

ETHEOSTOMA DITREMA, A NEW DARTER OF THE SUBGENUS
OLIGOCEPHALUS (PERCIDAE) FROM SPRINGS OF THE
ALABAMA RIVER BASIN IN ALABAMA AND GEORGIA

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ABSTRACT

Etheostoma (Oligocephalus) ditrema is described from 133 specimens from three localities in the upper Coosa-Alabama River basin. It is restricted in habitat to springs and spring-fed ponds above the fall line. It is a small, sexually dimorphic species most closely related to but sharply differentiated from *E. swaini* of the eastern Gulf Coastal Plain. Intraspecific variation is marked. *E. ditrema* is unusual among percids in typically possessing two coronal pores, which, when considered with other characters, suggests that it is a pedomorphic species of the *E. asprigene* species group.

The subgenus *Oligocephalus* is the most complex and speciose group of those comprising the North American darter genus *Etheostoma*. The members of the group were delimited by Bailey and Gosline (1955), who recognized 19 nominal species. Strawn and Hubbs (1956) recognized *Etheostoma lepidum* (Baird and Girard) as a species distinct from *E. grabami* (Girard). Yerger (1960) resurrected *E. okaloosae* (Fowler) from the synonymy of *E. swaini* (Jordan), and included it in the subgenus *Villora*. *Etheostoma spilotum* Gilbert was reduced to a subspecies of *E. sagitta* (Jordan and Swain) by Kuehne and Bailey (1961). Distler and Metcalf (1962) described *E. pallididorsum*, which may prove to be a subspecies of *E. cragini* Gilbert. With the definition of the subgenus *Oligocephalus* and the redescription

of *E. hopkinsi* (Fowler) by Bailey and Richards (1963), the number of recognized nominal species in the group was brought to 21.

Etheostoma ditrema was first collected by Jordan (1876) in millponds of the region of Rome, Floyd Co., Georgia. However, he misidentified his specimens as *Boleichthys elegans* Girard, which is probably a synonym of *E. grabami*, a species of southwestern United States and northeastern Mexico.

We discovered the new darter during the spring of 1962, in a spring tributary to the Coosa-Alabama river system in northwestern Georgia. Later another spring locality in northeastern Alabama was brought to our attention.

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collection in the region of Rome, Georgia. He allowed us to examine this specimen while he had it on loan from the Academy of Natural Sciences of Philadelphia (ANSP). Miss Winona H. Welch (De Pauw University) identified aquatic mosses from the type locality. Assistance in field work was made through National Institutes of Health grants WP-00082-04, 05 and 3-T1-ES-27-01S1, 02S1, and National Science Foundation NSF G-23598 to Suttkus, and NSF G-17005 to Ramsey through the Highlands Biological Station, Inc., North Carolina.

Etheostoma (Oligocephalus) ditrema
new species
Coldwater darter
(Figs. 1-3)

Boleichthys elegans.—Jordan, 1876: 308-309 (misidentification).

Material.—Description is based on 133 specimens from three localities in the Coosa-Alabama river drainage. The holotype, TU 35703, an adult male 33.9 mm in standard length, was collected in a spring flowing into a small tributary to Mills Creek, tributary to Chattooga River, 4.3 airline miles due west of Lyerly, Chattooga Co., Georgia (0.2 miles ENE of the Alabama boundary), on the Broomtown (Ala.)-Foster's Store-Lyerly road (T7S, R11E, Section 28) on 18 July 1962. Taken with the holotype were 21 paratopotypes (TU 29153, 15-35 mm s.l.). Other paratopotypes were taken 19 April 1962 (TU 26086, 8: 24-31), 30 May 1962 (TU 27566, 9: 18-34), 1 June 1964 (TU 32762, 34: 19-42), and 23 June 1964 (TU 32981, 43: 20-39). Five paratopotypes from TU 32981 have been distributed to each of the following institutions: USNM 198607, United States National Museum; MCZ 43123, Museum of Comparative Zoology, Harvard University; ANSP 101231, Academy of Natural Sciences of Philadelphia; UMMZ 187501, University of Michigan, Museum of Zoology; CU 47872, Cornell University; SU 62401, Stanford University.

A paratype (ANSP 20649, 1: 23) was collected during the summer of 1876 from a millpond (Etowah River drainage) near Rome, Floyd Co., Georgia.

Specimens from a third population, not designated as type material, were captured in Coldwater Creek, tributary to Choccolocco

