THE AMERICAN PERCID FISHES OF THE SUBGENUS *VILLORA*

BRUCE B. COLLETTE,

Ichthyological Laboratory, Fish and Wildlife Service
U.S. National Museum, Washington 25, D.C.

and

RALPH W. YERGER,

Department of Biological Sciences,
Florida State University,
Tallahassee, Florida

I. Introduction

The aims of this paper are threefold: to define the subgenus *Villora,* to resurrect and define *Etheostoma (Villora) okaloosae* (Fowler), and to examine intra-specific variation in *E. (Villora) edwini. Villora* was described as a new genus by Hubbs and Cannon (1935) on the basis of the new species *edwini.* Bailey (1951), in Bailey Winn and Smith (1954), and in Bailey and Gosline (1955) reduced the many nominal genera of darters to three: *Percina, Ammocrypta* and *Etheostoma.* In 1955 (Fig. 1), Bailey and Gosline arranged the darters in order of increasing specialization and some former genera were utilized as subgenera. *Etheostoma edwini* was listed under the subgenus *Hololepis,* without further comment. We cannot subscribe to this view. During his study of the subgenus *Hololepis,* the senior author (Collette, 1960) became convinced that *Villora* should be regarded as distinct from *Hololepis.* Through extensive collecting in western Florida, the junior author (Yerger, 1960) discovered that *Etheostoma okaloosae* (Fowler) is a valid species referable to the subgenus *Villora,* and concluded that it must be removed from the synonymy of *E. swaini* (Jordan) where it was placed by Bailey, Winn and Smith (1955).

The methods of this study are similar to those of Collette (1962). However, here we present the counts of the unpored (Table 3) as well as the pored and total lateral-line scales. This character is unimportant in the subgenus *Hololepis,* but proves most useful in *Villora.* Measurements were made following the technique described by Hubbs and Cannon (1935). In the course of this study, more than 1100 specimens of *E. edwini* and nearly 200 of *E. okaloosae* were examined. For purposes of comparison, summary counts for the two species of *Villora* are being presented along with those for the species of *Hololepis* in another paper (Collette, 1962, Tables 38-49).

II. Acknowledgments

The section on *Etheostoma edwini* is based on part of a doctoral dissertation presented to Cornell University by the senior author. Professor Edward C. Raney, who served as chairman of the committee, provided, in addition to constant interest, support for the study through National Science Foundation Grants 2893 and 9038.

The section on *E. okaloosae* is part of a study on the fishes of the Florida panhandle undertaken by the junior author with support from a National Science Foundation Grant G-6260 and from the Research Council of the Florida State University. The many contributions to this project by Ardith B. Cochran are gratefully acknowledged, as are the services rendered by W. Bruce Walden and Robert F. Christensen, graduate students at Florida State University. Colonel John N. Reynolds, Commander, Eglin Air Force Base, Florida, granted permission to collect on the military reservation and extended many courtesies. James E. Böhlke compared the type of *E. okaloosae* with several specimens sent to him by the junior author.

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III. Subgenus *Villora*

Villora Hubbs and Cannon, 1935:11-13 (type species *Villora edwini* Hubbs and Cannon, 1935, by original designation).

Lateral line slightly arched upward, incomplete to complete; pored lateral-line scales 20 to 36, unpored 0 to 18, total 32 to 42; infraorbital canal always complete, usually with 8 pores; supratemporal canal usually complete in adults; coronal pore present; interorbital pores usually 2; preoperculomandibular pores usually 9 or 10; vomer and palatine toothed; preopercle entire or crenulate; branchiostegal membranes separate or narrowly conjoined; branchiostegal rays usually 6; breast naked to entirely covered with scales; nape, preopercle, and opercle completely covered with imbedded cycloid to exposed ctenoid scales; parietal and interorbital regions naked; belly covered with unmodified ctenoid scales; flesh opaque; body rather stocky and somewhat compressed; vertebrae 33 to 38; premaxillary frenum broad; first dorsal fin moderately high, with 8 to 11 spines that lack thickened fleshy tips; second dorsal fin somewhat higher than first dorsal, with 9 to 13 rays; anal spines usually 2, the first thicker than the second; anal soft-rays 5 to 9; pectoral rays usually 12 or 13; segmented caudal rays: upper 8 to 13, lower 7 to 10, total 15 to 22; genital papilla of breeding female a low tube crowned with villi; pelvic fins closely approximated, separated by a distance equal to about one-half the pelvic base; dark humeral spot behind the opercle and above the pectoral fin origin usually prominent; breeding tubercles absent; males reaching a larger maximum size than females; habitat moderately fast, clear streams with patches of vegetation; range northern and western Florida and below the Fall Line in southwestern Georgia and in Alabama.

Hubbs and Cannon (1935) placed *Villora* between *Hololepis* and the catch-all *Poecilichthys*. They felt that many of the features of *Villora* were primitive and suggested that it may have evolved from an ancestor of *Hololepis*. The relationships of *Villora*, however, do not seem to lie with *Hololepis* (see Collette, 1962). The rediscovery of *E. okaloosae*, which is obviously closely related to *E. edwini* and more different from *Hololepis* than *edwini*, gives support to our view that *Villora* should stand as a subgenus separate from *Hololepis*. In a number of characters *E. okaloosae* is somewhat intermediate between *E. edwini* and E. *(Oligocephalus) swaini* (Jordan). There seems to be a trend toward a shorter genital papilla (Fig. 7), a more highly arched lateral line, a slenderer caudal peduncle, and fewer pored lateral-line scales as one moves from *E. (O.) swaini* through *E. (V.) okaloosae* to *E. (V.) edwini*. In the last three characters the evolutionary trend parallels that of the subgenus *Hololepis*, resulting in a superficial similarity between the *Villora* and *Hololepis* lines. *Villora* differs from the subgenus *Hololepis* by lacking breeding tubercles and by having a nearly complete lateral line, extending past the origin of the second dorsal fin (occasionally complete in *E. okaloosae*); a much less arched lateral line; the genital papilla in the form of a low tube crowned with villi (Collette, 1962: Fig. 1); and a dark humeral spot. The species live in clear, moderately fast-flowing, sandy-bottomed streams. *Villora* differs from many of the species of the subgenus *Oligocephalus* in having a somewhat arched lateral line and in the shape of the genital papilla. We have not studied thoroughly the differences between *Oligocephalus* and *Villora*. This matter deserves further study.

IV. Species of *Villora*

The two species that we refer to the subgenus *Villora* differ in a number of respects (Table 1). Frequency distributions of the more important characters are presented in

Tables 2-8. Table 9 compares the proportional measurements of the two species.

Etheostoma (Villora) edwini (Hubbs and Cannon)

Villora edwini—Hubbs and Cannon, 1935:13-16 (original description); Carr, 1937:83 (Fla.); Fowler, 1941:242, fig. 13 (not 3 as given) (Fla.); Bailey and Hubbs, 1949:10 (*edwini* one of a group of endemic species, probably relicts, in sinkhole region of N. Fla.).

Etheostoma edwini—Bailey, Winn, and Smith, 1954:144, 156 (range extension W to Perdido R., and N into S Ala.); Bailey and Gosline, 1955:20, 43-44 (number of vertebrae); Carr and Goin, 1955: 31, 101-102, pl. 30 (description, Fla.); Eddy, 1957: 220, 223, fig. 552; Moore, 1957:197; Neill, 1957:196 (distribution in Fla. stops at the Suwannee Straits, although habitat continues); Briggs, 1958: 275 (distribution); Crittenden, 1958:218 (Bay Co., Fla.); Yerger, 1960:41 (comparison with *E. okaloosae*); Collette, 1961: 1051.

Fowler's reports (1945: 251-252, 293-294) of *Villora edwini* from Ware County, Georgia and from Florida were based on *E. fusiforme barratti.*

Types—Holotype UMMZ 87892; 38 mm male; Fla., Santa Fe R., at Poe Springs; Feb. 8, 1928; E. T. Boardman. Paratypes, the rest of the specimens examined by Hubbs and Cannon (1935:13).

