

A NEW DARTER OF SUBGENUS *OLIGOCEPHALUS*, GENUS *ETHEOSTOMA*,
FROM SOUTHEASTERN TEXAS AND SOUTHWESTERN LOUISIANA

ROYAL D. SUTTKUS

Tulane University Biodiversity Research Institute, Belle Chasse, LA 70037-3098

HENRY L. BART, JR.

Tulane University Biodiversity Research Institute, Belle Chasse, LA 70037-3098

AND

DAVID A. ETNIER

University of Tennessee Knoxville, TN 37996-1610

ABSTRACT

A new species of darter of subgenus *Oligocephalus*, genus *Etheostoma*, is herein described relative to three similar and geographically proximal *Oligocephalus* – *E. asprigene* (Forbes), *E. collettei* Birdsong & Knapp, and *E. swaini* (Jordan) – largely confined to the Gulf Coastal Plain and the Central Lowlands of the eastern United States. The new species occurs in the Neches, Sabine and Calcasieu river systems of east Texas and western Louisiana. It is most closely related to *E. asprigene*. It differs from all of the above species primarily in having a longer spinous dorsal fin base and a narrower transpelvic width. Nuptial males of the new species differ in breeding coloration and have significantly shorter snouts and caudal peduncles, and narrower bodies than nuptial males of *E. asprigene* and other *Oligocephalus* compared. The new species is most similar to *E. asprigene* in physiognomy and body pigmentation.

Keywords: New species, *Etheostoma asprigene*, *Oligocephalus*, Neches River, Sabine River, Calcasieu River

INTRODUCTION

In this paper we describe a new species of darter of subgenus *Oligocephalus*, genus *Etheostoma*, and diagnose it relative to three similar and geographically proximal *Oligocephalus*–*E. asprigene* (Forbes), *E. collettei* Birdsong & Knapp, and *E. swaini* (Jordan). We compare meristic and morphometric data of the new species with that of *E. asprigene* and *E. collettei* from localities throughout their ranges, and with that of *E. swaini* from only eastern tributaries to the Mississippi River and from the Pearl River system (type locality). The new species is most closely related to *E. asprigene*. We follow Lang and Mayden (2007) in placing the new species in the *E. asprigene* species group, along with *E. asprigene*, *E. swaini*, *E. collettei* and the geographically restricted and spring-adapted *E. ditrema* and *E. nuchale*.

MATERIALS AND METHODS

Specimens of the new species and comparative material of *E. asprigene*, *E. collettei*, and *E. swaini* were borrowed from the collections at Illinois Natural History Survey (INHS), Louisiana State University (LSUMZ), Mississippi Museum of Natural Science (MMNS), Stanford University (SU) housed at California Academy of Sciences, Tulane University (TU), University of Arkansas at Fort Smith (UAFS), University of Tennessee (UT), and United States National Museum of Natural History (USNM). Paratypes of the new species were deposited at the following institutions not already identified above as detailed in the material listing below: Academy of Natural Sciences Philadelphia (ANSP), Cornell University Vertebrate Museum (CUVM), Texas Natural History Collection (TNHC), University of Alabama (UAIC), University of Florida Museum of Natural History (UF) and University of Michigan Museum of Zoology (UMMZ).

In the listing of type material, each catalog number is followed by the number of specimens seen and range of standard length (SL) in millimeters, e.g. (15, 28-50). In addition to standard compass directions (with the following “of” deleted), the following abbreviations are used: Cr. = Creek, R. = River, mi = mile(s), trib. = tributary, Hwy = Highway, Rd = Road, FM = Farm Road, jct. = junction, Co. = County. In lists of materials not designated as types, the catalog number is followed by the number of specimens seen, enclosed in parentheses. Although catalog numbers identify “lots” of specimens, we intentionally use mileage figures, rather than metric figures, in listing of materials because mileage figures are so recorded in the catalog and perhaps more importantly on the original labels in the jars. Collection dates are not included in the listing of nontype materials. Materials examined of *E. asprigene*, *E. collettei*, and *E. swaini* are listed only by institutional acronym and catalog number under “Additional Material Examined” after the Literature Cited; for each subdivision of a species' range listed in Tables 1-6 (*E. asprigene*, Ohio River basin, etc.), the mean (\bar{x}), number of specimens counted (N), and range (W) are listed for subsystems (Wabash River system, Green River system, etc.) that appear to have identical values. Meristic ranges listed in text include 90% or more of the counts bracketed by parenthetical extreme values, e.g., 16-21 (14-22).

