Geographic Variation in Gulf Slope Populations of the Bluntnose Darter, *Etheostoma chlorosomum* (Hay)

Henry L. Bart, Jr.
and
Robert C. Cashner

Department of Biological Sciences, University of New Orleans, New Orleans, LA 70148. (Present address of first author: Department of Ecology, Ethology, and Evolution, University of Illinois, Urbana, IL 61801).

Abstract

A total of 452 specimens of the bluntnose darter, *Etheostoma chlorosomum* from throughout the Gulf Slope portion of its range was examined for geographic variation in several morphological characters. Significant variation occurred in scale counts, the lateralis system, fin and branchiostegal rays, and body squamation, with the latter exhibiting the strongest patterns of geographic variation. Western populations (Colorado River, Texas) showed a consistent divergence with significantly higher means for otherwise conservative characters. However, there was little evidence to support the taxonomic recognition of any group of Gulf Slope populations of *E. chlorosomum*. Variation in *E. davisoni* is included for comparison. Relationships within *Vaillantia* and evolution of the group are discussed.

Introduction

The bluntnose darter, *Etheostoma chlorosomum*, is a widely distributed species found throughout much of the Mississippi River Valley and along the Gulf Coast (Gilbert, 1980). Despite its wide occurrence and relatively long history in the taxonomic literature, the bluntnose darter remains poorly known in many parts of its range. This study was undertaken to characterize the variation of the species over the southern part of its range (along the Gulf Slope), to compare morphological features for populations in the coastal drainages, and to classify relationships between *E. chlorosomum* and its reported closest relative, *E. davisoni*, the Choctawhatchee darter.

Nomenclatoral History and Relationships

The species was originally described as *Boleosoma camurum* by Forbes in 1878 from specimens collected in the Illinois River drainage, Illinois (Collette and Knapp, 1967). In 1881, Hay described *Vaillantia chlorosoma* from a tributary to the Tuscumbia River in Mississippi. Jordan and Gilbert (1883) recognized the similarity between *B. camurum* and *V. chlorosoma* and assigned *B. camurum* to *Vaillantia*. Bailey and Gosline (1955) recognized just one valid species, *Etheostoma chlorosomum* (the earlier name *camurum* was preoccupied in *Poecilichthyes*), which they assigned to the subgenus *Boleosoma*. Cole (1967) reallocated *E. chlorosomum* to the subgenus *Vaillantia* because the species exhibited character states that were inconsistent with other members of *Boleosoma*.

In addition to the bluntnose darter, the subgenus *Vaillantia* presently includes *E. davisoni*, which was resurrected from the synonomy of *E. stigmaeum* by Howell (1968). Although *E.*

chlorosomum has been considered in a number of taxonomic revisions, this study represents the first in depth treatment of variation and relationships for the species.

Page (1981) grouped *Vaillantia* with five other subgenera, including *Etheostoma, Nanostoma, Doration, Boleosoma,* and *Ioa.* Members share a tendency toward reduction of characters. Although *E. chlorosomum* and *E. davisoni* failed to cluster in phenograms, Page (1981) argued that *Vaillantia* should be retained due to important synapomorphies.

Distribution

The bluntnose darter is distributed in the Mississippi River basin from Minnesota southward to Louisiana, occurring in the lowlands and plains as far west as Oklahoma and to Indiana in the east (Gilbert, 1980). The species is also widely distributed across Gulf Coastal drainages east and west of the Mississippi River, where it is primarily restricted to low-gradient, Coastal Plain situations (i.e., below the Fall Line, Fig. 1). West of the Mississippi River *E. chlorosomum* occurs across coastal streams to the Colorado River drainage in Texas. Eastward the species occurs in major coastal streams from Louisiana to the Mobile Bay basin in Alabama. East of Mobile Bay, the the bluntnose darter is replaced by the Choctawhatchee darter, *E. davisoni,* which is confined to drainages of Pensacola and Choctawhatchee bays. Throughout its range, the bluntnose darter inhabits sluggish, low gradient streams, lower channels of large rivers, sloughs, backwaters and small lakes. The species prefers sandy to muddy bottomed streams with slight flow.

Pflieger (1971) classified *E. chlorosomum* as a lowland species, autochthonous to the central Mississippi Valley. This region is the apparent center of distribution and perhaps the center of origin as well. The bluntnose darter has undoubted followed the Mississippi Valley in its dispersal, except for its invasion of Gulf Slope drainages. There it likely crossed several southward flowing streams as it spread east and west. Populations of *E. chlorosomum* occurring in these streams are presently isolated from the more continuously distributed populations in the Mississippi River basin. In the case of *E. davisoni,* isolation in coastal streams was sufficiently long for speciation to occur. Thus, we expected variation to be most pronounced among Gulf Slope populations of the bluntnose darter, and therefore concentrated on this portion of its range. Data on variation of *E. davisoni* (included for comparison) was kindly provided by W. M. Howell (based on Howell, 1968).

Material Examined

Numbers in parentheses following major drainages are the total number of specimens examined and are applicable to the drainages listed in figures 3-9. Numbers in parentheses following museum numbers indicate specimens examined from that collection. Museum acronyms are identified in the acknowledgments.

Colorado River Drainage (6): Texas, Colorado Co., TU 73402 (5) Cummings Creek 0.5 mi above confluence with Colorado River; Travis Co., TNHC 1068 (1) Colorado River at Austin. Brazos River Drainage (12): Texas, Grimes Co., TNHC 8544 (8) Sulfur Creek 2.5 mi SW Singleton; TNHC 8511 (4) Gibbons Creek 2 mi NW Carlos. San Jacinto River Drainage (30): Texas, Harris Co., TU 66493 (20) Willow Creek at rear North Hampton subdivision; Montgomery Co., TU 61898 (10) San Jacinto River at FM 2854, 3 mi W Conroe. Trinity River Drainage (8): Texas, Liberty Co., TU 70123 (1) Trinity River at FM 1620, 5.3 mi W Moss; San Jacinto Co., TU 66447 (7) Big Creek at Texas Hwy 150, 2.3 mi N Shepard. Neches

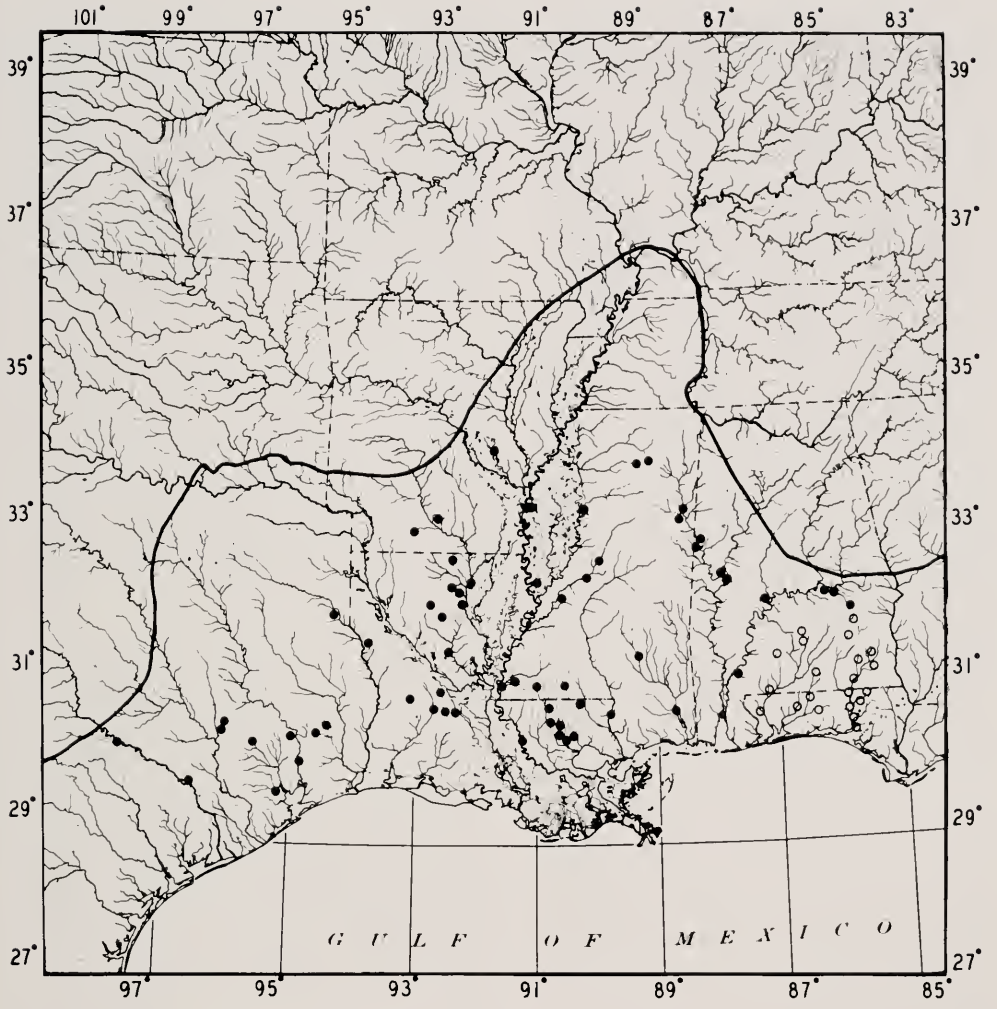

Fig. 1. Gulf Slope Region and its northern boundary, represented by the geographic Fall Line (heavy line), sample sites for *Etheostoma chlorosomum* populations (solid circles), and the distribution of *E. davisoni* (open circles).

