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Fundulus blairae, a New Species of the *Fundulus nottii* Complex (Teleostei, Cyprinodontidae)

E. O. WILEY, III,[1] AND DARRELL D. HALL[2]

ABSTRACT

Fundulus blairae is described from material from eastern Texas, southeastern Oklahoma, and western Louisiana. A phylogenetic analysis indicates that *F. blairae* is a member of the *Fundulus nottii* species group and is most closely related to *F. dispar*. The analysis also indicates that *F. cingulatus* is most closely related to the *F. nottii* species group. *Fundulus nottii* and *F. lineolatus*, the other members of the species group, are sympatric with each other, whereas *F. dispar* and *F. blairae* are allopatric, both with each other and with the other two species. A phylogeny of the *F. nottii* complex and three other species of *Fundulus* is presented.

INTRODUCTION

The *Fundulus nottii* species complex currently includes three named taxa: *F. nottii* (Agassiz),[a] *F. dispar* (Agassiz), and *F. lineolatus* (Agassiz).[b] Brown (1958) studied the geographic variation of these taxa and regarded them as subspecies of a single species, *Fundulus nottii*. He described the range of *F. n. nottii* as extending from the New River, Florida, westward along the Gulf Coast into East Texas. Citing Knapp (1953), Brown (1958) commented that the status of the Texas populations was uncertain and "Variation in the populations to the west and north of Louisiana has yet to be analyzed, but it is thought that significant variation does occur there. In particular the forms inhabiting Texas and Oklahoma should be studied." Rivas (1966) recognized *lineolatus* as a full species based on its supposed sympatry with *nottii* in northern Florida. Moore (1968) suggested that the taxonomic status of *lineolatus* cannot be decided until more is known of the western populations of the *F. nottii* complex.

The present investigation deals with populations of the *F. nottii* complex from Texas, Oklahoma, and Louisiana not studied by Brown

[a]The species name *nottii* has been incorrectly spelled *"notti"* by most recent authors.

[b]Griffith (1974) has used the name *Fundulus swampinus* (Lacépède) as the senior synonym of *F. lineolatus* (Agassiz). I use the accepted name *F. lineolatus* but recognize that a ruling by the International Commission may be in order.

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(1958). Most of these populations differ from those of *F. nottii*, *F. dispar*, and *F. lineolatus* and are considered here as representatives of a new species. In the course of our study we found that *F. nottii* showed geographic variation in color patterns. For convenience we herein recognize "eastern" and "western" populations of *F. nottii*. Eastern populations are distributed from the Escambia River east to the Suwannee River, Florida; western populations are distributed from the Mobile Bay drainage westward to the Lake Pontchartrain drainage, Louisiana.

METHODS AND MATERIALS

Body color patterns were determined by visual inspection of preserved specimens. Dots on the side of the body were of two types: large dots, which are distinctly rounded; and smaller dashes, which are elongate. Large dot patterns were grouped into three states: (1) dots in regular rows on all parts of the body except the caudal peduncle, each dot appearing at the approximate center of the exposed field of the scale; (2) dots irregularly arranged over the entire body; and (3) dots missing on all parts of the body except the caudal peduncle (although dashes may be present). Subocular teardrop intensity was also arranged in three states: (1) teardrop very diffuse (melanophores widely spaced, the lower border of the teardrop ill defined); (2) teardrop diffuse (melanophores separate but teardrop with a well-defined lower border); and (3) teardrop solid (melanophores fused forming a solid pigment area). Dash patterns and the number and intensity of stripes were noted but not coded.

Fin ray and scale row counts follow Brown (1958). We examined the same specimens of *F. dispar* studied by Brown (1958) from the University of Michigan Museum of Zoology and found no statistically significant differences between his counts and ours. Body measurements follow Hubbs and Lagler (1947). Subocular teardrop length was measured from the edge of the orbit ventrally to the last melanophore of the teardrop. Head squamation patterns and supraoccipital canal pores were determined by visual inspection; the former follows the terminology of Hoedeman (1958), the latter of Gosline (1949).

MATERIAL EXAMINED

Specimens of *Fundulus blairae* studied in detail are listed by state, county, and locality, whereas other specimens are listed by catalogue number only. Specimens of other species are listed by state, except those specimens that represent significant range extensions. The following abbreviations are used:

AMNH, the American Museum of Natural History
BU, Baylor University
CU, Cornell University
LPI, Louisiana Polytechnic University
NLU, Northeastern Louisiana University
OAM, Oklahoma State University
SHSU, Sam Houston State University
TAM, Texas A&M University
TNHC, Texas Natural History Collection
TU, Tulane University
UMMZ, University of Michigan Museum of Zoology
USNM, National Museum of Natural History, Smithsonian Institution

The following abbreviations are used in locality data:

B., bayou
Cat., catalogue
Co., county
Cr., creek
dr., drainage
Hwy., highway
jct., junction
L., lake
Par., parish
R., river
R.R., railroad
sect., section
spec., specimens
trib., tributary
uncat., uncatalogued

Fundulus blairae

Louisiana: Caddo Par.: Cr. S Lakeside Drive, 6.25 mi. W La. Hwy. 7173 (NLU 1347, 11 spec.). Grant Par.: sect. 9-T6N-R1.3E (NLU 3370, 4 spec.); Saline R., 1 mi. E Hwy. 229 on Co. Rd., 2.5 mi. N Pogen (NLU 16402, 2 spec.). Jefferson Par.: Calcasieu R. at Hwy. 10 (TU 44596, 5 spec.). La Salle Par.: Caster Cr., 6.5 mi. W jct. Tullos R. R. bridge and Hwy. 84 (SHSU 469, 7 spec.). Rapids Par.: B. Boeuf, 15 mi. NE Elmer on Hwy. 488 (SHSU 450, 7 spec.). St. Martin Par.: jct. B. Teche and La. Hwy 96 in St. Martinsville (SHSU 449, 5 spec.). Vernon Par.: Bear Cr., sect. 23-T8N-R6W (NLU 1792, 5 spec.); Six Mile Cr., sect. 3-T1S-R6W (NLU 1945, 6 spec.). *Oklahoma*: McCurtain Co.: Bar-

