Rediagnosis of the Tuckasegee Darter, *Etheostoma gutselli* (Hildebrand), a Blue Ridge Endemic

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In 1932, the Tuckasegee Darter was originally described as *Poecilichthys gutselli*, from the Tuckasegee River (Little Tennessee River system), North Carolina. In 1968, Miller, citing perceived areas of intergradation, relegated it to a subspecies of *Etheostoma blennioides*. Recent authors, however, re-elevated *E. gutselli* to the species level without providing any supporting data. We present morphological, meristic, and nuptial male pigmentation data that support the distinctiveness of *E. gutselli*. *Etheostoma gutselli* can be distinguished from proximal populations *E. blennioides newmanii* in the Tennessee River system by lower lateral-line (49–63 vs. 63–81) and caudal-peduncle (18–24 vs. 23–29) scale counts and differences in nuptial male pigmentation. *Etheostoma gutselli* primarily is restricted to the upper (Blue Ridge) portions of the Little Tennessee and Pigeon river drainages, generally upstream of the Tennessee-North Carolina state line.

COLLETTE (1967) described the middle third of the 20th century, an era characterized by numerous studies of morphological variation and taxonomic descriptions, as a period of "re-awakening" in darter taxonomy. Most studies published on darters during this period (e.g., Hubbs and Black, 1941; Distler, 1968; Tsai and Raney, 1974) followed an approach that is conservative by today's standard, recognizing species as wide-ranging entities comprising multiple subspecies. Subspecies were recognized when populations exhibited morphologically intermediate characteristics, which were interpreted as "intergrades," signifying ongoing gene flow between otherwise morphologically distinctive forms. In recent decades, across many groups of organisms, the recognition of subspecies has fallen out of favor because of the arbitrariness of the subspecies concept (Cracraft, 1983; McKitrick and Zink, 1988; Frost and Hillis, 1990; Burbrink et al., 2000). Contemporary studies of darters have followed the same philosophical approach in regards to the recognition of subspecies, which has resulted in a number of former subspecies being elevated to full species (Etnier and Starnes, 1986; Ceas and Page, 1997; Piller et al., 2001). Taking an objective approach and including information from different data sets including molecular, morphometric, nuptial male pigmentation, and traditional meristics have allowed for more comprehensive data-driven, taxonomic decisions to be made for darters, rather than the subjective approach incorporated in earlier studies.

The taxonomic history of the Greenside Darter, *Etheostoma blennioides* (Percidae), is rich with lumping and splitting based on varying amounts of data. Morphological variation of the species was reviewed by Miller (1968). The species was found to comprise four subspecies, several morphological races, and three zones of morphological intergradation. Two species, *Etheostoma gutselli* (Hildebrand) and *E. newmanii* (Agassiz), were placed in the synonymy of *E. blennioides* because of what Miller (1968) perceived to be morphological intergrades between these forms in the Hiwassee River System (Fig. 1). Additionally, genetic studies by Piller et al. (2008) and Piller and Bart (2009) provided additional evidence for recognition of *E. gutselli*, and the paraphyly of several of the subspecies, suggesting that a taxonomic revision of the entire *E. blennioides* complex was warranted.

In an addendum to the second printing of *The Fishes of Tennessee*, Etnier and Starnes (2001) recommended that *E. b. gutselli* (Hildebrand) be elevated to a full species. They provided no morphological or molecular data to support this decision, only the sympatric occurrence of *blennioides* and *gutselli* in the Pigeon River and the lack of intergradation between the two forms. Subsequently, other authors followed this recommendation and recognized *E. gutselli* at the specific level, also without supporting data (Nelson et al., 2004; Near et al., 2011; Page and Burr, 2011; Page et al., 2013).

In this paper, we provide meristic and nuptial male pigmentation evidence for recognizing the Tuckasegee Darter, *E. gutselli*, as a distinct species within the *E. blennioides* species complex. We also rediagnose the species and compare populations of *E. gutselli* in the Upper Pigeon and Little Tennessee rivers to populations of the closely related form, *E. b. newmanii* (Piller et al., 2008; Piller and Bart, 2009), in lower portions of both of these river systems. However, we take no position on the taxonomic status of the more widely distributed *E. b. newmanii*, or the status of the supposed intergrades in the Hiwassee River, as a more thorough investigation is needed to re-assess their taxonomic status.