Coloration—The first dorsal fin of the female varies from almost clear to having four rows of rectangular blotches on each interspinous membrane. The second dorsal fin is colored like the first dorsal but has additional pigment on the rays, producing a barred appearance. Melanophores usually outline the anal and pectoral rays; the anal membranes are clear or have a few pigment cells. The pelvic fin is clear, with occasional melanophores on the rays. The caudal rays are barred; the membranes sometimes have pigment. Both belly and breast vary from being immaculate to having scattered large melanophores. The cheek has small and medium melanophores. All four orbital bars are developed; the suborbital is the most prominent; the supraorbital and suborbital both enter the eye. The pored portion of the lateral line is light, with pigment underneath some scales. Most specimens lack distinct basi-caudal spots; some have blackish median spots and vestiges of dorsal and ventral spots. Eight to twelve lateral blotches are sometimes present along the sides; they may extend down to the underside of the caudal peduncle. There are usually about nine dark brown dorsal saddles. Melanophores on the sides below the lateral line are generally arranged in a prominent X-pattern as described by Hubbs and Cannon (1935). Chromatophores below the lateral line are mostly black; those above the lateral line are brown. The genital papilla is usually devoid of pigment, but the dorsal surface of the distal portion is sometimes pigmented. Figure 1 shows the pattern of a breeding female.

In the non-breeding male the pectoral and caudal fins, orbital bars, basi-caudal spots and sides of the body are colored as in the female. The first dorsal fin is similar to but darker than that of the female. Small melanophores occur between the blotches on the second dorsal fin. The proximal three-fourths of the anal fin and and the proximal seven-eighths of the pelvic fin membranes are covered with small melanophores. Both belly and breast are covered almost entirely with small melanophores. The cheek is darker than that of the female. The light, pored portion of the lateral line stands out more sharply against the dark sides of the male. The lateral blotches and the dorsal saddles are usually more prominent in the male. The genital papilla is free from pigmentation and there is no pigment on the belly dorsal to it.

The basi-caudal spots, orbital bars, cheek and genital papilla of the breeding male are colored as in the non-breeding male. The blotches in the dorsal fins have orange centers. Most breeding males have three or four rows of such spots on the membranes of the first dorsal fin and three to five rows on the membranes of the soft-dorsal. Black pigment is concentrated anterior and posterior to the last dorsal spine. The anal fin also has orange spots which are usually arranged in one or two rows, and the entire fin is darkened by melanophores. The pelvic fin is covered with small melanophores. The pectoral fin differs from that of the species of the subgenus *Hololepis* in having at least the basal half of its membranes covered with small melanophores. In addition to the barring of the caudal rays there are small mel-

Figures 1-3. Females of three species of *Etheostoma.* 1. (Upper) *E. edwini,* FSU 6178, Mar. 25, 1960, 35.4 mm. **2.** (Middle) *E. okaloosae,* FSU 6078, Jan. 25, 1960, 40.0 mm. **3.** (Lower) *E. swaini,* FSU 1632, Mar. 5, 1954, 35.8 mm.

anophores on the interradial membranes. The belly, breast and branchiostegal membranes are uniformly sprinkled with small melanophores. The narrow light streak along the lateral line is not prominent. There are light (orange in life) spots on the sides, both above and below the lateral line. The dorsal saddles are sometimes indistinct. Figure 4 shows the pigment pattern of a breeding male compared with males of *E. okaloosae* and *E. swaini.*

Fowler (1941) presented a drawing labeled as *Villora edwini* (Fig. 3), and another labeled as *Hololepis barratti* (Fig. 13). The labels on these drawings were apparently reversed, since the scale on Figure 3 indicates a fish of about 26 mm total length (close to the stated length of the specimen of *barratti,* 29 mm) and that on Figure 13 indicates a fish of about 41 mm (close to the stated length of the specimen of *edwini,* 44 mm). Figure 13 is clearly intended to represent *Villora edwini* since the pored portion of the lateral line extends behind the end of the second dorsal fin and there are no prominent basi-caudal spots. The pored portion of the lateral line in Figure 3 extends only to the end of the first dorsal fin, and there are three prominent basi-caudal spots, characters indicative of *barratti.* However, there are too few lateral-line scales in the figure to portray *Etheostoma fusiforme barratti* accurately.

The colors of *E. edwini* in life are very striking, and the presently accepted common name, brown darter, does not portray adequately the distinctive characters of this species. A more descriptive common name is redspot darter. The following descriptions are based on a composite of field notes (by Yerger) on series collected from January through April. Males in full breeding color have orange-red spots scattered over the body from the back of the oper-

Figures 4-6. Males of three species of *Etheostoma*. **4.** (Upper) *E. edwini*, FSU 6154, Mar. 26, 1960, 36.8 mm. **5.** (Middle) *E. okaloosae*, FSU 6078, Jan. 25, 1960, 43.4 mm. **6.** (Lower) *E. swaini*, FSU 6071, Jan. 23, 1960, 39.6 mm.

culum to the caudal fin, above the lateral line, and extending halfway from the lateral line to the ventral contour of the body. The largest spots, about the size of the pupil, are immediately above and below the lateral line. Each spot consists of a central red portion surrounded by a yellow ring. The spinous dorsal fin has a prominent basal row and a sub-marginal row of orange-red spots, with two irregular rows between them. A large black blotch is present on the posterior part of the membrane, centered between the last two spines. The second dorsal fin has four similar rows of slightly smaller orange-red spots, and lacks the black area. There are two incomplete rows of reddish spots on the anal fin, best developed on the posterior third of the membrane. The caudal has three to six vertical bands of elongate reddish or reddish-brown blotches, most prominent on the base of the fin. The pelvics are dusky. The general body color is tan to yellow brown, with irregular darker blotches below the lateral line. Males with less brilliant coloration and younger males are generally more yellow and possess fewer spots on the body and on the dorsal and anal fins. Neither *E. okaloosae* nor any species of the subgenus *Hololepis* has red spots on the body.

Females lack the brilliant orange-red spots on the fins, but have several rows of very small reddish spots just above and parallel

to the lateral line. The caudal fin is like that of the male, but has smaller and more numerous reddish to yellowish spots. The pelvics are clear. The black coloration below the lateral line contrasts more strikingly with the tan coloration above the lateral line than in the males.

Genital Papilla — Hubbs and Cannon (1935:14) described the genital papilla of *E. edwini* as follows: "In the breeding female scarcely developed as such, represented by matted villi surrounding the oviducal opening; some villi long enough to reach anal fin; in the non-breeding female shrunken but preserving the villous appearance." Examination of a large number of specimens indicates the need for modifying this description. The papilla of the breeding female is a short tube, containing rugae which form villi at the terminus of the papilla. The thin membrane connecting these rugae tends to break from excessive probing or from the use of an air jet; the ends of the rugae then appear as free villi. Figure 7a shows the genital papilla of a typical female in breeding condition.

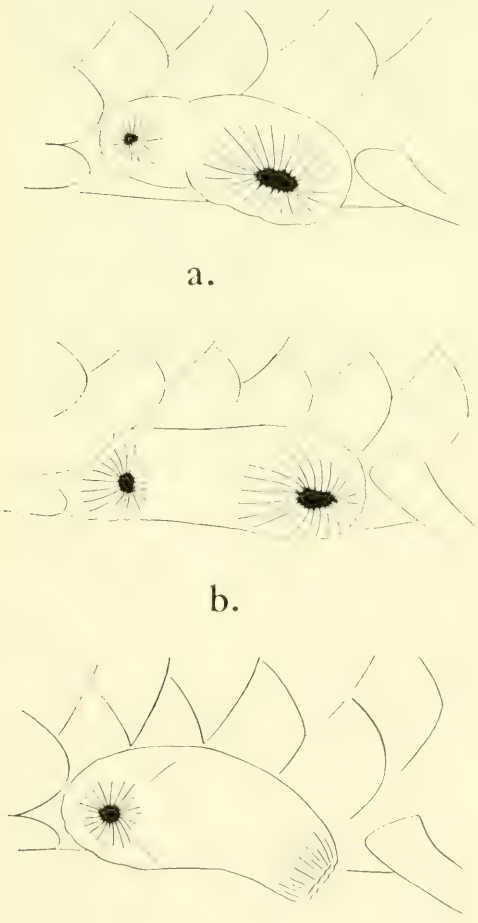

Figure 7. Genital papillae of breeding females of three species of *Etheostoma*. **a.** (Upper) *E. edwini*. **b.** (Middle) *E. okaloosae*. **c.** (Lower) *E. swaini*.

Development — Little information is available on the development of *E. edwini*. One collection (UF 6962) from the Apalachicola River system contains specimens as small as 11 mm SL. Plotting pored lateral-line scales against standard length for this collection (Fig. 8) gives about the same picture for their development as found in *E. fusiforme fusiforme* (Collette, 1962: Figs. 12 and 13). An 11.3 mm specimen lacked scales on the anterior portion of the body while another, 11.0 mm long, had the body completely scaled. The pored scales begin developing at about 12-13 mm. Figure 8 shows an intermediate group from about 15-21 mm which indicates that the definitive number of pored lateral-line scales may not be formed until a length of about 22 mm has been attained.