row Pits, 5 mi. S Broken Bow on U.S. Hwy. 259 (OAM 6648, 10 spec.); Oxbow L. near Eagleton (OAM 6637, 2 spec.) *Texas*: Bowie Co.: McKinney B. (TNHC 4998, 8 spec.); pond on Moser ranch (TNHC 5005, 11 spec.). Brazos Co.: Green L. (TAM W-2-a-46, 3 spec.; TAM W-2-a-47, 39 spec.). Cass Co.: Beach Cr., 1 mi. SW Atlanta (TNHC 33559, 1 spec.). Cherokee Co.: Striker's Cr., 15 mi. SW Henderson on Tex. Hwy. 79 (TAM W-2-a-40, 23 spec.). Hardin Co.: Pine Island B., 1 mi. W Saratoga (TNHC 971, 2 spec.). Harrison Co.: Caddo L. at Karnack (TNHC 938, 3 spec.); Caddo L. at State Park boat ramp (TNHC 1495, 1 spec.). Henderson Co.: Fincastle L. (TNHC 6124, 2 spec.). Houston Co.: Ratcliff L. (BU uncat., 2 spec.). Liberty Co.: Sand pits near Romayor (TAM 3396, 63 spec.); Neville B. at jct. Tex. Hwy. 105 (AMNH 32721, holotype; AMNH 32722, paratypes). Montgomery Co.: Cr., 15 mi. S Conroe on Hwy. 1314 (Tex. Parks and Wildlife Sheldon Reference Collection, 4 spec.). Sabine Co.: Toledo Bend Reservoir at jct. Tex. Hwy. 21 (SHSU uncat., 8 spec.). Walker Co.: pond 1 mi. W jct. Hwys. 150 and 1097 (SHSU 470, 43 spec.).

Other Material Examined: NLU 1914, 2282, 2736; SHSU 199, 228, 242, 444, 447, 448, 451, 452, 453, 456; TNHC 2882, 3628; TU 43285, 44596, 71432, 73757, 73973, 74072: UMMZ 110540, 110600, 131157, 146295, 146296, 159144.

Fundulus dispar

Arkansas: Ashley Co.: Overflow Cr., 12 mi. W Parksdale (NLU 11725, 12 spec.). *Illinois*: UMMZ 105834 (7 spec.); UMMZ 162874 (2 spec.). *Louisiana*: Franklin Par.: dr. canal ½ mi. N La. Hwy. 88, 3 mi. W La. Hwy. 17 (NLU 1899, 11 spec.). Ouachita Par.: Black L. (NLU 779, 13 spec.; NLU 840, 6 spec.). Union Par.: L. D'Arbonne (LPI 430, 18 spec.; NLU 16247, 13 spec.). *Michigan*: UMMZ 60564 (5 spec.); UMMZ 90149 (5 spec.); UMMZ 98010 (4 spec.). *Tennessee*: UMMZ 161023 (2 spec.).

Fundulus lineolatus

Florida: CU 12505 (12 spec.); CU 12814 (7 spec.); TU 12634 (9 spec.); TU 74396 (6 spec.). *North Carolina*: CU 14289 (56 spec.).

Fundulus nottii

Alabama: TU 2602 (11 spec.). *Florida*: Gilchrist Co.: Sante Fe R., ½ mi. upstream from mouth (TU 36514, 8 spec.); TU 1607 (25 spec.); TU 15256 (18 spec.); TU 18343 (23 spec.); TU 34823 (31 spec.). *Georgia*: Miller Co.: trib. Spring Cr., 4/10 mi. SW Colquitt (CU 23792, 7 spec.). *Louisiana*: BU (uncat., 13 spec.); TU 15466 (26 spec.).

Fundulus chrysotus

Florida: AMNH 22747 (2 spec.); AMNH 16126 (15 spec.). *Missouri*: UMMZ 139709 (2 spec.).

Fundulus cingulatus

Florida: CU 35355 (16 spec.). *Georgia*: CU 36315 (70 spec.); CU 39942 (12 spec.).

Fundulus sciadicus

Nebraska: CU 33811 (40 spec.).

Fundulus blairae, new species
Blair's Starhead Topminnow
Figures 1, 2, 3A

Fundulus dispar (Agassiz): Knapp, 1953, p. 89, fig. 122 (all Texas populations).

Fundulus notti[1] (Agassiz): Hubbs, 1957, p. 96; 1958, p. 8 (all Texas populations). Miller and Robison, 1973, pp. 155-156 (all Oklahoma populations).

Fundulus notti notti[1] (Agassiz): Brown, 1958, p. 477 (all populations west of the Mississippi River and south and west of the Ouachita River in Texas, Louisiana, and Oklahoma).

Holotype. AMNH 32721, adult male, 46 mm. SL, collected by dip net on the eastern bank of Neville Bayou at its intersection with Texas Highway 105, Liberty County, Texas, June 20, 1972, by Darrell D. Hall, Ralph R. Hammons, and E. O. Wiley.

Paratypes. AMNH 32722: 17 male, female, and juvenile specimens were taken with the holotype, and designated paratypes. All type specimens were originally catalogued SHSU 200. Meristic and morphometric data taken from the type specimens are given in table 1.

Diagnosis. *Fundulus blairae* differs from all other species of *Fundulus*, except those of the *nottii* species complex, in having a distinct subocular teardrop. *Fundulus blairae* differs from *F. lineolatus* and *F. nottii* in lacking vertical bars on the side of the body and in having a G-type head squamation pattern (fig. 3A). *Fundulus blairae*

[1]The species name *nottii* has been incorrectly spelled *"notti"* by most recent authors.