Except for recently collected specimens from the type locality used in color photographs, all of our collections of the new species extend from 25 January 1971 to 24 March 1979 from the Neches River system, from 14 July 1964 to 9 July 1985 from the Sabine River system, and from 7 June 1956 to 12 March 1981 from the Calcasieu River drainage. Names used for associated species follow Nelson et al. (2004).

Counts and measurements were made as described in Hubbs and Lagler (1958) except as follows: transverse body scales were counted from the origin of the anal fin diagonally upward to the base of the spinous dorsal fin, with scales of reduced size along base of dorsal fin included in the count; gill rakers, counted on the anterior arch on either the right or left side, included both dorsal and ventral rudiments. Presence or absence of scales on the nape, operculum, lower cheek, breast, and prepectoral area

was determined by passing a jet of compressed air over the area; deeply embedded scales might have been overlooked.

Twenty body measurements were made with needle-point dial calipers and recorded to the nearest 0.1 mm for samples of nuptial males and females from Neches and Calcasieu river populations of the new species (TU 200366, TU 111804, TU 106025, TU 111951, TU 200398), *E. asprigene* (MMNS 30684.0) and *E. swaini* (TU 55398, TU 66841, TU 66983) from the lower Mississippi River, and *E. collettei* from Ouachita and Red rivers (TU 55133, TU 76101, TU 93274). Caudal peduncle length was measured from the posterior insertion of the anal fin to the middle of the hypural plate. Trans-pelvic width was measured between the outer bases of the pelvic spines. Data for 19 of the measurements separated by sex were regressed on standard length to adjust the measurements to a common body size. The residuals from these regressions were subjected to unbalanced Analysis of Variance (ANOVA) and Canonical Discriminant Analysis (CDA) to test for differences in body proportions. Statistical Analyses were performed using the REG, GLM (unbalanced ANOVA) and CANDISC (CDA) procedures in the software package SAS 9.1 (SAS Institute, Inc., 2002-03).

Etheostoma thompsoni Suttkus, Bart, and Etnier, new species
Gumbo Darter
Figures 1, 2, and 3



Figure 1. *Etheostoma thompsoni*, Holotype. TU 200366, Adult male 53.7 mm SL, Neches River, along right (west) bank just below Town Bluff dam, at Town Bluff, Tyler County, Texas, 16 February 1979.

Etheostoma asprigene: Moore, 1968 (portion of range in Sabine and Neches river systems); Starnes, 1980 (distribution in Sabine and Neches river systems); Page, 1983 (portion of range in Sabine and Neches river systems); Cummings et al. 1984 (portion of range in Sabine and Neches river systems); Conner and Suttkus, 1986, (portion of range in Sabine Lake and Calcasieu drainage); Page and Burr, 1991 (portion of range in Sabine-Neches river drainage); Thomas et al. 1998 (portion of range in Sabine and Neches river systems).

Etheostoma collettei: Birdsong and Knapp, 1969 (portion of range in Sabine River system) Platania and Robison, 1980 (portion of range in Sabine River system); Douglas, 1974 (distribution in Sabine River system); Page, 1983 (portion of range in Sabine River system); Page and Burr, 1991 (portion of range in Sabine River system);

HOLOTYPE: Adult male, TU 200366, 53.7 mm SL, Neches River, along right (west) bank just below Town Bluff dam, at Town Bluff, Tyler County, Texas, 16 February 1979, R. D. Suttkus and Carolyn Miller (Fig. 1).