The same collection furnishes data on the size at which the supratemporal canal becomes complete. Specimens from 36.6 mm to 21.7 mm long are about equally divided between those with the canal complete and those with the canal incomplete, but all from 21.7 to 11.0 mm long have incomplete canals. A 12.0 mm specimen has only a shallow groove and completely lacks a roofed-over supratemporal canal. Adults of *E. edwini* typically have this canal complete, but individuals in a number of collections retain the juvenile incomplete condition.

Habitat — *E. edwini* usually lives in clear to slightly turbid streams varying in depth from six inches to two or three feet. The current is usually moderate. The bottom consists chiefly of sand with an occasional light overlay of fine silt, or some gravel, and occasionally rock outcrops. The vegetation varies from sparse to dense. The list of plants is long, and varies to some extent from one locality to another, but frequently consists of species of *Ludwigia, Scirpus, Orontium, Nitella,* and *Batracho-*

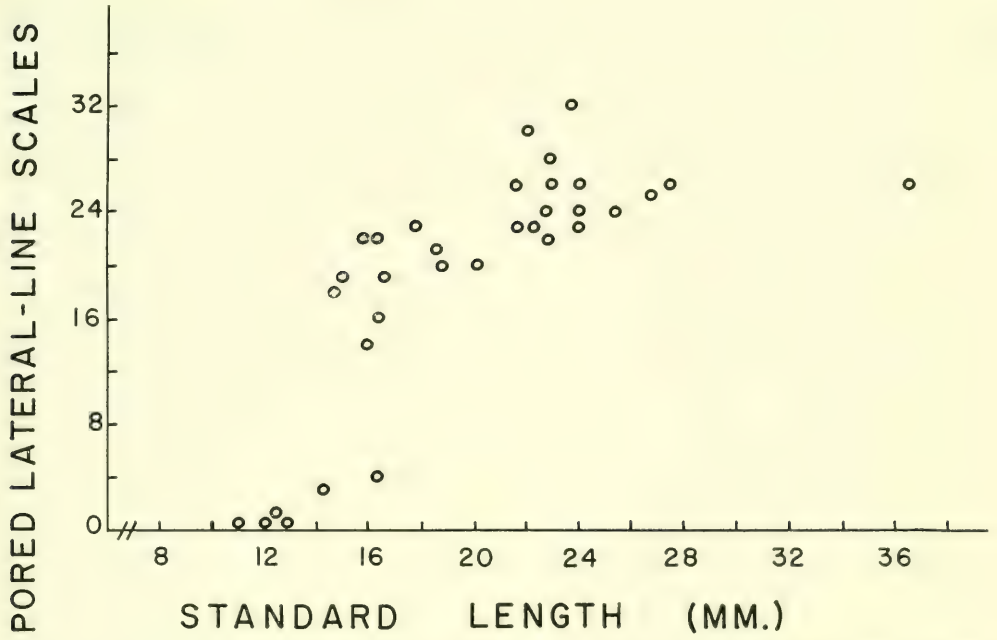

Figure 8. Change in number of pored lateral-line scales with size in *Etheostoma edwini*. (UF 6962, Fla., Apalachicola Dr., Dec. 2, 1939).

spermum. The pH varies from 6.4 to 7.8, the more alkaline readings having been recorded in spring runs with limestone outcrops.

Both species of the subgenus *Villora* prefer faster, clearer and more alkaline situations than do the species of the sugenus *Hololepis*. Crittenden (1958) gave some of the physical and chemical characters of two streams in Bay Co., Fla., one of which is inhabited by *Etheostoma edwini* and the other by *Etheostoma (Hololepis) fusiforme barratti*. The stream with *E. edwini* — Econfina Creek—"is spring-fed, clear, fast-flowing fresh water creek over most of its course; depths are three to ten feet near the mouth; and the bottom is of sand and limestone in its upper reaches." The pH was 7.5-7.8 and the methyl orange alkalinity was 45.5-56.0 p.p.m. The stream containing *E. f. barratti*—Cedar Creek—"is a sluggish slow-moving stream with currents noticeable only at low tide; the sand and mud bottom had a vegetable detritus overlay; depths vary from three to ten feet and the water is stained." The pH was 7.3 and the methyl orange alkalinity 35.0 p.p.m.

Habits—These darters are most frequently found beneath the leaves of scattered clumps of vegetation toward the margins of the streams rather than in the main current. Nothing is known about their spawning behavior, but since the genital papilla and the ecological requirements of *E. edwini* are so similar to those of *E. okaloosae*, it is highly probable that in behavior the two species are very much alike.

Examination of the ovaries of females and the development of breeding color in males indicates that the breeding season is at its height in February, March, and early April. Ripe ova occasionally observed in specimens collected as late as June indicate that the spawning season may be prolonged. Specimens as small as 11.0 mm SL. (UF 6962, Chipola R., Florida) were collected by William MacLane on December 2 in dense clumps of filamentous algae. The presence of fry in the beginning of December indicates that some individuals may spawn in the fall, at least in some years. Since this river originates from springs, its ecological conditions may differ from those in neighboring streams.

The males of *E. edwini* are considerably larger than the females. The largest male examined is 48.8 mm long (FSU 3404, Ochlockonee R.) and the largest female

39.9 mm (FSU 2218, Apalachicola R.). In the subgenus *Hololepis* the females are larger or the sexes are of equal size. Males of *E. edwini* have much brighter colors than do the males of the species of *Hololepis*. These characters would seem to be of advantage only to territorial species. Winn (1958:172) stated that for the darters he studied: "The male is larger than the female in all the species studied that have a well-developed territory . . ." with the exception of two species in which sex recognition and territoriality are easily disrupted. Hubbs and Cooper (1936), Noble (1938) and Raney and Lachner (1943) have also noted correlations between territorial behavior and degree of sexual dimorphism in color, size, or structure in various groups of freshwater fishes.

Distribution—Etheostoma edwini is limited to the Coastal Plain from the St. Johns River in northeastern Florida, west to the Perdido River of western Florida and southern Alabama, and north into Georgia as far as the Fall Line (Fig. 9). It is replaced by its relative *E. okaloosae* in several small streams tributary to Choctawhatchee Bay (Fig. 10).

Neill (1957) listed *E. edwini* as one of a group of species that has not crossed the Suwannee Straits to penetrate peninsular Florida. However, since the range of *E. edwini* does extend into Marion and Putnam counties in the St. Johns drainage, *edwini* should be added to Neill's list of species that barely penetrate the peninsula.

On the basis of present knowledge it is impossible to determine where or when *E. edwini* differentiated. Its wide range east to west and northward to the Fall Line would indicate that it probably was in existence before the Pleistocene. Periodic encroachments of the sea must have forced it to retreat toward the headwaters, where it survived only in those larger river systems along the Gulf Coast that were not completely inundated by salt water. As sea-level receded, it moved downstream to occupy all suitable habitats, and surrounded the restricted range of *E. okaloosae*. At the

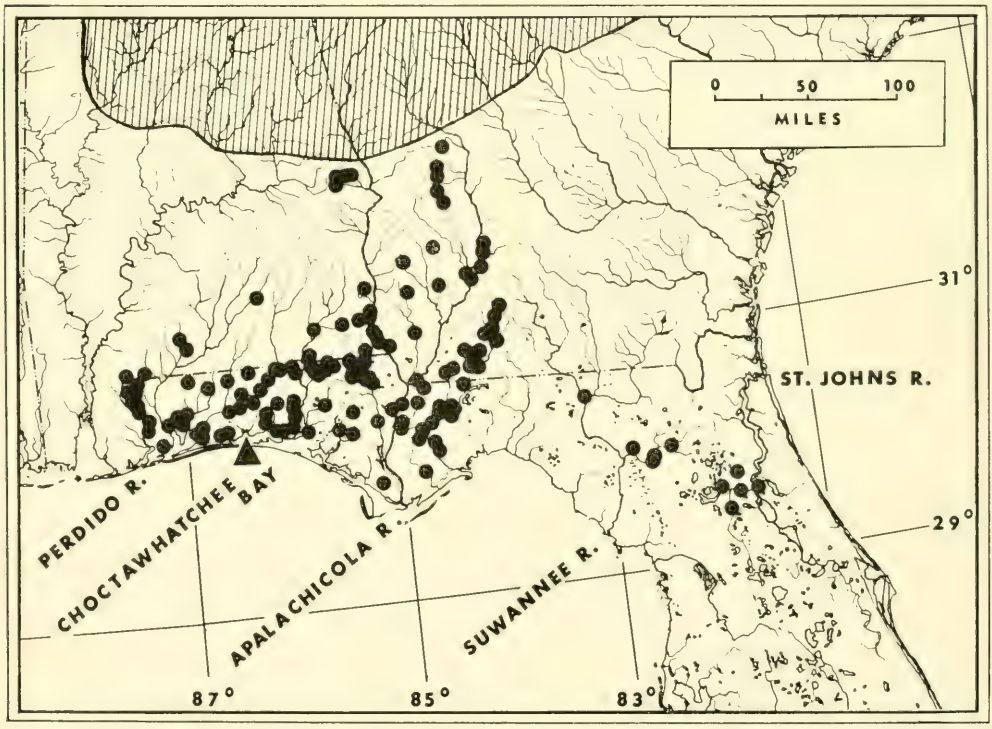

Figure 9. Distribution of *Etheostoma edwini* (dots) and of *E. okaloosae* (two streams at end of triangle) with reference to the Fall Line (taken from Fenneman, 1938 and 1946). (Based on specimens examined.)

present time, at several localities, streams occupied by *okaloosae* originate less than one mile from the headwaters of streams inhabited by *edwini,* but since the two species have never been taken together, there is no possibility of interbreeding under present conditions.