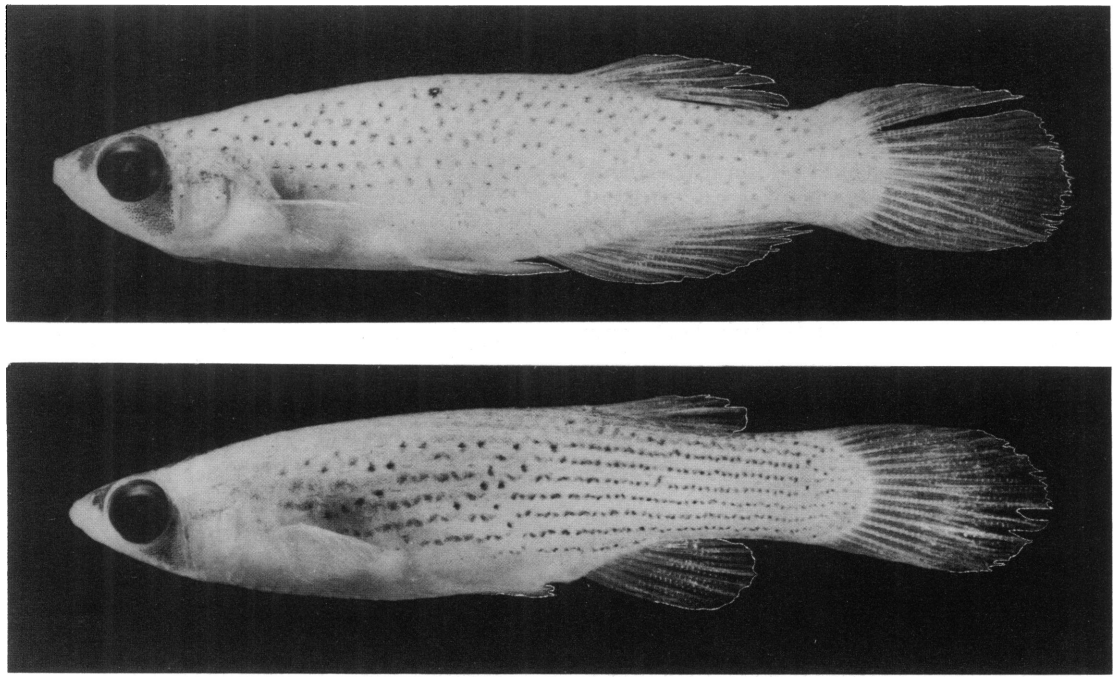

FIG. 1. Male holotype (above) and female paratype (below) of *Fundulus blairae*.

males differ from male *F. dispar* in lacking vertical bars on the side of the body, whereas female *blairae* differ from female *dispar* in having numerous dashes and less discrete melanophore development between the stripes on the body.

Description and Comparisons. Fundulus blairae is referable to the *F. nottii* species complex by the presence of a subocular teardrop, numerous stripes on the side of females, and numerous rows of dots on the side of males. It is a species of moderate length and proportions, neither as long as *F. nottii* nor as relatively deep bodied as *F. dispar*.

Body color patterns were taken from 245 preserved specimens distributed throughout the range of the species. Color patterns of the type

TABLE 1
Morphometric and Meristic Data of Type Specimens of *Fundulus blairae*

	Holotype Male	8 Paratype Males	9 Paratype Females
Standard length (mm.)	45	24-47	19-42
Body depth (mm.)	10.8	5.4-11.1	4.0-9.8
Caudal peduncle depth (mm.)	6.5	3.3-6.8	2.5-5.7
Snout length (mm.)	2.9	1.7-3.4	1.2-2.3
Teardrop length (mm.)	2.2	1.3-2.7	0.9-2.2
Number of:			
anal rays	10	10(2), 11(6)	10(1), 11(8)
dorsal rays	8	8(8)	7(1), 8(7), 9(1)
pectoral rays	13	13(5), 14(3)	13(8), 14(1)
lateral line scales	33	32-33	32-33
scales around body	26	24-26	24-26
scales around caudal peduncle	20	18-20	18-20

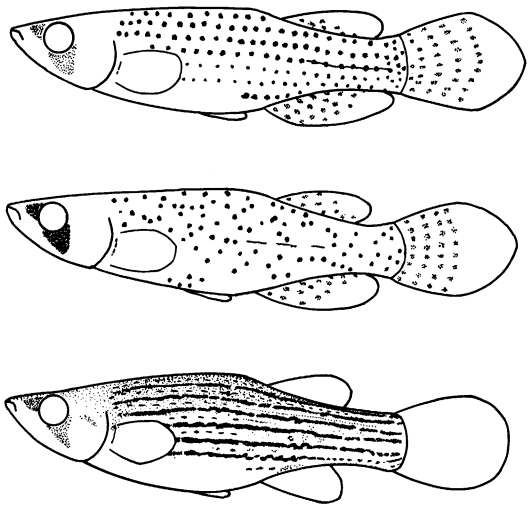

FIG. 2. Semidiagrammatic drawings showing color patterns of *Fundulus blairae*. *Above*: male paratype, southern male color pattern. *Middle*: male from the Red River (SHSU 450), Red River male color pattern. *Below*: female paratype, female color pattern.

specimens are those of the southern populations of the species. Vertical bars are missing on all but two males and on all juveniles. One male, from Toledo Bend Reservoir, may be an *F. blairae-F. chrysotus* hybrid. The other, from Caster Creek, may be an *F. blairae-F. dispar* hybrid. Dots on the side of the body are reddish in life, brown preserved, forming regular rows in males from the southern drainages and irregular rows in males from the Red River drainage (fig. 2, table 2). Dots are found both dorsally and ventrally in male *blairae* and *nottii*, and on male *dispar* they appear to be restricted to the upper three or four scale rows. In male *lineolatus* dots are large dorsally and there may be smaller dots or none ventrally. All males of *dispar* and *lineolatus* examined have stripes ventrally, a condition similar to some male *blairae* we examined from the Calcasieu and Red rivers. The ventral stripes of male *dispar* are occasionally disconnected, giving the impression of dots. These "dots," however, are found between the scale rows. Male *blairae* from other drainages do not have prominent stripes. Females of all four taxa have stripes. Female *blairae* have seven to nine stripes of moderate intensity, neither as dark and wide as in female *lineolatus* nor as light and thin as in eastern female *nottii* (in this form the stripes may be very light and not apparent on casual inspection). The stripes of female *blairae* are weakly serrate and are most similar to those of female *dispar*. Eastern female *nottii* are polymorphic with some females being rather similar to *lineolatus* and others having very light stripes and regular rows of dots similar to the pigment patterns of male *blairae*. Western female *nottii* have stripes that are interrupted by vertical "bars" formed by pigment on the posterior edges of the body scales, giving the appearance of a series of light blotches along the side of the body (as noted by Brown, 1958). Female *dispar* and *lineolatus* have little or no melanophore development between the stripes. Female *blairae* have many dashes and less discrete melanophore development between the stripes, whereas female *nottii* have dots either regularly or irregularly arranged. Female *blairae* and *dispar* lack the subdermal vertical bars found on female *nottii* and *lineolatus*. The southern populations of *blairae* have very diffuse to diffuse teardrops, whereas the Red River populations have a solid teardrop similar to that of *dispar*, *nottii*, and northern *lineolatus*. The teardrop exhibits age variation in its proportions; young have teardrops much wider that long, whereas adults have teardrops about as wide as long. The teardrops of adult *nottii* are usually longer than wide. That of *lineolatus* apparently shows geographic variation with specimens from Florida having very short and diffuse teardrops, and those from North Carolina having solid teardrops about as wide as long.