River Drainage (31): Texas, Polk Co., TU 106050 (9) Big Sandy Creek, 3.5 km SE Camp Ruby, FM 1276; Tyler Co., TU 21457 (22) Little Cypress Creek at Rte 287, 6 mi N Woodville. Sabine River Drainage (25): Texas, Panola Co., CU 34924 (2) trib 2.8 mi NE Carthage, Rte 79; Louisiana, Sabine Par., TU 4566 (23) trib to Bayou San Patricia 4.4 mi NW Noble Hwy 171. Calcasieu River Drainage (36): Louisiana, Allen Par., TU 43299 (30) Calcasieu River at Hwy 10, 2 mi W Oakdale; Vernon Par., NLU 4437 (6) Calcasieu River at Hwy 339, sec 9, T1S, R7W. Mermentau River Drainage (5): Louisiana, Evangeline Par., TU 41473 (4); TU 44568 (1) Boggy Bayou at Hwy 106, 3 mi W Hwy 13. Vermilion-Teche River Drainage (23): Louisiana, Evangeline Par., TU 87389 (2) Lake Chicot at Chicot Park, sec 21, R2E, T3S; Rapides Par., TU 40013 (15); TU 50150 (6) trib to Bayou Cocodrie at Hwy 12, 1 mi E Melder. Little River Drainage (5): Louisiana, Grant Par., NLU 3273 (5) Fish Creek at Rte 123, sec 27, T8N, R1W; Jackson Par., TU 55132 (2) Dugdemona River 0.3 mi S Quitman; NLU 3708 (8) Flat Creek sec 30, T16N, R1W. Ouachita River Drainage (26): Louisiana, Ouachita Par., NLU 1439 (2) Edgewater Dam-Bayou at Desaird, sec 40, T1N, R4E; NLU 2827 (4) Cypress Creek, sec 5, T15N, R2E; NLU 3552 (5) Choudrant Bayou, sec 16, T18N, R1E; NLU 3553 (4) South Chenniere, sec 4, T16N, R1E; Union Par., NLU 2967 (4) Meridian Creek, sec 33, T23N, R1E; Arkansas, Cal-

houn Co., TU 97748 (3) Focus Creek at Hwy 4, 1 mi NW Focus Bayou; Columbia Co., TU 84264 (2) trib to Smackover Creek at Hwy 98, sec 2, T16S, R20W; TU 84254 (2) Sloan Creek, 8 mi NE Magnolia. MISSISSIPPI RIVER BASIN (11): Louisiana, West Baton Rouge Par., TU 112533 (7) Mississippi River at river mi 252; Mississippi, Issaquena Co., TU 48286 (1) Steele Bayou at Hwy 1, 4.6 mi W Onward; Bolivar Co., TU 86036 (1) Lake Whittington 2 mi W Benoit; Wilkinson Co., TU 71178 (1) Piney Creek at Hwy 563, 4.2 mi E Wilkinson; TU 86254 (1) Lake Mary 14.7 air mi NW Woodville. ARKANSAS RIVER DRAINAGE (30): Arkansas, Arkansas Co., TU 97370 (20) Crooked Creek at Hwy 79, 10 mi SW Stuttgart; TU 2219 (10) trib to Bayou Meto 2 mi N Humphrey. BIG BLACK RIVER DRAINAGE (30): Mississippi, Holmes-Attala Co., TU 88220 (11) Big Black River at Pickens, Hwy 17; Hinds Co., TU 75443 (9) Porter Creek 9.5 mi. NE Edwards; Madison-Yazoo Co., TU 73064 (10) Big Black River at Hwy 16, 4 mi WNW I-55. YAZOO RIVER DRAINAGE (6): Mississippi, Lafayette Co., TU 87649 (3) Little Kettle Creek at Hwy 334, 7.3 ml W Toccopoda; Pontotoc Co., TU 87623 (2) Mud Creek at Hwy 334 1.1 mi W of Springville; Mississippi, Tallahatchie Co., TU 86102 (1) Slough of Tallahatchie at Hwy 8, River E of Phillip. AMITE RIVER DRAINAGE (21): Louisiana, Livingston Par., UNO 2525 (10, 40-45) Colyell Creek at Hwy 1024, 3 mi S I-12; St Helena Par., NLU 1118 (2); NLU 1119 (5) Birch Creek at Rte 448, sec 82, T2S, R4E; Mississippi, Amite Co., UAIC 1576 (2) Little Beaver Creek at Hwy 23, 4 mi E Centreville, sec 26, T1N, R2E; Lincoln Co., TU 76079 (2) East Branch of East Fork Amite River 2.6 mi W Arlington. TICKFAW RIVER DRAINAGE (30); Louisiana, Livingston Par., NLU 4120 (23) Blood River, sec 24, T5S, R5E; TU 3807 (1) Big Branch of Hog Branch 0.8 mi W Holden at Rte 190; TU 83128 (2) West Hog Branch at Hwy 442, 13.2 mi W Tickfaw; St Helena Par., NLU 3732 (4) West Hog Branch sec 70, T4S, R4E. NATALBANY RIVER DRAIANGE (7): Louisiana, Tangipahoa Par., NLU 1002 (4) Pontchatoula Creek at Rte 190, E Hammond sec 19, T6S, R8E; TU 86459 (2) Natalbany River 4.2 mi W Hammond, at I-12; TU 4440 (1) trib to Natalhany River 3.1 mi W Hammond at Rte 51. TANGIPAHOA RIVER DRAINAGE (8): Louisiana, Tangipahoa Par., CU 13948 (4) trib to Selser Creek 3.3 mi E Hammond al Rte 190; Mississippi, Pike Co., UNO 521 (1) Tangipahoa River 2.1 mi W Magnolia; TU 67116 (3) Tangipahoa River 0.7 mi S Magnolia. PEARL RIVER DRAINAGE (31): Louisiana, Tangipahoa Par., NLU 1009 (1) Wilson's Branch at Hwy 38, 12 mi E Kentwood sec 39, T1S, R8E; Washington Par., TU 39678 (30) Pearl River at Pools Bluff, 4 mi S Bogalousa. PASCAGOULA RIVER DRAINAGE (11): Mississippi, George Co., TU 100183 (10) Pascagoula River at Hwy 26; Jones Co., TU 84718 (1) Leaf River below Rte 84. TOMBIGBEE RIVER DRAINAGE (41): Mississippi, Lowndes Co., UAIC 1786 (6) trib to Catalpa Creek, sec 33, T19N, R16E; TU 54805 (3) Tombigbee River at Hwy 50, 9 mi NW Columbus; Alabama, Greene Co., UAIC 1898 (4) Taylor Creek 2.1 mi W Rte 43; TU 76896 (12) Taylor Creek 4.7 mi S Boligee; UAIC 696 (1) Needham Creek, sec 5, T20N, R2E; TU 76976 (3) Needham Creek 4.4 mi N Demopolis; TU 76856 (3) trib to Tombigbee River., 2.5 mi SW Forkland; CU 21899 (1) trib 11 mi N of Black Warrior at Hwy 40; Pickens Co., UAIC 1892 (1) Beaver Creek at Hwy 14, 4.4 mi NW Aliceville; TU 76997 (1) Beaver at Hwy 14 Creek 5.2 mi SE of Pickensville; Sumpter Co., TU 48920 (2) Noxubee Creek at Hwy 17 4.4 mi N Gieger; TU 85729 (4) Tombigbee River 3 mi N Gainsville. ALABAMA RIVER DRAINAGE (10): Alabama, Dallas Co., UAIC 2394 (3) Tatum Creek 2.5 mi N Orville; Monroe Co., TU 114915 (1) Alabama River along right bank at river mi 102; TU 44426 (2) Little River 13.1 mi W Uriah, at Hwy 59; Montgomery Co., UAIC 1510 (1) Johnson's Creek W Montgomery sec 18, T15N, R21E; UAIC 1238 (1) Miller Cr. at I-85, 2 mi E Mt Meigs; Bullock Co., UAIC 1483 (2) trib to Slaughter Creek 0.5 mi N Thompson sec 23, T14N, R22E.