Geographic Variation — Since there is no appreciable variation in the number of pectoral rays (11-14, modes 13), condition of supratemporal canal (usually complete), number of interorbital pores (0-3, usually 2), or the squamation of the preopercle, opercle, and breast, summed frequency distributions have been presented in comparison with the data for *E. okaloosae* and the species of the subgenus *Hololepis* elsewhere (Collette, 1962: Tables 38-49).

The three easternmost populations (St. Johns, Suwannee, and Ochlockonee) have slightly more pored lateral-line scales ($\bar{x}$: 28.0, 29.9, 28.3) than the other populations ($\bar{x}$: 24.6 to 27.8) (Tables 2). This difference is correlated with the difference in number of total lateral-line scales. Populations in the St. Johns and Suwannee have higher means ($\bar{x}$: 38.1, 39.3); the westernmost population, the Perdido, also has a high mean (38.1); in the other populations the means vary from 37.1-37.6 (Table 4). The modal number of the scale rows above the lateral line is usually 3; the Suwannee and Ochlockonee populations have a mode of 4; the numbers are of about equal frequencies in the Flint system (Table 5). Most populations have a mode of 7 scale rows below the lateral line; the Suwannee population has a mode of 8; the westernmost populations, Pensacola Bay and Perdido drainage, have a mode of 6 (Table 5).

The modal number of first dorsal spines in most populations is 9 ($\bar{x}$:9.40 or less); the St. Johns and Suwannee populations again stand out with a modal number of 10 spines ($\bar{x}$: 9.69 and 9.55) (Table 6). The modal number of second dorsal rays is 11 in most populations; 10 in the Chipola and Choctawhatchee; 12 in the Chattahoochee population (Table 6). The modal number of anal soft-rays is 7 in all but two populations; the Chipola and Choctawhatchee populations have a mode of 6 rays (Table 8).

Most populations have modes of 10 preoperculomandibular pores but the three easternmost show a tendency toward fewer pores that is especially evident in the Ochlockonee population which has a mode of 9, thus resembling *E. okaloosae* (Table 7).

There is no evident geographic variation in extent of squamation except in the nape region. The eastern populations, through the Apalachicola, have the nape mostly I/PX-C/T to PX/X-T,* while the populations west of the Apalachicola (Choctawhatchee, Pensacola, Perdido) have modes of X T (Table 8).

Three slightly differentiated races of *edwini* may be distinguished: (1) an eastern race (St. Johns and Suwannee) with more pored lateral-line scales, more total lateral-line scales, and more dorsal spines; (2) an Ochlockonee race with a modal number of nine preoperculomandibular pores and a high number of pored lateral-line scales; and (3) a western race (Pensacola, Perdido, Choctawhatchee) having more scales on the nape. The Apalachicola River is inhabited by a population lacking any differentiating characters. If other characters are used, these races may be further subdivided. The Suwannee population has on the average more scale rows above and below the lateral line than does the St. Johns population. The Choctawhatchee population has fewer dorsal and anal soft-rays, and more scale rows below the lateral line than do the Pensacola and Perdido populations. Even the Apalachicola populations can be subdivided: the Chipola population has more total lateral-line scales and fewer second dorsal rays; the Chattahoochee population has more second dorsal rays; the Flint population has an intermediate number of second dorsal rays.

Specimens Examined—Full locality data are given only for collections from the St. Johns River (range extension) and for the type locality. For the other collections, drainage, state, county, and museum number are listed. Complete data for most of the collections are contained in Collette (1960).

St. Johns Drainage, Fla.—Marion Co.: UF 6963 (6 specimens, 32-43 mm. in standard length), small spring cr., 5¾ mi. NE Bruceville on Salt Springs Rd., Oct. 13, 1948. Oklawaha R. at Davenport Landing, 6-7 mi. upstream from mouth: UF 6968 (22, 22-38), Mar. 26, 1949; UF 6966 (7, 25-27), Oct. 2, 1949; and UF 6967 (2, 27-28),

* Squamation designation follows Collette, 1962. I, PX, X refer to the relative imbedding of the scales (imbedded, partially exposed, exposed respectively); C and T stand for cycloid and ctenoid.

Oct. 7, 1949. CU 35138 (1), Oklawaha R. just E of Eureka on Fla. 316, Mar. 27, 1960. Putnam Co.: Acosta Cr., 1.5 mi. N Welaka on Fla. 309; UF 6969 (4, 33-39), Dec. 28, 1946; and UF 6970 (1, 34), Mar. 24, 1947. UF 1911 (11, 25-37), 9 mi. W Palatka on Keystone Heights Rd., Mar. 24, 1947. UF 99 (1, 38), Little Orange Cr., 6 mi. S Johnson, May 22, 1947.

Suwannee Drainage, 131 specimens. Fla.—Alachua Co.: Santa Fe R. at Poe Springs, type locality; USNM 94684 (1, 33) and UF 2674 (2, 32-33), Feb. 8, 1928, paratypes; UF 209 (2, 33-38), Mar. 19, 1934; CU 10198 (1, 34), Apr. 6, 1940; UF 2910 (5, 29-35), May 8, 1947; UF 52 (13, 24-35), Oct. 13, 1947; UF 6964 (35, 22-38), July 27, 1947; UF 298 (6, 22-36), July 15, 1952. Columbia Co.: ANSP 69160; UMMZ 166571; TU 8441; UF 2676, 8091, 8087, 8106, 8100, 8095, 8074, 8125, 8078, 8131, 8115, 8116, 8126, 8122, 8123, 8030. Gilchrist Co.: UF 6960, 8028. Hamilton Co.: UF 2675. Suwannee Co.: FSU 1742. Union Co.: UF 2677.

Ochlockonee Drainage, 125 specimens. Ga.—Colquitt Co.: CU 17768; FSU 4447, 4069. Decatur Co.: FSU 2979, 3011. Grady Co.: CU 29759; FSU 2885, 2863, 4201, 4191, 4489. Thomas Co.: FSU 3990, 3969. Fla.—Franklin Co.: FSU 4865. Gadsden Co.: UF 6959; FSU 1657, 1637, 2524, 2205, 3404, 4431. Leon Co.: UF 6935; FSU 654, 5174, 3927. Liberty Co.: UMMZ 158182; UF 6965; FSU 228, 166, 2797, 3754, 3872. Wakulla Co.: FSU 3851.

Apalachicola River

Flint-Apalachicola Drainage, 110 specimens. Ga.—Calhoun-Dougherty cos.: UMMZ 164083. Decatur Co.: UF 595, 4493; FSU 1736, 2218. Dougherty Co.: CU 17322; UMMZ 163969, 164033; BU uncat. coll.; Early Co.: CU 18235. Miller Co.: CU 23794. Randolph Co.: CU 17752. Schley Co.: CU 29751, 29754. Seminole Co.: UF 4560. Sumter Co.: CU 29757. Taylor Co.: CU 21147, 29750. Terrell Co.: CU 15795. Worth Co.: UMMZ 164013; BU 2 uncat. coll. Fla.—Gadsden Co.: FSU 4029, 6272.

Chattahoochee-Apalachicola Drainage, 34 specimens. Ga.—Early Co.: CU 29745; FSU 6627. Ala.—Henry Co.: CU 17487; TU 2560; FSU 6572. Houston Co.: TU 2542, 2338, 2325. Lee Co.: UMMZ 128786; CU 15995; FSU 6649. Russell Co.: API 551; CU 15600, 13977; TU 10716; FSU 6586, 6655.

