Morphological Variation of the Redfin Darter, *Etheostoma whipplei*, with Comments on the Status of the Subspecific Populations

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The redfin darter, Etheostoma whipplei (Percidae: subgenus Oligocephalus) has been the subject of several taxonomic treatments over the past 50 years. At the present, two subspecies are recognized: Etheostoma whipplei whipplei in the Ozark and Ouachita Highlands and Etheostoma whipplei artesiae on the Gulf Coastal Plain. We examined variation in meristics and pigmentation to assess the distinctiveness of eastern populations of E. w. artesiae. The results indicated that E. w. artesiae differs significantly from E. w. whipplei in meristics and features of male breeding pigmentation. We conclude that all populations currently recognized as E. w. artesiae should be elevated to full species status.

THE redfin darter, Etheostoma whipplei (Percidae: subgenus Oligocephalus), is a wideranging species that has been the subject of several taxonomic treatments (Hubbs and Black, 1941; Moore and Rigney, 1952; Retzer et al., 1986). At present, two subspecies are recognized. Etheostoma whipplei whipplei (Girard) is confined to the Arkansas and White River drainages above the Fall Line in Missouri, Arkansas, Kansas, and Oklahoma, and Etheostoma whipplei artesiae (Hay) occurs in Gulf Coast drainages east and west of the Mississippi River, lower tributaries of the Mississippi River, disjunctly in Halawakee Creek in the Chattahoochee River System in east-central Alabama, and in Bear Creek, tributary to the Tennessee River in northwestern Alabama (Fig. 1; Wall, 1968; Retzer et al., 1986; Mettee et al., 1996).

The taxonomic status of *E. w. artesiae* has been in a state of flux for some time. Described *Poecilichthys artesiae* by Hay (1881), the species was synonymized with *Poecilichthys whipplei* by Hubbs and Black (1941). Moore and Rigney (1952) and Moore (1968) recognized *artesiae* as a full species, whereas others, including Page (1983), Kuehne and Barbour (1983), and Retzer et al. (1986), treated it as a subspecies of *E. whipplei*. A thorough review of the nomenclatural history of *E. whipplei* is provided by Retzer et al. (1986).

We conducted this study to investigate the distinctiveness of *E. w. artesiae* in upland portions of the Mobile Bay System (Black Warrior River drainage). Retzer et al. (1986) grouped both upland (above the Fall Line) and lowland (below the Fall Line) populations of *E. w. artesiae* in the Mobile Bay Basin together as a single population. We also assessed the taxonomic status of a disjunct population of *E. w. artesiae* in Halawakee Creek (Chattahoochee River system).

MATERIALS AND METHODS

Material for study was obtained from the Tulane University Museum of Natural History (TU), Auburn University Museum (AUM), and Oklahoma Museum of Natural History (OMNH). A complete listing of this material is provided in the Material Examined section at the end. Counts and measurements followed Hubbs and Lagler (1958), with the exception of transverse scales, which were counted anteriodorsally from the origin of the anal fin to the base of the dorsal fin. Only specimens 25 mm SL or greater were used in this study; *t*-tests were used to test for significant differences (P < 0.05) in meristics for the subspecific populations. Nuptial male breeding pigmentation was observed either from live specimens or from photographs of freshly preserved specimens.

RESULTS

Significant variation was noted in several meristic characters. In the following summary, ranges of meristics are provided followed by the mode in brackets. Populations from the White and Arkansas River systems (E. w. whipplei) have significantly higher counts in all characters analyzed. These populations are characterized by high lateral line scales 59–73 [67] (t = 29.69, P< 0.0005; Table 1), pored lateral line scales 45-58 [51] (t = 17.16, P < 0.0005), caudal peduncle scales 26–32 [30] (t = 39.27, P < 0.0005; Table 2), and transverse scales 17–25 [20] (t =10.99, P < 0.0005). Populations of E. w. artesiae from the Gulf Coast, lower Mississippi, and Mobile Bay drainages have the following counts: lateral line scales 45-63 [54], pored lateral line scales 35–53 [42], caudal peduncle scales 18–26 [21], and transverse scales 14-22 [17]. Lateral line scale counts of ≤ 61 separate 97.9% (520/

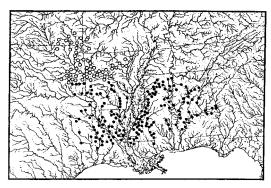


Fig. 1. Distribution of *Etheostoma whipplei whipplei* (open circles) and *Etheostoma whipplei artesiae* (solid circles, modified from Retzer et al. (1986).