MATERIALS AND METHODS

Counts and measurements followed Hubbs and Lagler (1958), with the exception of transverse scales, which were counted anterodorsally from the origin of the anal fin to the base of the dorsal fin. A portion of the meristic data presented in this study was derived from 28 specimens of *E. gutselli* examined and reported by Miller (1968). We gathered data for an additional 186 specimens of *E. gutselli*. Data from 116 specimens of *E. b. newmanii* from the Little River and the portions of the Little Tennessee (downstream of the TN/NC state lines) and Pigeon river systems (downstream of the TN/NC state lines) were taken from Miller (1968). All data are presented in a supplemental file (Table S1; see Data Accessibility). 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 between populations. Nuptial male pigmentation was observed from dozens of live specimens or from photographs of freshly preserved specimens across multiple years during the months of March–

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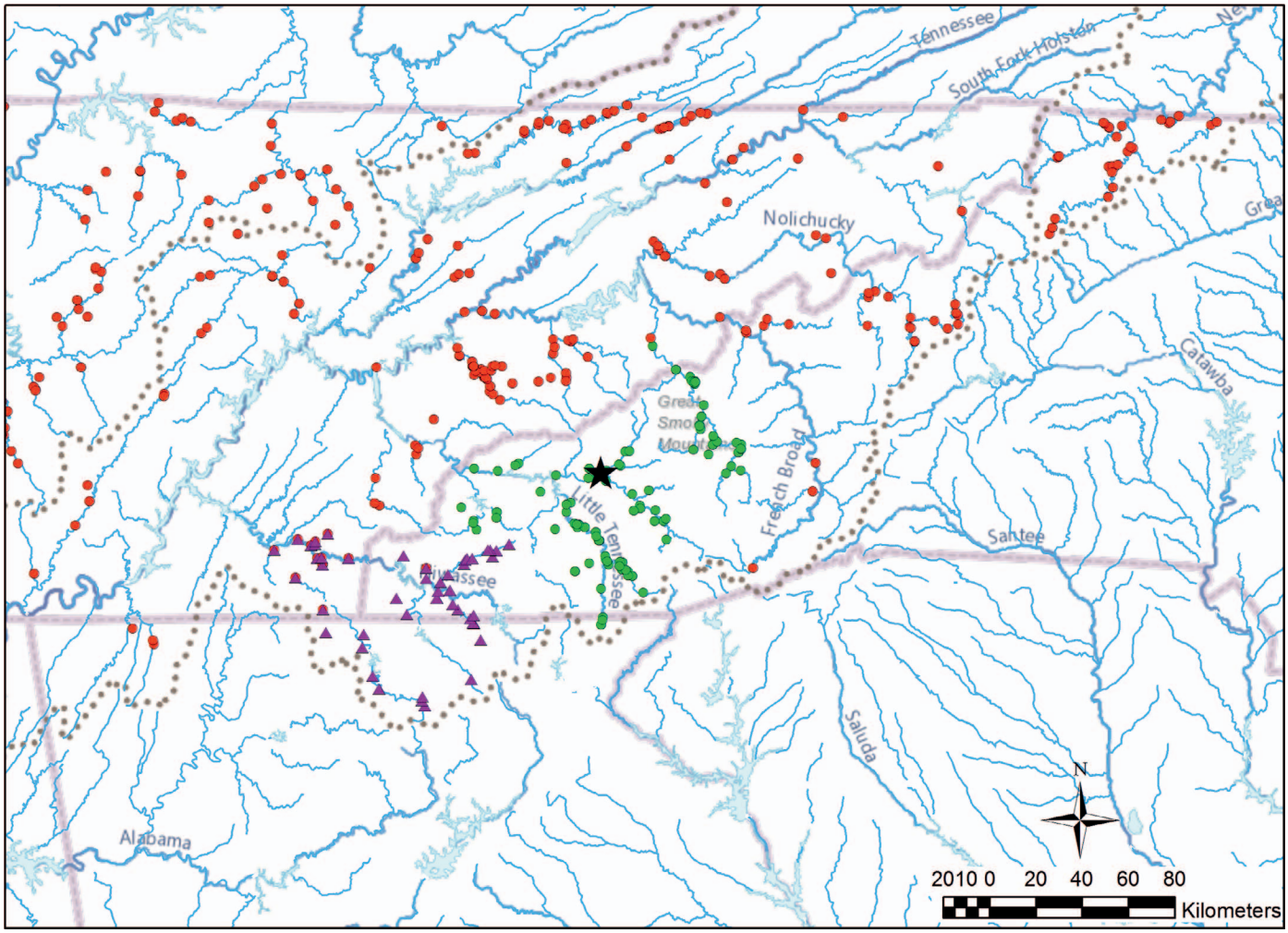

