A New Species of the Darter Subgenus *Doration* (Percidae: *Etheostoma*) from the Caney Fork River System, Tennessee

Steven R. Layman[1] and Richard L. Mayden[2]

***Etheostoma akatulo*, the Bluemask Darter, is described from upper Caney Fork River System of the middle Cumberland River drainage, Tennessee. It is presently known from four tributaries of Great Falls Reservoir on the eastern Highland Rim and is listed as federally endangered. The new species differs from other species of the subgenus *Doration* by having fully scaled cheeks, complete lateral line, breeding males with bright blue pigment completely covering the lower face, and breeding males with soft dorsal and anal fins lacking orange and blue pigment. Specimens are compared with nominate *E. stigmaeum* from four drainages and *E. jessiae*. *Etheostoma akatulo* typically occurs over sand and gravel substrates downstream of riffles, in moderate runs, or along margins of pools. It inhabits a 37-km reach of Collins River but is found in reaches of 4.3 km or less in Rocky River, Cane Creek, and Caney Fork River. Threats to the species include gravel dredging, pesticides, siltation, and acid mine drainage.**

DARTERS of the subgenus *Doration* of the percid genus *Etheostoma* are distributed widely in creeks and rivers of the southeastern United States, occurring from Gulf Coastal drainages, north into the lower Mississippi River basin, west into the Arkansas and White river drainages, and east into the Tennessee, Cumberland, and Green river drainages. Members of this group are occasionally among the most abundant benthic fishes collected on sand and gravel substrates in slow to moderate current, yet the subgenus is taxonomically one of the most poorly known groups in the genus *Etheostoma*. Based on a study of meristic variation (Howell, 1968), *Doration* often has been equated with a single polytypic species, the Speckled Darter, *Etheostoma stigmaeum*, with nominate and undescribed forms treated as subspecies, presumably under the Biological Species Concept (Starnes and Etnier, 1986; Etnier and Starnes, 1993; Jenkins and Burkhead, 1994). Many authorities also recognize the Blueside Darter, *Etheostoma jessiae*, endemic to the Tennessee River, as a distinct species (Page, 1981; Boschung and Mayden, 2004; Nelson et al., 2004). Howell (1980a, 1980b, 1980c) recognized a total of five species, including the nominate *Etheostoma meadiae* of the upper Tennessee River drainage and two undescribed forms from the Cumberland River drainage. Presently, only *E. stigmaeum* and *E. jessiae* are recognized widely as distinct species (Nelson et al., 2004).

The new species described here is endemic to the upper Caney Fork River system and is listed by the U.S. Fish and Wildlife Service as federally endangered (Federal Register 58:68480–68486). Caney Fork is a major southern tributary of the middle Cumberland River drainage in Tennessee. The species was first recognized and diagnosed in a dissertation by Howell (1968). Etnier and Starnes (1993) allied this form to the nominate taxon *E. stigmaeum*. As part of a comprehensive systematic investigation of the subgenus *Doration*, we recognize this form as a distinct species diagnosable on the basis of both morphological and biochemical evidence, and a distinct and diagnosable monophyletic group, thus satisfying the criteria of the Biological, Morphological, Phylogenetic, and Evolutionary species concepts (Mayden, 1997, 1999, 2002; Wiley and Mayden, 2000a, 2000b, 2000c).

MATERIALS AND METHODS

Scale and fin-ray counts followed Hubbs and Lagler (1974) with the following exceptions. Transverse scale rows were counted from the origin of the anal fin anterodorsally to the spinous dorsal fin (Page, 1983). Cheek, nape, opercle, and belly squamation was estimated to the nearest ten percent. The cheek was defined as the region bounded dorsally by the lateral and infraorbital canals, anteriorly by the suborbital bar or the position normally occupied by one, and ventrally and posteriorly by the preoperculomandibular canal. The nape was delimited as a subrectangular area centered on the dorsal midline between the occiput and spinous dorsal-fin origin; at the occiput it extended laterally on each side about one-half the distance to the lateral canal, and at the spinous dorsal-fin origin it extended laterally about one-third the distance to the lateral line. The belly was defined as a rectangular area about as wide as the trans-pelvic width (see below) and extending between the rear margin of the pelvic-fin bases and the anus. The opercle included the area covering the opercle, subopercle, and interopercle bones.

Body measurements were made under a dissecting microscope using digital calipers and followed Hubbs and Lagler (1974) with the following exceptions. Body width was measured as the distance between the dorsal insertions of the pectoral fins; trans-pelvic width was the distance between the outer bases of the pelvic spines (Bailey and Etnier, 1988); and caudal peduncle depth (least) was measured between the dorsal and ventral insertions of the caudal fin. Landmark-based truss distances, measured to more fully characterize body shape (Bookstein et al., 1985), included: spinous dorsal-fin origin to occiput; occiput to tip of snout; occiput to midline at least interorbital width; occiput to lateral insertion of pelvic fin; midline at least interorbital width to tip of snout; lateral pelvic-fin insertion to tip of snout; spinous dorsal-fin origin to lateral pelvic-fin insertion; spinous dorsal-fin origin to soft dorsal-fin origin; spinous dorsal-fin origin to anal-fin origin; lateral pelvic-fin insertion to anal-fin origin; soft dorsal-fin origin to lateral pelvic-fin insertion; and soft dorsal-fin origin to anal-fin origin. Standard length (SL) is used throughout.

Means of meristic counts and morphometric proportions within species were tested for sexual dimorphism using a

[1] CH2M HILL, 1000 Abernathy Road, Suite 1600, Atlanta, Georgia 30328; E-mail: steve.layman@ch2m.com.
[2] Department of Biology, 3507 Laclede Avenue, Saint Louis University, St. Louis, Missouri 63103-2010; E-mail: cypriniformes@gmail.com. Send reprint requests to this address.
Submitted: 3 June 2007. Accepted: 29 September 2008. Associate Editor: C. J. Ferraris.
 DOI: 10.1643/CI-07-129

Student's t-test. Meristic variation between populations of the new species was evaluated using the GT2-method of multiple comparisons among means (Sokal and Rohlf, 1981) for unequal sample sizes. Ratios of morphometric proportions were arcsine square root transformed for statistical tests (Sokal and Rohlf, 1981). Multivariate analysis of meristic and morphometric variation between species was conducted using principal component analysis. For the meristic data, principal components were obtained from a correlation matrix; sexes were combined. Morphometric data were assessed using sheared principal component analysis to remove the effects of size, with principal components factored from a covariance matrix of log-transformed variables (Humphries et al., 1981; Bookstein et al., 1985; program by D. L. Swofford, modified by M. L. Warren, Jr.); for each species the number of specimens examined was: *E. stigmaeum* ($n = 80$), *E. akatulo* (51), and *E. jessiae* (20). Sexes were analyzed separately due to significant dimorphism in body proportions.

Specimens of the new species are compared critically with forms of nominate *E. stigmaeum* from the Mobile Basin (type locality in Coosa River system), Duck River, Cumberland River, and Green River, and with *E. jessiae*. Color descriptions and comparisons are based on live and freshly preserved specimens and color slides thereof; color plates in Page (1983), Kuehne and Barbour (1983), Johnson (1987), and Burkhead and Jenkins (1991); and color notes and slides provided by colleagues. Institutional abbreviations follow Leviton et al. (1985) and Leviton and Gibbs (1988).

Etheostoma akatulo, new species
Bluemask Darter
Figure 1

Holotype.—UAIC 10382.02, breeding male, 45.5 mm, Tennessee, Warren Co., Caney Fork River system, Collins River between mouths of Scott and Hillis creeks, 1.6 air km SE Irving College, 35°34.188′N, 85°42.064′W, 11 April 1992, S. R. Layman, A. M. Simons, J. R. Shute, P. W. Shute, and P. L. Rakes.

Paratypes.—UAIC 10382.01 (7), SIUC 70039 (4), TU 167868 (4), USNM 328258 (4), and UT 91.4426 (4), same data as holotype; INHS 77585 (4), Tennessee, Grundy Co., Caney Fork River system, Collins R. 3.2 km N Tarlton, 35°31.068′N, 85°40.445′W; UMMZ 187464 (1) and UMMZ 187465 (22), Tennessee, Grundy Co., Caney Fork River system, Collins R. along TN Hwy 56, 1.6 km S Tarlton, 35°28.785′N, 85°38.927′W.

Non-type material.—Tennessee. Collins River system. Grundy Co.: UMMZ 175293 (6), Collins R. 3.2 km N Tarlton, TN Hwy 56; UT 91.4427 (10), Collins R. at TN Hwy 56, 1.2 km E Mt. Olive near Warren Co. line; Warren Co.: UT 91.4175 (1), Collins R. at S terminus of Camp Woodley Rd., 1.8 air km N Grundy Co. line; UAIC 9818.16 (14), 10061.17 (21), Collins R. at mouth of Scott Cr., 13.9 air km SSE McMinnville; UAIC 10106.09 (9), Collins R. along Turners Bend Rd., 0.5 km N Hillis Creek Rd., 1.9 km NE Irving College; UAIC 10105.01 (3), Collins R. at Meyers Cove Rd., 9.4 air km SE McMinnville; UAIC 2539.16 (2), 10107.15 (9), Collins R. at TN Hwy 127, Shellsford, 7.2 km E McMinnville. Rocky River system. Van Buren Co.: UT 91.2362 (6), UAIC 10124.19 (2), Rocky R. at Laurelburg Rd. ford, second crossing upstream TN Hwy 30; UAIC 10114.15 (7), Rocky R. at old bridge just off Laurelburg Rd., 0.8 km W Laurelburg; TU 30323 (44), UT 91.335 (5), UAIC 10368.01 (5), Rocky R. at TN Hwy 30, 24 km E McMinnville. Calfkiller River system. White Co.: AUM 3221 (10), Town Cr. at W limit of Sparta, US Hwy 70; AUM 3237 (3), Calfkiller R. at US Hwy 70, Sparta. Cane Creek system. Van Buren Co.: UT 91.675 (6), Cane Cr. on Co. Rd. 4251; UAIC 9816.11 (4), 9849.01 (1), Cane Cr. along TN Hwy 285, 2.0 km ESE Lemont Rd. jct., 7.2 km NE Spencer; KU 16380 (9), 4.8 km E Cummingsville. Upper Caney Fork River system. White Co.: UAIC 10060.07 (11), Caney Fork R., 7.2 air km S Lost Creek at unpaved rd., 3.2 river km upstream of bridge at Dodson; UT 91.4428 (11), Caney Fork R., 2.2 air km ESE Dodson, 1.3 river km upstream Dry Cr., 0.6 road km upstream point where unpaved rd. approaches river and turns SE.