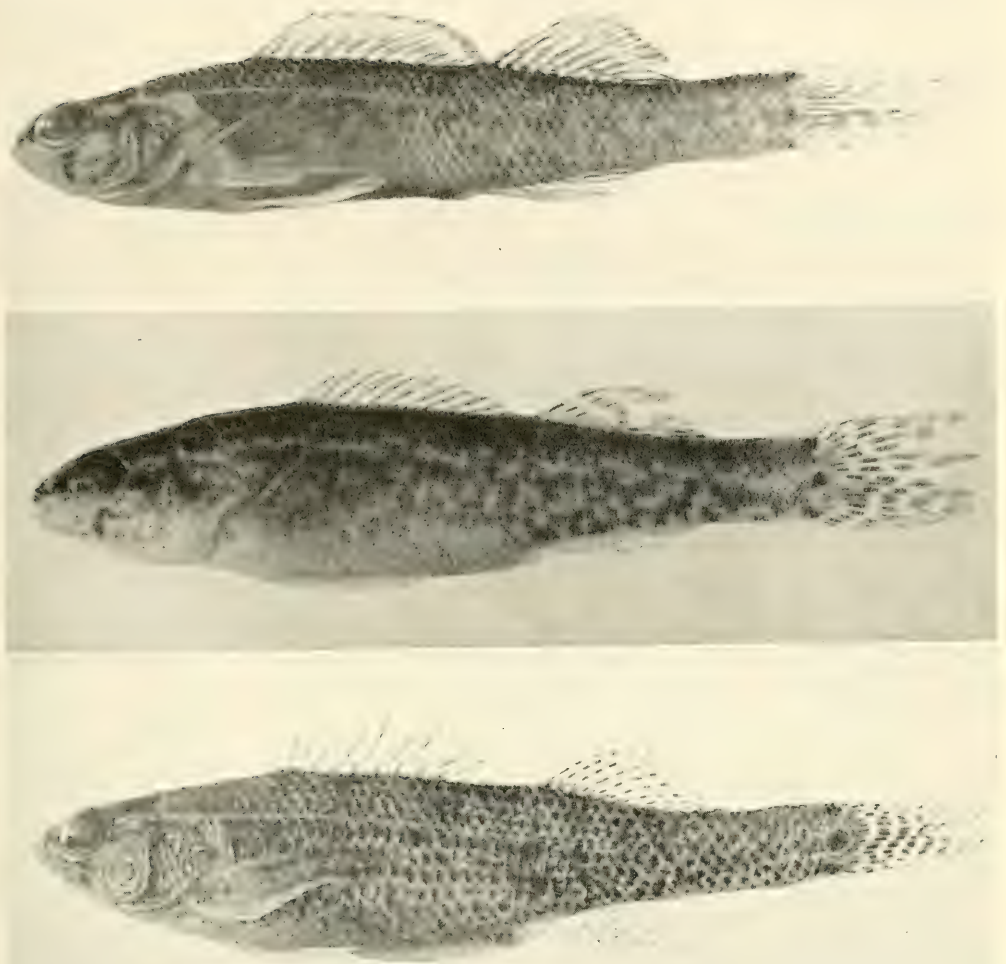
Creek, immediately below Coldwater Spring (T16S, R7E, Section 29), at Coldwater, 5.7 miles W of Oxford, Calhoun Co., Alabama, about 500 yards north of U. S. Highway 78, on 28 January 1964 (UAIC 1138, 1: 38), 1 June 1964 (TU 32746, 9: 26-41), and 31 August 1964 (TU 34400, 6: 20-32).

Several series of *Etheostoma swaini* from the Alabama River drainage were used for comparison with **ditrema**. These include TU 9497 (2: 43-55), Ala., Montgomery Co., creek 12.6 miles east of Montgomery, Highway 80; TU 34016 (5: 20-38), Ala., Clarke Co., Sand Hill Creek 1.1 miles west of Choctaw Bluff; TU 35176 (37: 22-48), Ala., Dallas Co., Pine Flat Creek 6 miles south of Selma. The problem of geographic variation in *swaini* and in the *asprigene* complex is being reported elsewhere.

Counts and measurements were made following Hubbs and Lagler (1958), except transpelvic width, the distance between the outer bases of the pelvic spines when held parallel (Bailey and Richards, 1963). The cephalic lateralis canals were analyzed following Hubbs and Cannon (1935).

Diagnosis.—A small, moderately robust species of the subgenus *Oligocephalus*. Lateral line moderately arched and incomplete, pored lateral-line series terminating between the level of the posterior base of the spinous dorsal fin and posterior soft dorsal base; total lateral-line scales 41 to 54, pored scales 19 to 35, unpored scales 13 to 30. Coronal canal incomplete, usually two coronal pores; infraorbital canal complete; supratemporal canal usually interrupted. Branchiostegal membranes overlapping anteriorly. Nape naked to completely scaled; breast usually scaled, rarely naked; prepectoral region, cheeks, opercles, and posterolateral corners of top of head scaled. Dorsal fin-rays VIII to XII—9 to 12; anal II, 6 to 8; pectoral 11 to 13. Nuptial tubercles absent. Vertebrae 35 to 37. Breeding male dark brown with orange pigment on belly and lower caudal peduncle; female indistinctly mottled with dark brown. Submarginal orange band present in spinous dorsal fin of both sexes. Humeral dark spot absent. Three dark blotches (rarely somewhat ocellate) in a vertical series at caudal fin base.

Description.—*Etheostoma ditrema* is a dwarfed species of the subgenus *Oligocephalus*. The largest specimen available is a



Figures 1-3. *Etheostoma ditrema*, new species. 1. (Upper) TU 32762, male paratopotype, 39.0 mm standard length. 2. (Middle) TU 32762, female paratopotype, 31.9 mm. 3. (Lower) TU 32746, female, Coldwater Creek, 40.7 mm. Photographs by C. D. Barbour.

male 42.1 mm in standard length, the largest female, 40.7 mm. Adulthood is apparently reached when a standard length of 25 mm is attained. The body is moderately robust but somewhat compressed. The body is widest just behind the head, and deepest at the level of the pelvic fin insertion, except in gravid females. There is a moderate nuchal hump in about half of adult males and in a third of adult females. The caudal peduncle is moderately slender. These and

other proportional measurements are listed in Table 1.