TABLE 2
Frequency Distribution of Dot Patterns in Male *Fundulus blairae* and Two Related Species

Species and Drainage	Dots Regular	Dots Irregular	Dots Missing	N
F. blairae				
Red River	3	23	2	28
B. Teche and Calcasieu	3	–	1	4
Sabine	7	3	–	10
Neches	5	6	1	12
Trinity	10	–	–	10
San Jacinto	30	–	–	30
Brazos	16	–	–	16
F. blairae (total)	74	32	4	110
F. nottii	48	4	2	54
F. dispar	36	8	–	44

TABLE 3
Frequency Distribution of Subocular Teardrop Intensity in *Fundulus blairae* and Two Related Species

Species and Drainage	Teardrop Very Diffuse	Teardrop Diffuse	Teardrop Solid	N
F. blairae				
Red River	1	50	24	75
B. Teche and Calcasieu	–	9	–	9
Sabine	3	8	8	19
Neches	–	25	–	25
Trinity	–	15	5	20
San Jacinto	9	39	–	48
Brazos	25	14	–	39
F. blairae (total)	38	160	37	235
F. nottii	–	6	150	156
F. dispar	–	4	68	72

The dorsal, anal, and caudal fins of male *blairae* have small melanophores that border the edges of the fin rays, and larger blotches (reddish in life, brown preserved) found on the membrane between the rays. The caudal fin of *dispar* and western *nottii* males is similar to that of *blairae*. That of *lineolatus* and eastern *nottii* shows a reduction or loss of the blotches. Females of all four taxa have the bordering melanophores on the dorsal and caudal fin, and may have one or two rows of light blotches proximally on the anal fin. The dorsum of both sexes of all taxa is darkened as a result of general melanophore development.

Fundulus blairae resembles most *Fundulus*, including *F. dispar* and *F. lineolatus*, in having both pores 4a and 4b of the supraoccipital sensory canal series (figs. 3A-C, E, F). *Fundulus nottii* differs in lacking pore 4b (fig. 3D). *Fundulus blairae* is similar to *F. dispar* in having the single or paired "E" scale overlain by the "G" scale (figs. 3A, B). *Fundulus lineolatus* and *F. nottii* have the opposite arrangement (figs. 3C, D). These are herein termed the G-type and E-type head squamation patterns respectively. The usual pattern in the genus is the A-type pattern where the "A" scale overlies the "E" scale(s) which in turn overlies the "G" scale(s) (fig. 3F). These conditions apply only to specimens with no regenerated scales on the head.

Meristically *F. blairae* resembles *dispar* and differs from *nottii* and *lineolatus* in having a modal anal fin ray count of 11 (10 in *nottii* and *lineolatus*) and fewer lateral line scales (modally 33 or fewer in the former two and 34 or more in the latter two species). *Fundulus blairae* differs from *nottii* and *dispar* and is similar to *lineolatus* in scales around the body (modally 24 or fewer in *blairae* and *lineolatus*, 25 or more in *nottii* and *dispar*). *Fundulus blairae* is similar to *nottii* and *dispar* and differs from *lineolatus* in the number of scales around the caudal peduncle (modally 18 or more in *blairae*, *nottii*, and *dispar*, 16 or fewer in *lineolatus*). Frequency distributions of the various meristic counts taken are shown in tables 4-9. Meristic counts for *lineolatus* are those reported by Brown (1958) and are shown here for comparison.

Intraspecific Variation. Fundulus blairae from the Red River differ in two color patterns from *blairae* to the south and west: subocular teardrop shading (table 3) and male dot pattern (table 2). Frequency distributions of meristic characters do not indicate any significant east-west or north-south trends. Populations from the Red River do have a lower anal fin ray count.

Range. Known from Bayou Teche, St. Martin Parish, Louisiana, northward along the Red River drainage to the Little River of southeastern Oklahoma, westward to the middle Brazos River drainage in Brazos County, Texas, and southwestward along the Gulf Coast to the Galveston Bay drainage, Texas (fig. 4).

Habitat. Fundulus blairae is a topminnow found in relatively clear ponds, lakes and bayous, in shoreline vegetation, and in streams where current is slow. It is also commonly found in barrow ditches that receive regular overflow from larger bodies of water.

Etymology. Fundulus blairae is named for Blair Knies for her assistance in all the field work associated with the project.