Chipola-Apalachicola Drainage, 125 specimens. Ala.—Houston Co.: CU 17676, 17667; TU 2406; UAIC 381. Fla.—Calhoun Co.: FSU 3814. Jackson Co.: UMMZ 158204, 163469, 163478; UF 6936, 6962, 4896; CU 29749; TU 127, 2292, 2380; FSU 1698, 2826, 4090, 4174.

Other Apalachicola Drainage, 19 specimens. Fla.—Calhoun Co.: TU 2042. Gadsden Co.: UF 4916, 4941. Gulf Co.: FSU 3298. Liberty Co.: UF 6971, 6972.

St. Andrews Bay Drainage, 4 specimens. Fla.—Bay Co.: FSU 552, 5766; TU 21449.

Choctawhatchee Bay Drainage, 197 specimens. Fla.—Holmes Co.: UMMZ 163502; CU 12116; TU 183, 1091, 1598, 2283, 2485, 2461, 2304, 2309, 20409; UMMZ 166327; FSU 1702, 1619, 2805, 4129, 4408, 6309. Holmes-Jackson Cos.: FSU 4168. Okaloosa Co.: FSU 5165, 6048. Walton Co.: TU 1073, 310; CU 21773; TU 1694, 1610, 22750; FSU 368, 4154, 5378, 5411, 6026, 6178, 6125, 6154. Washington-Bay Cos.: TU 3643. Washington Co.: FSU 5053. Ala.—Dale Co.: TU 4037, 2520. Geneva Co.: TU 1763, 14286, 16383. Houston Co.: CU 29758; TU 2512.

Pensacola Bay Drainage, 249 specimens. Ala.—Conecuh Co.: UMMZ 155518. Crenshaw Co.: TU 14194. Escambia Co.: TU 14177; UAIC 417, 420. Fla.—Okaloosa Co.: UF 6961, 3359; UMMZ 166239; FSU 4732, 4744, 4996, 6094, 6183. Santa Rosa Co.: UF 1456; UMMZ 155506, 166220, 165134; TU 4590, 20535; UF 7879; FSU 4670, 4940, 4950. Walton Co.: UMMZ 166246, 166351; FSU 6060.

Perdido Drainage, 76 specimens, Ala.—Escambia Co.: CU 15603; TU 14183, 16366, 23978, 21188. Fla.—Escambia Co.: UMMZ 134605, 166173, 166188; FSU 2958, 4799, 4761, 4726, 5956, 5843, 5799, 5862, 5880.

Etheostoma (Villora) okaloosae (Fowler)

Villora okaloosae—Fowler, 1941:242, 244 (original description), fig. 12 (holotype); Fowler, 1945:40, 294 (reference to holotype).

Etheostoma okaloosae — Carr and Goin, 1955:100 (characters and range mixed with that of *E. swaini*); Neill, 1957:185 (endemic in Florida panhandle); Yerger, 1960: 41 (validity of species, range).

Etheostoma swaini—in part; Bailey, Winn, and Smith, 1954: 143-144 *(E. okaloosae* synonymized with *E. swaini);* Moore, 1957:195 *(E. okaloosae* included under *E. swaini).*

Type—Holotype ANSP 69159; 24.4 mm female; Fla., Okaloosa Co., Little Rocky Cr., 7 mi. NE of Niceville on rt. 218 (now Fla. 285); June 20, 1939; F. Harper.

Since Fowler (1941:242) omitted counts of the cephalic pores, the following should be added to the original description (from examination of the holotype by the senior author): supratemporal canal complete, infraorbital with 8 pores, preoperculomandibular with 9 pores, both interorbital pores and coronal pore present. Counts of the lateral-line scales differ from Fowler's account of 30+3=33; there are 33+3=36 on the left and 35+2=37 on the right.

Comparisons—Etheostoma okaloosae is compared with *E. edwini* in Table 1. As previously indicated, it appears to be somewhat intermediate between *E. edwini* and *E. (Oligocephalus) swaini,* with which it has been confounded. *E. okaloosae* differs from *E. swaini* in the much shorter and more rugose genital papilla of the female (Fig. 7); in the higher arch in the lateral line, in the slenderer caudal peduncle, in the smaller number of unpored lateral-line scales, and in various details of pigmentation (Figs. 1-6); in having the preopercular margin at least slightly crenulate; and the prepectoral area at least partly scaled. *E. okaloosae* usually has 9 preoperculomandibular pores while both *E. edwini* and *E. swaini* usually have 10.

Coloration—On the first dorsal fin of the non-breeding female small to medium-sized melanophores are arranged in two or three irregular bands. The membrane of the soft dorsal fin is clear, with dark spots in four to six (usually four) rows. On the anal fin a few small melanophores are scat-

TABLE 1.
Comparison of Etheostoma edwini and E. okaloosae

Character	*E. edwini*	*E. okaloosae*
Branchiostegal membranes	Separate	Narrowly conjoined
Unpored lateral-line scales	4-18 (usually 7-15)	0-4
Pored lateral-line scales	20-34 (usually 23-32)	30-36 (usually 32-34)
Total lateral-line scales	34-42 (usually 36-40)	32-37 (usually 34-35)
Preoperculomandibular pores	Usually 10 (but often 9, and usually 9 in the Ochlockonee drainage)	Usually 9
Preopercular margin	Entire	At least slightly crenulate
First anal spine	Shorter than second	Longer than second
Red spots on body of males in life	Conspicuous	Lacking

tered, chiefly on the basal portion, occasionally on the rays. The rays of the pectoral fins are indistinctly outlined with pigment cells, which may also be scattered on the rays. The pelvic fins are similar to the pectoral fins. The caudal fin is indistinctly barred with five dark bands. The interradial membranes are clear or have a few melanophores on their distal portions. The belly and breast are usually immaculate white, but may possess a few brownish chromatophores. The cheek, throat, chin and branchiostegal membranes are usually white with numerous freckles formed by clusters of medium to large melanophores. All four orbital bars are developed. The supraorbital enters the eye. The suborbital is slightly to moderately developed and rarely enters the eye. The snout is almost uniformly pigmented. A single, median black spot is present at the base of the caudal fin and diffuse, brownish spots usually occur dorsal and ventral to the median spot. A well defined black spot covers one to two and one-half scales in the humeral region. Lateral-line scales are pigmented like the scales above and below, but the pores are unpigmented and appear as a thin, light-colored line. Excluding the humeral and basi-caudal spots, a series of 9-11 (usually 9) rectangular lateral blotches, wider than high, are located immediately below the lateral line. Dorsal spots or saddles are absent or indistinct; if present, two are on the nape, three under the first dorsal, two to four under the soft dorsal, and one, rarely, at

TABLE 2.
Number of pored lateral-line scales in Etheostoma edwini and E. okaloosae [1]

Species and Drainage	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	N	$\bar{x}$
E. edwini																			
St. Johns							3	10	7	4	5	1						30	28.03
Suwannee							4	5	10	15	13	10	11	4	3			75	29.87
Ochlockonee			1	—	—	2	7	18	20	8	8	6	5	1				76	28.30
Apalachicola																			
Flint				1	4	9	12	27	14	7	—	2	2					78	27.00
Chattahoochee				1	3	5	6	3	2	3								23	26.09
Chipola	1	4	6	13	26	14	18	3	5	—	2	—	1					93	24.62
Total Apalachicola	1	4	6	15	33	28	36	33	21	10	2	2	3					194	25.75
West of Apalachicola																			
Choctawhatchee	1	1	2	8	13	27	40	25	12	3	1	—	1					134	25.79
Pensacola Bay					2	5	10	17	21	7	11	3	—	—	1			77	27.79
E. okaloosae							1	4	6	1								12	27.58
Perdido											3	4	19	27	19	6	2	80	33.01

[1] To eliminate developmental variation, counts on specimens below 22 mm. have not been used.

TABLE 3.
Number of unpored lateral-line scales in Etheostoma edwini and E. okaloosae

Species and Drainage	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	N	$\bar{x}$
E. edwini																					
St. Johns								1	4	4	6	12	2	1	—	—	1			31	10.32
Suwannee					1	3	6	11	15	19	13	4	1	1						74	9.41
Ochlockonee					4	6	3	8	12	23	10	5	3	1	1					76	8.43
Apalachicola																					
Flint						2	—	1	10	16	19	13	7	4	3	2				77	10.16
Chattahoochee								1	1	7	3	8	1	2	5	2				30	11.13
Chipola								2	1	1	2	12	14	20	29	9	7	2		99	13.11
Total Apalachicola						2	—	4	12	24	24	33	22	26	37	13	7	2		206	11.72
West of Apalachicola																					
Choctawhatchee							1	—	2	7	19	42	29	20	15	4	1	3	1	144	11.81
Pensacola Bay					1	1	4	5	9	21	13	12	9	1	2					78	9.49
Perdido										3	4	4	1							12	10.25
E. okaloosae	5	33	26	12	4															80	1.71

the origin of the first caudal ray. The sides of the body are marked with longitudinal rows of dark dots, which extend from head to tail. There are two or three rows above and three to five rows below the lateral line. The center of each scale bears a pigment spot which is darker than the remainder of the scale. The genital papilla is usually immaculate, but occasionally a patch of melanophores appears posterior to its base. In breeding females there is a general increase in the number of small melanophores over most of the body and fins, and the submarginal orange-red band in the first dorsal becomes brighter. Figure 2 illustrates a female in breeding condition.