The head is of moderate length, about 30 percent of standard length. The snout is gently to abruptly decurved and short, its length usually less than orbit length. The upper and lower profiles of the snout meet at an angle of 55° to 85° . The projected angle formed by the upper and lower head surfaces behind the eye ranges from 19° to 30° . The frenum is always well-developed,

TABLE 1.
Measurements of *Etheostoma ditrema* in thousandths of standard length

Catalog Number	TU 35703 Holotype	TU 26086 27566, 29153 Paratypes	TU 26086 29153 Paratypes
Number of specimens	1	9	10
Sex	♂	♂	♀
	Range	$\bar{x}^1$	Range $\bar{x}$
Standard length (mm)	33.9	24.9-33.7 (30.4)	26.7-35.3 (31.3)
Predorsal length	348	346-367 (353)	358-371 (358)
Anal origin to snout	644	619-656 (641)	634-668 (650)
Body depth	209	190-208 (199)	190-228 (206)
Distance from soft dorsal origin to anal origin	180	157-175 (169)	149-176 (161)
Body width	142	121-138 (130)	124-153 (139)
Caudal peduncle length	233	227-265 (244)	227-272 (245)
Caudal peduncle depth	106	97-109 (103)	90-111 (100)
Head length	307	294-312 (320)	280-317 (300)
Head depth	174	165-177 (171)	159-180 (166)
Head width	136	125-145 (137)	129-149 (137)
Lower jaw symphysis to junction of gill membranes	127	115-149 (132)	126-152 (136)
Pelvic insertion to junction of gill membranes	192	167-192 (180)	180-198 (185)
Orbit length	74	76-89 (80)	72-90 (80)
Snout length	71	54-72 (66)	59-75 (65)
Upper jaw length	86	80-96 (87)	82-95 (87)
Width of gape	74	72-85 (79)	70-83 (76)
Interorbital width, least fleshy	50	48-64 (55)	37-54 (50)
Spinous dorsal base	274	260-289 (276)	252-288 (269)
Longest dorsal spine	97	85-112 (99)	67-99 (85)
Soft dorsal base	177	158-197 (176)	142-184 (166)
Longest dorsal soft ray	174	131-159 (143)	127-153 (139)
Soft dorsal, depressed length	254	218-273 (252)	221-257 (236)
Longest anal soft ray	142	119-154 (140)	113-138 (128)
Anal base	124	94-136 (121)	96-115 (107)
First anal spine	86	69-95 (84)	65-87 (74)
Anal, depressed length	200	205-230 (216)	192-214 (199)
Longest pectoral ray	200	187-245 (207)	158-216 (191)
Pelvic fin length	209	186-223 (205)	173-194 (185)
Pelvic fin base	32	32-39 (35)	33-39 (36)
Interpelvic distance	15	10-16 (13)	10-19 (14)
Transpelvic width	71	61-67 (65)	62-72 (66)
Caudal length	206	190-232 (209)	187-216 (203)

¹ Holotype included in mean for males.

although frequently narrow. The mouth is terminal or slightly subterminal, and projects posteriorly and downward to or slightly beyond the anterior edge of the eye. The prevomer and palatine bones bear teeth. The upper surface of the eye in lateral aspect is even with the top of the head. The gill membranes are usually separate and overlapping anteriorly, occasionally very slightly conjoined. There are six branchiostegal rays on each side.

The lateral line is incomplete, and is elevated and arched anteriorly, beginning the downward arc at about the level of the

spinous dorsal origin. The pored lateral line terminates at the level of a point between the posterior spinous dorsal and posterior soft dorsal bases.

The infraorbital canal is usually complete (interrupted on one side in one of 22 type specimens and in two of 16 specimens from the Choccolocco Creek drainage; interrupted on both sides in one specimen from the Choccolocco locality, pores 2+5-5+2). Infraorbital pores usually number 8 (5 to 9). The preoperculomandibular canal is typically complete, usually with 10 pores (rarely 8 or 11, frequently 9). The supratemporal

canal is usually interrupted, each branch having 2 pores (Table 5). The lateral canal normally has 5 pores.

An unusual diagnostic feature is the possession of two well defined coronal pores in most specimens (Table 5), which results from the non-fusion of the two coronal canals branching mesially from the supra-orbital canals. In all other species of *Oligocephalus*, and in other percid subgenera, these branches fuse to form a backward-projecting tube terminating at the coronal pore. In *E. ditrema* the two coronal branches emerge side-by-side just posterior to a line between the upper orbital rims. The two pores may fuse as one, but there is rarely a tube directed caudad to the pore. There are in addition four pores in the supraorbital canal, although infrequently one interorbital pore is absent. Rarely, one of the coronal branches has failed to develop.

