fins have dark margins. In *Nothonotus*, darkly margined median fins are absent only in *acuticeps*, *juliae*, and *tippecanoe* (presumed symplesiomorphy), and as a presumed synapomorphy in *aquali*, *maculatum*, and *sanguifluum* of the *maculatum* species group. Other *Nothonotus* have dark margins on these fins consistently evident in males and often apparent in females.

17. Rounded caudal fin. This character is

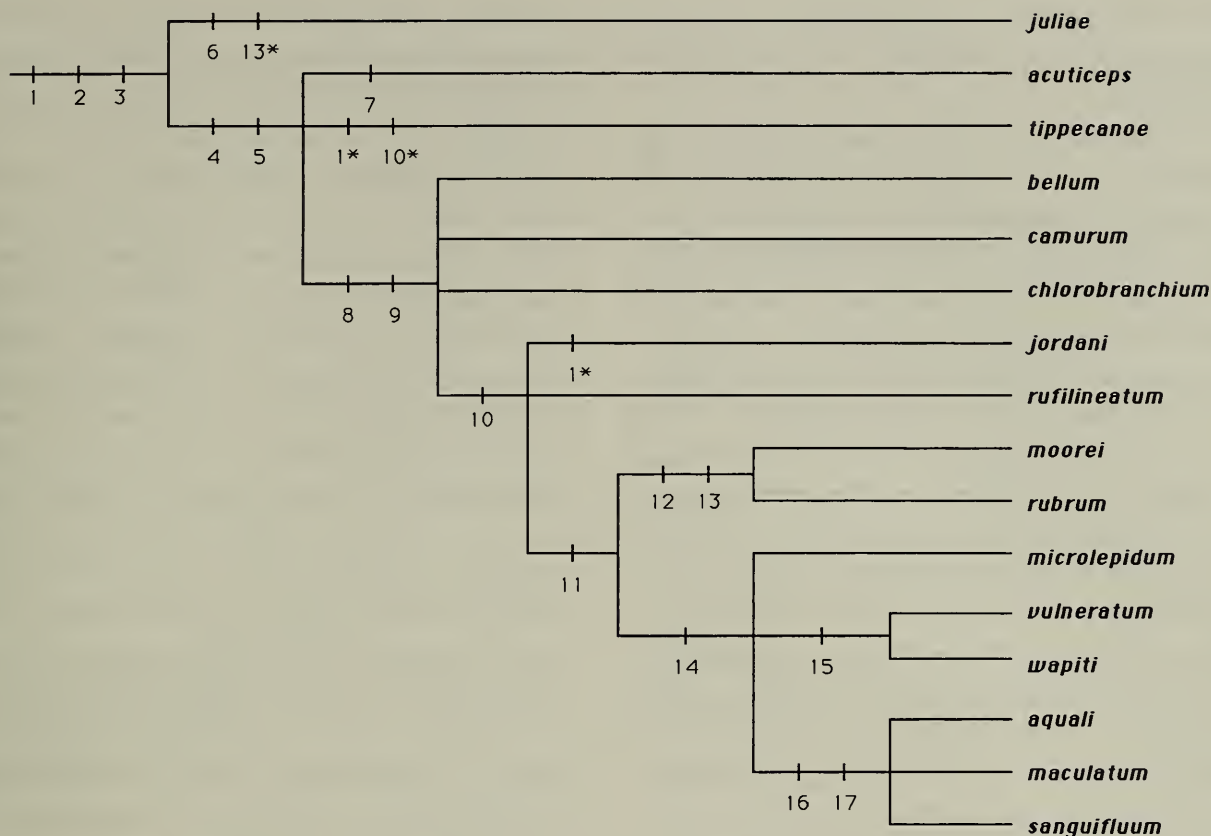


Fig. 3. Hypothesized phylogenetic relationships within subgenus *Nothonotus*. Characters 1–17 are discussed in the text. Asterisks indicate suspected homoplasies.

somewhat subjective, but we and Zorach & Raney (1967) find it useful, if somewhat variable, within the *maculatum* species group. The caudal fin is truncate to slightly forked in outgroups, and *Nothonotus* except for *aquali*, *maculatum*, and *sanguifluum*. We do note some sexual and size dimorphism in this character, with extremely large males of *vulneratum* occasionally having the caudal fin rounded, and occasional *sanguifluum*, especially females and smaller males, having the caudal fin truncate.