METHODS

In order to reduce sample bias, drainages were represented by as many localities as the material allowed, rather than large series from a single locality. An effort was made to obtain at least 30 specimens per drainage but due to the limited amount of material available, this was not always possible. To lessen the effects of developmental variation, counts were limited to specimens above 30 mm in standard length (Collette 1962).

Counts were made following the methods of Hubbs and Lagler (1958), except as noted below. Scale rows in transverse series were counted according to Howell (1968). The cephalic canals of the lateralis system were examined following Hubbs and Cannon (1935), with special reference to cephalic canal patterns discussed by other authors (Cole, 1967; Page, 1977; Burr, 1978). Squamation of the nape, breast, anterior belly, head and prepectoral regions was scored according to the methods of Cole (1957, 1967) and Howell (1968).

Sex was determined primarily by examination of the genital papillae. Specimens were also examined for breeding tubercles and other sexually dimorphic characteristics. Intrapopulational variation in morphological characters was analyzed to determine if significant differences existed between sexes. The t test was used to determine significance.

Statistical Techniques

All statistical computations were performed on the University of New Orleans Computer System using the DEC system 10/20 version of the SPSS batch system. The SPSS subprograms used were CONDESCRIPTIVE (a package of descriptive statistics) and ONEWAY (oneway analysis of variance). A multiple range test using the Student Newman Keuls (SNK) procedure was conducted to assign statistical significance to group separations. SNK produced a series of homogeneous subsets of groups whose highest and lowest means did not differ by more than the shortest significant range for a subset of that size (Nie et al., 1975). In the graphs (Figs. 10 & 11) the means were arranged from highest to lowest value on the lower axis. Above each subset means were arranged in geographic sequence from east to west.

Graphical analyses of morphological characters follow Hubbs and Hubbs (1953). The analyses were performed with ranges, means, standard deviations, and standard errors from frequency distributions.

Character Selection

Originally, Gulf Slope populations of the bluntnose darter were scored for approximately 30 morphological characters. The character set was later reduced by eliminating invariant or redundant characters. This report is based on variation in 13 characters, including those used to delimit taxa in previous studies of percid systematics. However, it was not clear from these studies which characters would be most important for separating groups.

Collette (1962) stated that the number of pored lateral line scales was valuable in distinguishing subspecies of the swamp darter, *Etheostoma fusiforme*, while total lateral line scales was valuable in distinguishing some species of the subgenus *Hololepis*. Burr (1978) found that species in the subgenus *Microperca* could be separated based on pored lateral line scales. Cole (1967) based separation of subspecies of the tesselated darter, *E. olmstedi*, on total lateral line scales and percent squamation. Tsai and Raney (1974) used only total lateral line scales to separate the banded darter, *E. zonale*, into subspecies, stating that separation based on percent squamation was meaningless.

It was evident very early in our study that squamation of the breast and anterior belly showed considerable geographic variation among Gulf Slope populations of *E. chlorosomum* (Fig. 8). Other characters, including total lateral line scales, pored lateral line scales, caudal peduncle scale rows, nape squamation, and branchiostegal rays, showed either continuous variation from one population to the next, or varied abruptly after appearing nonvariable. Finally, characters such as anal rays, dorsal rays, and branched caudal rays showed little variation across the Gulf Slope range of the species.

Results

Etheostoma chlorosomum is a species of the subgenus *Vaillantia*, distinguished from the only other member, *E. davi-*

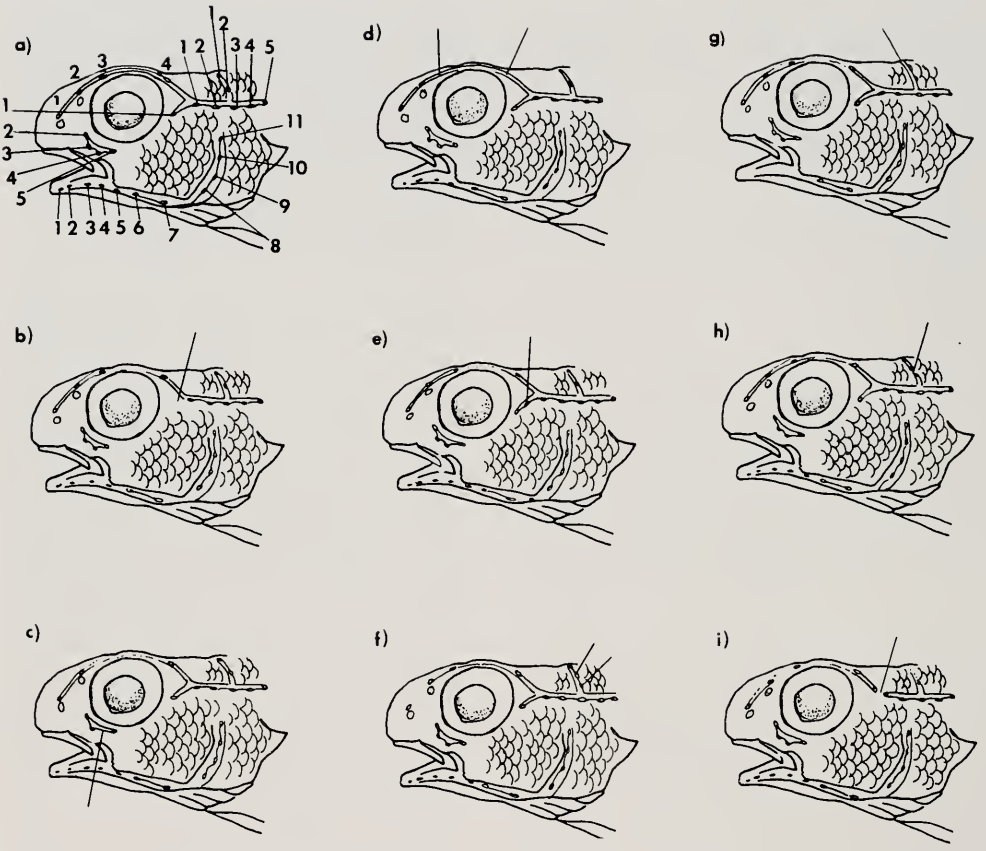

Fig. 2. Variation in development of the cephalic lateralis system in Gulf Slope populations of *Etheostoma chlorosomum*. a) Typical condition with numbers of pores and breaks in canals indicated. b,h & i) Deletions of portions of canals. c & d) Deletions of pores. e & f) Additions of pores. g) supratemporal canal complete across nape.

soni, by the morphology of the genital papillae of breeding females, the presence of breeding tubercles and having only one anal spine (Howell, 1968). It differs from all members of the subgenera *Boleosoma* and *Doration* in the morphology of the female genital papillae (Cole, 1967). The following results are based on an examination of 452 specimens from the Gulf Slope range of *E. chlorosomum*.

Along the Gulf Coast, *E. chlorosomum* is characterized by an incomplete lateral line, not arched upward anteriorly; 47-64 scales in lateral series of which 1-41 are pored; 10-17 scales in transverse series; 15-23 caudal peduncle scale rows. Fin rays: dorsal VII to XII (usually VIII to X), 8 to 13; anal I (rarely II), 6 to 11 (usually 8 or 9); branched caudal 11 to 15 (usually 13); total pectoral 24 to 30 (usually 26); pelvic I, 5 (always). Branchiostegal rays total 9 to 12 (usually 10), membrane slightly connected across isthmus.

The cephalic lateralis system displays random and developmental variation in number of pores and completeness of canals (Fig. 2). Infraorbital canal usually interrupted (Page, 1977), with 4 pores above the angle of the jaw and one behind the eye near the branch of

the lateral canal; lateral canal usually complete with 5 pores (incomplete in only one case); supratemporal canal complete across the head (2 pores) or interrupted laterally (3 pores); supraorbital canal always complete with 4 pores or with the number of pores reduced to 2 or 3; coronal pore present or absent; preoperculomandibular canal complete (9 pores) or interrupted (10 to 12 pores).