Scale row counts (Tables 2 and 3): total lateral-line scales number 41 to 54 (usually 44 to 50), pored lateral-line scales 19 to 35

(usually 22 to 32); unpored lateral-line scales 13 to 30 (usually 16 to 26); transverse body scales (from soft dorsal origin posteroventrally to anal fin base) 11 to 14 (usually 12 or 13); scales above lateral line 3 to 5 (usually 4); scales below lateral line 6 to 9 (usually 7 or 8); caudal peduncle scales 17 to 22 (usually 19 to 21).

Squamation: The opercles, cheeks, belly, and prepectoral region are wholly invested with exposed ctenoid scales. There are a few scales embedded on the head just above and anterior to the junction of the supra-temporal and lateral canals. The breast is naked anteriorly. The posterior breast is usually scaled, although some infraspecific variation exists. The type material from the Chattooga and Etowah drainages in Georgia usually has exposed ctenoid breast scales. Occasionally the scales are embedded, or a narrow median strip is naked, but the breast is never entirely scaleless. Of the 16 specimens available from Coldwater Spring, only one has exposed ctenoid breast scales, 10

TABLE 2.
Distribution of scale row counts in *Etheostoma ditrema* and *E. swaini*. Value for holotype of *ditrema* in boldface

Species and drainage	Total lateral-line scales																	
	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	N	
<i>ditrema</i>																		
Chattooga			1	1	3	6	16	22	18	11	16	10	4	—	—	1	109	
Etowah									1 ^r	—	1 ^l						1	
Choccolocco					1	3	4	—	2	2	2	—	1				15	
<i>swaini</i>																		
Alabama	1	4	3	2	8	7	10	1	5	2	—	1					44	
	Caudal peduncle scales												Soft dorsal origin to anal base					
	17	18	19	20	21	22	N						11	12	13	14	N	
<i>ditrema</i>																		
Chattooga			3	41	33	28	3	108					2	65	40	2	109	
Etowah			1					1						1			1	
Choccolocco	1	1	8	3	1			14						14	1		15	
<i>swaini</i>																		
Alabama	1	4	11	15	10	3	44						5	23	14	2	44	
	Scales above lateral line												Scales below lateral line					
	3	4	5	6	7	N							6	7	8	9	10	N
<i>ditrema</i>																		
Chattooga	3	53	20				76						2	30	31	7	70	
Etowah		1					1							1			1	
Choccolocco		14	1				15						1	10	4		15	
<i>swaini</i>																		
Alabama			3	35	5	1	44						5	20	15	3	1	44

r, l Both sides of single specimen used: r = right, l = left

TABLE 3 (continued on opposite page)

Lateral line scales in Etheostoma ditrema and E. swaini. Value for holotype in boldface.

Species and drainage	Pored lateral-line scales										
	19	20	21	22	23	24	25	26	27	28	29
<i>ditrema</i>											
Chattooga	3	2	2	3	7	8	11	15	12	12	11
Etowah								1 ¹	1 ^r		
Choccolocco		1	1	1	2	1	—	2	3	3	—
<i>swaini</i>											
Alabama											
	Unpored lateral-line scales										
	4	5	6	7	8	9	10	11	12	13	16
<i>ditrema</i>											
Chattooga										1	7
Etowah										2	
Choccolocco										3	
<i>swaini</i>											
Alabama	1	3	9	10	10	3	2	5	1		

have scattered, embedded ctenoid scales, and 5 have the breast completely naked.

Nape squamation is variable (Table 6). Specimens from Coldwater Spring tend to have the nape more fully scaled than in type specimens. The notation used for the degree of nape squamation in Table 6 was derived from a relative scale. A value of zero signifies that at least the median portion of the nape from the spinous dorsal origin to the occiput is naked; I through III represent successive increases in posterior nape squamation; IV, nape wholly scaled but scales embedded at least anteriorly; V, nape completely invested with exposed scales.

Fins (measurements in Table 1): The spinous dorsal is composed of 8 to 12 slender spines. Many specimens have small postapical fleshy enlargements at the spine tips similar to those in other species of *Oligocephalus*. The fin is low; the length of the longest spine (located at the fin center) is about two-fifths to one-half the length of the fin base, and can be stepped into head length two and one-half to three times. The fin border in both sexes usually forms a gentle arc rearward to the dorsum (not subquadrate in outline, as in *E. swaini*). The soft dorsal fin is usually well separated from the spinous dorsal (as in Fig. 2). There is typically a much broader hiatus between the fins in the Choccolocco population (Fig. 3). Though low, the soft dorsal is higher than the spinous dorsal. Dorsal soft rays number 9 to 12. Total dorsal rays range

from 18 to 23. The Choccolocco population has fewer dorsal rays (Table 4), which probably is correlated with the greater dorsal fin separation.

The anal fin is also small. There are usually two spines (one specimen out of 133 has a single spine, and two have three spines). The second spine is usually more slender than the first. The second spine in the Choccolocco population is usually stiff, but is typically very slender and flexible in specimens from Georgia. Anal soft rays number 6 to 8 (usually 7).