In the non-breeding male the pigmentation of the pectoral fins, orbital bars, snout, basi-caudal spots, humeral spot, lateral blotches, and longitudinal rows of dots is very similar to that of the female. Melanophores are more numerous on the first dorsal, anal, pelvic, and caudal fins. One-half to seven-eighths of the anal and pelvic fin membranes are darkened by these melanophores. The second dorsal fin is dark with light spots, just opposite to the condition in the female. The belly, breast, cheek, throat, and branchiostegal membranes possess numerous small melanophores. The genital papilla is immaculate, except for a few small melanophores around the base posteriorly.

The pigmentation of the breeding male is characterized by an enormous increase in the number of small melanophores over the entire body and fins. The submarginal orange-red band on the first dorsal fin is more vivid. Numerous melanophores are concentrated between spines VIII and IX to form two dark blotches. The anal fin is darkened by numerous melanophores, and one or two blotches are frequently evident between the first and second or between the second and third soft-rays. Melanophores are present on the basal one-third to one-half of the pectoral fin membranes. The pelvic fins are dusky, with an occasional blotch. The barring on the caudal fin may be indistinct, and the entire membrane is speckled with tiny melanophores. The presence of more melanophores on the lateral line renders the pores less distinct than in non-breeding individuals. The lateral blotches usually become more promi-

TABLE 4.
Total number of lateral-line scales in Etheostoma edwini and E. okaloosae

Species and Drainage	32	33	34	35	36	37	38	39	40	41	42	N	$\bar{x}$
E. edwini													
St. Johns						7	18	6	1	1		33	38.12
Suwannee					2	1	13	27	22	8	3	76	39.34
Ochlockonee				5	25	44	5	4	1			84	36.77
Apalachicola													
Flint			3	5	13	30	24	8	1			84	37.13
Chattahoochee					4	12	4	3	2			25	37.48
Chipola					9	40	46	15		2		112	37.67
Total Apalachicola			3	5	26	82	74	26	3	2		221	37.44
West of Apalachicola													
Choctawhatchee				1	15	53	46	14	5	2		136	37.59
Pensacola Bay			1	1	11	25	29	10	3			80	37.53
Perdido						5	4	4		1		14	38.14
E. okaloosae	1	6	24	34	13	1						79	34.70

TABLE 5.
Number of scale rows above and below the lateral line in Etheostoma edwini and E. okaloosae

	Above the lateral line						Below the lateral line								
Species and Drainage	2	3	4	5	N	$\bar{x}$	5	6	7	8	9	10	11	N	$\bar{x}$
E. edwini															
St. Johns		16	5		21	3.24		2	15	4				21	7.10
Suwannee		22	40	1	63	3.67		4	11	24	20	4		63	8.14
Ochlockonee		15	56	5	76	3.87		10	40	23	3	1		77	7.29
Apalachicola															
Flint		38	39	2	79	3.54		21	42	15	1			79	6.95
Chattahoochee	2	13	10		25	3.32	1	6	15	3				25	6.80
Chipola		44	20		64	3.31	1	8	19	20	11	3	1	63	7.71
Total Apalachicola	2	95	69	2	168	3.42	2	35	76	38	12	3	1	167	7.22
West of Apalachicola															
Choctawhatchee	2	86	50		138	3.35	1	43	75	19				138	6.81
Pensacola Bay	1	58	23		82	3.27	4	42	29	6	1			82	6.49
Perdido		12	2		14	3.14		10	3	1				14	6.36
E. okaloosae		10	70		80	3.88	5	74						79	5.94

nent, increase in size, become deeper than wide, and extend above the lateral line to within one or two scale rows of the dorsal fin, as well as below the lateral line. In some specimens these lateral blotches are barely discernible. The darkened appearance of the fish in breeding color renders the longitudinal rows of dots on the sides of the body less distinct. Melanophores are formed on the margins of the upper and lower surfaces of the genital papilla, as well as on the basal portion. Other areas are similar but darker than in the non-breeding male. Figure 5 shows the pattern of a male in breeding condition.

In life, the colors are far less striking than in *E. edwini.* The general color of the adult male is reddish-brown to yellow-brown, becoming lighter on the lower flanks and yellow-white to dusky white on the throat. An olive-green cast is especially prominent below the lateral line and on the caudal peduncle. The areas around the bases of the pectoral and pelvic fins are golden-yellow. The margin of the first dorsal is dusky with a bright submarginal orange-red stripe. The basal two-thirds of the fin is dusky. The membranes of the dorsal and pelvic fins are dusky with a papilla of a typical female of *E. okaloosae* is fin is usually barred with vertical bands of light and reddish brown, the dark bands are the broader. Females generally resemble the males, but the fins and body are lighter, and the orange-red stripe in the spinous dorsal is less bright.

Genital Papilla—In breeding females, the genital papilla is very similar to that of *E. edwini,* except that the tube is somewhat longer. Misuse of an air jet or excessive probing will create the appearance of free villi, as in *E. edwini.* The genital papilla of a typical female *E. okaloosae* is compared with that of *E. edwini* and *E. swaini* in Figure 7.

Development—Development in *E. okaloosae* is probably similar to that in *E. edwini.* Two 15 mm specimens have only 22 and 28 pored lateral-line scales while all specimens over 20 mm long have at least 32. Both 15 mm specimens have incomplete supratemporal canals, ten specimens 17.5-20.0 mm long are equally divided between incomplete and complete, and almost all specimens over 20 mm long have complete canals.

Habitat—The terrain in that portion of Okaloosa and Walton counties inhabited by *E. okaloosae* is sandy, deeply dissected, and covered by pines, scrub oaks and mixed hardwoods. Stream valleys are marked by the presence of alder, titi, wax myrtle, blackgum, and pines and oaks. The clear streams are small to medium-sized, with a moderate to swift current. The bottom consists chiefly of clean, light-colored sand, with some mud and detritus around patches of vegetation in areas with reduced circulation. Depths vary from six inches to four feet, and widths from five to 40 feet. The water is nearly neutral or slightly acid (pH 6.6-6.9). Vegetation is absent in some areas, sparse and scattered where clumps of bullrushes *(Scirpus etuberculatus)* are found, or dense with *Mayaca, Orontium, Nuphar, Nitella,* and *Potamogeton capillaceus.* The red alga, *Batrachospermum,* is present throughout the year, and occasionally forms thick concentrations. Other common fishes in these streams included: *Ichthyomyzon gagei, Esox americanus, Erimyzon sucetta, Notropis hypselopterus, N. petersoni, Hybopsis harperi, Noturus leptacanthus, Gambusia affinis, Aphredoderus sayanus, Micropterus salmoides, Ambloplites rupestris ariommus, Lepomis punctatus,* and *Percina nigrofasciata.*

Habits—The two species of darters in this stream system occupy different niches. *Etheostoma okaloosae* is most common around clumps of the bullrush *(Scirpus)* over a clean sandy bottom in areas with reduced current. It is usually in water from six inches to two feet deep and has rarely been collected at depths of three feet or greater. Few specimens have been taken from sections of the stream where *Mayaca* and other aquatic plants provide dense cover. Apparently this species avoids the large amounts of silt and organic sediments that accumulate in these heavily vegetated areas.

The other darter, *Percina nigrofasciata,* frequents the swifter areas of the stream, in the channels and deeper pools where vegetation is sparse or absent, but where logs or brushy cover are available. Only occasionally is it taken in areas with little water movement.