Fig. 1. Georeferenced Fishnet2 records (www.fishnet2.org, 24 May 2017) of *Etheostoma gutselli* (green circles), *E. blennioides newmanii* (red circles), and Hiwassee River populations of uncertain taxonomic status (purple triangles). The type locality for *E. gutselli* is represented by a star symbol.

May. Institutional abbreviations follow Sabaj (2016). A complete listing of all specimens examined is provided in the Material Examined section.

RESULTS

Significant variation was found for several meristic characters. In the following paragraphs, ranges are presented for each character followed by the mode in brackets, and t -test statistic and *P*-value in parentheses. In comparison to *E. b. newmanii* (Lower Pigeon, Little, and Little Tennessee rivers), *E. gutselli* possesses significantly lower meristic counts: lateral-line scales 63–81 [71] versus 49–63 [56] ($t = 37.636$, $P < 0.0001$; Table 1), least caudal-peduncle scales 23–29 [26] versus 18–24 [22] ($t = 38.339$, $P < 0.0001$; Table 2), and transverse scales 18–22 [19] versus 15–20 [17] ($t = 21.319$, $P < 0.0001$; Table 3).

Slight meristic variation exists between populations of *E. gutselli* from the Pigeon and Little Tennessee river systems; however, both populations are clearly assignable to *E. gutselli*. In comparison to Pigeon River populations, Little Tennessee River populations have lower meristic counts for two characters: lateral-line scales 50–63 [58] versus 49–62 [56] and transverse scales 15–20 [17] versus 15–19 [17].

Lateral-line scale counts of ≤63 separate 98.7% (297/301) of specimens of *E. gutselli* and *E. b. newmanii*, based on the sample used in this study. Least caudal-peduncle scale counts of ≤24 separate 96.3% of specimens of *E. gutselli* and *E. b. newmanii* specimens (290/301). The combination of lateral-line (≤63) and least caudal-peduncle (≤24) scales completely separates the two species (Fig. 2). No specimens of *E. gutselli* had ≥63 lateral-line and ≥24 least caudal-peduncle scales, and none of the specimens of *E. b. newmanii* had <63 lateral-line and <24 least caudal-peduncle scales.

In addition to meristic differences, *E. gutselli* differs from *E. b. newmanii* in the degree of opercular squamation and development of a premaxillary frenum. All specimens of *E. gutselli* examined in this study lack a distinct lip tip, a nipple-like formation on the upper lip as described in Miller (1968), and most possess an unscaled opercle. Specimens from the Little Tennessee River System rarely (5/107 specimens) possess partially scaled opercles, while all specimens from the Pigeon River have opercles that are unscaled.

Patterns of nuptial male pigmentation are also diagnostic for *E. gutselli* (Fig. 3A). The spinous dorsal fin has three bands, a basal red-orange, middle green, and distal red-orange band. A thin blue-green border occurs along the distal edge of the spinous dorsal fin. Nuptial males of *E. b. newmanii* from the Tennessee River drainage also typically possess three bands in the spinous dorsal fin, including, a basal reddish-orange band, a dark-blue middle, and a distal green band (Fig. 3B).

Table 1. Lateral line scale counts for selected populations of *Etheostoma gutselli* and *E. blennioides newmanii.*

Population	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	*n*	X	SD
Etheostoma gutselli																																				
Upper Little Tennessee River	1	2	4	3	11	11	19	21	11	7	9	6	2	1																				108	55.69	2.59
Upper Pigeon River		1		2	2	5	7	9	12	11	10	6	6	4	3																			78	57.62	2.79
Etheostoma blennioides newmanii																																				
Lower Pigeon and Little rivers															1	1	3	4	2	6	6	3	16	7	9	4	7	3		1			1	74	71.04	3.41
Lower Little Tennessee River																1		2	1	7	3	6	7	3	3	7	1						1	42	70.76	3.07