531) of *E. w. whipplei* and *E. w. artesiae*. Caudal peduncle scale counts of ≤ 26 separate 95.4% (503/527) of *E. w. whipplei* and *E. w. artesiae*. The combination of lateral line scales and caudal peduncle scales best separate *E. w. artesiae* and *E. w. whipplei* (Fig. 2). No specimens of *E. w. artesiae* has the combination of ≤ 61 lateral line and ≤ 26 caudal peduncle scales; no specimens of *E. w. whipplei* have the combination of ≤ 61 lateral line and ≤ 26 caudal peduncle scales.

With the exception of the degree of red spotting on the side of the body of nuptial males, coloration of the subspecies are similar. Nuptial males of *E. w. artesiae* develop more brilliant and higher degree of red spotting on the side of the body than males of *E. w. whipplei*. This difference in pigmentation patterns of nuptial males was first recognized by Moore and Rigney (1952).

Meristics of the Upper Mobile population of artesiae are slightly higher than lowland populations in the Mobile Bay Basin but are clearly assignable to E. w. artesiae. Breeding male coloration of the Upper Black Warrior population differs from that seen in other populations of E. w. artesiae. Nuptial males lack the brilliant red spotting pattern typical of other populations of E. w. artesiae and, in this regard, are more similar to E. whipplei. Upper Black Warrior males also develop dark blue bars on the caudal peduncle, a pattern atypical of other populations. Based on nuptial male coloration and meristic data, the population from the Chattahoochee River System agrees with lowland populations of artesiae.

DISCUSSION

In arguing that *Etheostoma lynceum* (formerly regarded as a subspecies of *E. zonale*) should be

TABLE 1. LATERAL LINE SCALE COUNTS FOR SELECTED POPULATIONS OF Etheostoma whipplei whipplei AND Etheostoma whipplei artesiae.

SD	3.15		3.29	2.62	2.88	2.37	2.63	2.87	2.44
			٠.,						
Mean	65.60		55.81	54.83	50.71	52.87	51.25	54.45	50.71
n	29		58	45	120	30	85	84	45
73	1								
72									
71	21								
20	4								
69	70								
89	6								
29	11								
99	9								
65	4								
64	6								
63	4		_						
62	9		_					П	
19	r0		3					01	
09	1		50	81				1	
59	21		2		1	1		01	
28			9	01				3	
22			∞	7		П	П	∞	
99			П	∞	9	01	\mathcal{D}	11	_
55			13	9	9	33		16	_
54			60	9	11	$r_{\mathcal{C}}$	11	13	70
53			3	4	10	3	12	^	8
52			20	9	13	\mathcal{L}	12	9	6
51			50	П	6	$r_{\mathcal{O}}$	14	7	∞
20			87	01	16	4	6	$r_{\mathcal{O}}$	9
49					18	1	∞		7
48					5 19 18		ಸ	П	\mathcal{L}
47				П	\mathcal{D}		01		8
46					01		9	П	8
45					4				
Population 45 46 47 48 49	E. w. whipplei Arkansas-White	E. w. artesiae	Ouachita-Red	Neches-Sabine	Lower Mississippi 4	Pearl	Lower Mobile	Upper Mobile	Chattahoochee

	SD	1.39		1.47	1.12	1.25	1.13	1.27	1.26	1.95
Table 2. Caudal Peduncie Scale Counts for Selected Populations of Etheostoma whipplei whipplei and Etheostoma whipplei artesiae.	Mean	99.4		22.8	21.2	20.5	9.61	21.1	22.0	22.5
	u	69		58	42	120	30	85	84	39
	32	4	4							
	31	6	,							
	30	20	ī							
	53	19	2							
	28	19	!							
	27	4	4		9					
	56	-	•	23	12					4
	25			7	12				6	99
	24			6	10	П		П	67	9
or Selec	23			15	2	œ		6	15	4
OUNTS FO	22			15		16	2	25	29	7
CALE CC	21			7		31	4	23	21	10
UNCLE S	20			33		45	10	16	9	4
OAL PEDI	19					17	6	10	67	П
2. CAUI	18					ъс	ъс	-		
TABLE	Population	E. w. whipplei Arkansas-White	E. w. artesiae	Ouachita-Red	Neches-Sabine	Lower Mississippi	Pearl	Lower Mobile	Upper Mobile	Chattahoochee