Squamation of the body shows considerable geographic variation. Nape in western populations between 0-100% scaled (means from 0-40%); lower Mississippi River populations east through Lake Pontchartrain drainages with between 0-100% scaled nape (means 30-70%); Pearl and Pascagoula populations have less than 5% scaled nape; easternmost populations 20-50%. Breast squamation higher (70%) in extreme west; lower in Brazos population (20%) and increasing clinally to 100% in the lower Mississippi and Pontchartrain populations; less than 10% in the Pearl and Pascagoula; and between 70-100% in eastern most populations. Anterior belly scaled 50% in western most population; lower in Brazos; increasing clinally to 100% in central Gulf Slope populations; virtually scaleless in Pearl and Pascagoula; and between 70-100% scaled in extreme eastern populations. Cheek and opercle always fully scaled.

There is little variation in coloration and pigmentation along the Gulf Slope. Juveniles and nonbreeding adults are pale yellow to straw colored dorsally and somewhat lighter ventrally. In life the body is greenish-yellow and transparent with olive-brown markings. The opercle and cheek has an iridescent blue-green hue. The body of preserved specimens is marked with zig-zagging brown blotches which irregularly form X's or M's on the sides, giving the appearance of a broken lateral stripe. The dorsum is crossed by six brown saddles separated by wider unpigmented interspaces. On the head, a faint suborbital bar extends from the orbit to the edge of the preoperculum. A postorbital blotch is usually visible near the posterior margin of the orbit on level with the pupil. A brown preorbital bar originates at the anterior edge of the orbit and continues around the snout, narrowing and being reflected ventrally onto the premaxilla. This feature is important in the diagnosis of *Vaillantia*. A frenum is usually absent, however, in some western populations there is a slight degree of connection between the tip of the snout and the premaxilla.

Geographic Variation

Populations of *E. chlorosomum* from more northern drainages of the Mississippi River were little different from those in lower Mississippi River drainages. All of these populations were characterized by high squamation, and they displayed similar variation in other characteristics. While the survey of northern populations was not exhaustive, it suggested little divergence within the Mississippi River Basin. Divergence was observed in populations from Gulf Slope drainages east and west of the Mississippi River. The patterns of geographic variation discussed below are based on comparisons of divergent Gulf Slope populations with populations from the lower Mississippi River basin.

Distinct patterns of variation were noted for four suites of characters: lateralis system (cephalic and lateral line), scale counts (lateral line and circumferential series), squamation, and ray counts (fin rays and branchiostegals). Fin ray characters were the most conservative. With the exception of the

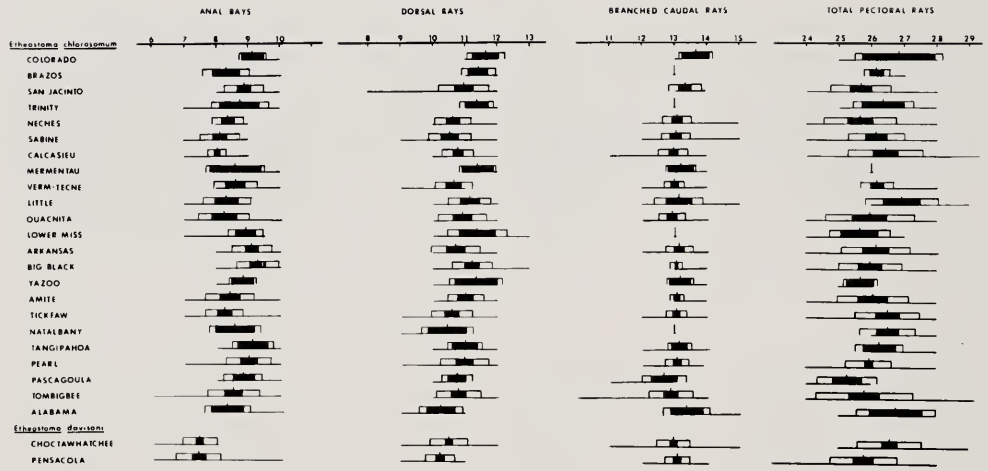

Fig. 3. Results of the graphical analysis showing variation in four ray count characters for Gulf Slope populations of *Etheostoma chlorosomum* and *E. davisoni*.

Colorado River population, variation in these characters was slight (Fig. 3). Scale meristics were less conservative (Figs. 4 & 5). Squamation showed the greatest amount of variation across the Gulf Slope (Figs. 6 & 7). Considerable variation was also observed in the lateralis system.

Conservative characters showed a consistent divergence in the Colorado River population, where the highest means for a number of these characters were recorded (Figs. 3, 4 & 5). The separation was significant in the case of caudal peduncle scale rows and branchiostegal rays (Fig. 10). The Brazos River population was also somewhat divergent with regard to scale count characters. In general, scale counts averaged higher in western populations, but the variation was clinal eastward to the lower Mississippi River drainage (Figs. 4 & 5). Fin ray and scale row characters did not support the separation of any other Gulf Slope populations of *E. chlorosomum*.

The pattern of variation in the lateralis system involved reductions in some populations. Considerable reduction was observed in the cephalic lateralis system (Fig. 2), resulting in confusion concerning the number of pores present and completeness of canals. In some instances canals were incompletely roofed or had large breaks, giving the appearance of additional pores. An analysis based on the number of pores present was meaningless under these conditions, and therefore was excluded.

Based on the pattern of variation of pored lateral line scales (Fig. 4), the reduction was most pronounced in lower Mississippi River basin, the Sabine River, and extreme eastern and western populations. Between these areas populations of *E. chlorosomum* showed a greater degree of lateral line development, a condition similar to that of *E. davisoni* (Fig. 4). The Choctawhatchee darter also showed complete development of the cephalic lateralis system (Howell, 1968).

The greatest degree of geographic variation was shown by squamation characters (Figs. 6 & 7). Squamation of the prepectoral region and anterior belly was complete for lower Mississippi River, and the adjacent Gulf Slope pop-

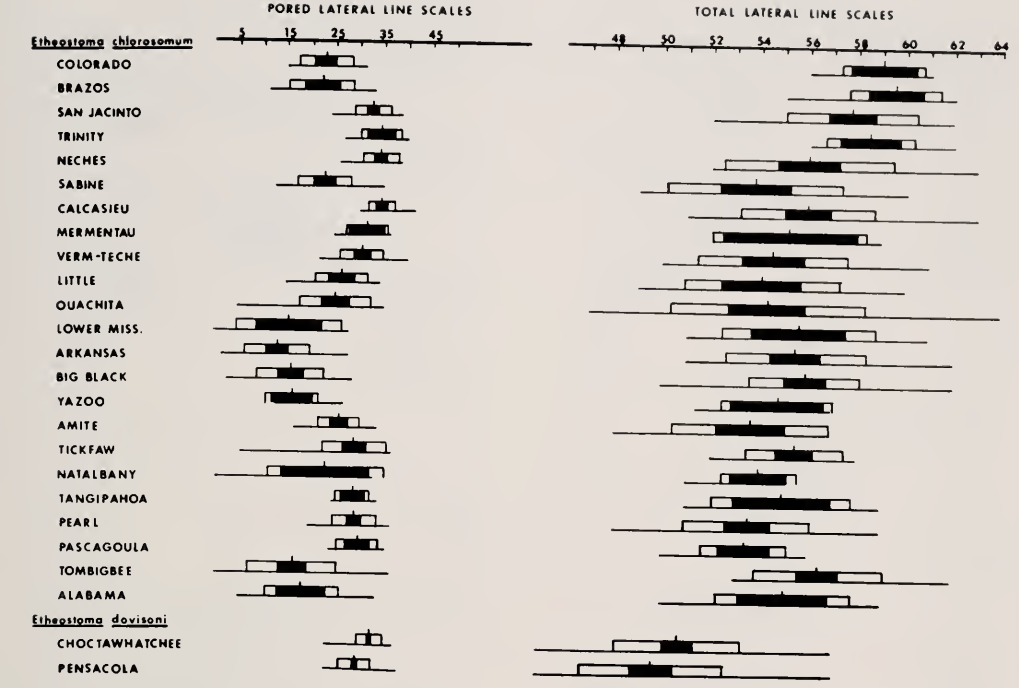

Fig. 4. Graphical analysis results for pored lateral line scales and total lateral line scales in Gulf Slope populations of *Etheostoma chlorosomum* and *E. davisoni*.