Discussion. — While characters 1–17 above are not sufficient to resolve relationships within subgenus *Nothonotus*, the consensus tree generated (Fig. 3, consistency index = 0.654) indicates that (1) *Nothonotus* is monophyletic; (2) *Etheostoma juliae* is sister to all other *Nothonotus*; (3) *Etheostoma acuticeps*, *E. tippecanoe*, and all other *Nothonotus* (except *juliae*) form an unresolved trichotomy; (4) although *E. bellum*, *E. camurum*, and *E. chlorobranchium* share all

17 characters analyzed, none is a synapomorphy for the three species, and their monophyly is not established; (5) the *E. maculatum* species group is monophyletic as are its branches of *moorei* + *rubrum*, *aquali* + *maculatum* + *sanguifluum*, and *vulneratum* + *wapiti*; (6) *Etheostoma moorei* and *E. rubrum* are sister to remaining members of the *maculatum* species group; and (7) *Etheostoma microlepidum* is included in an unresolved trichotomy with *aquali* + *maculatum* + *sanguifluum* and *vulneratum* + *wapiti*.

Prior to availability of sufficient material of *Etheostoma aquali* and *E. wapiti*, Zorach & Raney (1967) recognized *E. maculatum* as polytypic, including *E. m. sanguifluum* and *E. m. vulneratum*. They pointed out (p. 296) that “Three allopatric forms are recognized as subspecies, but might properly be considered as species.” Our data indicate that *vulneratum* and *wapiti* are sister taxa and that *aquali* + *maculatum* + *sanguifluum*

fluum comprise a monophyletic branch, rendering their polytypic *E. maculatum* paraphyletic.

Our hypothesis concerning relationships between the taxa *aquali*, *maculatum*, *microlepidum*, *sanguifluum*, *vulneratum*, and *wapiti* differs from Page's (1985) hypothesized relationships between the species *aquali*, *maculatum*, *sanguifluum*, and *microlepidum* in which he treated *vulneratum* as a subspecies of *sanguifluum*. In his scheme, the polytypic *E. sanguifluum* and *E. aquali* are considered sister species based on the presumed synapomorphy of adult males with "two red spots at the front and one red spot at the rear" of the spinous dorsal fin. Although this pattern is distinctive, there is considerable variation within *aquali*, *sanguifluum*, and *vulneratum* in the extent of red margination, and a complete or nearly complete marginal band may be present. Marginal red pigment can occur in spinous dorsal fins of both *maculatum* and *wapiti* in subnuptial males (description, this paper, and Zorach & Raney 1967), but is absent in nuptial males. Red to orange margination in dorsal fins of male *Nothonotus* is variously expressed in all species except *acuticeps*, and perhaps *chlorobranchium*, and is often brighter anteriorly. Since red margination of the spinous dorsal fin of males is present in subgenera *Allohistium* and *Liticara*, and often present although more submarginal in subgenus *Oligocephalus*, we treat this character as a symplesiomorphy within *Nothonotus*, and anterior and posterior concentration of this pigment, also variously expressed in several *Nothonotus*, is very suspect as a synapomorphy uniting *aquali*, *sanguifluum*, and *vulneratum*. Page's scheme conflicts with additional characters (rounded caudal fin, lack of bright colors in pelvic and anal fins of males, lack of dark spots on anal fin of females and lack of dark margins on median fins) that are supported by outgroup analysis as being synapomorphies within more derived *Nothonotus* species. We elevate *vulneratum* to species status based