E. okaloosae was observed spawning by W. Bruce Walden and Ray Birdsong in Tom's Creek on March 25, 1961, in the swiftest part of the stream in water 12 to

TABLE 6.
Number of first dorsal spines and second dorsal rays in Etheostoma edwini and E. okaloosae

Species and Drainage	First dorsal spines						Second dorsal rays						
	8	9	10	11	N	$\bar{x}$	9	10	11	12	13	N	$\bar{x}$
E. edwini													
St. Johns		9	16	1	26	9.69		1	19	6		26	11.19
Suwannee	1	27	33	1	62	9.55		6	34	20	2	62	11.29
Ochlockonee	2	47	34	1	84	9.40		18	59	7		84	10.87
Apalachicola													
Flint	9	53	17		79	9.10	1	14	39	23	2	79	11.14
Chattahoochee	6	17	2		25	8.84	1	4	8	11	1	25	11.28
Chipola	5	44	15		64	9.16	4	35	22	3		64	10.38
Total Apalachicola	20	114	34		168	9.08	6	53	69	37	3	168	10.87
West of Apalachicola													
Choctawhatchee	15	98	22	1	136	9.07	1	72	58	6		137	10.50
Pensacola Bay	14	60	9		83	8.94		22	49	10	2	83	10.90
Perdido		13	1		14	9.07		3	8	3		14	11.00
E. okaloosae	2	31	4		37	9.05		3	32	40	5	80	11.59

TABLE 7.
Number of pores in the infraorbital and preoperculomandibular canals in Etheostoma edwini and E. okaloosae

Species and Drainage	Infraorbital pores							Preoperculomandibular pores					
	6	7	8	9	10	N	$\bar{x}$	8	9	10	11	N	$\bar{x}$
E. edwini													
St. Johns			12	3		15	8.20	1	7	11	1	20	9.60
Suwannee		2	38	2	1	43	8.05	1	26	33	1	61	9.56
Ochlockonee		4	75	4		83	8.00	3	70	5		78	9.03
Apalachicola													
Flint		8	75	1		84	7.92	2	14	62	1	79	9.78
Chattahoochee		1	21	2		24	8.04			24		24	10.00
Chipola		5	55	5	1	66	8.03		2	57		59	9.97
Total Apalachicola		14	151	8	1	174	7.98	2	16	143	1	162	9.88
West of Apalachicola													
Choctawhatchee	1	6	124	6	1	138	8.00	1	24	108	4	137	9.84
Pensacola Bay		12	69	1		82	7.87	3	18	54		75	9.68
Perdido		1	13			14	7.93		2	12		14	9.86
E. okaloosae		2	39			41	7.95	1	46	4		51	9.06

TABLE 8.
Number of anal soft rays and squamation of nape in Etheostoma edwini and E. okaloosae

Species and Drainage	Anal soft-rays							Nape squamation*				
	5	6	7	8	9	N	$\bar{x}$	I-C	I/PX-C/T	PX-T	PX/X-T	X-T
E. edwini												
St. Johns		4	14	3		21	6.95					
Suwannee		13	29	3		45	6.78	1	6	2	1	
Ochlockonee	1	31	43	3		78	6.62		7	1	3	
Apalachicola								1	5	7	2	
Flint		8	41	29	1	79	7.29	1	15	3		
Chattahoochee	1	4	13	6	1	25	7.08		7	6	1	
Chipola	1	34	25	3	1	64	6.52		1	3	5	2
Total Apalachicola	2	46	79	38	3	168	6.96	1	23	12	6	2
West of Apalachicola												
Choctawhatchee	2	70	62	4		138	6.49		1	—	1	7
Pensacola Bay		31	49	3		83	6.66		1	1	—	9
Perdido			10	4		14	7.29					3
E. okaloosae		8	65	7		80	6.99	5	26	1		

*See Text, page 223.

18 inches deep over a sandy bottom at the edge of clumps of *Nitella.* The male mounted the back of the female. Then, while remaining in a horizontal position, both moved forward a short distance, paused, and moved again. The pair spawned a few moments later, while lying side by side. Both male and female rotated their bodies slightly until their ventral surfaces were opposed, and quivered for several seconds. Examination of the vegetation revealed that several eggs had been deposited singly within the branches of *Nitella.* The vegetation and eggs were taken to the laboratory where one 5.5 mm larva hatched on March 27.

Several mature adults captured on March 25 were placed in aquaria in the laboratory. Although spawning behavior was not witnessed, six eggs were discovered on April 1, individually attached to masses of *Nitella.*

This spawning behavior is quite different from that observed by Winn (1958: 173) for other darters, where species with

flattened, flower-like genital papillae demonstrated a complex, inverted spawning behavior and laid their eggs on the underside of rocks.

Examination of adult females collected in January, March, August, September, and October revealed that large ova were present from late January to early August. The smallest young (15 mm SL.) in existing collections were taken August 11 and September 9. Breeding coloration appears to be most highly developed in January and March collections. It seems likely that this species has a rather long breeding period, probably from midwinter through early summer. The onset of spawning may vary from year to year, for temperature conditions in January and February in western Florida are mild in some years and severe in others.

Males are larger than females but the difference appears to be less than in *E. edwini*. The largest male of *okaloosae* examined is 43.5 mm long and the largest female 40.0 mm (both FSU 6078, Tom's Cr.). Differences in sexual coloration are likewise less pronounced. Although these differences in size and coloration are slight, limited observations both in the field and in aquaria indicate that this species exhibits territorial behavior to some extent. Studies on the reproductive behavior of both species of *Villora* are being continued by the junior author.

Distribution—*E. okaloosae* is confined to those streams of Okaloosa and Walton counties in west Florida that empty into Rocky and Boggy bayous near the western end of Choctawhatchee Bay, in the vicinity of Niceville. From east to west these streams are known as Rocky Creek, Lone Creek, Swift Creek, Turkey Creek, Tom's Creek, and their various tributaries. Although several of the streams inhabited by *E. okaloosae* originate less than a mile from the headwaters of streams inhabited by *E. edwini*,

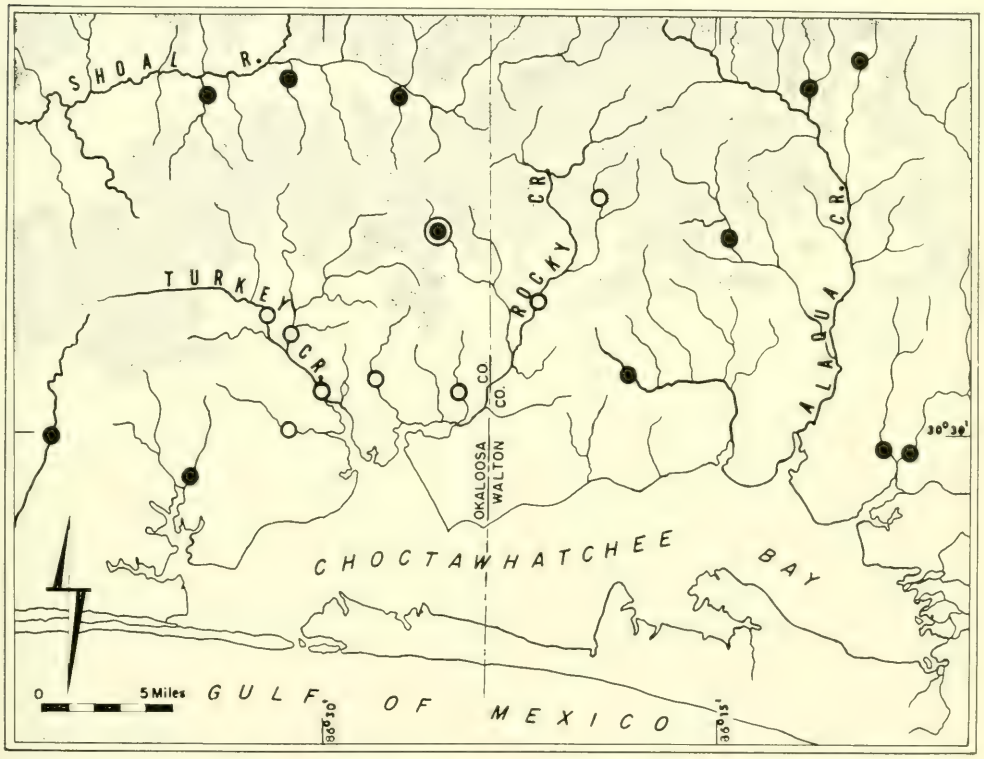

Figure 10. Distribution of *Ethcostoma edwini* (dots) and of *E. okaloosae* (open circles; encircled dot is the type locality) in the Choctawhatchee Bay region of western Florida. The stippling indicates the area of the hypothetical Pleistocene peninsula or island (see text) above the 150-foot contour line.

the two species are allopatric. The greatly restricted range of *E. okaloosae* is encircled by the range of the much more widely distributed *edwini* (Figs. 9 and 10). The collection sites for the specimens examined in this study together with the distribution of adjacent populations of *E. edwini* are shown in Fig. 10.