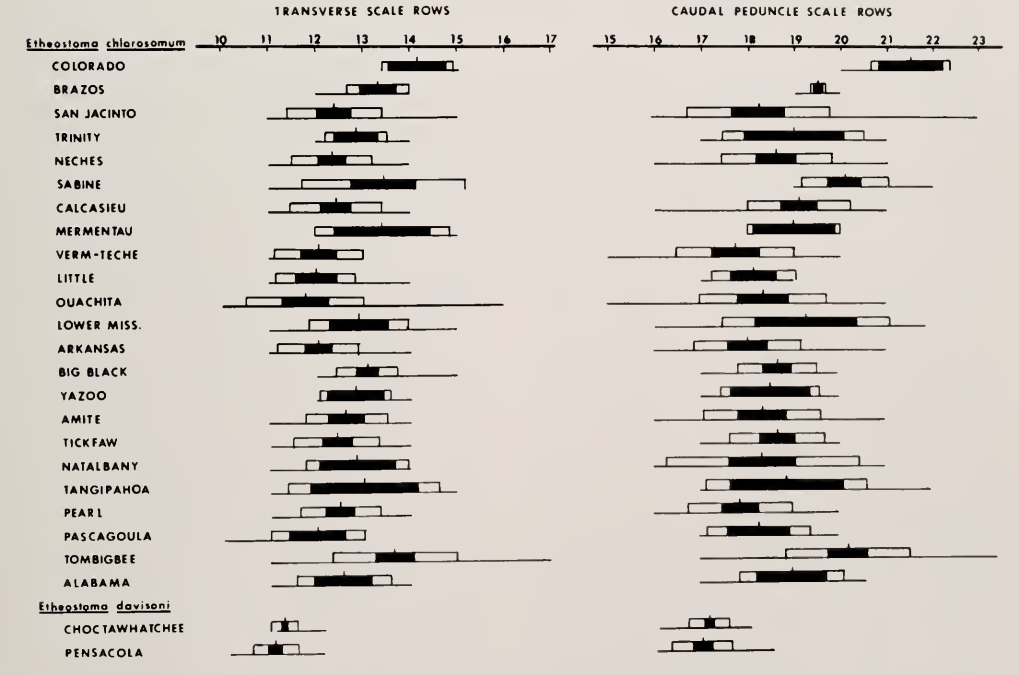

Fig. 5. Graphical analysis results for transverse and caudal peduncle scale rows in Gulf Slope populations of *Etheostoma chlorosomum* and *E. davisoni*.

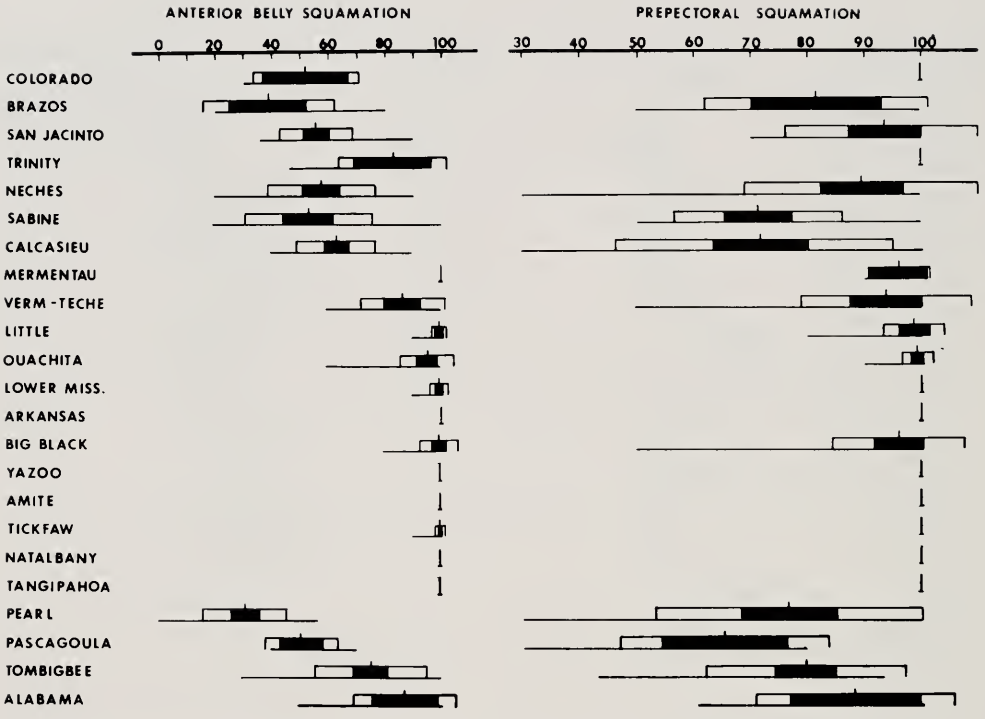

Fig. 6. Graphical analysis results for percent squamation of the anterior belly and prepectoral regions in Gulf Slope populations of *Etheostoma chlorosomum*.

ulations. We noted higher proportions of scales on the breast and nape for these populations as well. Variation in squamation was clinal west of the Mississippi River with gradual decreases in anterior belly squamation and more abrupt changes in prepectoral, breast and nape squamation. Higher squamation of the prepectoral, breast and anterior belly regions was observed west of the Neches River, primarily in the Trinity and Colorado River populations.

Step clines were observed east of the Lake Pontchartrain drainages for all squamation characters (Figs. 6 & 7). Pearl and Pascagoula river populations of *E. chlorosomum* had greatly reduced squamation. For extreme eastern populations in the Mobile Bay basin (Tombigbee and Alabama rivers), squamation was intermediate between that of lower Mississippi-Pontchartrain populations, and Pearl-Pascagoula populations. In general, the pattern was reversed east of the Pearl River and squamation increased clinally to a condition more similar to lower Mississippi populations. Figure 8 illustrates the pattern of squamation for a number of Gulf Slope populations of *E. chlorosomum*.

Page (1981) stated that character reduction was an important trend in darter evolution. Primitive darters in the genus *Percina* are characterized by higher mersitics and complete development of the lateralis system. These characters are often reduced in more derived forms. Howell (1968) assigned *E. davisoni* to the subgenus *Vaillantia* as a distant relative of *E. chlorosomum*. In characterizing the evolutionary divergence of these species, we assumed

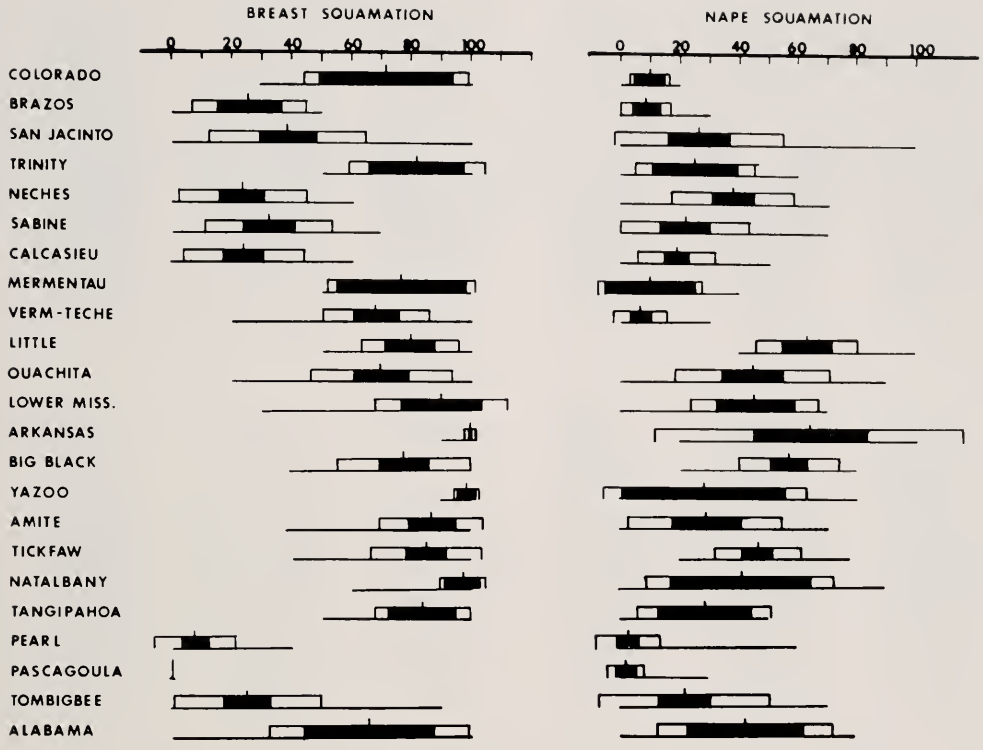

Fig. 7. Graphical analysis results for percent squamation of the breast and nape regions for Gulf Slope populations of *Etheostoma chlorosomum*.

that reduced character states represented the derived condition.