Relationships. A phylogenetic analysis of the *Fundulus nottii* species complex and three possible sister taxa, *F. chrysotus*, *F. sciadicus*, and *F. cingulatus*, is shown in figure 5. This kind of analysis is used to determine cladistic relationships. The common possession of shared derived characters (synapomorphies) between two or more taxa indicates that they are more closely related to each other than to taxa without the character. Common possession of primitive characters (symplesiomorphies) neither indicates nor precludes a close relationship. Overall similarity is

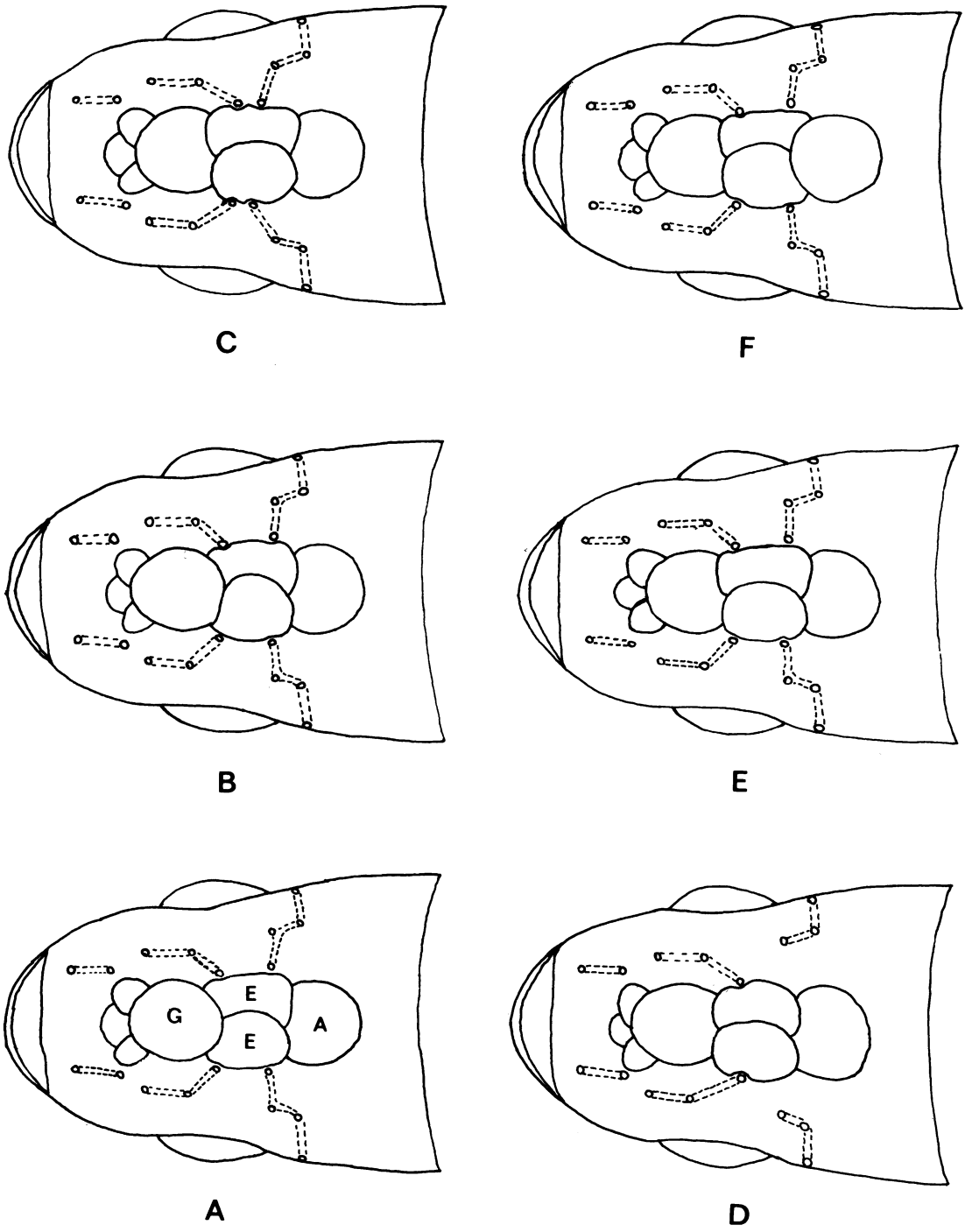

FIG. 3. Head squamation patterns and supraoccipital pores of six species of *Fundulus*. A, *F. blairae*; B, *F. dispar*; C, *F. lineolatus*; D, *F. nottii*; E, *F. cingulatus*; F, *F. chrysotus*. A and B, G-type pattern; C to E, E-type pattern; F, A-type pattern.

TABLE 4
Frequency Distribution of Anal Fin Rays in *Fundulus blairae* and Two Related Species

Species and Drainage	Number Anal Fin Rays 9	10	11	12	N
F. blairae					
Red River	3	49	27	3	82
B. Teche and Calcasieu	–	3	6	–	9
Sabine	–	8	10	1	19
Neches	–	13	10	2	25
Trinity	–	15	46	5	66
San Jacinto	–	13	35	5	53
Brazos	–	22	16	1	39
F. blairae (total)	3	123	150	17	293
F. nottii	18	123	7	–	148
F. dispar	–	18	50	5	73

rejected as a criterion for showing cladistic relationships. The philosophy and methodology of this type of analysis is dealt with by Hennig (1966), Brundin (1966), Kavanaugh (1972), and Griffiths (1972).

The *F. nottii* species complex, the three other *Fundulus* named above, and *F. luciae* are characterized by the derived nature of their karyotypes. Chen (1971) characterized this group as the "LSA-V" group based on the predominance of "long short-armed" acrocentric chromosomes ($> 50\%$), and a total chromosome count of less than 2N=48 (2N=46 in this group). The number of chromosomes alone is sufficient to characterize this group from all other karyotypically known North American *Fundulus* (20 of 27 species) except *F. notatus* which may be distinguished by the predominance of "short short-armed" acrocentric chromosomes. We conclude that the chromosome characteristics of "long short-armed" acrocentric chromosomes, a chromosome count of $2N \leqslant$ than 46, and the presence of two or more long chromosomes is a shared derived character uniting the *F. nottii* complex with *F. chrysotus*, *F. cingulatus*, *F. sciadicus*, and *F. luciae*.

Fundulus chrysotus and *F. sciadicus* are provisionally considered sister species as a working hypothesis. We have not examined these species in detail and cannot form a definite hypothesis of relationship between them. Their karyotypes are sufficiently apomorphic to distinguish both from *F. cingulatus* and the *nottii* species complex. Chen's (1971) karyotype analysis indicates that *F. chrysotus* is the intermediate in a transformation series between the primitive karyotype of the LSA-V group (as exhibited by known samples of *F. cingulatus* and the *nottii* complex) and the more apomorphic *F. sciadicus*.