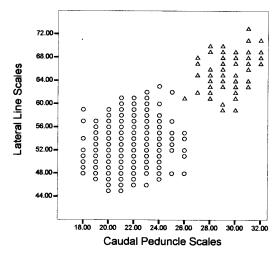


Fig. 2. The relationship between caudal peduncle and lateral scale counts of *Etheostoma whipplei whipplei* (triangles) and *Etheostoma whipplei artesiae* (circles).

recognized as a species, Etnier and Starnes (1986) commented on the difficulty of "assessing the taxonomic status of closely related allopatric forms whose level of differentiation appears to be intermediate between that of species and subspecies." At present, no universally accepted level of differentiation exists for the delineation of species versus subspecies. Subspecies have traditionally been recognized where morphologically intermediate populations (intergrades) are found in zones of contact between otherwise differentiated groups of populations. In recent years, the subspecies category has been abandoned even where intergrades are known (Warren, 1992). Warren (1992), following the phylogenetic species concept (PSC; Nixon and Wheeler, 1990), argued that subspecies of Lepomis punctatus should be recognized as full species, despite the presence of a broad zone of intergradation. We also follow the PSC (Nixon and Wheeler, 1990), which treats species as the smallest diagnosable unit. Diagnosability is the central premise of the PSC.

We found no intergrades between *E. whipplei* and *E. artesiae*, which further strengthens the recognition of these taxa as full species. Moreover, the species are diagnosable by meristics and other morphological characters. Although our results are similar to those obtained by Retzer et al. (1986), our interpretation differs. Both studies found higher meristics in populations of *E. whipplei* than in populations of *E. artesiae*, and both note the absence of a zone of intergradation. Retzer et al. (1986) interpreted the presence of modal differences in meristics as evidence of subspecific differentiation. We inter-

pret the very small degree of overlap in certain meristics as evidence of species level differentiation.

There is little evidence to support recognition of additional taxa within *E. artesiae*. The Upper Black Warrior (Upper Mobile) population has slightly higher transverse, lateral line, and pored lateral line scale counts than lowland Mobile populations, but the differences are not statistically significant. Retzer et al. (1986) noted the presence of blue bars along the caudal peduncle of nuptial males of *E. whipplei* and upland populations of *E. artesiae*. We only observed the blue barring pattern in nuptial males of *E. artesiae* from the Upper Black Warrior River Drainage.

Etheostoma whipplei is an upland form confined to portions of the White and Arkansas River systems above the Fall Line. Etheostoma artesiae is a lowland form widely distributed across the Coastal Plain. However, it occurs in streams in more elevated portions of the Coastal Plain (Pre-Wisconsin Glacial stage deposits). Etheostoma artesiae extends immediately above the Fall Line in the Ouachita, Red, and Western Mobile Bay Systems. The ranges of E. whipplei and E. artesiae are separated by the low (Holocene) Valley of the Mississippi River. Prior to (and possibly during) the Pleistocene, the Mississippi River flowed along the eastern edge of the Ozark Plateau, west of Crowley's Ridge, transforming the hilly topography in this region to alluviated flood plain. The Mississippi River shifted to its current position on the eastern side of Crowley's ridge during the Pleistocene (Fenneman, 1938). The Arkansas River formed to the south and west of Crowley's Ridge. Etheostoma whipplei is common in the gravelly streams along the edge of the Ozark Plateau but avoids the alluviated low gradient streams on the valley floor.

Etheostoma artesiae primarily inhabits small to moderate sized Gulf Coast Plain streams with substrates of mixed sand and gravel. It inhabits rockier streams in the Ouachita Uplands of Arkansas and Appalachian Plateau of Alabama. In the western portion of the range, Etheostoma artesiae is sympatric with E. radiosum immediately above the Fall Line in the Red and Ouachita River drainages. Further expansion into the upper reaches of the Red and Ouachita Rivers is probably prohibited by the presence of E. radiosum (Moore and Rigney, 1952) or by habitat differences. Etheostoma radiosum is an upland species endemic to the Ouachita highlands (elevations of 76-793 m; Fenneman, 1938; Robison, 1986). In the areas of sympatry with E. artesiae, E. radiosum inhabits smaller, high-gradigravel-cobble swift-flowing, bottomed streams, whereas *E. artesiae* inhabits larger, lower gradient, moderate flowing, gravel-sand bottomed streams (Moore and Rigney, 1952).