With respect to the characters analyzed in this study, ancestral *Vaillantia* characteristics apparently included complete squamation of the breast, prepectoral and anterior belly regions, complete development of the lateralis system, higher numbers of scale rows, fin and branchiostegal ray elements, and breeding tubercles. The divergence of *E. chlorosomum* apparently involved reductions in spiny ray elements (dorsal, anal and branchiostegal) and the cephalic lateralis system, while that of *E. davisoni* involved reductions in numbers of scale rows and squamation, and loss of breeding tubercles. The reduction in squamation observed for some Gulf Slope populations of *E. chlorosomum* is interpreted as subsequent to the divergence of the species. Squamation was more or less complete for presumed ancestral populations in the Mississippi River basin.

Sexual Dimorphism

Although male *E. chlorosomum* do not develop bright colors in the breeding condition, there was obvious sexual dichromatism. The bodies of breeding males were highly flecked with melanophores (more concentrated dorsolaterally) and heavy black pigment was observed on the interradial membranes of the spinous dorsal fin. Less intense pigmentation developed across the base and margin of the dorsal fin producing a flag like appearance which

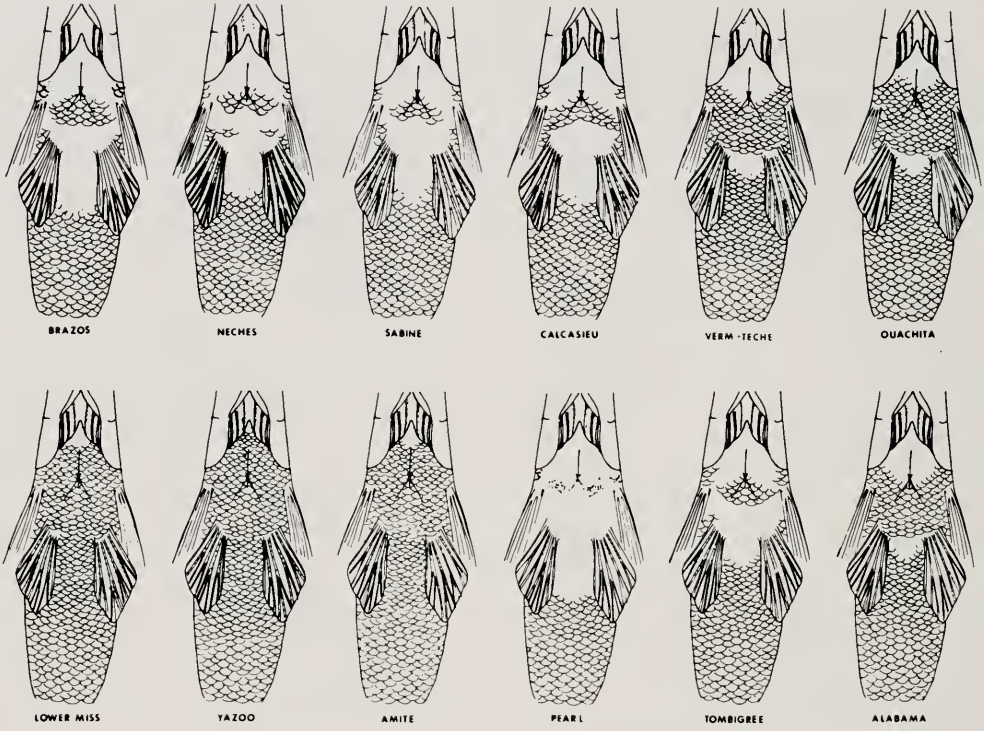

Fig. 8. Variation in squamation of the anterior belly and breast regions for a number of Gulf Slope populations of *Etheostoma chlorosomum*.

apparently serves for sexual or species recognition.

Sexual dimorphism was evident in a number of characters. Breeding males had small, tubular shaped genital papillae and thickened, fleshy pelvic and anal spines (Fig. 9). Tubercles were observed on the pelvic and anal fins of breeding males but showed considerable variation in development. Tubercles were usually seen on the anterior rays of these fins but in some instances occurred on all rays and the spine (Fig. 9a). There was no geographic pattern to the variation in tubercle development. Females had large, fleshy, heart-shaped genital papillae, which increased in size as they approached the height of the breeding condition (Fig. 9d & e). In most areas, females retained normal, nonbreeding coloration in the breeding condition.

Mature males and females had two rows of tubercle-like structures on the interradial membrane of the caudal fin. These structures apparently differ from the tubercles observed on the caudal rays of males darters in the subgenera *Ericosoma*, *Imostoma*, *Ammocrypta*, and *Etheostoma* (Collette, 1965). Their distribution and fleshy nature, however, suggests a function similar to contact organs during spawning. Examination of *E. davisoni* revealed similar structures with an identical distribution on the caudal fin. Males had higher numbers of scale rows around the caudal peduncle and greater anterior belly and prepectoral squamation (Table 1). On the average males were larger than females, suggesting that the differences were size related. Both sexes were equally represented in the population samples to

reduce bias resulting from sexual variation.

Discussion

The patterns of variation in *E. chlorosomum* were similar to those observed by Burr (1978) for the cypress darter, *E. proeliare,* a species with a distribution similar to that of *E. chlorosomum.* Burr (1978) described the following patterns of geographic variation: 1) variation slight and random; 2) unusual variation in certain drainages; and 3) Gulf Coast populations in Texas somewhat divergent. However, in *E. chlorosomum* most slight and randomly variable characters showed a consistent divergence in the Colorado River population. The bluntnose darter was recorded west of the Colorado River, in the San Antonio Bay drainage (Gilbert, 1980), although the material on which this record was based no longer exists (Clark Hubbs, pers. comm.). These extreme western populations may warrant special taxonomic consideration. Attempts to collect additional material from these drainages, however, have been fruitless thus far.

Clinal variation was observed in populations west of the Mississippi River. Clines were seen in gradually changing characters such as lateral line scales (Fig. 4) and anterior belly and breast squamation (Figs. 6 & 7). These characters, together with pored lateral line scales, were important in establishing the limits of subspecies in previous studies of percid species. The clines originated in the lower Mississippi and continued westward to the Brazos River population. The divergence noted in the Trinity River for squamation may be attributed to small sample size. A similar shift was seen for the Mermentau River population, which was also based on a small sample.

Reductions in the lateralis system did not follow a clear geographic pattern. Considerable reduction was observed for the Colorado, Brazos, Sabine, lower Mississippi, and Mobile Bay populations. The trend was best illustrated by variation in pored lateral line scales (Fig. 4), with the above populations showing distinctly lower numbers of pored lateral line scales. The peculiar pattern involved extreme western populations which were divergent in other respects, extreme eastern populations which were somewhat intergraded in other respects, central Gulf Slope populations (lower Mississippi), and the Sabine River population.

Information from other darter studies suggests that reduction in the lateralis system may be environmentally induced. Significant reductions in the system were observed for darters in the subgenera *Hololepis* (Hubbs and Cannon, 1935; Collette, 1962), *Catonotus* (Page and Braasch, 1976), and *Microperca* (Burr, 1978). Burr (1978) suggested that the reduction was correlated with ecological parameters. In the three groups mentioned above, the species showing the greatest reduction in the lateralis system were associated with quietwater habitats (swamps, low gradient streams, springs and lakes). The populations of *E. chlorosomum* showing the trend were from large, sluggishly flowing river systems. The habitat of the bluntnose darter in these systems is described as quiet backwaters, oxbows and sloughs (Pflieger, 1975). Additional comparisons of populations from large versus small streams or quiet vs. running water habitats are needed before it can be determined whether development of the lateralis system is environmentally controlled. However, such an explanation seems more plausi-

ble than one based on genetic relationships.

Nape squamation (Fig. 7) produced irregular clines with rather abrupt changes between the Vermilion-Teche and the lower Mississippi, the boundary between the western Gulf Slope and the Mississippi River basin. All squamation characters showed abrupt changes in the Pearl and Pascagoula populations. The differences were significant in some instances. The results suggest that eastern populations stabilized at greatly reduced squamation due to isolation from the fully scaled central stock found in the Mississippi River and its tributaries. These populations were similar or slightly variable in other respects.

There was evidence for isolation between the Pearl River population and populations in and around the lower Mississippi River based on variation in squamation. However, squamation was variable and intermediate in the Mobile Bay basin populations to the east, suggesting intergradation between populations with greatly reduced squamation (Pearl and Pascaqoula), and those populations with high to complete squamation (Mississippi and its tributaries).