Fundulus cingulatus is considered the sister group of the *nottii* species complex based on the head squamation patterns shown in figure 3, and the presence of regular rows of reddish dots on the side of males of the five taxa. We interpret the E-type head squamation pattern exhibited by *F. cingulatus*, *F. nottii*, and *F. lineolatus* as intermediate in a transformation series from the typical A-type pattern shown by most species of *Fundulus* and the more apomorphic G-type pattern shown by *F. blairae* and *F. dispar*. Dots on the side of the body appear in several groups of cyprinodont fishes. *Fundulus cingulatus* and members of the *nottii* complex seem to be the only *Fundulus* that have regular rows of reddish dots associated with the center of scales on the body. The dots of *F. cingulatus* males are not well preserved in the material we examined, but their presence is indicated in several color photographs we have seen. *Fundulus chrysotus* has reddish dots, but these seem to be confined mostly to the caudal peduncle and are less regularly distributed.

That *F. nottii* and *F. lineolatus* are more closely related to *F. blairae* and *F. dispar* than to *F. cingulatus* is indicated by the presence of two synapomorphies shared by the members of the *nottii* complex but not by *cingulatus*: a subocular teardrop and numerous stripes on the

TABLE 5
Frequency Distribution of Dorsal Fin Rays in *Fundulus blairae* and Two Related Species

Species and Drainage	Number Dorsal Fin Rays 7	8	9	N
F. blairae				
Red River	19	59	3	81
B. Teche and Calcasieu	1	8	–	9
Sabine	4	15	–	19
Neches	3	21	–	24
Trinity	7	53	1	61
San Jacinto	–	36	16	52
Brazos	2	35	–	37
F. blairae (total)	36	227	20	283
F. nottii	13	114	1	128
F. dispar	9	41	2	62

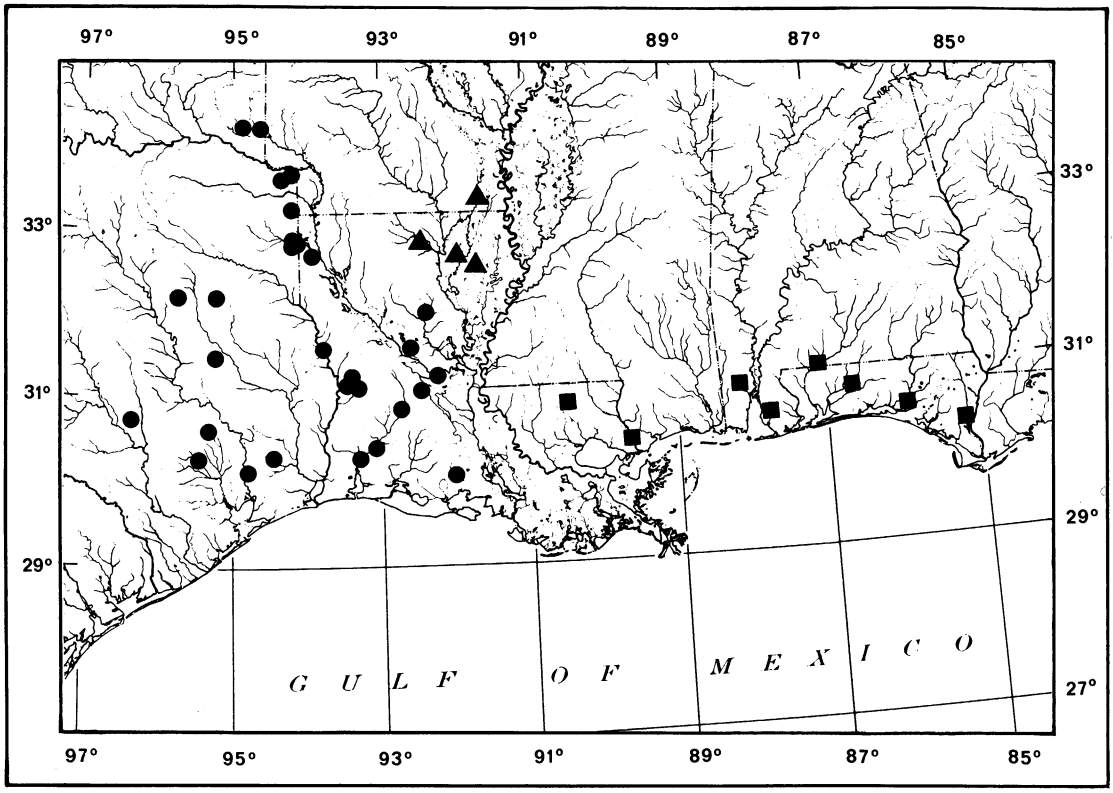

FIG. 4. Geographic distribution of *Fundulus blairae* (circles), southern populations of *F. dispar* (triangles), and populations of *F. nottii* (squares) west of the Apalachicola River.

side of females. These characters are not shared in combination by any other species of *Fundulus* and the presence of the subocular teardrop is a diagnostic character of the complex.

Relationships within the *nottii* complex are not fully resolved by our analysis (note the trichotomy in fig. 5). Although *F. lineolatus* is similar in some characters to *F. nottii* (presence of vertical bars in females, number of lateral line scales, etc.), these characters either appear to be primitive or their state cannot be determined. Neither *F. lineolatus* nor *F. nottii* shares a synapomorphy with each other that is not shared by *F. blairae* and *F. dispar*. *Fundulus nottii* complicates the problem by being polymorphic for several male and female color patterns and this species might be found to include two recognizable taxa. *Fundulus blairae* and *F. dispar* share two derived characters: the head squamation pattern discussed above and the absence of vertical bars on the side of females. The latter character is considered derived based on two lines of evidence: vertical bars are present on female *nottii*, *lineolatus*, and *cingulatus*, and a variety of other *Fundulus*; young of *nottii*, *lineolatus*, and *dispar*

TABLE 6
Frequency Distribution of Pectoral Fin Rays (Total of Both Fins) in *Fundulus blairae* and Two Related Species