Diagnosis.—A species of the subgenus *Doration* as diagnosed by Page (1981) and emended by Bailey and Etnier (1988). Distinguished from all other species of *Doration* by the combination of having completely scaled cheeks (or nearly so); usually complete lateral line; breeding males with intense blue mask of pigment completely covering lower face and operculum, snout, lips, underside of head, and branchiostegal membranes; and breeding males with soft dorsal and anal fins dark gray to black with no orange spots on rays or blue pigment in membranes.

Description.—*Etheostoma akatulo* is a slender, medium-sized species of *Doration* with a moderately produced snout and a long, narrow caudal peduncle. Males average larger than females ($P < 0.05$); largest male 47.6 mm, largest female 45.0 mm. Sexes exhibit dimorphism in 12 of 18 body proportions (Table 1) with males having a longer head, snout, and upper jaw, larger fins, and a deeper and wider body.

Frequency distributions of scale and fin-ray counts appear in Tables 2–8. Usual counts refer to those in more than 85% of specimens. Lateral line complete, or nearly so; lateral scale rows usually 42–48 (39–51). Unpored lateral scales 0 (180 specimens), 1 (15), 2 (3), 3 (4), or 8 (1); $\bar{x} = 0.2$, SD = 0.77. Transverse scale rows usually 11–13 (10–14), modally 12. Scale rows below lateral line usually 6–7 (5–8), modally 6. Scale rows above lateral line usually 4–5 (3–6), modally 4. Caudal peduncle scale rows usually 14–16 (12–18), modally 15. Cheek squamation usually 80–100% (40–100), modally 100%. Opercle squamation 60% (1 specimen), 70 (2), 80 (8), 90 (45), or 100 (147); $\bar{x} = 96.5$, SD = 6.53. Nape squamation 40% (2), 50 (3), 60 (12), 70 (41), 80 (26), 90 (35), or 100 (84); $\bar{x} = 86.0$, SD = 14.87. Belly fully scaled. Breast usually naked, but 89 (44%) of 203 specimens with 1–5 exposed or partly embedded prepectoral scales on one or both sides.

Dorsal-fin spines modally 11 or 12 (10–13). Dorsal soft rays modally 11 (10–12). Principal caudal-fin rays 14 (2 specimens), 15 (154), 16 (38), or 17 (9); $\bar{x} = 15.3$, SD = 0.55. Anal-fin spines 2; anal soft rays modally 8 (7–9). Pectoral-fin rays usually 14–15 (13–15). Branchiostegal rays 6, rarely 5 or 7; membranes narrowly connected.

Frenum absent in 200 (99%) of 203 specimens. Vomerine teeth present; palatine teeth absent in 201 (99%) of 203 specimens. Infraorbital canal uninterrupted with 6 (1 specimen), 7 (11), 8 (176), 9 (14), or 10 (1) pores; $\bar{x} = 8.0$, SD = 0.40. Preoperculomandibular canal pores 8 (1), 9 (28), 10 (169), or 11 (5); $\bar{x} = 9.9$, SD = 0.41. Supratemporal canal

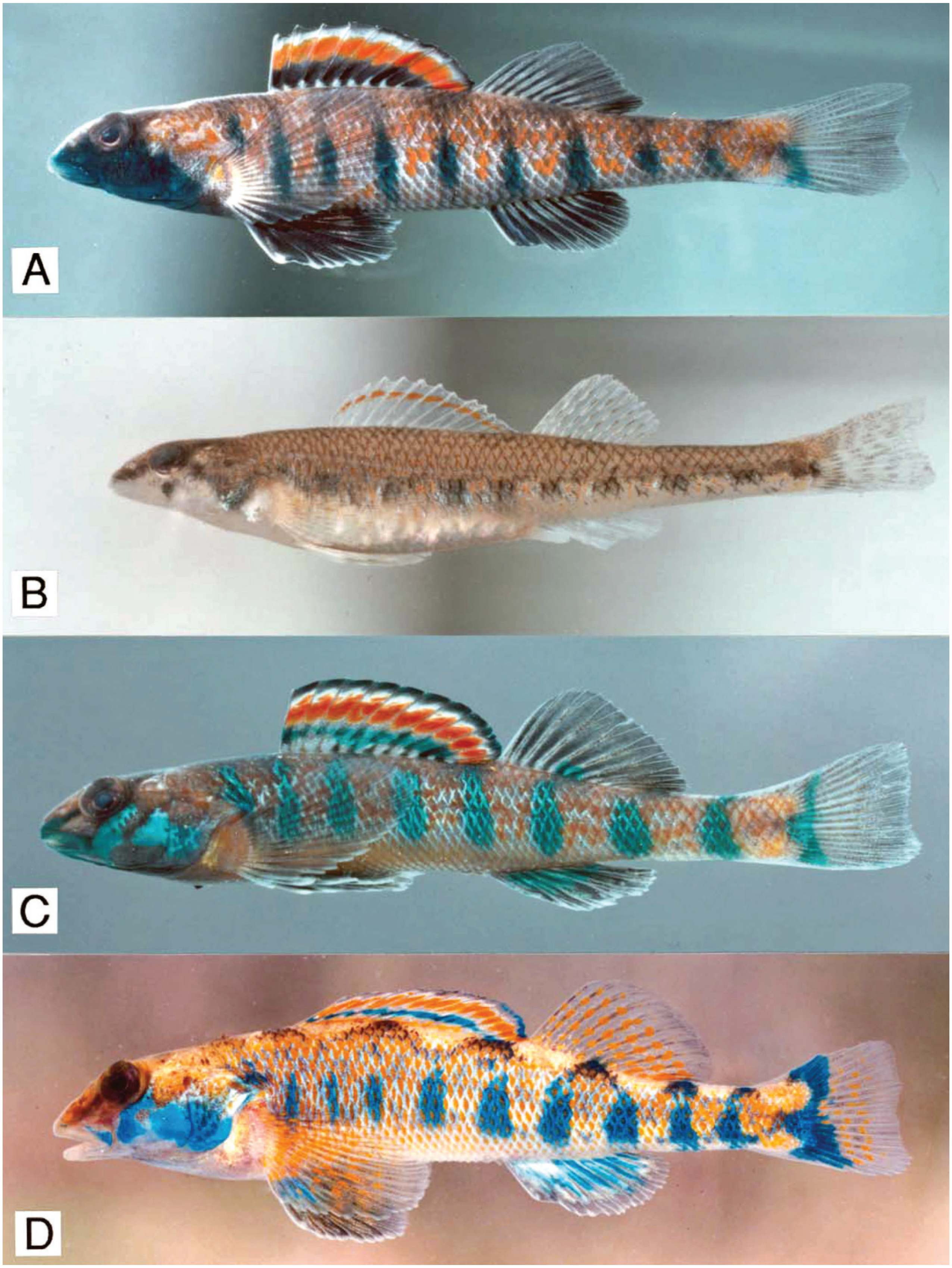

Fig. 1. (A) *Etheostoma akatulo*, UAIC 10382.02, holotype, breeding male, 45.5 mm SL. (B) *Etheostoma akatulo*, UAIC 10382.01, adult female, 41.5 mm SL. (C) *Etheostoma stigmaeum*, UAIC 10791.01, breeding male, 44 mm SL, Alabama, Tuscaloosa Co., Black Warrior River system, Hurricane Creek at US Hwy 11, 5 April 1993. (D) *Etheostoma jessiae*, UAIC 10372.01, breeding male, 59 mm SL, Alabama, Franklin Co., Tennessee River drainage, Little Bear Creek at AL Hwy 187, 8.0 km S Belgreen, 14 March 1992. Photos by S. R. Layman.

Table 1. Measurements in Thousandths of Standard Length for *Etheostoma akatulo*, *E. stigmaeum* from Four Drainages, and *E. jessiae*. D1 = spinous dorsal-fin origin; D2 = soft dorsal-fin origin; P2 = lateral pelvic-fin insertion; A = anal-fin origin. Measurements of *E. akatulo* are from UAIC 10382.01 (19), 9818.16 (10), 10061.17 (5); see Material Examined for museum numbers for *E. stigmaeum* and *E. jessiae*.