Populations of *E. chlorosomum* could have gained access to the Mobile Bay drainage via the Big Black, Yazoo, or other more northern Mississippi River tributary. The distributions of a number of other species, most notably, *E. nigrum*, reflect this type of dispersal pattern; occurring in the lower eastern tributaries of the Mississippi River and the Mobile Bay basin, but not in the intervening coastal drainages. The decline in squamation from the Alabama River westward to the Pearl River suggests separate invasion of the Mobile Bay basin from the west (via the Pascagoula

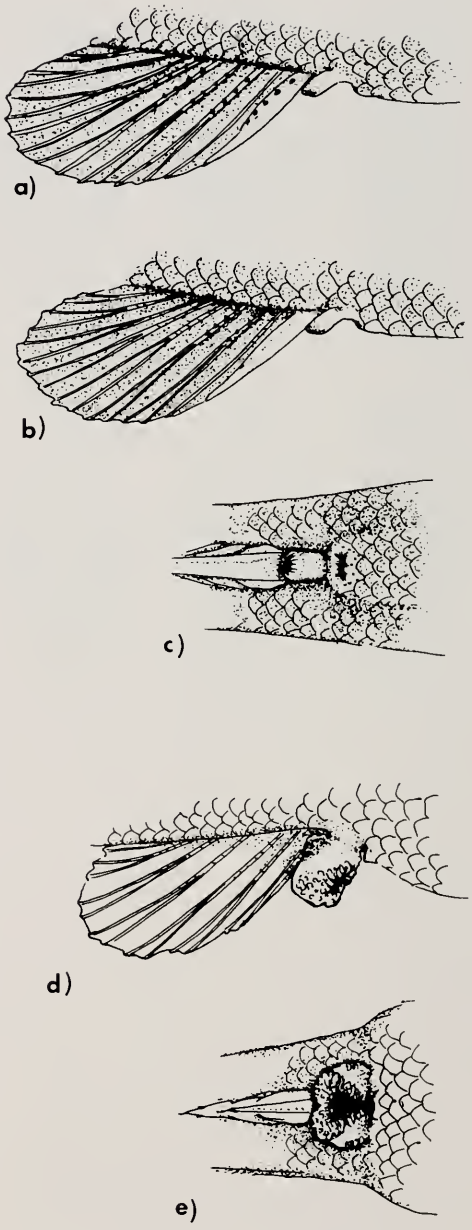

Fig. 9. Sexual dimorphism in Gulf Slope populations of *Etheostoma chlorosomum:* a-c) Male breeding condition showing tubular genital papillae, thickened (fleshy) anal spine and development of tubercles on anterior rays on the anal fin or on all rays and the spine. d & e) Lateral and ventral view of the large heart shaped genital papilla of breeding females.

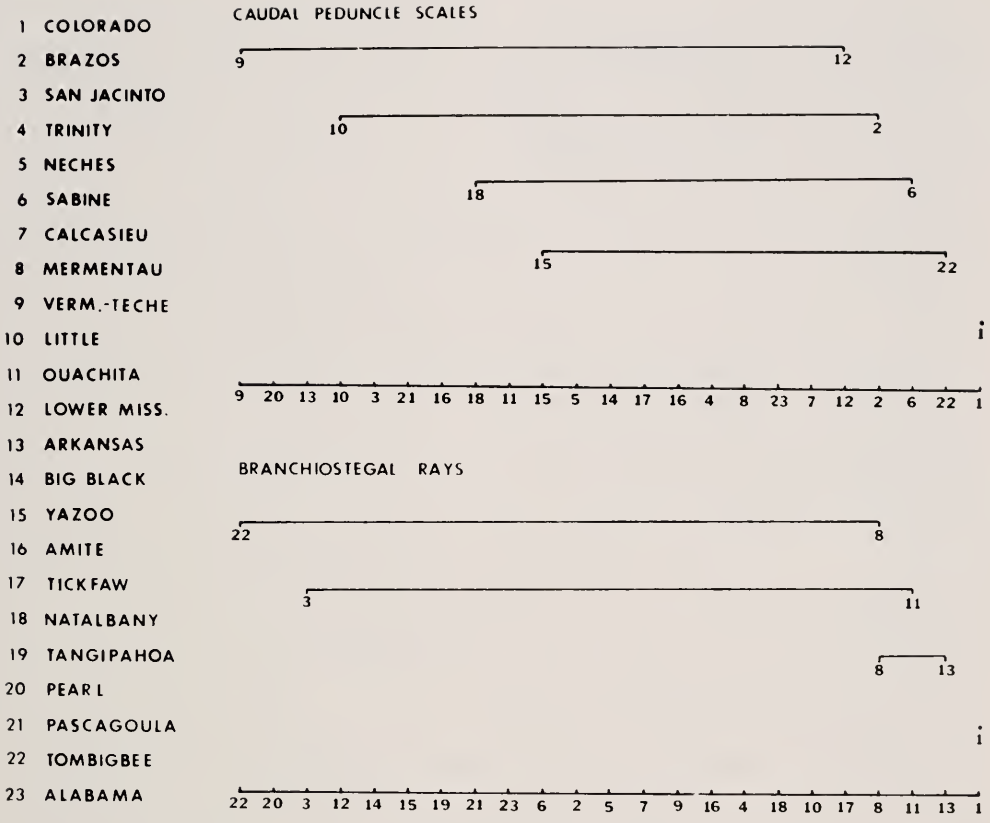

Fig. 10. Results of the SNK multiple range test for caudal peduncle scale rows and branchiostegal rays showing divergence for the Colorado River population. Numbers below subsets and ranges correspond to numbered drainages (populations) on the left.

River) and subsequent exchanges between these populations.

Results of the multiple range test indicated considerable overlap for most groups, but similar patterns of variation emerged (Figs. 8-9). The Colorado River population was distinct in the number of branchiostegals and caudal peduncle scale rows (Fig. 10). The Pearl and Pascagoula populations were distinct with respect to percent squamation of the anterior belly and breast (Fig. 11). The Tombigbee and Alabama populations were intermediate between the Pearl and Pascagoula, and the lower Mississippi and Pontchartrain populations for these characters.

Causes of Variation

Of particular importance to the interpretation of geographic variation is distinguishing between nongenetic causes of phenotypic variation (direct modification by the environment, sexual variation, and developmental variation) and causes of true genetic variation. Causal factors of true genetic variation include selection, random genetic drift, founder effect, and on a short temporal scale, recent migration without time to adapt to local conditions (Gould and Johnston, 1972).

There are no pronounced environmental differences between Gulf Slope drainages that would offer a high adap-

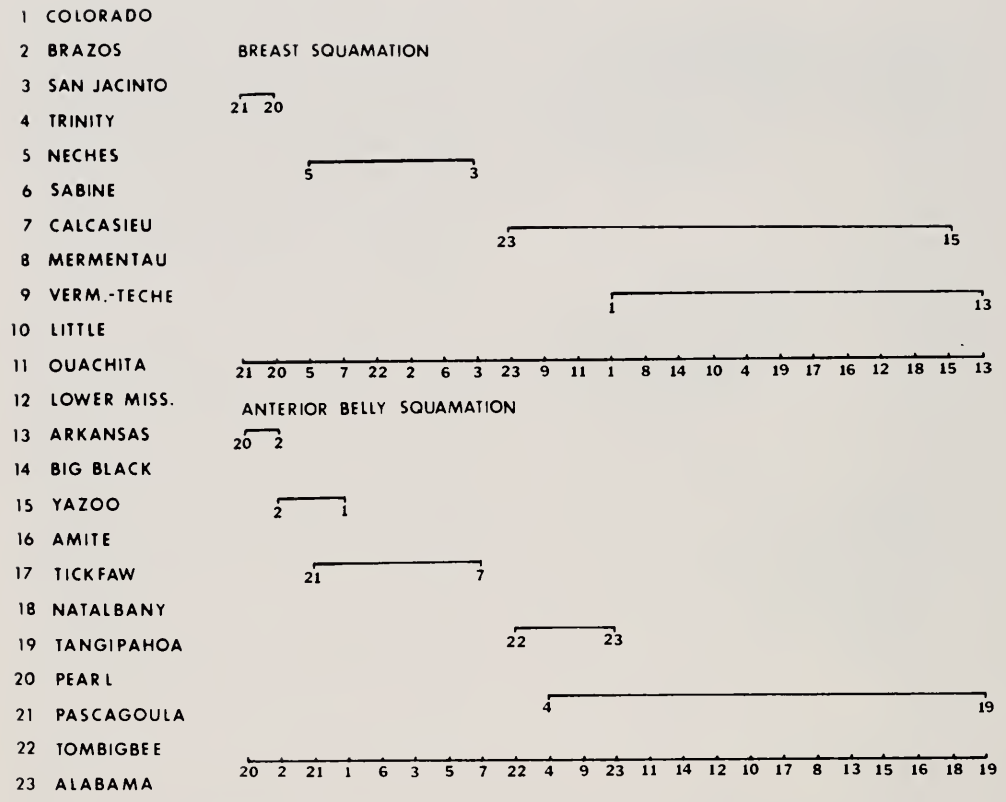

Fig. 11. Results of the SNK multiple range test for anterior belly and breast percent squamation showing the isolated nature of the Pearl River population.

tive value to the divergent character states observed for some *E. chlorosomum* populations. If these divergent character states resulted from true genetic variation it is more likely that they were the product of random genetic effects.