Species and Drainage	Total Pectoral Fin Rays 23-24	25-26	27-28	N
F. blairae				
Red River	31	37	12	80
B. Teche and Calcasieu	–	4	1	5
Sabine	10	9	–	19
Neches	18	5	–	23
Trinity	–	14	4	18
San Jacinto	11	36	1	48
Brazos	17	16	3	36
F. blairae (total)	87	121	21	229
F. nottii	45	92	16	153
F. dispar	8	51	9	68

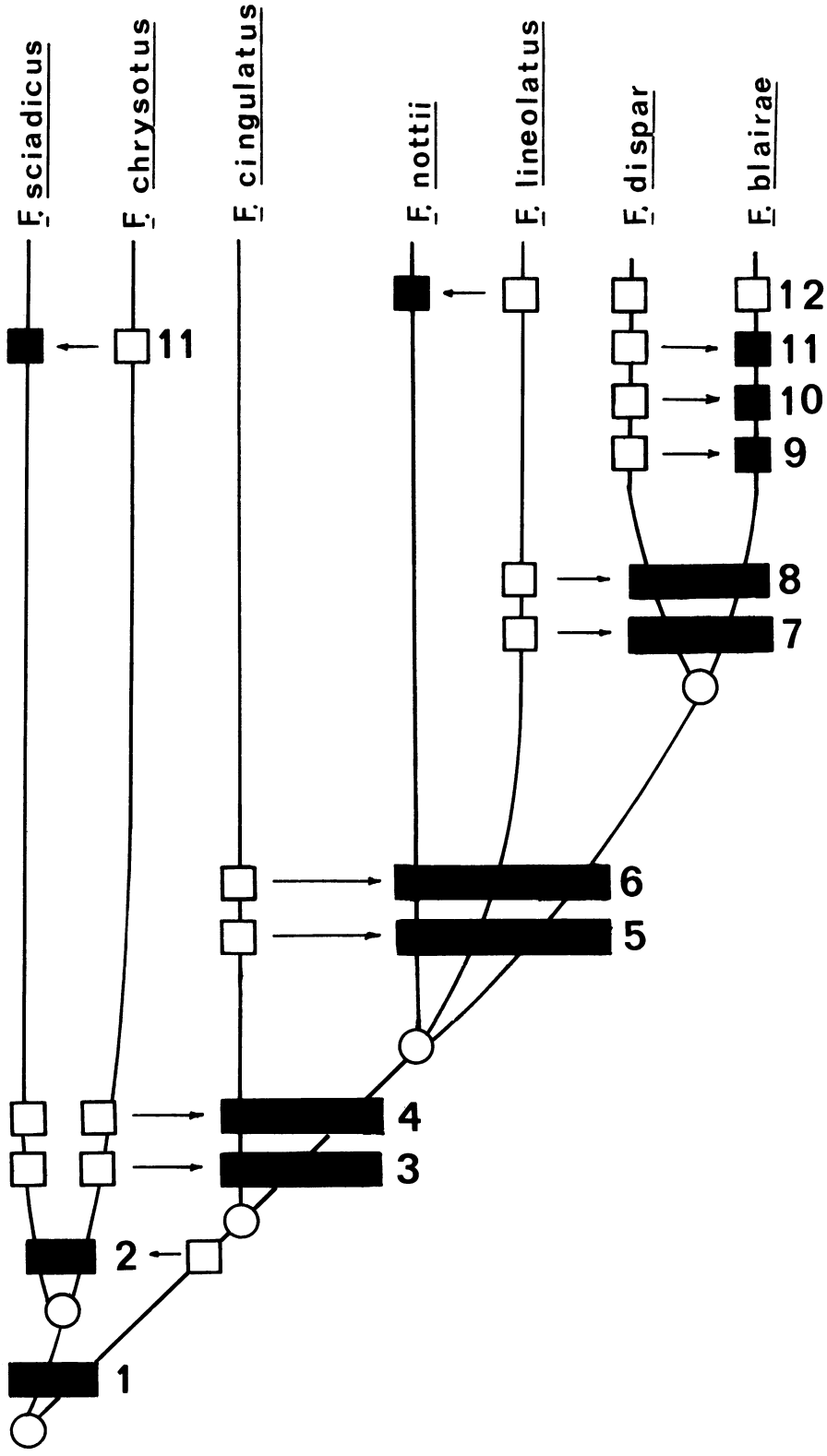
F. sciadicus
F. chrysotus
F. cingulatus
F. nottii
F. lineolatus
F. dispar
F. blairae
12
11
10
9
8
7
6
5
4
3
2
1
11

TABLE 7
Frequency Distribution of Lateral Line Scales (Total from Each Side of the Body) in *Fundulus blairae* and Two Related Species

Species and Drainage	Total Lateral Line Scales							
	60-61	62-63	64-65	66-67	68-69	70-71	72	N
F. blairae								
Red River	10	4	16	28	12	1	–	71
B. Teche and Calcasieu	–	–	–	8	2	–	–	10
Sabine	1	4	1	2	–	–	–	8
Neches	–	–	–	1	–	–	–	1
Trinity	–	1	7	8	2	–	–	18
San Jacinto	8	11	5	17	3	2	–	46
Brazos	2	3	11	15	4	1	–	36
F. blairae (total)	21	23	40	79	23	4	–	190
F. nottii	–	–	7	39	61	38	10	145
F. dispar	2	14	25	15	2	–	–	58

females have vertical bars (Brown, 1958), but mature female *dispar* lose them. It is reasonable to assume that the vertical bars on both sexes seen in the young are primitive expressions and that the absence of vertical bars in female *dispar* and *blairae* (as well as in male *blairae*) is a derived condition compared with the retention of these bars in female *nottii* and *lineolatus*.

DISCUSSION

The phylogenetic analysis has proven useful in establishing: the relationship between *F. cingulatus* and the *F. nottii* species complex, the monophyletic nature of the *nottii* complex, and the sister-species relationship between *F. blairae* and *F. dispar*. Further analysis is necessary to establish the relationship of *F. chrysotus*, *F. sciadicus*, and *F. luciae* with the *cingulatus-nottii* group, and the relationship of *F. nottii* and *F. lineolatus* with the *blairae-dispar* species pair.