	Males (*n* = 17)			Females (*n* = 17)			
Etheostoma akatulo	Mean	Range	SD	Mean	Range	SD	*P*-value
Standard length (mm)	42.0	34.0–47.6	3.6	39.0	30.0–45.0	3.2	0.0145
Head length	272	263–284	5.2	264	252–277	6.0	0.0002
Snout length	78	72–89	4.5	74	67–80	4.1	0.0110
Predorsal length	334	316–355	9.4	333	310–348	9.6	0.5840
Orbit length	62	58–67	2.3	63	58–70	3.4	0.6336
Upper jaw length	79	71–84	3.1	74	68–83	3.5	0.0001
D1 to P2 body depth	167	143–183	10.7	173	160–187	7.4	0.0526
D1 to D2	295	278–309	9.6	297	283–308	8.4	0.6572
Sixth dorsal spine length	118	107–140	7.6	101	69–116	11.9	0.0000
D2 to A body depth	149	130–163	8.3	137	125–149	6.1	0.0000
Soft dorsal-fin base length	156	140–171	9.7	152	139–165	7.9	0.1356
Caudal peduncle length	261	246–280	9.8	255	240–268	8.1	0.0511
Caudal peduncle depth	77	69–84	4.2	74	67–79	3.6	0.0212
Anal-fin base length	131	120–142	6.4	120	109–140	8.3	0.0002
First anal spine length	74	63–93	6.7	68	54–81	6.8	0.0118
Pectoral-fin length	260	246–290	10.9	248	225–270	10.0	0.0022
Pelvic-fin length	213	175–231	12.9	199	188–211	7.5	0.0005
Trans-pelvic width	71	65–82	4.2	65	57–72	4.1	0.0000
Body width	124	111–135	6.9	117	106–127	6.0	0.0018

Etheostoma stigmaeum	Males (*n* = 10)			Females (*n* = 10)			
Mobile Basin (Coosa River)	Mean	Range	SD	Mean	Range	SD	*P*-value
Standard length (mm)	42.0	37.4–48.6	3.4	38.7	33.9–42.0	2.8	0.0299
Head length	282	273–296	7.3	274	265–291	7.5	0.0220
Snout length	82	75–91	4.7	75	67–86	4.8	0.0076
Predorsal length	350	342–359	6.1	343	334–353	6.8	0.0324
Orbit length	68	62–75	3.8	68	66–71	1.7	0.8506
Upper jaw length	86	77–93	4.2	79	73–84	3.5	0.0015
D1 to P2 body depth	185	167–210	12.4	172	160–180	5.6	0.0062
D1 to D2	295	280–308	7.5	291	276–303	8.4	0.3553
Sixth dorsal spine length	122	114–132	6.5	112	105–119	5.2	0.0018
D2 to A body depth	162	149–175	8.0	142	130–148	5.3	0.0000
Soft dorsal-fin base length	159	152–178	8.4	158	149–168	6.9	0.8631
Caudal peduncle length	243	231–256	7.3	251	240–265	8.1	0.0202
Caudal peduncle depth	97	88–104	4.7	90	84–96	3.8	0.0026
Anal-fin base length	130	118–139	6.6	112	102–120	5.6	0.0000
First anal spine length	69	60–81	7.7	64	58–75	5.6	0.0904
Pectoral-fin length	266	241–283	14.2	267	257–287	9.0	0.8479
Pelvic-fin length	226	213–242	8.4	211	183–223	11.9	0.0059
Trans-pelvic width	78	74–83	3.0	73	66–78	4.4	0.0165
Body width	129	117–140	6.2	123	116–130	4.5	0.0338

Etheostoma stigmaeum	Males (*n* = 10)			Females (*n* = 10)			
Duck River	Mean	Range	SD	Mean	Range	SD	*P*-value
Standard length (mm)	39.8	36.1–43.4	2.8	35.6	31.4–39.1	2.1	0.0013
Head length	276	270–284	4.6	267	252–277	8.4	0.0137
Snout length	76	70–82	4.1	72	64–77	4.1	0.0859
Predorsal length	340	330–348	5.0	337	326–353	7.6	0.3316
Orbit length	68	64–71	2.6	67	62–73	3.8	0.5329
Upper jaw length	78	75–82	2.4	71	69–76	2.2	0.0000
D1 to P2 body depth	185	176–191	4.9	183	171–201	8.2	0.6412
D1 to D2	318	308–336	10.0	321	311–332	7.4	0.4010
Sixth dorsal spine length	131	119–147	10.1	117	107–125	5.9	0.0011
D2 to A body depth	157	149–162	3.7	140	121–151	7.9	0.0000
Soft dorsal-fin base length	172	161–180	5.8	166	146–180	9.3	0.0623

Table 1. Continued.

Etheostoma stigmaeum	Males (n = 10)			Females (n = 10)			
Duck River	Mean	Range	SD	Mean	Range	SD	*P*-value
Caudal peduncle length	233	223–248	7.6	232	209–253	12.5	0.7920
Caudal peduncle depth	85	82–91	3.2	80	74–83	2.8	0.0020
Anal-fin base length	157	141–166	8.5	134	124–148	7.3	0.0000
First anal spine length	75	65–86	6.6	69	63–75	3.7	0.0305
Pectoral-fin length	308	287–329	12.2	290	272–319	13.0	0.0054
Pelvic fin length	250	237–262	8.4	227	217–241	8.8	0.0000
Trans-pelvic width	76	70–81	3.5	71	68–77	3.2	0.0021
Body width	135	129–141	4.1	127	117–135	6.4	0.0039

Etheostoma stigmaeum	Males (n = 10)			Females (n = 10)			
Cumberland River (Stones River)	Mean	Range	SD	Mean	Range	SD	*P*-value
Standard length (mm)	38.5	34.4–42.3	2.3	35.8	33.0–39.3	2.2	0.0166
Head length	266	260–282	6.7	261	253–274	6.5	0.0825
Snout length	73	66–80	4.4	71	61–79	5.1	0.4803
Predorsal length	340	327–353	8.1	339	318–351	8.8	0.6350
Orbit length	67	60–71	3.4	65	60–71	3.3	0.2219
Upper jaw length	71	67–75	2.6	68	61–73	3.6	0.0104
D1 to P2 body depth	176	156–187	8.5	178	167–185	5.9	0.8044
D1 to D2	298	286–310	7.5	305	289–321	10.1	0.1277
Sixth dorsal spine length	117	111–125	4.9	109	101–119	6.8	0.0051
D2 to A body depth	156	148–163	5.0	144	135–153	6.9	0.0003
Soft dorsal-fin base length	168	148–191	10.7	161	149–171	8.2	0.1275
Caudal peduncle length	235	221–254	10.1	243	219–263	12.8	0.1299
Caudal peduncle depth	87	82–93	4.2	82	78–87	2.9	0.0130
Anal-fin base length	139	126–152	7.8	128	98–142	12.3	0.0374
First anal spine length	76	65–83	6.0	67	59–77	5.5	0.0043
Pectoral-fin length	302	279–316	11.6	277	254–307	15.3	0.0005
Pelvic-fin length	245	220–263	12.2	220	207–239	11.1	0.0002
Trans-pelvic width	79	69–85	5.1	73	68–79	3.9	0.0098
Body width	127	121–133	4.4	121	117–126	3.3	0.0081

Etheostoma stigmaeum	Males (n = 10)			Females (n = 10)			
Green River (Trammel Fork)	Mean	Range	SD	Mean	Range	SD	*P*-value
Standard length (mm)	42.9	35.9–51.8	4.2	38.2	33.0–41.5	2.6	0.0077
Head length	271	263–280	5.2	263	256–274	5.7	0.0030
Snout length	78	70–86	5.4	73	67–79	4.0	0.0378
Predorsal length	334	325–345	7.5	331	324–343	6.3	0.3328
Orbit length	63	59–68	3.0	65	61–70	2.8	0.1019
Upper jaw length	77	74–81	1.9	70	66–73	2.6	0.0000
D1 to P2 body depth	185	170–197	9.1	189	178–199	7.8	0.2874
D1 to D2	317	302–326	8.5	318	299–239	10.9	0.8166
Sixth dorsal spine length	129	115–138	7.8	118	105–139	10.9	0.0169
D2 to A body depth	155	145–166	6.8	146	140–156	5.3	0.0035
Soft dorsal-fin base length	160	146–181	10.0	156	148–166	5.8	0.2896
Caudal peduncle length	238	227–257	9.3	243	223–252	8.2	0.1607
Caudal peduncle depth	86	82–92	3.0	83	78–90	4.0	0.0549
Anal-fin base length	145	131–161	10.7	124	112–136	7.7	0.0000
First anal spine length	82	76–87	3.5	72	65–79	4.9	0.0001
Pectoral-fin length	296	275–316	12.6	291	275–308	10.3	0.3775
Pelvic-fin length	240	230–257	7.1	229	219–243	8.8	0.0067
Trans-pelvic width	77	71–83	3.3	73	68–78	3.4	0.0061
Body width	135	126–140	4.6	129	120–143	7.0	0.0301

Table 1. Continued.

Etheostoma jessiae	Males (*n* = 10) Mean	Range	SD	Females (*n* = 10) Mean	Range	SD	*P*-value
Standard length (mm)	48.8	36.9–57.7	6.7	46.4	36.4–51.7	4.6	0.3571
Head length	288	278–308	9.1	276	263–290	7.1	0.0047
Snout length	86	80–94	4.1	79	72–85	4.1	0.0009
Predorsal length	354	342–373	9.4	347	337–356	6.4	0.0634
Orbit length	65	58–75	4.4	64	57–70	3.7	0.4696
Upper jaw length	87	81–95	4.2	81	71–90	5.7	0.0216
D1 to P2 body depth	187	171–203	10.8	180	165–206	11.3	0.2049
D1 to D2	308	291–326	12.2	313	290–336	13.9	0.3475
Sixth dorsal spine length	124	113–133	7.6	104	92–118	9.1	0.0001
D2 to A body depth	150	137–163	9.2	141	134–147	4.2	0.0100
Soft dorsal-fin base length	170	166–177	4.1	167	150–178	8.2	0.3173
Caudal peduncle length	219	209–234	8.0	221	210–240	8.7	0.6226
Caudal peduncle depth	89	85–94	2.9	85	83–89	1.7	0.0049
Anal-fin base length	146	134–170	11.3	132	123–144	6.7	0.0022
First anal spine length	75	65–85	6.3	62	55–71	5.4	0.0001
Pectoral-fin length	267	233–282	14.5	256	234–295	20.0	0.1769
Pelvic-fin length	227	194–249	14.0	204	184–230	13.1	0.0017
Trans-pelvic width	77	70–81	3.3	71	65–77	4.1	0.0025
Body width	134	124–146	7.0	125	111–136	8.6	0.0197

uninterrupted with 3 pores, occasionally interrupted. Lateral canal pores 5, supraorbital canal pores 4, coronal pore single.