Hubbs and Black (1941), Moore and Rigney (1952), Retzer et al. (1986), and others have noted the close affinities between E. whipplei, E. artesiae, and E. radiosum. However, until recently, no phylogenetic hypotheses for the subgenus Oligocephalus were available. A recent morphology based phylogenetic study of the Oligocephalus group of darters, which included E. radiosum and E. artesiae, suggested that E. radiosum and E. artesiae were sister taxa (Shaw, 1996). Morphologically, E. radiosum is very similar to both E. whipplei and E. artesiae, differing from them mainly in male breeding coloration (no red spotting). Etheostoma radiosum and E. artesiae share lower meristics when compared to E. whipplei; E. whipplei and E. radiosum occupy similar upland habitats.

The occurrence of E. whipplei in the Ozark Highlands, E. artesiae over a broad area of the Coastal Plain, and E. radiosum in the Ouachita Highlands suggests that the common ancestor of these three species was widely distributed in the Interior Highlands and along the Gulf Coast. It is difficult to hypothesize patterns or modes of speciation for these taxa without a well-supported phylogenetic hypothesis. However, the virtually parapatric distribution of these taxa argues for vicariant origin in the areas occupied today. Peripheral isolation, likely in a preglacial plains drainage system, best explains the divergence of E. radiosum from a common ancestor of E. whipplei/artesiae. Current distribution suggests that the divergence of E. whipplei from E. artesiae involved similar, but more recent, peripheral isolation of upland Arkansas and White River populations from more widespread Coastal populations.

Nixon and Wheeler (1990) stated that a species is "the smallest aggregation of populations diagnosable by a unique combination of characters." We conclude that the meristic differences coupled with the habitat differences and the allopatric distribution of the populations strongly supports the recognition of *E. artesiae* and *E. whipplei* as distinct species.

Etheostoma whipplei (Girard) REDFIN DARTER

Types.—Syntype of Boleichthys whipplei Girard 1859: MCZ 24569 (ex USNM 1333 and MCZ 41). Coal Creek, Tributary to Arkansas River, eastern Oklahoma.

Diagnosis.—Etheostoma whipplei is distinguished from E. artesiae by higher meristics: lateral line scales 59 or higher; scales around caudal peduncle 26 or greater (all specimens examined). Etheostoma whipplei can be distinguished from E. radiosum by the presence of red lateral spots and high meristics.

Etheostoma artesiae (Hay) REDSPOT DARTER

Types.—Holotype of Poecilichthys artesiae Hay 1881: USNM 27434, collected from a small branch of Catawba Creek (Catalpa Creek), at Artesia, Lowndes Coounty, Mississippi.

Diagnosis.—Etheostoma artesiae can be distinguished from E. whipplei by lower counts of lateral line scales (< 63) and caudal peduncle scales (< 27). Etheostoma artesiae can be distinguished from E. radiosum by the presence of red lateral spots in breeding males.

Etymology.—Apparently in reference to the type locality. We suggest the vernacular name of "redspot darter" in reference to the brilliant red lateral spots of nuptial males.

MATERIALS EXAMINED

ARKANSAS-WHITE RIVER: Illinois Bayou, Pope County, AR, TU 15588 (19); Petit Jean River, Yell County, AR, TU 10268 (7); Departe Creek, Independence County, AR, TU 49971 (16); Little Raccoon Creek, Stone County, AR, TU 182886 (15); Departe Creek, Independence Co, AR, TU 49971 (30). LOWER MOBILE BAY DRAINAGE.: Chilatchee Creek, Dallas-Wilcox County, TU 60893 (30); Beaver Creek, Wilcox County, TU 178334 (3); Chilatchee Creek, Wilcox County, AL, TU 162587 (5), Salt Creek, Clarke County, AL, TU 41432 (4), Chilatchee Creek, Wilcox County, TU 153097 (2); Chilatchee Creek, Dallas-Wilcox County, AL. TU 153198 (2); Sandy Creek, Montgomery County, AL, AUM 11822 (1); Bear Creek, Wilcox County, AL, TU 60865 (27); Wolf Creek, Choctaw County, AL, TU 166722 (2); Chilatchee Creek, Dallas-Wilcox County, TU 121395 (2); Tributary to Little Sourwilpa Creek, Choctaw County, AL, TU 152520 (11); Salt Creek, Clarke County, AL, TU 151777 (1); Tributary to Salt Creek, Clarke County, AL, TU 37395 (2); Capsey Creek, Winston County, AL, TU 179473 (4); Tombigbee River, Sumter County, AL, TU 85733 (4); UP-PER MOBILE: Little Cove Creek, Etowah County, AL, TU 183122 (18); Five Mile Creek, Jefferson County, AL, TU 163019 (3); Tributary to