There are 11 to 14 (usually 12 or 13) branched caudal rays. The posterior edge of the caudal fin is usually truncate, frequently slightly emarginate or convex. The pectoral fins are short and rounded, the longest ray about two-thirds of head length. Left pectoral rays number 11 to 13 (usually 12). The pelvic fins (rays I, 5) usually extend beyond the posterior edge of the pectoral fin, and are inserted very close together. Interpelvic distance is less than half the width of the pelvic fin base.

Analysis of radiographs of 35 specimens from the type locality revealed the following vertebral counts: 35 vertebrae (one specimen), 36 (17), and 37 (17).

Coloration of males.—The most conspicuous feature of nuptial males is the somewhat muted red-orange pigmentation of the lower body. In several male paratopotypes captured on 1 June 1964, this pigment was distributed almost uninterruptedly from just

TABLE 3 (continued)

Pored lateral-line scales															N
30	31	32	33	34	35	36	37	38	39	40	41	42	43		
7	5	8	2	—	1									109	
—	1													1	
														15	
	2	2	7	4	3	2	7	5	6	3	2	—	1	44	
Unpored lateral-line scales															N
17	18	19	20	21	22	23	24	25	26	27	28	29	30		
5	19	5	18	19	11	3	6	1	5	3	—	—	1	109	
			1 ^r	—	—	1 ^l								1	
4	—	—	1	3	4	—	2	—	1					15	
														44	

behind the pectoral base to immediately posterior to the anal fin origin, and on the lower caudal peduncle in the form of about five indefinite bar-like groupings of orange scales separated by dull olive-green bars. The orange pigmentation on the caudal peduncle extended dorsad only to the level of the lateral line. Other males had orange pigment before the vent only. Two to four upper body scales in some males also bore orange pigment, but these were scattered and inconspicuous.

In life, and in alcohol, the dorsum is usually uniformly dark brown, broken in most by a predorsal buff-colored nuchal patch of varying width. In some there are about nine very ill-defined darker saddles crossing the dorsal midline and extending laterad on about two scale rows to either side. The intermediate areas between the saddles are brown, similar to the background color, but occasionally are a light brown or buff color. The body at the base of each dorsal fin is buff. In some, the centers of the exposed fields of scales of the dorsum have a slightly darker brown color, giving the impression of vague longitudinal lines extending from the sides of the occiput to the posterior soft dorsal base. The striped pattern extends downward (excluding the lateral line) to the anal base. The stripes are irregularly if at all developed on the lower body, generally being limited to an area on the lateral belly anterior to the anal fin origin and for a short distance on the lower body above the

anal fin. There is no humeral dark blotch. The lateral line is less pigmented along the pored portion than on adjoining areas, and appeared yellowish in life, somewhat as in *E. parvipinne* Gilbert and Swain. The unpored lateral-line series appears as an irregular light line. Very faint lateral bars (dull olive-green in life) showing some connection with the dorsal dark saddles are present in many individuals.

There are three black spots (sometimes connected) in a vertical series at the caudal base. Occasionally the lower and/or median spots are faint or absent. The central spot lies at the termination of the lateral-line series just at or immediately behind the posterior edge of the hypural plate. The upper and lower spots lie at the bases of the posterior procurent caudal rays. The caudal base between the spots is usually lighter than on adjoining areas of the peduncle, and in life there was a small spot of red-orange immediately posterior and mesial to the upper and lower basicaudal dark spots.

The genital papilla and anal rugae are immaculate white. The genital papilla in males takes the form of a short subquadrate flap extending posteriorly to the base of the first anal spine. Occasionally a median short fingerlike projection extends beyond the shorter lateral portions of the papilla.

The lower belly is evenly stippled with micromelanophores. The breast has larger melanophores distributed to the gular region. There is a prepectoral dark blotch.

The head dorsum to the snout is dark brown. The upper snout was buff-colored in life. A dark diffuse line extends from the anterior edge of the orbit below the nostrils to the snout tip, expanding on the anterior third of the upper lip to either side of the buff-colored frenum. The remainder of the upper lip has one or two dark blotches. The posterior maxillary is darkened. The lower lip and lower jaw rami are mottled, and the mandibular symphyseal region usually has a dark blotch. The gular region and branchiostegal membranes are diffusely stippled. There is a postorbital dark streak. The suborbital bar is well-developed, beginning behind the lower orbital midpoint and curving downward and slightly forward on the cheek. The iris was golden-orange in life.

The spinous dorsal fin in life was bordered by a narrow dusky blue band. Proximal to this was a band of red-orange, about three times as wide as the marginal band anteriorly, tapering to an equal width posteriorly. Below this was a slightly wider dusky blue band extending almost to the base of the fin. There was a basal spot of

dark red behind each dorsal spine. Nuptial males have melanophores irregularly distributed on the spines.

The soft dorsal fin was dusky blue throughout, always having a basal spot of dark red behind each ray. There was usually some red-orange arranged in one or two indefinite narrow bands mesially and submarginally. There are three or four dark blotches on the rays.

The anal fin was dusky blue-green on both the spined and soft-rayed portion, with basal red-orange spots on the membranes between the soft rays. Some nuptial males had a median band of orange on the rays. Others had several quadrate dark blotches on yellowish rays. The edge of the fin was colorless.