Males ($n = 120$) and females ($n = 83$) differed significantly ($P < 0.05$) in the mean number of principal caudal-fin rays. Males have a slightly higher mean number of rays (15.4) than females (15.1).

Male breeding coloration.—Color descriptions of live and freshly preserved breeding adults are based on April 1990–1992 collections from Collins River, Cane Creek, and upper Caney Fork River. Breeding males (Fig. 1) with conspicuous spinous dorsal-fin banding: very thin gray to black marginal band, darkest in posterior third of fin; narrow white to clear submarginal band; wide red-orange medial band; wide black submedial band, sometimes with narrow pale zone between it and red-orange band above; and narrow clear basal band with black pigment extending vertically through posterior portions of membranes connecting submedial band above to base of fin (clear areas may appear as windows). Soft dorsal-fin membranes black in basal half with pigment concentrated in centers of membranes and clear areas bordering rays; distal portion evenly dusky gray. Soft dorsal rays with scattered dark pigment. Caudal-fin membranes clear basally to dusky in distal third; rays with scattered melanophores, many at segment junctions. Blue bar or wedge on base of caudal fin extending ventroposteriorly from two small dark spots at medial fin base (sometimes obscured by blue and dusky pigment) to ventral edge of fin. Anal-fin membranes dark gray to black with clear areas bordering rays in basal half; rays paler than membranes. Pelvic-fin membranes black, rays dusky. Pectoral fin clear to dusky with pale streaks of orange-yellow at base of rays.

Intense blue mask of pigment completely covering entire lower head of breeding males from middle of eye ventrad, including snout, lips, lower three-fourths of cheek, lower

Table 2. Lateral Scale Row Counts in *Etheostoma akatulo*, *E. stigmaeum* from Four Drainages, and *E. jessiae*. Value for holotype is in boldface.

	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	*n*	Mean	SD
Etheostoma akatulo																									
Collins River				6	**16**	14	24	18	12	14	3	2											109	45.4	1.94
Rocky River	1	1	1	4	7	9	10	10	3	1	1		1										49	44.6	2.16
Calfkiller River				1				1	3		3	1											9	47.3	2.40
Cane Creek				1		5	6	3	3		1	1											20	45.5	1.85
Upper Caney Fork River					2		7	1	4	2													16	45.7	1.54
Totals	1	1	1	12	25	28	47	33	25	17	8	4	1										203		
Etheostoma stigmaeum																									
Mobile Basin				3	3	6	5	9	8	8	10	9	11	4	3	1							80	48.0	2.95
Duck River				2	3	1	8	15	7	12	8	3	1										60	46.8	2.00
Cumberland River		2	1	7	8	11	12	13	11	9	3	5											82	45.5	2.40
Green River		1	2	6	6	9	9	9	8	3	4	3											60	45.2	2.43
Totals		3	3	18	20	27	34	46	34	32	25	20	12	4	3	1							282		
Etheostoma jessiae				1		2	1	2	3	3	13	19	9	12	16	6	6	4	1	1		1	100	51.2	3.01

Table 3. Transverse Scale Row Counts in *Etheostoma akatulo*, *E. stigmaeum* from Four Drainages, and *E. jessiae*. Count for holotype is in boldface.

	10	11	12	13	14	15	16	17	18	*n*	Mean	SD
Etheostoma akatulo												
Collins River	9	26	**67**	6	1					109	11.7	0.75
Rocky River		3	16	21	9					49	12.7	0.84
Calfkiller River			5	4						9	12.4	0.53
Cane Creek			10	7	3					20	12.7	0.75
Upper Caney Fork River	1		9	4	2					16	12.4	0.96
Totals	10	29	107	42	15					203		
Etheostoma stigmaeum												
Mobile Basin		2	11	31	21	12	3			80	13.5	1.10
Duck River		4	31	20	4	1				60	12.5	0.79
Cumberland River		5	39	23	14	1				82	12.6	0.89
Green River		8	31	17	3		1			60	12.3	0.89
Totals		19	112	91	42	14	4			282		
Etheostoma jessiae			5	14	35	26	14	4	2	100	14.5	1.27

Table 4. Counts of Scale Rows below and Scale Rows above Lateral Line in *Etheostoma akatulo*, *E. stigmaeum* from Four Drainages, and *E. jessiae*. Values for holotype are in boldface.

	Scale rows below lateral line									Scale rows above lateral line							
	5	6	7	8	9	10	*n*	Mean	SD	3	4	5	6	7	*n*	Mean	SD
Etheostoma akatulo																	
Collins River	13	**87**	9				109	6.0	0.45	2	**70**	34	3		109	4.3	0.57
Rocky River	1	23	21	4			49	6.6	0.68		21	26	2		49	4.6	0.57
Calfkiller River		6	3				9	6.3	0.50		2	7			9	4.8	0.44
Cane Creek		10	10				20	6.5	0.51		10	10			20	4.5	0.51
Upper Caney Fork River	1	9	6				16	6.3	0.60		10	5	1		16	4.4	0.63
Totals	15	135	49	4			203			2	113	82	6		203		
Etheostoma stigmaeum																	
Mobile Basin	1	17	43	16	3		80	7.0	0.79	1	20	42	17		80	4.9	0.72
Duck River		39	20	1			60	6.4	0.52		18	38	4		60	4.8	0.56
Cumberland River		45	32	5			82	6.5	0.61	2	39	41			82	4.5	0.55
Green River	9	38	12	1			60	6.1	0.65		10	47	3		60	4.9	0.45
Totals	10	139	107	23	3		282			3	87	168	24		282		
Etheostoma jessiae		10	43	38	7	2	100	7.5	0.85			31	57	12	100	5.8	0.63

Table 5. Caudal Peduncle Scale Row Counts in *Etheostoma akatulo*, *E. stigmaeum* from Four Drainages, and *E. jessiae*. Count for holotype is in boldface.

	12	13	14	15	16	17	18	19	20	21	*n*	Mean	SD
Etheostoma akatulo													
Collins River	1	10	31	**62**	5						109	14.6	0.76
Rocky River				10	24	14	1				49	16.1	0.75
Calfkiller River				4	5						9	15.6	0.53
Cane Creek				8	10	2					20	15.7	0.66
Upper Caney Fork River				5	10		1				16	15.8	0.75
Totals	1	10	31	89	54	16	2				203		
Etheostoma stigmaeum													
Mobile Basin			2	7	35	28	6	2			80	16.4	0.94
Duck River				3	29	19	8	1			60	16.6	0.85
Cumberland River		1	8	22	39	9	3				82	15.7	0.97
Green River		1	9	7	42	1					60	15.6	0.83
Totals		2	19	39	145	57	17	3			282		
Etheostoma jessiae				1	15	19	37	18	9	1	100	17.9	1.23

Table 6. Percent Cheek Squamation in *Etheostoma akatulo*, *E. stigmaeum* from Four Drainages, and *E. jessiae*. Value for holotype is in boldface.

	0	10	20	30	40	50	60	70	80	90	100	*n*	Mean	SD
Etheostoma akatulo														
Collins River									3	30	**76**	109	96.7	5.28
Rocky River					2	3	1	3	13	13	14	49	83.9	16.31
Calfkiller River								1	1	6	1	9	87.8	8.33
Cane Creek						2	1	1	5	5	6	20	84.0	16.03
Upper Caney Fork River								1	7	8		16	84.4	6.29
Totals					2	5	2	6	29	62	97	203		
Etheostoma stigmaeum														
Mobile Basin	15	7	20	20	4	7	5	2				80	25.3	18.62
Duck River	4	15	25	14	2							60	19.2	9.44
Cumberland River	46	27	9									82	5.5	6.88
Green River	41	15	4									60	3.8	6.13
Totals	106	64	58	34	6	7	5	2				282		
Etheostoma jessiae	1	14	47	31	5	2						100	23.1	8.84

Table 7. Dorsal Spine and Soft Ray Counts in *Etheostoma akatulo*, *E. stigmaeum* from Four Drainages, and *E. jessiae*. Counts for holotype are in boldface.