However, males in peak breeding condition appear to have only two bands (green and red). The dark middle band blends in with and is indistinguishable from the distal green band (see also photos in Page, 1983; Etnier and Starnes, 1993; Jenkins and Burkhead, 1994). Both nuptial and non-nuptial males of *E. gutselli* also possess a small blotch of dark pigment near the origin of the spinous dorsal fin. This pigment is primarily distributed on the membrane between the first and second dorsal fin spines, but often occurs on the membrane between the second and third dorsal fin spines as well. The blotch is evident on both live and preserved specimens. The soft dorsal fin of *E. gutselli* has an orange or yellow hue and possesses dark reddish-brown vermiculations and a narrow proximal reddish-brown band. For males in peak reproductive condition, the vermiculations become obscured by intense bands of red and blue chromatophores. The soft dorsal fin of *E. b. newmanii* also has a yellow hue; however, it also possesses a basal red band and a median green band. It lacks the vermiculated fin pattern of *E. gutselli*.

The venter from the head to the caudal fin, cheeks, anal fin, and the first few dorsal and ventral rays of the caudal fin of *E. gutselli* are blue-green in color. The ventral edge of the pectoral fin of nuptial males often develops a narrow green band. The pectoral of *E. gutselli* contains dark reddish-brown vermiculations similar to the pattern seen in the soft dorsal fin, caudal, pectoral, and pelvic fins of females and non-breeding males. These vermiculations also are present on nuptial males; however they become obscured by pigment in individuals in peak nuptial condition.

Physiographic and elevational differences, rather than habitat differences per se, seem to be important physical factors separating *E. gutselli* and *E. b. newmanii*. Based on spring time point habitat measurements, *E. gutselli* and *E. b. newmanii* occupy streams with similar average flow (0.50 vs. 0.49 m/sec), substrate composition (rock and cobble), average depth (32.3 vs. 30.3 cm), and amount of instream vegetation (K. Piller, unpubl.). However, *E. gutselli* is confined to streams above 350 meters elevation and presumably cooler water temperatures.

DISCUSSION

Comparisons of morphological traits from pigmentation patterns to meristic counts highlight the distinctiveness of *E. gutselli*. Results from this study clearly indicate that *E. gutselli* is a distinct species and can be readily diagnosed from *E. b. newmanii*. In addition to the distinguishing characteristics reported here, Miller (1968) reported that *E. gutselli* possesses fewer lateral blotches (mean = 8.43) than *E. b. newmanii* (mean = 7.25). *Etheostoma gutselli* also has a distinct frenum and possesses prevomerine teeth (47%) more often than specimens of *E. b. newmanii* which possess a long lip tip and less often (<10%) have prevomerine teeth (Miller, 1968).

Despite its distinctiveness, the taxonomic status of *E. gutselli* has been debated for some time (Hubbs and Greene, 1928; Hildebrand, 1932; Miller, 1968). Miller (1968) relegated it to a subspecies of *E. blennioides*; however, he suggested that "differences in coloration and opercle squamation between *E. gutselli* and *E. b. newmanii* are probably great enough to warrant specific recognition of the former, were it not for the *E. b. newmanii* x *gutselli* intergrades in the Hiwassee River." Populations of Greenside Darters from the Hiwassee River were previously identified as intergrades between *E. b. newmanii* and *E. gutselli*. However, Piller et al. (2008) showed that this population possesses mitochondrial

Table 2. Caudal peduncle scale counts for selected populations of *Etheostoma gutselli* and *E. blennioides newmanii*.

Population	18	19	20	21	22	23	24	25	26	27	28	29	*n*	X	SD
Etheostoma gutselli															
Little Tennessee River	1	2	12	24	47	17	4						107	21.69	1.10
Pigeon River		1	12	20	26	15	4						78	21.69	1.14
Etheostoma blennioides newmanii															
Lower Pigeon and Little rivers							1	8	33	24	4	4	74	26.46	1.00
Lower Little Tennessee River						1		2	22	15	2		42	26.33	0.85

haplotypes distinct from those observed within both *E. b. newmanii* and *E. gutselli* and may either represent a distinct taxon with meristics intermediate between these taxa, or a divergent population of *E. b. newmanii*. A more thorough investigation of the taxonomic status of the "intergrades" in the Hiwassee River System is needed before a taxonomic decision is presented for this population.