PARATOPOTYPES: TU 111804 (15, 38-50), collected with holotype, 16 February 1979, (10 specimens removed and distributed as follows: CUVM 9511 (2), UAIC 15593.01 (2), UMMZ 248782 (2), USNM 396516 (2), UT 91.7977 (1)); TU 111873 (2, 41-45), 17 February 1979; TU 111951 (6, 40-51), 9 March 1979 (two specimens removed and cataloged as UF 174326); TU 112130(2, 45-46), 23 March 1979; TU 112163 (11, 36-51), 24 March 1979; TU 116112(5, 37-38), 25 January 1980; TU 116149 (19, 34-43), 25 January 1980; TU 120675(2, 38-42), 1 March 1981; TU 200398 (2, 45), 1 March 2008.

OTHER PARATYPES: TU 120711(1, 35), Neches River, along right (west) bank, 1.0 mi below Town Bluff dam, Tyler County, Texas, 2 March 1981; TU 120762 (2, 33-42), Neches River, along left (east) bank, 1.0 mi below Town Bluff dam, Jasper County, Texas, 2 March 1981. TU 111222 (1), Neches R. along right (west) bank, 7.5 mi below Cowart Bend; TU 66915 (1), Neches R. 4.9 mi W Mt. Union, 5.0 airmi E Spurger, FM 1013, TU 103202 (3), TU 103935 (5), TU 104484 (3), TU 105178 (1), TU 106025 (5, four specimens removed and distributed as follows: ANSP 189360 (2), TNHC 43091 (2)).

ADDITIONAL MATERIAL EXAMINED: **Neches River system, Texas, Tyler Co.:** TU 111222 (1), Neches R. along right (west) bank, 7.5 mi below Cowart Bend; TU 66915 (1), Neches R. 4.9 mi W Mt. Union, 5.0 airmi E Spurger, FM 1013, TU 103202 (3), TU 103935 (5), TU 104484 (3), TU 105178 (1), TU 106025 (5). **Jasper Co.:** TU 123850 (1), Neches R.1.5 mi below Old Stone Bend. **Hardin Co.:** TU 67564 (11), Neches R. at US Hwy 96, 6.0 mi ENE Silsbee, TU 69331 (2). **Jasper Co.:** TU 103169 (1), Neches R. 1.0 mi w Evadale, US Hwy 96 bridge, TU 103964 (2), TU 104537 (6), TU 105208 (1), TU 105976 (1). **Hardin Co.:** TU 111322 (2), Neches R. opposite Wiess Bluff. **Jasper Co.:** TU 114803 (5), Neches R. opposite mouth of Village Cr. **Hardin Co.:** TU 113782 (1), Village Cr. 1.0 mi above US Hwy 96 bridge; TU 138875 (1), Village Cr. at US Hwy 96 bridge. **Orange Co.:** TU 138893 (2), Neches R.at Lakeview; TU 114593 (2), Neches R.1.0 mi below Lakeview; TU114613 (1), Neches R.1.2 mi below Lakeview; TU 114676 (1), Neches R.0.7 mi below Four Oaks Ranch. **Jefferson Co.:** TU 127025 (1), Pine Island Bayou, trib. to Neches R. 1.0 mi above Horseshoe Bend.

Sabine River system, Texas, Gregg Co.: TU 127936 (1), Sabine R., 1.0 mi SW Longview at US Hwy 259; TU 141641 (17), Sabine R., 2.5 mi SE Longview at Texas Hwy 149. **Panola Co.:** TU 42816 (1), Sabine R. 4.0 mi NW Logansport, Louisiana. **Shelby Co.:** TU 50338 (1), Flat fork Cr., trib. to Tenaha Bayou, 2.2 mi NE James, Texas Hwy 7; TU 33424 (17), Tenaha Bayou, trib. to Sabine R. 13.3 mi S Logansport, Louisiana (preimpoundment collection, Toledo Bend Reservoir), Texas Hwy 139.