	Dorsal spines								Dorsal soft rays						
	10	11	12	13	14	*n*	Mean	SD	10	11	12	13	*n*	Mean	SD
Etheostoma akatulo															
Collins River	8	**63**	36	2		109	11.3	0.63	5	80	**24**		109	11.2	0.49
Rocky River		9	36	4		49	11.9	0.51	13	33	3		49	10.8	0.54
Calfkiller River		4	5			9	11.6	0.53	3	5	1		9	10.8	0.67
Cane Creek	1	9	9	1		20	11.5	0.69	4	11	5		20	11.1	0.69
Upper Caney Fork River	1	8	6	1		16	11.4	0.73		13	3		16	11.2	0.40
Totals	10	93	92	8		203			25	142	36		203		
Etheostoma stigmaeum															
Mobile Basin	5	46	27	2		80	11.3	0.63	14	56	10		80	11.0	0.55
Duck River		4	26	26	4	60	12.5	0.72	1	27	32		60	11.5	0.54
Cumberland River	1	36	43	2		82	11.6	0.57	5	48	29		82	11.3	0.58
Green River		1	23	34	2	60	12.6	0.58	2	39	18	1	60	11.3	0.56
Totals	6	87	119	64	6	282			22	170	89	1	282		
Etheostoma jessiae	1	5	47	46	1	100	12.4	0.65	1	18	72	9	100	11.9	0.55

Table 8. Anal Soft Ray and Left Pectoral Ray Counts in *Etheostoma akatulo*, *E. stigmaeum* from Four Drainages, and *E. jessiae*. Counts for holotype are in boldface.

	Anal soft rays								Left pectoral rays						
	5	7	8	9	10	*n*	Mean	SD	13	14	15	16	*n*	Mean	SD
Etheostoma akatulo															
Collins River		6	**91**	12		109	8.1	0.40		39	**70**		109	14.6	0.48
Rocky River		7	38	4		49	7.9	0.47	2	20	27		49	14.5	0.58
Calfkiller River		2	5	2		9	8.0	0.71	1	7	1		9	14.0	0.50
Cane Creek		3	15	2		20	8.0	0.51		9	11		20	14.6	0.51
Upper Caney Fork River		1	11	4		16	8.2	0.54		6	10		16	14.6	0.50
Totals		19	160	24		203			3	81	119		203		
Etheostoma stigmaeum															
Mobile Basin		10	54	16		80	8.1	0.57	24	49	7		80	13.8	0.59
Duck River			11	42	7	60	8.9	0.55	1	26	31	2	60	14.6	0.59
Cumberland River	1	1	43	34	3	82	8.4	0.70	7	60	15		82	14.1	0.51
Green River		1	31	28		60	8.5	0.53		22	38		60	14.6	0.49
Totals	1	12	139	120	10	282			32	157	91	2	282		
Etheostoma jessiae		1	22	65	12	100	8.9	0.61	1	37	55	7	100	14.7	0.62

half of operculum, underside of head, gular area, branchiostegal membranes, and often the anterior portion of breast; shade of blue varying from bright cobalt or royal to almost navy. Breast dark gray to black, belly and lower body dusky gray. Base color of upper body straw to olivaceous. Sides with usually 8–9 (7–11) cobalt or royal to dark blue vertical bars extending from humeral area to caudal peduncle (not including basicaudal bar). Anterior lateral bars more vertically elongate, extending from just above belly to dorsolateral area, making indistinct connections with lateral edges of dorsal saddles. Posterior lateral bars more quadrate and usually not extending above lateral line; posterior two bars may nearly encircle the caudal peduncle ventrally. Dusky blotch often present on body just anterior to basicaudal spots. Scales between lateral bars outlined in powder blue and forming crosshatched pattern. Sides with red-orange spots and X-markings between lateral bars and extending to dorsum and upper operculum; spots often coalescent, appearing as fiery red splotches. Dorsolateral area also with small scattered dark markings. Dorsum with six dark saddles, quadrate to somewhat medially constricted; often irregular in shape. First saddle located anterior to spinous dorsal fin, may be fainter and less discrete than others; second saddle slightly anterior to middle of spinous dorsal fin; third saddle at posterior end of spinous dorsal fin; fourth saddle at middle of soft dorsal fin; fifth saddle behind soft dorsal fin; sixth saddle at dorsal insertion of caudal fin. Entire body dusky, covered with tiny melanophores. Genital papilla a small dusky conical flap.

Howell (1968) described a submedial blue band and narrow basal orange band in the spinous dorsal fin of breeding males, but in live and freshly preserved nuptial specimens we observed the submedial band was always gray to black and the basal band was never orange. He remarked that the species has basically the same breeding color pattern as *E. jessiae*, except that *E. jessiae* has orange spots on the fins. Although it is true that *E. jessiae* has orange spots on the soft dorsal, caudal, and pectoral fins and *E. akatulo* does not, there are other conspicuous differences in breeding coloration between *E. akatulo* and *E. jessiae* (Fig. 1, Table 9). Most notably, *E. akatulo* has an entirely blue face and lacks blue pigment in the base of the soft dorsal and anal fins.

Female breeding coloration.—Coloration of breeding females of *E. akatulo* is more subdued than in males. Spinous dorsal fin with faint dusky marginal band, narrow clear submarginal band, narrow orange medial band, and broad clear basal zone; spines with scattered dark pigment. Soft dorsal-fin membranes clear; rays with 2–3 brown dashes. Caudal-fin membranes clear; rays with 4–5 brown dashes, often faint. Two small, vertically aligned, closely spaced dark spots on medial base of caudal fin, sometimes appearing fused. Anal-fin membranes clear; rays with faint dusky streaks. Pelvic-fin membranes clear; rays with tinge of yellow-orange and a few dark dashes or specks. Pectoral fins mostly clear with yellow-orange hue basally; rays with a few dark dashes or specks.

Cheeks, lips, underside of head, breast, belly, and lower sides white. Operculum and sometimes upper cheek with tinge of purple-blue. Head with dark preorbital bars extending onto upper lip but not meeting, dark suborbital bar or spot, and dark postorbital spot. Sides with usually 8–9 quadrate blotches (including humeral blotch) extending from lateral line ventrad 2–3 scale rows, formed by crosshatching of dark pigment along edges of scales (W-, V-, and X-markings); blotches with tinge of blue. Small dark X-markings also may occur between lateral blotches near ventral edges. Belly with faint yellow-orange iridescence laterally. Midlateral scales sometimes with tinge of powder blue along edges. Base color of upper body straw to beige, scales with small melanophores along edges, imparting overall sandy appearance. Sides and upper body also with scattered orange and dark brown markings. Dorsum with six quadrate saddles as described for males but usually more regular in shape; first saddle typically fainter and less discretely formed than others. All saddles may be faint, with dorsum nearly uniformly sand-colored. Genital papilla a long, pale, conical tube.

Nonbreeding coloration.—Sexual dichromatism is less pronounced in nonbreeding adults. Live nonbreeding males lack intense blue mask, blue lateral bars, blue basicaudal bar, conspicuous lateral red-orange splotches, and overall coverage with tiny melanophores. Red-orange medial band of spinous dorsal fin conspicuous but submedial band tending toward dusky gray rather than black. Second dorsal, anal, and pelvic fins dusky gray rather than black. Head with dark preorbital and suborbital bars and postorbital spot as described for females above; operculum and upper cheek with tinge of blue. Face, underside of head, and breast white; as the spawning season approaches, scattered melanophores appear and increase in density on these areas. Belly and lower sides white to light straw. Lateral blotches and dorsal body as described for females above. Coloration of live nonbreeding females similar to breeding females above with reduced intensity or absence of orange band in spinous dorsal fin and blue pigment lacking on lateral blotches and operculum.

Coloration in preservative.—In preservative, the blue pigment of breeding males fades quickly, and the heavily melanized face and lateral bars appear black. The lateral red-orange spots fade, and the red-orange band in the spinous dorsal fin turns pale brown. Most other aspects of pigmentation in breeding and nonbreeding specimens are retained.

Tuberculation.—Breeding males may develop low, crescent-shaped tubercles along posterior edges of ventral body scales. At maximum development, tubercles are present on belly scales from pelvic-fin bases to anus, scales along anal-fin base, and ventral caudal peduncle scales; development weakest on latter two regions. Tubercles occur on two midventral scale rows behind pelvic-fin bases, 5–6 midventral scale rows at mid-belly, 4–5 midventral scale rows at anus, 1–2 scale rows above anal-fin base, and 2–3 midventral scale rows on caudal peduncle. Most males with tubercles only on posterior three-fourths of belly.

Breeding males also may develop epidermal ridges on pelvic- and anal-fin rays. Pelvic spine with overall thickened epidermis; narrow ridges on ventral surfaces of rays 1–2 or 1–3, often extending entire length of element and ending in small fleshy tip. Rays 3–5 with weaker, broken ridges and occasional weak, individual projections. Anal spine and usually all but last anal ray with narrow ridges on basal three-fourths to entire length of element; more weakly developed posteriorly. Although the ridge surfaces are not rough in texture, they may contain keratin and possibly

Table 9. Characteristics Useful in Distinguishing *Etheostoma akatulo*, Nominal *Etheostoma stigmaeum* from Four Drainages, and *Etheostoma jessiae*.

		Nominal *E. stigmaeum* complex				
	E. akatulo	Mobile Basin	Duck R.	Cumberland R.	Green R.	*E. jessiae*
Frenum	absent	absent	absent	absent	absent	present
Usual number lateral scale rows	42–48	44–52	45–50	42–48	42–49	49–56
Mean number unpored lateral scales	0.2	13.8	14.6	11.2	15.4	7.5
Modal percent cheek squamation	100	20 or 30	20	0	0	20
Modal number caudal peduncle scales	15	16	16	16	16	18
Modal number scales above lateral line	4	5	5	5	5	6
Palatine teeth	absent	present	sometimes	absent	absent	present
Breeding males:						
Face coloration	entirely blue	gray with blue-green	orange with blue	orange with blue	orange with blue	gray with blue
Orange spots on soft-dorsal, caudal, and pectoral-fin rays	absent	absent	present	present	present	present
Blue in base of soft-dorsal and anal fins	absent	present	present	present	absent	present
Spinous dorsal-fin marginal and submedial bands	black	blue-green	blue	blue	black	blue
Orange in spinous dorsal-fin basal band	absent	absent	present	present	present	present
Orange spots on anal-fin rays	absent	absent	sometimes	present	present	absent

function like breeding tubercles in providing a frictional surface.