The distinctiveness of *E. gutselli* is also evident from recent genetic studies (Piller et al., 2008; Piller and Bart, 2009). Bayesian phylogenetic analysis of mitochondrial DNA (Cytochrome *b*) recovered an unresolved clade of *E. b. newmanii* (Lower and Middle Tennessee) and *E. gutselli* (Upper Little Tennessee; Piller et al., 2008). This clade, however, was sister to *E. gutselli* from the Upper Pigeon River. Nuclear S7-1 intron data, however, recovered each taxon, *E. b. newmanii* and *E. gutselli*, as monophyletic, which indicates ancestral mitochondrial introgression between *E. gutselli* (Upper Little Tennessee River) and *E. b. newmanii* (Lower and Middle Tennessee River; Piller et al., 2008).

Status and distribution.—*Etheostoma gutselli* has a geographically small range. It only occurs in the upper Blue Ridge portions of the Upper Pigeon and Little Tennessee river systems in Tennessee, Georgia, and North Carolina. The most downstream locality for *E. gutselli* in the Pigeon River is near Denton, Cocke Co., TN (UT 91.4796). In the Little Tennessee River drainage, Slick Rock Creek, Monroe Co., TN, along the Tennessee/North Carolina border, represents the downstream distributional extent of *E. gutselli* (UT 91.2706). The majority of the species' range is in North Carolina, where it is often locally common; however, several specimens also have been collected in Tennessee. As a result of its limited occurrence in the state, Tennessee recognizes *E. gutselli* as an endangered species. *Etheostoma gutselli* is replaced by *E. b. newmanii* in the lower Little Tennessee and Pigeon river systems (downstream of TN/NC border). *Etheostoma gutselli* and *E. b. newmanii* are only known to be sympatric at one locality (Pigeon River at Denton, Cocke Co., TN). However, multiple samples taken at this locality have not resulted in the collection of both taxa synchronously.

Results from this study indicate that *E. gutselli* and *E. b. newmanii* are maintaining separate evolutionary histories, despite the potential for sympatry. The two forms show evidence of past hybridization and mtDNA introgression. However, we found no evidence of ongoing hybridization. Meristic, morphological, and nuptial male pigmentation data presented here support the conclusion of Etnier and Starnes (2001), and subsequent works, that *E. gutselli* should be recognized as a distinct species. The taxonomic status of *E. b. newmanii* and remaining populations of *E. blennioides* species complex will be treated in several forthcoming papers.

Etheostoma gutselli
Tuckasegee Darter

Type material.—USNM 92402, holotype of *Poecilichthys gutselli*, by Hildebrand (1932) from the Tuckasegee River at Ela, Swain Co., NC, collected by James S. Gutsell, 26 August 1930.

Holotype meristics.—Counts of the holotype are derived from Miller (1968). Scale counts are as follows: lateral-line (53), least caudal-peduncle (22), and transverse (16). A distinct frenum is present and a lip tip is absent. The cheek is scaled, but the opercle is unscaled.

Diagnosis.—*Etheostoma gutselli* can be differentiated from *E. b. newmanii* by lower counts of lateral-line ($\leq$63) and least caudal-peduncle ($\leq$24) scales, an unscaled operculum, and the presence of a distinct frenum. *Etheostoma gutselli* also can be distinguished from *E. b. newmanii* by differences in nuptial male pigmentation including the presence of a distinct dark spot near the origin of the first dorsal fin, a blue-green belly, and reddish-brown vermiculations in the pectoral, pelvic, soft dorsal, and caudal fins.

Etymology.—The vernacular name of Tuckasegee Darter, which refers to the type locality, has been used extensively in the literature. We suggest retention of this name. The specific epithet, *gutselli*, is a patronym for James S. Gutsell, collector of the species.

Table 3. Transverse scale counts for selected populations of *Etheostoma gutselli* and *E. blennioides newmanii*.