on our contention that *wapiti* and *vulneratum* are sister species, with either *microlepidum* or the unresolved trichotomy of *aquali*, *sanguifluum*, and *maculatum* as sister to that pair. The presumed synapomorphy uniting *wapiti* and *vulneratum* is secondary loss of bright colors in the anal and pelvic fins of adult males plus absence of spots in anal fin of females. The clade of *aquali*, *sanguifluum*, and *maculatum* share the presumed synapomorphies of rounded caudal fin and loss of dark margination on the median fins. Additional characters, whose polarity is difficult to evaluate, support the above relationships. Vertebrae are modally 40 in both *vulneratum* and *wapiti*, but modally 39 or fewer in other *Nothonotus* except *chlorobranchium* (39 or 40). High vertebral counts in *chlorobranchium* are likely related to its being the largest and most cold-adapted member of the subgenus, but neither *vulneratum* nor *wapiti* is larger than nor more tolerant of cold water than most other *Nothonotus* species. Mean anal fin ray counts are 7.93 and 8.04 for *vulneratum* and *wapiti*, respectively, but 8.18 or more for other egg-clumping *Nothonotus*. Simon et al. (1987) noted that egg diameter (2.8–3.1 mm) and hatchling length (8.3 mm SL) for *vulneratum* (treated as *E. sanguifluum vulneratum*) were larger than for other *Nothonotus* studied (egg diameter range 1.3–2.1 mm, hatchling length range 3.8–7.2 mm). *Etheostoma aquali* and *E. maculatum* were the only other members of the *maculatum* group included in their study. Our examination of egg diameter in gravid females of the *maculatum* species group (their data were based on fertilized, water-hardened eggs) confirms the large egg size in *E. vulneratum*, but the two available gravid females of *wapiti* had eggs within the range of sizes seen in the other species.

Zoogeography.—Dr. R. E. Jenkins (in litt.) has noted that dark marginal bands on median fins are less well developed in Clinch/Powell/Emory river *E. vulneratum* specimens than elsewhere. He has suggested that

these might represent intergrades with *sanguifluum*, but this supposition demands a major headwater piracy event (members of the *maculatum* species group inhabit streams of order three or larger) between those systems and the Cumberland River drainage. Such a piracy has been alluded to (Ross 1971, Starnes et al. 1977), and similarities between fish faunas of the upper Cumberland River below the Falls and the adjacent Clinch/Powell/Emory systems certainly suggest such an event. Starnes & Etnier (1986) rethought and refuted this hypothesis based on the complete absence of geological evidence—Cumberland Gap was formed by faulting, and does not represent an extinct watercourse. They attribute faunal similarities to physiographic conditions (abundance of Silurian and/or Carboniferous sandstones in the watersheds and similar stream size and gradient) coupled with formerly more continuous distribution of ancestral forms throughout the Tennessee and Cumberland drainages. We accept this view as most likely, and any similarities between Cumberland *sanguifluum* and Clinch/Powell/Emory *vulneratum* are treated as homoplasies rather than as the result of recent contact. Assuming that main channel dispersal rather than headwater piracy has been responsible for present distribution, the ranges of *sanguifluum* and *vulneratum*, rather than abutting, are at maximum separation for the four taxa being considered (Fig. 2), with *aquali* and *wapiti* occupying geographically intermediate areas. These distributions and our proposed relationships of the four taxa conform nicely to the Starnes & Etnier (1986) hypothesis that, based on considerable geological evidence, the upper and middle portions of the Tennessee River drainage had a remote outlet from that of the present lower Tennessee and Duck river systems during the late Tertiary, and that the Tennessee achieved its present configuration in the Pleistocene. This development may have effected vicariance of the ancestral stock into a middle/upper

Tennessee component (*vulneratum/wapiti* precursor) and a Duck/lower Tennessee/Cumberland river component (*aquali/sanguifluum* precursor). Further speciation into the four taxa considered here may be attributable to strict habitat requirements and physiographic fidelity of these darters (see discussion in Starnes & Etnier 1986). Since *vulneratum/wapiti* and *aquali/maculatum/sanguifluum* are supported as being monophyletic groups with *aquali* and *sanguifluum* likely sister species in the latter, a polytypic *maculatum* including *vulneratum* and/or *sanguifluum* would be paraphyletic. Monophyly could be retained by considering all five taxa as subspecies of a polytypic *Etheostoma maculatum*, a move we consider unwarranted. The unusual situation of two species (*aquali* and *wapiti*) evolving independently from two taxa that maintain their subspecies status (*sanguifluum* and *vulneratum*, respectively) could occur if (a) a founder effect were present, or (b) the allopatric ranges of *aquali* and *wapiti* presented drastically different selective pressures from those prevailing in the total range of *sanguifluum* and *vulneratum*, or (c) if the original subspecies continue to have or more recently have had a more continuous distribution than their vicariates. Since none of these, perhaps not exclusive, conditions appears likely, we are uncomfortable in accepting the derivation of two relatively distinct species (*aquali* and *wapiti*) from two different subspecies of a polytypic species.

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