Gurley Creek, Jefferson County, AL, TU 163197 (1); Mill Creek, Blount County, AL, TU 151828 (3); Tributary to Mulberry Frk, Blount County, AL, TU 62657 (1); Gurley Creek, Jefferson County, AL, TU 61947 (4); Borden Creek, Lawrence County, AL, TU 176300 (1); Bristow Creek, TU 167934 (1); Six Mile Creek, Bibb County, AL, TU 152161 (1); Little Schultz Creek, Bibb County, AL, TU 176144 (1); Camp Branch, Tributary to Waxahatchee Creek, Shelby County, AL, TU 24190 (13); Camp Branch, Tributary to Waxahatchee Creek, Shelby County, AL, AUM 15887 (2); Camp Branch, Tributary to Waxahatchee Creek, Shelby County, AL, TU 23592 (2); James Creek, Blount County, TU 125431 (1); Little Cove Creek, Etowah County, AL, TU 167925 (18); Blevens Creek, Cullman County, AL, TU 179884 (6); Capsey Creek, Winston County, AL, TU 168299 (9). LOWER MIS-SISSIPPI RIVER: Coles Creek, Jefferson County, MS, TU 67161 (30); Little Sand Creek, Claiborne County, MS, TU 132868 (30); Raglan Creek, Claiborne County, MS, TU 80285 (15); Homochitto River, Copiah County, MS, TU 85991 (30); Tributary to Bliss Creek, Warren County, MS, TU 91995 (15). OUACHITA-RED RIVER: Horsepen Creek, Natchitoches Par., LA, TU 13690 (9); Red River, Natchitoches Par., LA, TU 13257 (9); Locust Bayou, Calhoun County, AR, TU 100995 (1); Sloan Creek, Columbia County, AR, TU 87107 (1); Unamed Tributary, Catahoula Par., LA, TU 76102 (4); Unnamed Tributary to Smackover Creek, Columbia County, AR, TU 84267 (6); Big Cornie Creek, Columbia County, AR, TU 93289 (18); Tributary to Big Cedar Creek, Leflore County, OK, OMNH 19137 (6); Kiamichi River, Leflore County, OMNH 7411 (1); Tributary to Kiamichi River, Leflore County, OMNH 7778 (2). NECHES-SABINE RIVER: Neches River, Tyler County, TX, TU 111999 (1); Dement Creek, Cherokee County, TX, TU 17771 (11); Tributary to Angelina River, Tyler County, TX, TU 36812 (2); Wall Creek, Sabine Par., LA, TU 33758 (4); Bayou Negret, Sabine Par., LA, TU 35404 (5); Hurricane Creek, Sabine Par., LA, TU 33946 (2); Palo Gaucho Bayou, Sabine County, TX, TU 35475 (2); Bayou Anococo, Vernon Par., LA, TU 60666 (2); Well Creek, Sabine Parish, LA, TU 38676 (8); Tributary to Sabine River, Vernon Par., LA, TU 14361 (1); Wall Creek, Sabine Parish, LA, TU 33758 (3); Laco Bayou, Nacogdoches County, TX, TU 3265 (1). PEARL RIVER: Tributary to Pearl River, Copiah County, MS, TU 43445 (15); Pearl River, Lawrence County, MS, TU 82713 (3); Tributary to Pearl River, Copiah County, MS, TU 26711 (9); Tributary to Strong River, Simpson County, MS, TU 26809 (3). CHATTA-

HOOCHEE RIVER: Tributary to Halawakee Creek, Lee County, AL, AUM 24028 (1); Tributary to Halawakee Creek, Lee County, AL, AUM 24045 (1); Halawakee Creek, Lee County, AL, TU 23997 (3); Tributary to Halawakee Creek, Lee County, AL, AUM 24044 (1); Tributary to Halawakee Creek, Lee County, AL, TU 24004 (1); Tributary to Halawakee Creek, Lee County, AL, TU 174597 (2); Tributary to Halawakee Creek, Lee County, AL, TU 174597 (2); Tributary to Halawakee Creek, Lee County, AL, TU 24042 (8); Tributary to Halawakee Creek, Lee County, AL, TU 183036 (8); Tributary to Halawakee Creek, Lee County, AL, TU 175137 (15).

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