The caudal fin has five to seven irregular dark bars (pigment on rays only). Between the dark bars the rays are yellowish. In a few individuals, the basal portion of the central rays had red-orange pigment extending two-thirds of the distance toward the fin edge. The anterior procurrent caudal rays are embedded in opaque whitish tissue.

TABLE 4.
Distribution of fin-ray counts in *Etheostoma ditrema* and *E. swaini*. Value for holotype in boldface.

Species and drainage	Dorsal spines						Dorsal soft rays						
	8	9	10	11	12	N	9	10	11	12	13	14	N
<i>ditrema</i>													
Chattooga		2	51	52	7	112		30	71	11			112
Etowah				1		1			1				1
Choccolocco	6	9	1			16	1	8	7				16
<i>swaini</i>													
Alabama		1	21	22		44			19	23	1	1	44
	18		19	20		Total dorsal rays							
					21	22	23	24	25				N
<i>ditrema</i>													
Chattooga			1	12	48	44	7						112
Etowah						1							1
Choccolocco	6		3	7									16
<i>swaini</i>													
Alabama				1	9	21	11	1	1				44
		Anal soft rays					Left pectoral rays						
	6	7	8	N		11	12	13	14				N
<i>ditrema</i>													
Chattooga	40	66	6	112			3	36	29				65
Etowah	1			1				1					1
Choccolocco	5	11		16				10	5				15
<i>swaini</i>													
Alabama	6	31	7	44				5	25	14			44

TABLE 5.
Supratemporal canal and coronal pores in Etheostoma ditrema and E. swaini.
Value for holotype in boldface.

Species and drainage	Supratemporal canal			Coronal pores		
	Complete	Interrupted	N	1	2	N
<i>ditrema</i>						
Chattooga	30	86	116	45	68	113
Etowah		1	1	1		1
Choccolocco	5	11	16	8	8	16
<i>swaini</i>						
Alabama	20	24	44	44		44

The pectoral fins are colorless save for a scattering of dusky along the entire length of the rays.

The tissue investing the pelvic spine is only very slightly thickened, and is colorless save for a sprinkling of micromelanophores. The soft-rayed portion had dusky blue-green (darkest between the posterior rays) along the basal two-thirds of the rays and inter-radial membrane. The distal third of the membrane is colorless. The distal portions of the rays have scattered melanophores.

Only two young males are available from the Choccolocco locality. These had submarginal and basal red-orange bands in the spinous dorsal fin, but lacked the orange pigment on the venter.

Coloration of females.—Females were devoid of erythric pigment on the body. In alcohol the general body coloration is similar to that of males, save they tend to be more mottled, especially on the venter. Choccolocco females are darker and less mottled, and occasionally the basicaudal dark spots are somewhat ocellate (Fig. 2 and 3).

Only one female from the Chattooga population had a submarginal pale orange band in the spinous dorsal, but all adult females from the Choccolocco locality possessed this coloration. Females usually have a dusky

marginal band, which tends to be obsolete anteriorly. There are brownish streaks in the median interrarial membranes along the spines. Dusky spots occur basally in the interrarial membranes. The spines are variously marked with one or two elongate dusky blotches.

The soft dorsal fin is marked with four or five indefinite bands of brownish pigment, which is distributed on the interrarial membranes distally and on the rays basally. There is a basal series of interrarial dark blotches. The soft dorsal bands are more discrete and narrower in Choccolocco females.

The caudal fin is barred with five to seven irregular rows of dark pigment. The anal fin bears one to three vague dusky brown series of blotches on or adjacent to the rays. The pectoral fin is pigmented as in the male. The pelvic fins are colorless or have scattered melanophores.

The immaculate, slightly crenulate genital papilla of the female projects posteriorly to the base of the first anal spine, and is as long as or slightly longer than broad.

Coloration of juveniles.—Juveniles are generally more lightly pigmented than adults. The smallest individuals have moderately well-defined dorsal saddles and lateral blotches.

TABLE 6.
Squamation of nape in Etheostoma ditrema and E. swaini (see text for explanation of symbols). Value for holotype in boldface.

Species and drainage	Degree of nape squamation					
	0	I	II	III	IV	N
<i>ditrema</i>						
Chattooga	24	13	16	8	6	76
Etowah					1	1
Choccolocco	1	—	—	—	6	16
<i>swaini</i>						
Alabama	25	5	3	1	10	44

Intraspecific variation.—The single specimen of *E. ditrema* from the Etowah drainage of Georgia is apparently of the same genetic stock as specimens from the type locality in the Chattooga drainage. Members of the Choccolocco population differ markedly in several respects: they have the nape more often fully scaled (Table 6); the breast tends to be naked or weakly scaled; the females are darker and less mottled than Chattooga females, and more consistently possess an orange submarginal band in the spinous dorsal; the basicaudal dark spots occasionally are ocellate; the second anal spine is stronger. The most striking difference is that the Choccolocco population has a reduced number of dorsal rays. If a separation point in Table 4 is determined as being between 20 and 21 total dorsal rays, the average divergence between the Choccolocco population and the Etowah and Chattooga population is about 94 percent. Concurrently, the dorsal fin bases are more widely separated. These observations suggest that the number of dorsal fin rays has been secondarily reduced, and that the Choccolocco race is a derivative of a common stock which has been preserved in a more primitive state in the upper Coosa area.