The possibility of sympatry between *F. lineolatus* and *F. nottii* has been unresolved, primarily because there has been no diagnostic feature with which to separate all *nottii* from all *lineolatus*. Rivas (1966) concluded that *lineolatus* and *nottii* were sympatric in northern Florida and therefore good species. Ramsey (personal commun.) also believes that the two forms are full species. We accept Rivas's conclusion but point out that the features he used to draw this conclusion are not diagnostic for either *nottii* or *lineolatus*. He stated that the relative length of the subocular teardrop could be used to separate the two species. This seems to work with the Florida material, but is not characteristic of *lineolatus* over its entire range. *Fundulus lineolatus* from North Carolina have teardrops that reach the preopercular canal. Rivas also cited the characters used by Brown (1958) to separate the two forms. Brown (1958) characterized "*F. n. notti*" males as having vertical bars which "fade" anteriorly, whereas those of *F. lineolatus* do not. This is true only when eastern male *nottii* are considered; western male *nottii* have vertical bars that

FIG. 5. A phylogenetic analysis of seven species of *Fundulus*. Open circles are hypothetical ancestors. Open squares are primitive (plesiomorph) character expressions and shaded squares are derived (apomorph) character expressions which are opposite of primitive expressions unless stated otherwise. Numbers refer to character expressions as listed below: 1, karyotype $2N = 46, > 50\%$ acrocentric chromosomes; 2, karyotype $2N < 46$; 3, dots on males in rows on the side of the body; 4, E-type head squamation pattern; 5, subocular teardrop; 6, six to eight stripes on the side of females between the scale rows; 7, G-type head squamation pattern derived from E-type pattern; 8, no vertical bars on the side of mature females; 9, no vertical bars on immature females; 10, no vertical bars on immature males; 11, no vertical bars on mature males; 12, pore 4b of supraoccipital canal series missing. Arrows are inferred directions of evolutionary change and do not imply ancestor-descendent relationships.

TABLE 8
Frequency Distribution of Scales around the Body in *Fundulus blairae* and Two Related Species

Species and Drainage	Number of Scales around Body 22	23	24	25	26	27	28	N
F. blairae								
Red River	10	20	15	11	9	6	–	71
B. Teche and Calcasieu	–	1	4	2	1	–	–	8
Sabine	1	4	9	3	–	–	–	17
Trinity	–	–	6	7	5	–	–	18
San Jacinto	19	13	15	2	1	–	–	50
Brazos	5	13	9	6	1	–	–	34
F. blairae (total)	35	51	58	31	17	6	–	198
F. nottii	2	19	40	65	11	2	–	139
F. dispar	2	8	8	24	16	8	1	66

do not "fade" anteriorly. Perhaps a better character employed by Brown is the scales around the caudal peduncle. This character seems to separate all but a few specimens of *nottii* (from the Apalachicola River) from most *lineolatus*. It certainly holds true for the specimens of *nottii* we examined from the Suwannee River (TU 36514). Female color patterns of Apalachicola River *nottii* seem to approach the patterns of female *lineolatus*, but most female *lineolatus* can be separated by their relatively wide stripes and their greater number of subdermal vertical bars. These characters, however, are of dubious value in determining sympatry because they are not diagnostic. The one character we have found that separates all *nottii* from all *lineolatus*, *dispar*, and *blairae* is the loss (or fusion with pore 4a) of the 4b supraoccipital canal pore in all *nottii*, leaving the derived pore pattern of 1-2a, 2b-3-4a, 5-6-7 (see fig. 3C). On the basis of this character we have examined two collections from the Suwannee River and find one (CU 23792) composed totally of *F. nottii*, and the other (CU 12505) composed totally of *F. lineolatus*. The forms, then, are sympatric and Rivas's conclusions are independently verified.

Determination of the taxonomic level at which allopatric forms should be placed is a problem that has been discussed by many authors. Gosline and Brock (1960) have clearly stated the problem in relation to endemic Hawaiian fishes. Rosen and Kallman (1969) have discussed it in relation to Middle American *Xiphophorus*. We adopt the view that recognizable taxa (at the 100% level) should be given species status. This is not our own concept but conforms closely to the attitudes expressed by Gosline and Brock (1960) and Rosen (personal commun.). In adopting this view we also adopt the attitude that the "biological species" concept is not operational unless there is sympatry between the most closely related species (sister species). *Fundulus blairae*, then, is not a "biological species" operationally because it is not sympatric with its closest relative, *F. dispar*. Further, *F. lineolatus* and *F. nottii* cannot be regarded as biological species operationally until they are demonstrated to be more closely related to each other than either is to the *blairae-dispar* species pair (see Croizat, Nelson, and Rosen, 1974, for discussion). We have followed our phylogenetic analysis in determining the status of the four forms of the *nottii* complex. Figure 5 suggests several conclusions. The most important is that *F. nottii* has not been shown to be more closely related to *dispar* and *blairae* than to *lineolatus*. To retain *lineolatus* as a full species while retaining the other forms as subspecies of a single species would be unwarranted because it would imply that *nottii* was more closely related to *dispar* and *blairae* than to *lineolatus*. This has not been demonstrated. Also following the phylogenetic analysis, we might place *dispar* and *blairae* in a single species. This might be warranted if the two forms were connected by a zone of intergradation. But, *blairae* and *dispar* are apparently not connected by such a zone. We therefore recognize *blairae* and the other three taxa of the *nottii* complex as full species.

TABLE 9
Frequency Distribution of Scales around the Caudal Peduncle in *Fundulus blairae* and Two Related Species

Species and Drainage	Number of Scales around Caudal Peduncle 16	17	18	19	20	21	N
F. blairae							
Red River	16	13	17	13	7	–	66
B. Teche and Calcasieu	–	–	3	4	1	–	8
Sabine	6	9	3	1	–	–	19
Trinity	–	–	1	1	6	–	8
San Jacinto	8	24	12	4	–	–	48
Brazos	8	15	8	4	–	–	35
F. blairae (total)	38	61	44	27	14	–	184
F. nottii	1	13	42	57	31	2	146
F. dispar	6	10	14	13	24	–	67

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