Population	15	16	17	18	19	20	21	22	23	24	25	26	*n*	X	SD
Etheostoma gutselli															
Little Tennessee River	7	35	49	12	4								107	16.73	0.89
Pigeon River	4	12	24	23	12	3							78	17.46	1.91
Etheostoma blennioides newmanii															
Lower Pigeon and Little rivers				9	34	24	6	1					74	19.41	0.86
Lower Little Tennessee River				2	16	18	5	1					42	19.69	0.84

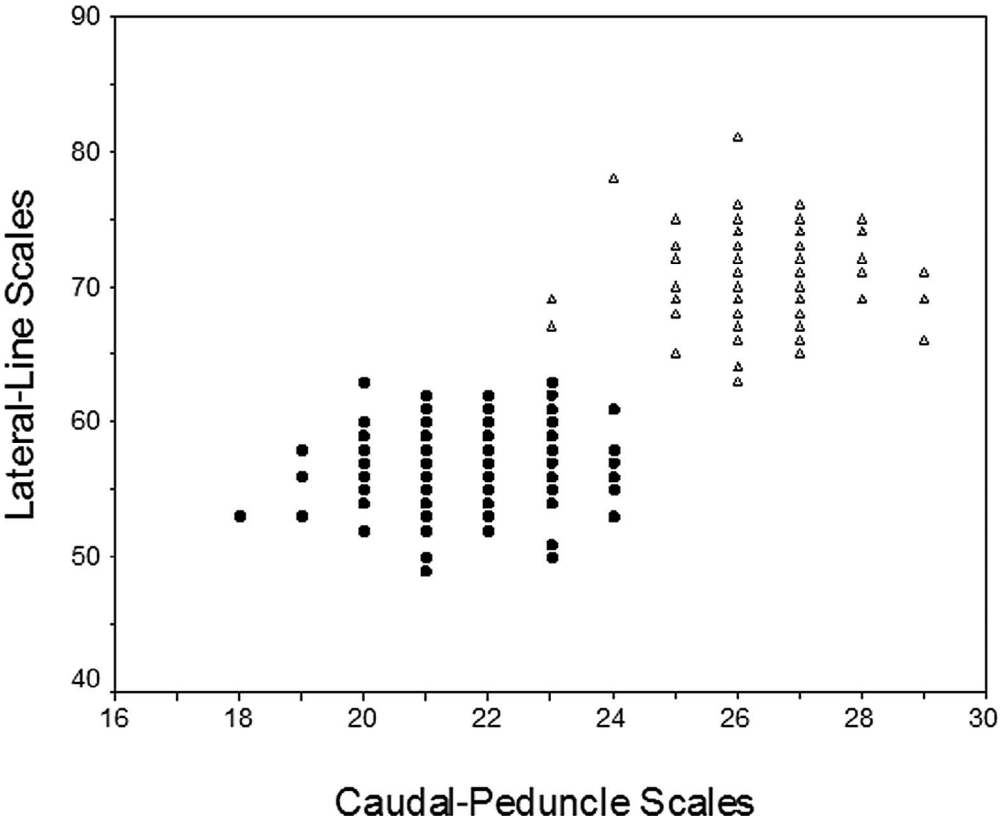

Fig. 2. Relationship between caudal-peduncle and lateral-line scale counts of *Etheostoma gutselli* (circles) and *E. blennioides newmanii* (triangles).