Comparisons.—*Etheostoma akatulo* is the only species of *Doration* having a usually complete lateral line, fully scaled cheeks (or nearly so; Table 6), breeding males with bright blue pigment completely covering the lower face and underside of the head, and breeding males with soft dorsal and anal fins lacking both orange and blue pigment (Table 9, Fig. 1). The new species differs further from *E. jessiae* in consistently lacking a frenum and palatine teeth, having usually 42–48 lateral scale rows (88% of *jessiae* have 49 or more), modally 15 caudal peduncle scale rows (vs. 18), modally 12 transverse scale rows (vs. 14), modally 6 scale rows below the lateral line (vs. 7), modally 4 scale rows above the lateral line (vs. 6), modally 11 soft dorsal rays (vs. 12), and modally 8 anal soft rays (vs. 9; Tables 2–5, 7–8). It differs from Mobile Basin and Duck River forms of *E. stigmaeum* and nominate *E. meadiae* in consistently lacking palatine teeth (palatine teeth present in 85% of Mobile Basin specimens, 25% of Duck River specimens, and 33% of *E. meadiae* specimens). It differs from *E. jessiae* and Duck, Cumberland, and Green river forms of *E. stigmaeum* in breeding males lacking bright orange pigment in the base of the spinous dorsal fin (Table 9). It differs further from *E. jessiae*, *E. meadiae*, and Mobile, Duck, and Cumberland River forms of *E. stigmaeum* in breeding males lacking blue or blue-green pigment in the marginal and submedial bands of the spinous dorsal fin and having a blue or blue-green basicaudal bar mainly developed ventrally and not extending to the dorsal margin of the caudal fin. Prepectoral scales are present in 44% of *E. akatulo* specimens vs. 0–20% of specimens in other *Doration* taxa.

Species of *Doration* are morphologically very similar. Proportional measurements (Table 1) indicate that *E. akatulo* has moderate head and snout length, narrower body depth at the spinous dorsal-fin origin in males, a longer and narrower caudal peduncle, and relatively short pectoral fins compared to other species of *Doration*.

Principal component analysis reveals that the overall variation in 17 meristic variables (sexes combined) largely distinguishes *E. akatulo* from other species of *Doration* (Fig. 2A). Principal component one (PC-I) completely separates *E. akatulo* from *E. jessiae*. Variables loading heavily on PC-I include body scale row counts (positive loading) and percent cheek squamation (negative loading), such that individuals with higher scale counts have higher scores along the axis and individuals with greater cheek squamation have lower scores (Table 10). PC-II largely separates *E. akatulo* from Mobile Basin *E. stigmaeum*. Variables loading heavily on PC-II include nape and belly squamation and pectoral-fin rays (Table 10).

Mensural data (Table 1) indicate that *E. akatulo* has a moderate head and snout length, narrower body depth at the spinous dorsal-fin origin in males, a longer and narrower caudal peduncle, and relatively short pectoral fins compared to other species of *Doration*. Sheared principal component analysis of 28 morphometric variables indicates that *E. akatulo* males largely can be distinguished from males of other species of *Doration* on the basis of overall shape differences (Fig. 2B). *Etheostoma akatulo* is completely separated from all forms of nominate *E. stigmaeum* in the plot of sheared PC-II versus sheared PC-III (Fig. 2B); furthermore, this analysis also provides considerable evidence for morphometric separation between *E. akatulo* and *E. jessiae*. Variables loading most heavily on sheared PC-II include snout, upper jaw, and caudal peduncle length, pectoral- and pelvic-fin length, anal-fin base length, and first anal-spine length (Table 11). Variables with the highest absolute loadings on sheared PC-III include first anal spine length and caudal peduncle length and depth. Sheared principal component analysis of mensural data for females reveals a similar trend in shape differentiation but with less overall separation as compared to males. Females of *E. akatulo* are completely separated from *E. stigmaeum* of the Mobile Basin and Duck and Green rivers, but display considerable overlap with *E. jessiae* in sheared PC-II vs. sheared PC-III (Fig. 2C, Table 11).

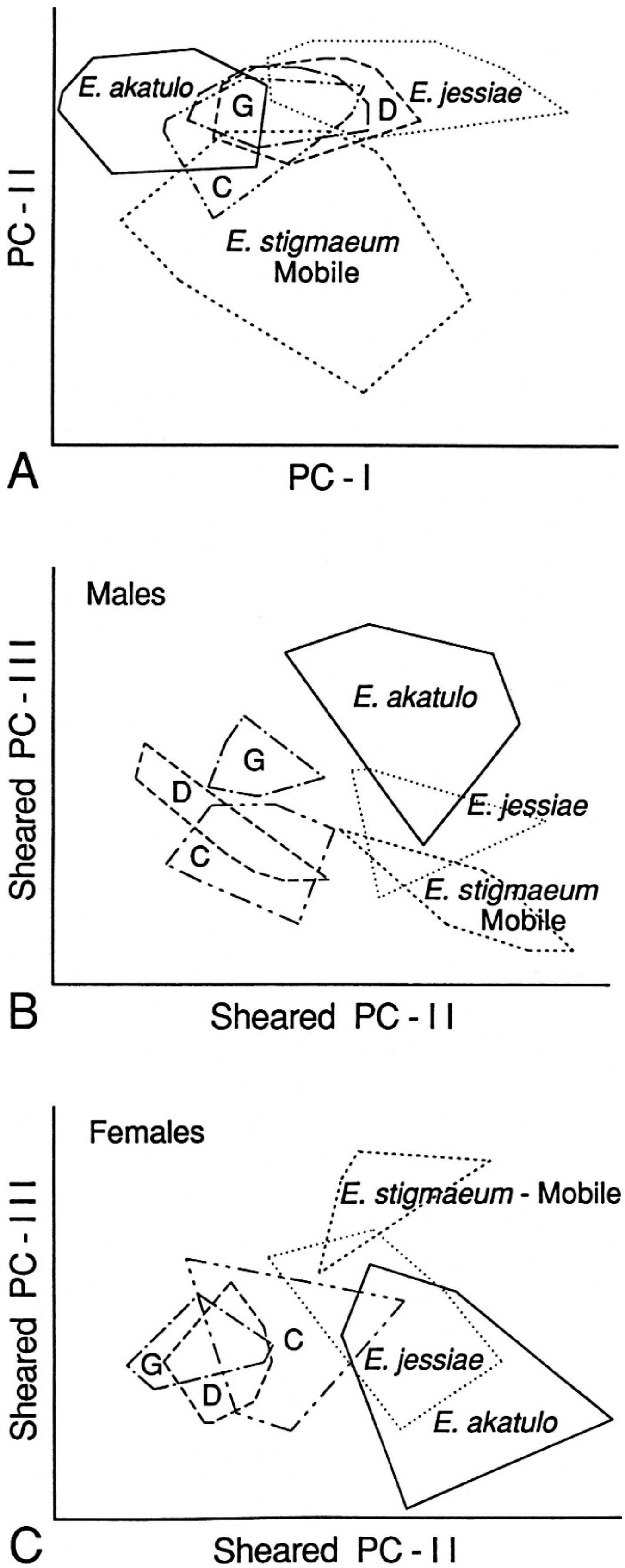

Fig. 2. Plots of principal component (PC) scores for *Etheostoma akatulo*, *E. stigmaeum* from Mobile Basin, Duck River (=D), Cumberland River (=C), and Green River (=G), and *E. jessiae*. (A) Plot of meristic PC-I and PC-II. (B) Plot of morphometric sheared PC-II and PC-III for males. (C) Plot of morphometric sheared PC-II and PC-III for females. Polygons bound all individuals.

Table 10. Principal Component Loadings for 17 Meristic Variables in 585 Specimens of *Etheostoma akatulo*, *E. stigmaeum* from Four Drainages, and *E. jessiae*.

	Principal component	
Variable	I	II
Dorsal-fin spines	0.414	0.260
Dorsal-fin rays	0.429	0.485
Principal caudal-fin rays	−0.078	0.127
Anal-fin rays	0.532	0.361
Pectoral-fin rays	−0.025	0.636
Lateral scale rows	0.678	0.081
Unpored lateral scale rows	0.536	−0.336
Transverse scale rows	0.802	−0.081
Scale rows below lateral line	0.714	−0.141
Scale rows above lateral line	0.687	0.118
Caudal peduncle scale rows	0.808	0.017
Percent cheek squamation	−0.671	0.240
Percent nape squamation	−0.012	0.857
Percent belly squamation	−0.117	0.810
Percent opercle squamation	−0.512	0.049
Infraorbital canal pores	0.044	−0.004
Preoperculomandibular canal pores	0.079	0.075

Distribution and habitat.—*Etheostoma akatulo* is known from five small rivers and large creeks of the upper Caney Fork River system, Tennessee, including Collins River, Rocky River, Calfkiller River, Cane Creek, and upper Caney Fork River (Fig. 3). All five streams originate on the Cumberland Plateau physiographic province and flow through the eastern Highland Rim physiographic province into Great Falls Reservoir, which was filled in 1916. All records of *E. akatulo* are from lower free-flowing reaches of these streams on the Highland Rim, extending downstream to the backwaters of Great Falls Reservoir.

Based on a 1990–1992 status survey, the Bluemask Darter presently persists in Collins River, Rocky River, Cane Creek, and upper Caney Fork River (Layman et al., 1993; Fig. 3). The species was not detected in the Calfkiller River system, where it was last collected twice in 1968 in the town of Sparta.