A slight lowering of sea level during Pleistocene glacial stages would have resulted in the conjoining of all the creeks inhabited by *E. okaloosae* into a single stream system originating in a highland area a few miles north of the Gulf of Mexico. The stippling on Fig. 10 indicates the land areas above the 150-foot contour line, which according to MacNeill (1957), is the maximum height to which sea-level rose during Pleistocene interglacial stages. It is likely, then, that during maximum inundation of the Coastal Plain, a peninsula with a very narrow connection to the mainland, or possibly an island, with freshwater drainage would have remained above the sea, and served as a refuge for *E. okaloosae* and other freshwater and terrestrial species. Cooke (1945) postulated a maximum rise of the sea to the present 270-foot contour. Even if this were the case, some land would have been emergent, for elevations up to 294 feet occur along this high ridge. Under these conditions, an island would have been cut off from the mainland to the north. Since erosion has continuously lowered this land mass, elevations in the Pleistocene were undoubtedly considerably higher, and consequently the highlands would have been greater in area than at present.

During one of the oscillations of sea-level in the Pleistocene, the *Villora* population in the stream system now inhabited by *okaloosae* may have been cut off from other *Villora* populations in the Choctawhatchee River drainage. During this period of isolation, a series of mutations may have occurred and may have spread rapidly through this small inbred population. Since the headwaters of this stream system would have remained above the sea, differentiation might have been completed prior to the subsequent lowering of sea-level to the point where the differentiated population may again have come in contact with older *Villora* populations. In the meantime, the ancestral *Villora* stock would have been forced into the headwaters of adjacent streams, and with the lowering of sea-level, could have moved downstream into newly emerged habitats to the west, north, and east (in the Yellow, Shoal, and Choctawhatchee rivers), and thereby have surrounded the range of *E. okaloosae*.

TABLE 9.

Proportional measurements of adults of Etheostoma edwini and E. okaloosae in thousandths of standard length

Catalog Number, FSU	*E. edwini* 4799 (5 females) 6178 (3 males) 4950 (2 males)		*E. okaloosae* 5135 (3 males, 1 female) 5138 (2 males, 1 female) 6214 (3 females)	
Measurement	Range	$\bar{x}$	Range	$\bar{x}$
Standard length, mm	29.7 - 43.6	36.3	28.7 - 39.9	33.4
Head length	256 - 302	280.6	268 - 323	292.6
Greatest depth	197 - 228	212.7	200 - 235	215.2
Least depth	95 - 115	105.8	109 - 153	123.5
Body width	128 - 157	143.4	131 - 164	146.3
Caudal peduncle length	280 - 350	299.7	245 - 272	260.2
Highest dorsal spine	109 - 158	131.3	106 - 135	123.2
Highest dorsal soft-ray	140 - 174	153.0	137 - 153	145.7
Caudal length	221 - 249	231.3	205 - 221	213.4
First anal spine	71 - 93	79.6	85 - 120	94.5
Second anal spine	76 - 95	86.7	70 - 105	84.4
Highest anal soft-ray	135 - 194	151.0	132 - 155	142.8
Longest pectoral ray	241 - 269	255.4	246 - 273	255.1
Pelvic length	196 - 212	206.4	194 - 223	205.7
Pelvic base	26 - 35	29.6	30 - 37	32.8
Interpelvic distance	11 - 17	14.5	12 - 18	14.6
Head depth	165 - 185	162.8	163 - 186	172.1
Head width	139 - 167	155.0	151 - 173	162.2
Snout length	41 - 60	50.2	48 - 64	57.6
Orbit length	71 - 90	79.5	72 - 81	75.9
Fleshy interorbital width	51 - 60	55.0	46 - 62	55.4
Upper jaw length	70 - 79	74.7	64 - 88	80.2
Distance from tip of jaw to union of gill membranes	104 - 139	117.9	137 - 161	150.0
Distance from union of gill membranes to insertion of pelvic fin	146 - 191	165.1	135 - 165	150.5

However, a comparison of primitive and specialized characters in the two species of *Villora* indicates that *E. okaloosae* is the more primitive species. It has a more nearly complete lateral line and a deeper body, the genital papilla of the breeding female is not quite as specialized, and the male lacks red spots on the body. If it evolved at an earlier date than *E. edwini,* it is reasonable to assume that it formerly occupied a wider range, which was later restricted by changes in sea-level during the Pleistocene, and that today it persists only as a relict. Its presence in only one stream system tributary to Choctawhatchee Bay is definitely believed to be related to the Pleistocene peninsula or island conditions described previously.

The unusual distributional patterns of many plant and animal species in the Florida panhandle have been discussed by Neill (1957). The occurrence of a number of endemics and "northern disjuncts" in Okaloosa and Walton counties on or in proximity to the Pleistocene peninsula or island emphasizes the unusual ecological conditions prevailing there. Recent unpublished investigations have added several species to this list. Further investigations on these problems are in progress by the junior author.

Specimens Examined—Since *E. okaloosae* was heretofore known only from the type locality, complete data are given. All series are from the Choctawhatchee Bay drainage system of western Florida.

Rocky Creek—Walton Co.: FSU 6101 (6 specimens, 24-32 mm. in standard length), E. Rocky Cr., 11.2 (airline) mi. NE Niceville, on Eglin Air Force Base rd. 201, Jan. 24, 1960. FSU 6032 (2, 27-30), Rocky Cr., 7.75 (airline) mi. NE Niceville on EAFB 200, Jan. 24, 1960. Okaloosa Co.: Little Rocky Cr., 7.5 mi. NE of Niceville on Fla. 285, type locality; ANSP 69159 (1, 24), holotype, June 20, 1939; FSU 6045 (25, 23-39), Jan. 23, 1960. UF 6937 (2, 23), Big Rocky Cr. near Niceville, Nov. 13, 1938.

Lone Cr.—Okaloosa Co.: FSU uncat. coll., Lone Cr., 4 mi. E Niceville, Feb. 4, 1961.

Swift Creek—Okaloosa Co.: FSU 5158 (7, 26-40), Swift Cr., 1.2 mi. NE Niceville on Fla. 285, Sept. 9, 1959.

Turkey Creek-Okaloosa Co.: FSU 5135 (26, 15-35), Turkey Cr., 5.4 mi. NW Niceville on EAFB 232, Sept. 9, 1959. Tenmile Cr., 3.5 mi. NW Niceville on Fla. 85; USNM 196136 (10, 23-39), Oct. 19, 1960; TU 18364 (3, 27-34), May 31, 1958. Turkey Creek, at W edge of Niceville on Fla. 85; FSU 1937 (1, 28), May 24, 1953; FSU 6214 (21, 15-33), Aug. 11, 1959; TU 4716 (1, 25), Nov. 14, 1952.

Tom's Creek - Okaloosa Co.: Tom's Creek approx. 2 (airline) mi. W Valparaiso on Fla. 85; FSU 6078 (50, 30-44), Jan. 25, 1960; FSU 6138 (11, 31-43), Mar. 26, 1960; FSU 6748 (10, 25-40), Oct. 19, 1960; TU 2079 (3, 28-38), May 26, 1951.

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VI. Abstract

The subgenus *Villora* Hubbs and Cannon is removed from *Hololepis* Putnam where it has been placed by some authors. This decision is based upon the belief that *Villora* constitutes a separate phyletic line running somewhat parallel to *Hololepis* and probably originating from the subgenus *Oligocephalus*. Important differentiating characters of *Villora* include lack of breeding tubercles, moderately arched lateral line, genital papilla of breeding female a low tube crowned with villi, a prominent humeral spot and a somewhat incomplete lateral line.

Variation in a number of meristic characters between populations of *Etheostoma (Villora) edwini* (Hubbs and Cannon) is considered. Three slightly differentiated races of *edwini* may be distinguished using lateral-line scales, preoperculomandibular pores and squamation of the nape. This species occurs in nothern and western Florida and below the Fall Line in southwestern Georgia and in Alabama.

E. okaloosae (Fowler) is resurrected from the synonomy of *E. swaini* (Jordan). It differs from *E. (Oligocephalus) swaini* in number of preoperculomandibular pores, shape of the genital papilla of breeding females, arching of the lateral line, squamation of the breast, nape, and prepectoral area, and in habitat. Several of these characters show that *E. okaloosae* is most closely related to *E. edwini* and belongs to the subgenus *Villora*. Possible reasons for the isolation of *E. okaloosae* in several small streams tributary to one arm of Choctawhatchee Bay are discussed and it is concluded that this is a relict species.

Photographs of both species and figures of the genital papillae are presented along with those for *E. swaini*. Discussions of habits, habitat, and relationships are included.