Most discussions of environmental factors that produce morphological variation in fishes deal with temperature effects in northern versus southern populations of a species. In this study east-west variation was analyzed in populations distributed across a relatively homogeneous (humid subtropical) climatic region. Thus, the variation in meristic elements observed here is not readily explained by the effects of temperature on growth rates. Other growth retardants such as high salinity or low dissolved oxygen, which parallel the effects of temperature (Barlow, 1961), may operate along the Gulf Slope. The role of these factors in producing the observed variation is not known.

Pflieger (1971) suggested that the bluntnose darter evolved in the central Mississippi River Valley. Presumably, the species then spread east and west along the Gulf Slope where it colonized new habitats. Hubbs (1928) stated that a species new to an area would be altered by the environment and these differences, when associated with adaptive changes would become genetically fixed. Based on the high degree of variability in the patterns of variation observed, it appeared that of the many characters analyzed, few were geneti-

cally fixed in Gulf Slope populations of *E. chlorosomum*. Instead, there was evidence of varying degrees of isolation and intergradation.

The variation observed was not explained by sexual differences. Although a few important characters showed significant differences between sexes (Table 1), character trends were not disturbed by combinations of data from different sexes as long as both were equally represented. An attempt was made to avoid the effects of ontogenetic variation by restricting examinations to individuals presumed to be adult sized. Collette (1962) suggested that variation in the lateralis system was developmental for members of the subgenus *Hololepis*. However, based on the pattern of variation observed here and elsewhere (Burr, 1978), development of the lateralis system appears to be environmentally controlled.

According to Barlow (1961) characters that are the last to develop ontogenetically are more adaptable. Collette (1962) noted that scales originate in the caudal peduncle region and then spread anteriorly during the early development of *E. fusiforme*. The last areas to develop scales were the nape, belly, breast and head (Collette, 1962). Squamation characters showed high degrees of reduction across the Gulf Slope range of *E. chlorosomum* and little variation (from the fully scaled state) in the Mississippi River basin. These character states probably originated ontogenetically, but they showed true genetic variation in Gulf Slope populations of *E. chlorosomum*.

Zoogeography and Evolution

The distribution of extant *Vaillantia* species suggests that the common ancestor of the group occupied lowland areas

TABLE 1. Sexual variation among lower Mississippi populations of *E. chlorosomum*. Significance determined by t test. Probabilities (P) greater than 0.05 nonsignificant (ns).

		Sexual variation				
Character	Sex	X	SD	N	t	p
Standard length	M	37.49	3.61	42		
					3.70	<.005
	F	34.51	3.16	33		
Total l.l. scales	M	59.11	2.26	4		
					1.29	ns
	F	59.67	1.12	33		
Pored l.l. scales	M	23.44	5.90	42		
					1.22	ns
	F	21.67	6.44	33		
Caudal peduncle	M	20.44	1.15	42		
					1.95	<.05
	F	19.89	0.60	33		
Anterior belly	M	47.78	19.86	42		
					1.93	<.05
	F	37.78	24.38	33		
Prepectoral	M	96.67	7.07	42		
					4.96	<.005
	F	78.89	21.47	33		
Nape	M	10.00	10.00	42		
					1.17	ns
	F	7.78	4.41	33		
Breast	M	43.33	26.46	42		
					0.61	ns
	F	38.89	35.86	33		

of the Gulf Coastal Plain, including the Mississippi River Valley and the eastern *Gulf Slope*. *E. davisoni* is restricted to Gulf Slope drainages east of Mobile Bay. Bailey et al. (1954) stated that due to isolation, drainages east of Mobile Bay form a common faunal block that was predominantly derived from the Mississippi River. Evidence from this study suggests long-term isolation of *E. davisoni* from its presumed ancestor in the Mississippi River, and a more recent history for *E. chlorosomum* in Gulf Slope drainages east and west of the Mississippi River.

Most of the present Gulf Coastal Plain (including the Mississippi Embayment up to the southern lowlands of Missouri and Kentucky) was below sea level until the late Oligocene. A precipitous drop in sea level occurred during that period (Vial and Hardenbol, 1979), which could have exposed the region to colonization by primary freshwater fishes for the first time. We hypothesize that the common ancestor of *E. chlorosomum* and *E. davisoni* was a lowland form, autochthonous to the Mississippi River basin, that attained a widespread Gulf Coastal distribution in late Oligocene or early Miocene times. *Etheostoma davisoni* likely evolved from ancestral *Vaillantia* populations that were isolated in Gulf Slope drainages east of Mobile Bay during the middle Miocene, when a sustained, 100 m elevation in sea level caused reflooding of the Mississippi Embayment (Vial and Hardenbol, 1979). A marine transgression of this magnitude could have also restricted ancestral populations to northern areas of the Mississippi Embayment; the presumed area of origin of *E. chlorosomum* (Pflieger, 1971). The isolation of ancestral *Vaillantia* populations that produced the extant species may have occurred more recently, as a result of a subsequent transgression (similar in magnitude, but much shorter in duration) in Pliocene times (Vial and Hardenbol, 1979).

The bluntnose darter most likely invaded Gulf Slope drainages during glacial periods when heavy precipitation caused high degrees of flooding (Bailey et al., 1954), crossgrading (Distler, 1968) and headwater stream captures (Burr, 1978; Conner, 1977) in the region. Regression of sea water during glacial maxima, coupled with increased deposition in large rivers may have also allowed transfers of primary freshwater fishes across bays and bayous into adjacent drainages (Conner, 1977).

Burr (1978) stated that *E. proeliare* may have used a lowland transfer to enter the Pearl River from the Mississippi River in fairly recent times. An earlier transfer from lower eastern tributaries of the Mississippi River, such as the Big Black (Snelson, 1972; see also Suttkus and Clemmer, 1977), seems more likely for the Pearl River population of *E. chlorosomun* due to its isolated nature.

Lake Pontchartrain was suggested to have been isolated as a totally freshwater basin at least once during its formation as the Mississippi River flowed eastward along the St. Bernard Delta (Saucier, 1963). Populations of *E. chlorosomum* in the Pontchartrain drainages were similar to lower Mississippi River populations in a number of respects.

Burr (1978) cited evidence for stream captures between eastern tributaries of the Mississippi River and western tributaries of the Tombigbee River which could explain the entrance of *E. chlorosomun* into the Mobile Bay basin. Extant populations in the Mobile basin were apparently intergraded with

divergent stocks from the Pearl and and Pascagoula Rivers.

To the west, clines indicated a more gradual divergence of populations. The distribution of *E. chlorosomum* was more continuous west of the Mississippi River, suggesting a higher degree exchange and intergradation in the past. The spread of *E. chlorosomum* westward along the Gulf Coast could be explained by any of the above mentioned processes. Burr (1978) favored lowland transfers of *E. proeliare* west of the Mississippi because the species was only known from lower portions of western Gulf Slope drainages. The same may have been true for *E. chlorosomum* which has a similar distribution west of the Mississippi River. Transfers via captures or cross-graded streams may have occurred as well (Distler, 1968). Conner (1977) cited evidence for Kansan and preKansan glacial period captures between the Red and Brazos rivers and the Colorado and Brazos, which could explain the spread of *E. chlorosomum* to these far western areas.

Taxonomic Conclusions

We found little evidence to support the taxonomic recognition of any group of *E. chlorosomum* populations from the Gulf Slope region. Instead, we observed: 1) conservative variation (slight and random) for some characters; 2) evidence of isolation and intergradation in some populations for characters that were adaptable; and 3) evidence for enviromental control of variation in other characters. Extreme western populations were divergent for important, (otherwise conservative) characters. However, an insufficient amount of material was available to make a definite conclusion regarding their status.

Based on the patterns of variation observed in comparisons among *E. chlorosomum* populations and between *Vaillantia* species, adaptable characters such as those from the lateralis system and body squamation would have a questionable value in taxonomic decisions below the genus level. Adaptation or random fixation of new states was better suggested by variation in characters that were otherwise more conservative.

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