Etheostoma akatulo occurs in slow to moderate current over sand and fine gravel at depths of 10–50 cm, typically just downstream of riffles, in runs, or along margins of pools (Layman et al., 1993). Breeding males collected in April at the type locality were most abundant in gravelly runs, and breeding females were more common in slower water over sandier substrates adjacent to runs. Simmons and Layzer (2004) observed Bluemask Darters spawning in May and June in gravelly runs, burying their eggs in small sand patches among the gravel (Simmons and Layzer, 2004), similar to the behavior of *E. stigmaeum* in aquaria (Green River form; Winn, 1958). After the spawning period, Bluemask Darters move to sandy substrates in low-velocity areas of intermediate depth (Layzer and Brady, 2003). Headwaters of the four streams occupied by the Bluemask Darter descend the Cumberland Plateau through subterranean channels and emerge from springs on the Highland Rim. During summer and other low-flow periods, upper portions of the main channels, which may exceed 30 m width, convey little to no surface flow, thereby limiting perennial habitat for the species mainly to reaches below springs.

Table 11. Sheared Principal Component (PC) Loadings for 28 Morphometric Measurements in 134 Specimens of *Etheostoma akatulo*, *E. stigmaeum* from Four Drainages, and *E. jessiae*. D1 = spinous dorsal-fin origin; D2 = soft dorsal-fin origin; IOW = midline at least interorbital width; P2 = lateral pelvic-fin insertion; A = anal-fin origin.

	Males (n = 67)			Females (n = 67)		
		Sheared PC			Sheared PC	
Measurement	Size	II	III	Size	II	III
Standard length	0.171	0.086	0.144	0.178	0.138	−0.085
Head length	0.165	0.159	0.060	0.172	0.150	0.062
Snout length	0.190	0.358	0.086	0.212	0.237	−0.012
Orbit length	0.145	0.059	−0.195	0.162	0.034	0.213
Upper jaw length	0.201	0.352	0.033	0.220	0.310	0.222
Predorsal length	0.177	0.132	0.019	0.180	0.144	0.023
D1 to occiput	0.192	0.061	−0.144	0.208	0.237	0.034
Occiput to snout	0.162	0.137	−0.011	0.169	0.110	0.034
Occiput to IOW	0.158	0.052	−0.064	0.152	0.000	0.165
IOW to snout	0.186	0.169	0.019	0.181	0.123	−0.055
P2 to snout	0.174	−0.012	−0.060	0.187	0.048	0.108
Occiput to P2	0.221	−0.050	−0.086	0.202	−0.131	0.007
D1 to P2	0.243	−0.041	−0.155	0.219	−0.115	−0.151
D1 to D2	0.187	−0.107	0.159	0.185	−0.074	−0.235
D1 to A	0.197	−0.019	0.054	0.209	−0.001	−0.115
P2 to A	0.194	0.079	−0.006	0.194	0.095	−0.077
D2 to P2	0.194	−0.046	0.020	0.193	0.055	−0.166
D2 to A	0.230	0.028	−0.100	0.216	−0.012	0.024
Soft dorsal-fin base length	0.187	−0.099	−0.067	0.205	−0.004	−0.086
Caudal peduncle depth	0.193	0.127	−0.472	0.169	−0.036	0.403
Caudal peduncle length	0.157	0.314	0.451	0.166	0.339	−0.002
Anal-fin base length	0.203	−0.344	0.071	0.174	−0.158	−0.530
First anal spine length	0.177	−0.283	0.558	0.154	−0.086	−0.417
Pectoral fin length	0.180	−0.385	−0.078	0.192	−0.365	0.112
Pelvic fin length	0.167	−0.326	−0.165	0.162	−0.269	0.076
Trans-pelvic width	0.210	−0.104	−0.116	0.221	−0.189	0.191
Sixth dorsal spine length	0.178	−0.151	0.185	0.174	−0.489	0.211
Body width	0.215	−0.063	0.048	0.202	−0.141	0.029

The Bluemask Darter is most abundant and widely distributed in Collins River, where it occurs in a 37-km reach between Shellsford, Warren Co., and Tennessee Highway 56, 1.2 km east of Mt. Olive, Grundy Co. (Fig. 3). In Rocky River, the species inhabits only a 4.3-km reach from Tennessee Highway 30 upstream to Laurelburg Road ford, Van Buren Co., including a 1.7-km reach that alternates between backwater and free-flowing conditions as Great Falls Reservoir fluctuates between maximum (244 m) and minimum (240 m) pool elevations (Layman

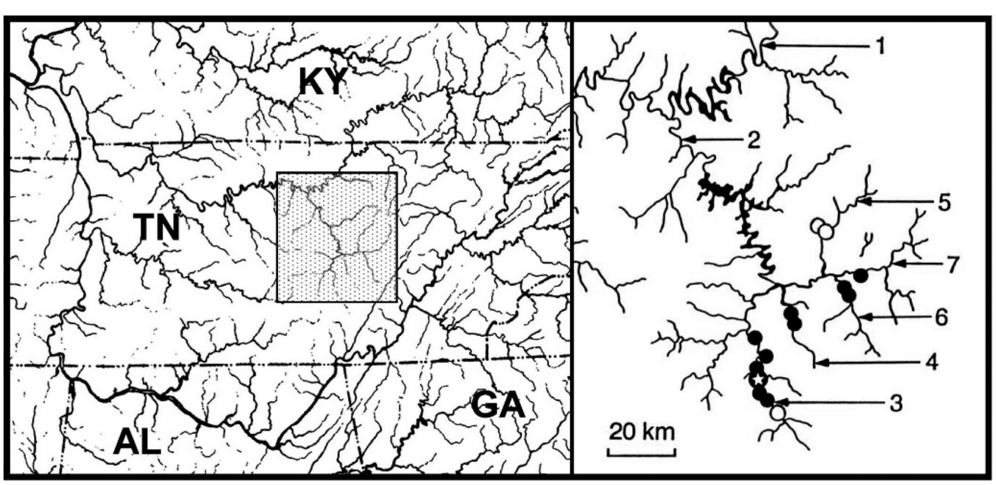

Fig. 3. Distribution of *Etheostoma akatulo*. Inset of Caney Fork River system enlarged on right. Type locality indicated by dot with star. It and solid dots represent current distribution. Open circles represent historic localities. 1–Cumberland River; 2–Caney Fork River; 3–Collins River; 4–Rocky River; 5–Calfkiller River; 6–Cane Creek; 7–upper Caney Fork River.

et al., 1993). In Cane Creek, recent collections are from the lower 200 m of free-flowing waters in Van Buren Co. In upper Caney Fork River, the species has been collected in an intermittent reach located only 1.8 river km upstream of reservoir maximum pool in White Co. The species also possibly uses portions of the reservoir fluctuation zones in Cane Creek and Caney Fork River, depending on the occurrence of sufficient current velocities or spring inflow to moderate silt deposition.

Etheostoma akatulo is restricted in distribution to the Caney Fork River system in free-flowing streams upstream of Great Falls. All four extant populations apparently are isolated from one another by the impounded waters of Great Falls Reservoir. Other darters endemic to Caney Fork River above Great Falls are *E. etnieri*, *E. forbesi*, and *E. basilare*.

Conservation.—*Etheostoma akatulo* is federally endangered. Existing and potential threats to continued survival of the species include habitat destruction from gravel dredging, which has already eliminated habitat once occupied by the species in Collins River; pesticides in runoff or groundwater from plant nurseries; siltation from gravel mining, agricultural runoff, or land-disturbing activities; and acid mine drainage from headwater streams (Layman et al., 1993). Water quality degradation, siltation, and low-head main-channel impoundments may have contributed to decline of the population in Calfkiller River. Gravel dredging has extensively altered an intermittent upper reach of Collins River at Tennessee Highway 56, 1.6 km south of Tarlton, Grundy Co., a site where 23 Bluemask Darters were collected in 1967 (Fig. 3). Sand and gravel substrates that once existed there (J. D. Williams, pers. comm.) are no longer present.

Etymology.—The species epithet *akatulo* is derived from the Cherokee noun for mask (King, 1975) and, like the common name Bluemask Darter, calls attention to the uninterrupted, intense blue pigment covering the lower face of breeding males.

MATERIAL EXAMINED

The first number in parentheses indicates specimens examined for meristic counts or identification; the second number, when present, indicates specimens measured.

Etheostoma stigmaeum. Mobile Basin. Coosa River system, Georgia. Floyd Co.: ANSP 20645 (1; lectotype); Bartow Co.: UAIC 10116.07 (12); Paulding Co.: UF 80126 (0, 7), UF 84743 (0, 5), UAIC 10103.12 (11, 3). Coosa River system, Alabama. Etowah Co.: UAIC 9821.09 (0, 5). Black Warrior River system, Alabama. Winston Co.: UAIC 4111.07 (9), UAIC 4329.16 (11). Tombigbee River system, Alabama. Marion Co.: UAIC 4316.19 (16). Alabama River tributary, Alabama. Monroe Co.: TU 44449 (20). Tennessee River drainage. Duck River system, Tennessee. Bedford Co.: UAIC 9862.15 (8, 4), UAIC 10337.27 (0, 5), UAIC 2534 (0, 1); Marshall Co.: UT 91.1538 (22), UAIC 6395.11 (0, 10); Maury Co.: NLU 50667 (2); Hickman Co.: UT 91.1292 (2); Humphreys Co.: UT 91.832 (3), UT 91.856 (3), UAIC 10319.09 (6); Lewis Co.: UAIC 10462.15 (14). Cumberland River drainage, Kentucky. Pulaski Co.: SIUC 7584 (6), UF 15405 (8); Cumberland Co.: UMMZ 154639 (3). Cumberland River drainage, Tennessee. Scott Co.: UT 91.426 (10); Pickett Co.: UT 91.196 (5); Jackson Co.: KU 11539 (12); Rutherford Co.: TU 19506 (1), CU 37282 (12, 7), CU 42008 (2), CU 51527 (1), UT 91.708 (3), INHS 84130 (1), UAIC 9865.19 (13, 10), UAIC 10328.08, NLU 15742 (0, 3); Cheatham Co.: UAIC 10707.01 (15); Robertson Co.: UMMZ 175059 (10). Green River drainage, Kentucky. Monroe Co.: SIUC 3948 (4); Barren Co.: UMMZ 165401 (10); Allen Co.: UT 91.780 (10), NLU 18876 (0, 10), UAIC 9853.19 (0, 10); Casey Co.: UMMZ 165267 (10); Green Co.: UMMZ 165302 (8), SIUC 1101 (2); Metcalfe Co.: UAIC 9852.14 (6); Larue Co.: UMMZ 165432 (10).