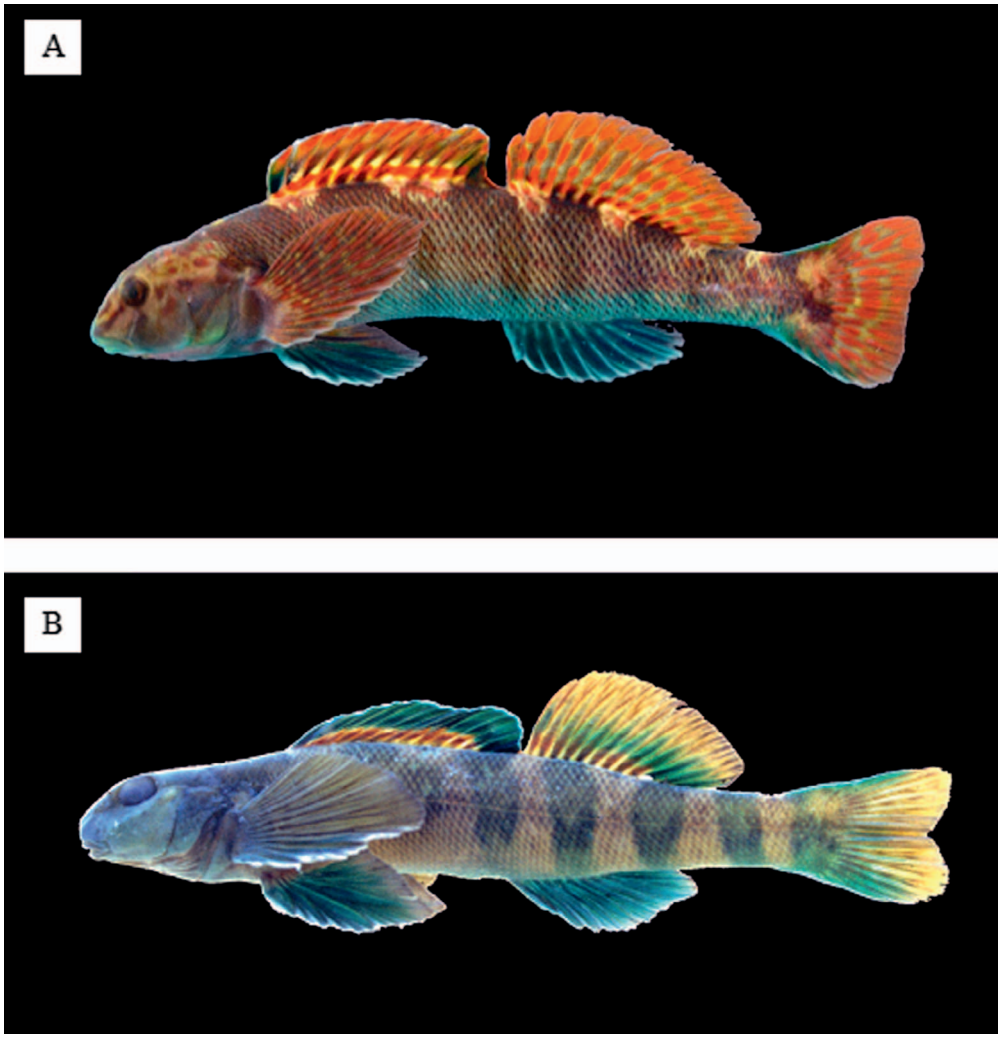

Fig. 3. Nuptial males of (A) *Etheostoma gutselli* (Jonathon Creek, Pigeon River System, NC, 24 May 2013) and (B) *E. blennioides newmanii* (Citico Creek, Lower Little Tennessee River System, TN, 9 April 2000).

MATERIAL EXAMINED

Etheostoma blennioides newmanii (from Miller, 1968): Little River Drainage: CU 24623, 12, CU 41384, 8, USNM 190864, 11. Lower Little Tennessee River Drainage: Abrams Creek: UMMZ 129472, 23, UMMZ 163284, 19. Lower Pigeon River Drainage: Cosby Creek: UMMZ 131501, 9; East Fork Little Pigeon River: CU 23457, 7, CU 46179, 2; Little Pigeon River: CU 40114, 6, CU 41337, 6, CU 41420, 2; Middle Prong Little Pigeon River: CU 37688, 2, UMMZ 129304, 2; Walden Creek: CU 41882, 3, CU 46718, 2; West Prong Little Pigeon River: CU 46176, 2.

Etheostoma gutselli: Upper Little Tennessee River Drainage: Cullasaja River: UGMNH 3039, 19; Eagle Creek: UT 91.3582, 14; Forney Creek: UT 91.3588, 12; Jones Creek: UGMNH 3031, 10; Tellico Creek: UGMNH 3027, 7; Tuckasegee River: TU 188865, 5, UT 91.1436, 18. Upper Pigeon River Drainage: Campbell Creek: UT 91.192, 3; Cold Spring Creek: UMMZ 156280, 8; East Fork Pigeon River: UT 91.5540, 6; Jonathon Creek: TU 190421, 2, TU 190427, 13, UT 91.4150, 10; Pigeon River: TU 188875, 10, TU 191493, 8, TU 191510, 2, UMMZ 156251, 3, UT 91.682, 2, UT 91.3506, 3, UT 91.4786, 2; West Fork Pigeon River: YPM 21727, 1.

DATA ACCESSIBILITY

Supplemental material is available at http://www.copeiajournal.org/ci-17-578.

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