The Choccolocco population likely represents a genetically valid subspecies, but we hesitate to designate it as such in view of the dearth of specimens and lack of knowledge of distribution of *ditrema* throughout the Coosa drainage. There may be a clinal type of variation in probable spring populations of the area surrounding the nearly 60

airline miles between Lyerly, Georgia and Coldwater, Alabama. In opposition to this view, Mr. Richard D. Caldwell of the University of Alabama informs us that *E. ditrema* was absent from numerous collections made by him in springs of northeastern Alabama.

Relationships.—The subgenus *Oligocephalus* retains in part the diversity of composition formerly possessed by the catch-all darter genus *Poeciliichthys* (now a synonym of *Etheostoma* s.s.). Although evaluation of evolution within *Oligocephalus* is confused by many secondarily developed characters in the species, it is clear that *E. ditrema* is closely allied with the *E. asprigene* species group. Members of this group are *E. asprigene* (Forbes), *E. swaini*, *E. ditrema*, and an undescribed species from the Black Warrior-Tombigbee drainage in Alabama. These forms share the following characteristics; nuptial tubercles absent; opercular membranes overlapping or scarcely connected; body robust at the level of the spinous dorsal origin; supratemporal canal usually or frequently interrupted (much variation in *swaini* and *asprigene*); lateral line slightly to moderately arched anteriorly; humeral blotch not enlarged, inconspicuous or absent (usually distinct in *swaini*); color pattern of red-orange and blue or olive-green on the lower body, red-orange and blue in dorsal and anal fins of males; 35 to 39 vertebrae.

Collette (in press) has found the presence and distribution of breeding tubercles among percids to be of systematic significance. The

TABLE 7.
A comparison of Etheostoma ditrema and E. swaini from the Alabama River basin.

Character	Species	
	<i>ditrema</i>	<i>swaini</i>
Snout shape	Decurved, blunt	Produced, acute
Spinous dorsal fin	Spines slender, short; posterior edge gently curved and diagonal to body	Spines thicker, longer; posterior edge abruptly curved and nearly perpendicular to body
Greatest known size (s.l.)	42 mm	55 mm
Horizontal streaks on body	Absent or indistinct	Distinct
Dorsal saddles	Absent or indistinct	Distinct
Breast	Usually scaled	Naked
Prepectoral region	Exposed ctenoid scales	Naked or with embedded cycloid scales
Left pectoral rays	Mode at 12	Mode at 13
Coronal canal	Incomplete, usually 2 pores	Complete, a single pore
Lateral line contour	Moderately arched	Slightly arched
Pored lateral-line scales	19-35	31-43
Unpored lateral-line scales	13-30	4-12
Scales above lateral line	Mode at 4	Mode at 5

asprigene species group forms a natural group among atuberculate species of *Oligocephalus*. Others which appear most closely related are *E. exile* (Girard), *E. grabami*, *E. lepidum*, and *E. pottsi* (Girard). *Etheostoma mariae* (Fowler) and *E. juliae* Meek also lack tubercles, but on the basis of morphology and pigmentation do not appear as closely related to the *asprigene* group.

Etheostoma asprigene comprises a complex whose most easterly range along the Gulf Coast is in tributaries of the lower Mississippi River in Louisiana and Mississippi. *Etheostoma swaini* ranges from the Amite River drainage of Louisiana and Mississippi eastward below the fall line to the Apalachicola River drainage of Florida and Georgia (Bailey, Winn, and Smith, 1954).

Etheostoma ditrema appears to be a highly specialized derivative of *swaini* stock which early surmounted the fall line in the Coosa River system. The nature of the characters by which *ditrema* is distinct from *swaini* suggests that *ditrema* has diverged through genetic fixation of developmental traits which in darters are associated with neoteny. Collette (1962) discussed apparently neotenic populations of *E. (Hololepis) fusiforme* (Girard), which are characterized by reduction in adult size, decrease in relative number of pored lateral-line scales, and incomplete development of cephalic canals. All of these characters are found in *ditrema* as compared with *swaini*. Collette (1962) found reduction in development of the coronal canal in a neotenic population of *fusiforme*, but did not report as great a degree of reduction as that present in *ditrema*, in which the coronal branches usually do not fuse at all. The assemblage of characters in which *E. ditrema* seems a paedomorphic species have probably arisen through adaptation to the cold spring environment, to which the species presently appears restricted.

Other species of *Oligocephalus* inhabiting the Alabama River system include *E. parvipinne* and *E. whiplii artesiae* (Hay), which have the lateral line complete or nearly so, and possess moderately conjoined opercular membranes. *Etheostoma parvipinne* apparently occurs only on the Coastal Plain. *Etheostoma whiplii* occurs above and below the fall line, but has never been collected with *ditrema*.