Etheostoma jessiae. Tennessee River drainage, Tennessee. Hawkins Co.: UT 91.3713 (8); Greene Co.: UT 91.4190 (8); Sevier Co.: CU 38184 (7); Blount Co.: CU 67581 (0, 7), UAIC 8591.12 (10, 10), UAIC 9845.01 (0, 3); Monroe Co.: UT 91.308 (6); Polk Co.: UAIC 9819.15 (7); Sequatchie Co.: UAIC 10110.15 (6); Giles Co.: UT 91.3697 (3); Lincoln Co.: CU 46607 (4); Hardin Co.: UT 91.685 (3), UT 91.2789 (8); Humphreys Co.: UAIC 9864.16 (5). Tennessee River drainage, Georgia. Catoosa Co.: UT 91.2726 (8). Tennessee River drainage, Alabama. Jackson Co.: UAIC 7123.20 (7); Lauderdale Co.: UAIC 4817.19 (10).

ACKNOWLEDGMENTS

This study was part of S. Layman's dissertation research and was supported by the Department of Biological Sciences and Graduate School of the University of Alabama, United States Fish and Wildlife Service (contract 14-16-0004-91-039), and National Science Foundation (BSR 90-07513 to R. L. Mayden). We are especially grateful to B. Kuhajda, A. Simons, and R. Wood for assisting with field collections and laboratory analyses. We thank R. Biggins, P. Rakes, J. Shute, and P. Shute for field assistance. For specimen loans and distributional records we thank: W. Saul and E. Bohlke (ANSP); H. Bart, Jr. and M. Taylor (AUM and TU); J. Humphries, Jr., R. Normark, and C. Dardia (CU); L. Page and K. Cummings (INHS); E. Wiley and J. Collins (KU); N. Douglas (NLU); B. Burr and M. Warren, Jr. (SIUC); J. Caruso (TU); B. Kuhajda (UAIC); C. Gilbert, G. Burgess, and S. Walsh (UF); D. Nelson (UMMZ); D. Etnier (UT). Color notes and/or photos of *Doration* males were generously shared by M. Braasch, N. Burkhead, D. Etnier, R. Jenkins, S. Ross, J. Tomelleri, and M. Warren, Jr. This study also benefited from discussions of breeding color variation with W. Howell.

LITERATURE CITED

Bailey, R. M., and D. A. Etnier. 1988. Comments on the subgenera of darters (Percidae) with descriptions of two new species of *Etheostoma* (*Ulocentra*) from southeastern United States. Miscellaneous Publications Museum of Zoology University of Michigan 175:1–48.

Bookstein, F. L., B. Chernoff, R. L. Elder, J. M. Humphries, Jr., G. R. Smith, and R. E. Strauss. 1985. Morphometrics in evolutionary biology. Academy of Natural Sciences of Philadelphia, Special Publication 15.

Boschung, H. T., Jr., and R. L. Mayden. 2004. Fishes of Alabama. Smithsonian Books, Washington, D.C.

Burkhead, N. M., and R. E. Jenkins. 1991. Fishes, p. 321–409. *In*: Virginia's Endangered Species. K. Terwilliger (coordinator). McDonald and Woodward Publishing Co., Blacksburg, Virginia.

Etnier, D. A., and W. C. Starnes. 1993. The Fishes of Tennessee. University of Tennessee Press, Knoxville, Tennessee.

Howell, W. M. 1968. Taxonomy and distribution of the percid fish, *Etheostoma stigmaeum* (Jordan), with the validation and redescription of *Etheostoma davisoni* Hay. Unpubl. Ph.D. diss., University of Alabama, Tuscaloosa, Alabama.

Howell, W. M. 1980a. *Etheostoma jessiae* (Jordan and Brayton), blueside darter, p. 656. *In*: Atlas of North American Freshwater Fishes. D. S. Lee et al. (eds.). North Carolina State Museum of Natural History, Raleigh, North Carolina.

Howell, W. M. 1980b. *Etheostoma meadiae* (Jordan and Evermann), p. 666. *In*: Atlas of North American Freshwater Fishes. D. S. Lee et al. (eds.). North Carolina State Museum of Natural History, Raleigh, North Carolina.

Howell, W. M. 1980c. *Etheostoma stigmaeum* (Jordan), speckled darter, p. 697. *In*: Atlas of North American Freshwater Fishes. D. S. Lee et al. (eds.). North Carolina State Museum of Natural History, Raleigh, North Carolina.

Hubbs, C. L., and K. F. Lagler. 1974. Fishes of the Great Lakes Region. University of Michigan Press, Ann Arbor, Michigan.

Humphries, J. M., Jr., F. L. Bookstein, B. Chernoff, G. R. Smith, R. L. Elder, and S. G. Poss. 1981. Multivariate discrimination by shape in relation to size. Systematic Zoology 30:291–308.

Jenkins, R. E., and N. M. Burkhead. 1994. Freshwater Fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Johnson, J. E. 1987. Protected Fishes of the United States and Canada. American Fisheries Society, Bethesda, Maryland.

King, D. H. 1975. A grammar and dictionary of the Cherokee language. Unpubl. Ph.D. diss., University of Georgia, Athens, Georgia.

Kuehne, R. A., and R. W. Barbour. 1983. The American Darters. University Press of Kentucky, Lexington, Kentucky.

Layman, S. R., A. M. Simons, and R. M. Wood. 1993. Status of the dirty darter, *Etheostoma olivaceum*, and bluemask darter, *Etheostoma* (*Doration*) sp., with notes on fishes of the Caney Fork River system, Tennessee. Journal of the Tennessee Academy of Science 68:65–70.

Layzer, J. B., and T. R. Brady. 2003. Summer microhabitat of the endangered bluemask darter *Etheostoma* (*Doration*) sp. Journal of the Tennessee Academy of Science 78:55–57.

Leviton, A. E., and R. H. Gibbs, Jr. 1988. Standards in herpetology and ichthyology. Standard symbolic codes for institution resource collections in herpetology and ichthyology. Supplement No. 1: additions and corrections. Copeia 1988:280–282.

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

Mayden, R. L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem, p. 381–424. *In*: Species: The Units of Biodiversity. M. F. Claridge, H. A. Dawah, and M. R. Wilson (eds.). Chapman and Hall Ltd., London.

Mayden, R. L. 1999. Consilience and a hierarchy of species concepts: advances towards closure on the species puzzle. Journal of Nematology 31:95–116.

Mayden, R. L. 2002. On biological species, species concepts, and individuation in the natural world. Fish and Fisheries 2:1–26.

Nelson, J. S., E. J. Crossman, H. Espinoza-Perez, L. T. Findley, C. R. Gilbert, R. N. Lea, and J. D. Williams. 2004. Common and Scientific Names of Fishes from the United States, Canada, and Mexico. American Fisheries Society, Special Publication 29, Bethesda, Maryland.

Page, L. M. 1981. The genera and subgenera of darters (Percidae, Etheostomatini). Occasional Papers of the Museum of Natural History of the University of Kansas 90:1–69.

Page, L. M. 1983. Handbook of Darters. TFH Publications, Neptune City, New Jersey.

Simmons, J. W., and J. B. Layzer. 2004. Spawning behavior and habitat of the endangered bluemask darter, *Etheostoma* (*Doration*) sp. Copeia 2004:412–417.

Sokal, R. R., and R. J. Rohlf. 1981. Biometry. Second edition. W. H. Freeman and Co., New York.

Starnes, W. C., and D. A. Etnier. 1986. Drainage evolution and fish biogeography of the Tennessee and Cumberland Rivers drainage realm, p. 325–362. *In*: The Zoogeography of North American Freshwater Fishes. C. H. Hocutt and E. O. Wiley (eds.). John Wiley and Sons, New York.

Wiley, E. O., and R. L. Mayden. 2000a. The evolutionary species concept, p. 70–89. *In*: Species Concepts and Phylogenetic Theory: A Debate. Q. D. Wheeler and R. Meier (eds.). Columbia University Press, New York.

Wiley, E. O., and R. L. Mayden. 2000b. Comments on alternative species concepts, p. 146–158. *In*: Species Concepts and Phylogenetic Theory: A Debate. Q. D. Wheeler and R. Meier (eds.). Columbia University Press, New York.

Wiley, E. O., and R. L. Mayden. 2000c. A reply to our critics, p. 198–208. *In*: Species Concepts and Phylogenetic Theory: A Debate. Q. D. Wheeler and R. Meier (eds.). Columbia University Press, New York.

Winn, H. E. 1958. Comparative reproductive behavior and ecology of fourteen species of darters (Pisces–Percidae). Ecological Monographs 28:155–191.