Etheostoma ditrema resembles species of

the subgenus *Hololepis* in the configuration of the lateral line. Two species of *Hololepis* are reported from the Alabama River system, including *E. fusiforme barratti* (Holbrook) and *E. zoniferum* (Hubbs and Cannon), and a third, *E. gracile* (Girard), is known from the Tombigbee River system (Collette, 1962). In the Mobile Bay system these occur only on the Coastal Plain. They differ from *E. ditrema* in possessing nuptial tubercles and in lacking red-orange body pigmentation in breeding males. The lateral line is more highly arched in *Hololepis* species. The moderately arched lateral line in *E. ditrema* seems to be a secondary specialization, and its similarity to that of *Hololepis* almost certainly represents convergence (probably as does the somewhat arched form of the lateral line in *E. exile*).

Etheostoma (Psychromaster) trisella Bailey and Richards is known from a unique specimen collected about midway between two of the known localities of *ditrema*. Repeated efforts by several groups to collect further specimens have been futile. Although the specimen is distinct in possessing a single weak anal spine, three intense dorsal saddles, and a complete lateral line, it is possible that the type of *trisella* is an aberrant hybrid between *ditrema* and another darter. This is rather tenuously suggested by the generally blotched color pattern, the overlapping opercular membranes, and presence of two coronal pores in *trisella* (which the authors mentioned was a probable anomaly, but which is the usual condition in *ditrema*), as well as its apparent absence in the region today. It is understandable that a large-stream form such as *E. (Nothonotus) acuticeps* Bailey might be collected only rarely, but all habitats (mainly springs and small streams) of the region in which *trisella* might occur have been surveyed intensively.

Habitat and life history.—*E. ditrema* has been collected recently only in or near large springs. We suspect that the "mill-ponds" in which Jordan (1876) found specimens were springfed impoundments, as the region of Rome, Georgia has many large springs.

The spring at the type locality boiled from a bed of dolomitic limestone at a rate of about 30 cubic feet per second. The water was cold (16 to 18 C), colorless, and was clear even after heavy rains had roiled neigh-

boring streams. The bottom was composed of a deep bed of soft whitish clay overlaid by detritus and a dense growth of aquatic mosses (*Fontinalis filiformis* and *Fissidens debilis*). The greatest depth of water was about two meters. The spring pool was about 15 m in diameter, and was surrounded by brush and open woods. An abrupt break in habitat type occurred with the beginning of moderate flow at the head of the gravelly effluent stream, which was about 2 m wide and choked in place with submerged *Sparganium americanum*.

E. ditrema was the only darter present in the spring pool. It was always associated with dense aquatic vegetation, and individuals could occasionally be seen perching at the surface of moss clumps. It was most commonly captured in less than a meter of water, but was also taken as deep as 1.3 m.

Associated fish species in the spring pool at the Chattooga locality included *Esox americanus*, *E. niger*, *Minytrema melanops*, *Moxostoma duquesnei*, *Notropis chrosomus*, *N. lirus*, *Semotilus atromaculatus*, *Ictalurus melas*, *Lepomis cyanellus*, *Micropterus s. salmoides*, and *Cottus carolinae zopherus*. In the effluent stream, the above were taken (except for *E. ditrema*), as well as *Hypentelium etowanum*, *Camptostoma anomalum*, *Notropis c. chrysocephalus*, *N. xenocephalus*, *Rhinichthys atratulus*, *Lepomis m. megalotis*, *Micropterus coosae*, *Etheostoma (Ulocentra) coosae*, and *Percina caprodes carbonaria*.

As Coldwater Spring is the chief water supply for the city of Anniston, Alabama, we were forced to collect in Coldwater Creek just below the spring overflow. The spring flows from a thrust in the Weisner Quartzite formation, and yields 32 million gallons per day. The flow in Coldwater Creek was estimated at 100 cfs. The water was clear, colorless, and cold (18 C). *Etheostoma ditrema* was the only darter present, and was taken from dense silted patches of *Myriophyllum* growing in protected pockets along the left stream edge (right edge was polluted from a tributary a short distance below). Several specimens were captured in a muddy ditch near its junction with Coldwater Creek.

Associated species at the Coldwater locality were *Lampetra aepyptera*, *Esox americanus*, *E. niger*, *Gambusia affinis*, *Lepomis*

cyanellus, *L. macrochirus*, and *Cottus carolinae zopherus*.

Jordan (1876) took *Notropis lirus*, *Etheostoma stigmaeum*, and *Percina n. nigrofasciata* with *E. ditrema*.

Males had assumed nuptial coloration by the end of April. They were still brightly colored in mid-July. It is probable that bright coloration is maintained year-round.

Females were gravid in collections made in April through July, but were largely spent by the latter date. Coldwater females were greatly swollen with eggs on June 1 (Fig. 3), but did not yield eggs when gently pressed. Ovarian eggs were large and few in number. Chattooga females had eggs of an average diameter of 1 mm on June 1, and 1.2 mm on June 23. One at 40.5 mm s.l. had 25 large ova in the left ovary and 19 in the right. Another at 33.1 mm had 23 (left) and 14 (right). A third at 31.7 mm had 23 ripe eggs in the right ovary. The smallest gravid female was 24.4 mm long.

The smallest young available (15.2 mm s.l.) was taken at the Chattooga locality on 18 July. Spawning likely occurs throughout the month of June.

The name *ditrema* refers to the typical possession of two coronal pores.

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