Sabine River system, Louisiana, Sabine Parish: TU 50044 (2), Sabine R. at temporary bridge, 0.6 mi below precompleted Toledo Bend dam, TU 50317 (2). **Vernon Parish:** TU 50306 (1), Sabine R. at lower end of Toledo Bend, 13.2 mi SW Anacoco; TU 61442 (1), Sabine R. 2.5 mi above mouth of Anacoco Bayou, TU 67755 (1). **Beauregard Parish:** TU 183227 (1), Bayou Anacoco 2.5 mi N jct. US Hwy 190 and Louisiana Hwy 111 at Louisiana Hwy 111. **Texas, Newton Co.:** TU 115032 (5), Sabine R. along right (west bank), 1.0 mi below Armstrong Lake; TU 67881 (4), Sabine R. along right (west) bank, opposite Moon Lake; TU 104627 (2), Sabine R. 1.9 mi E Bon Wier, US Hwy 190. **Louisiana, Beauregard Parish:** TU 67477 (1), Sabine R. 0.7 mi below US Hwy 190 bridge.

Texas, Newton Co.: TU 63409 (1), Sabine R. at upper end of Middle R.; TU 86889 (1), Big Cow Cr., 0.2 mi NE jct. FM 1416 and TX Hwy 87, at FM 1416, TU 86951 (1), TU 183790 (1); TU 63477 (3), Sabine R. at mouth Big Cow Cr. **Louisiana, Beauregard Parish:** TU 63503 (4), Sabine R. at River Mile 74, opposite Skinner Lake.

Calcasieu River drainage, Louisiana, Rapides Parish: TU 120457 (6), Calcasieu R. 1.2 mi SSW Hineston, LA Hwys 121 and 112; TU 120437 (2), Calcasieu R. 1.0 mi SSW Calcasieu. **Allen Parish:** TU 14051 (5), Calcasieu R. 2.5 mi W Oakdale, LA Hwy10, TU 41475 (1), TU 41509 (1), TU 43300 (33), TU 44613 (6), TU 50222 (6), TU 120480 (5), TU 120855 (1); TU 120499 (6), Calcasieu R. 1.9 mi W Reeds; TU 120452 (3), Mill Cr., trib. to Calcasieu R. 4.0 airmi NW Oberlin; TU 120520 (8), Calcasieu R. 3.7 mi NW Oberlin, LA Hwy 26, TU 120890 (10); TU 120378 (6), Calcasieu R. above dam, upstream of LA Hwy 141 (1147), 3.0 mi NW Kinder, TU 120390 (4); TU 120413 (52), Calcasieu R. just below dam, downriver of LA Hwy 141 (Hwy 1147), 3.0 mi NW Kinder; TU 64296 (18), Calcasieu R. 4.0 mi W Kinder, US Hwy 190 bridge, TU 79861 (4).

Diagnosis: *Etheostoma thompsoni* is a member of the subgenus *Oligocephalus* as diagnosed by Page (1981) and Bailey and Etnier (1988). It is most like *E. asprigene* of other members of the subgenus *Oligocephalus*, especially in its physiognomy. The spinous dorsal fin base is longer in *E. thompsoni* than in *E. asprigene*, *E. collettei* and *E. swaini*, averaging >30% of standard length in males and females (<30% in *E. asprigene* and other *Oligocephalus* compared) and the transpelvic width is distinctly narrower than in *E. asprigene*, *E. collettei* and *E. swaini*. Nuptial males of *E. thompsoni* have significantly shorter snouts and caudal peduncles, and narrower bodies than nuptial males of *E. asprigene* and other *Oligocephalus* compared.

Nuptial males of *E. thompsoni* also differ from those of *E. asprigene* in fin and body coloration. Nuptial males of *E. thompsoni* have numerous small red blotches or flecks on the sides of body anterior to the dark blue bars that alternate with bright red bars on posterior part of body and caudal peduncle. The central blue-gray band of the spinous dorsal fin is nearly uniform in width in *E. thompsoni*, whereas it is narrow anteriorly and progressively widens posteriorly in *E. asprigene*. Color on lateral areas of the belly and between blue bars on the caudal peduncle is a more intense red-orange in *E. thompsoni* than in *E. asprigene*. Lastly, *E. thompsoni* typically has a naked nape, whereas, the nape is fully scaled in *E. asprigene*.

Description: Our description is based on 371 specimens: 126 from Neches River system; 68 from Sabine River system; and 177 from Calcasieu River drainage.

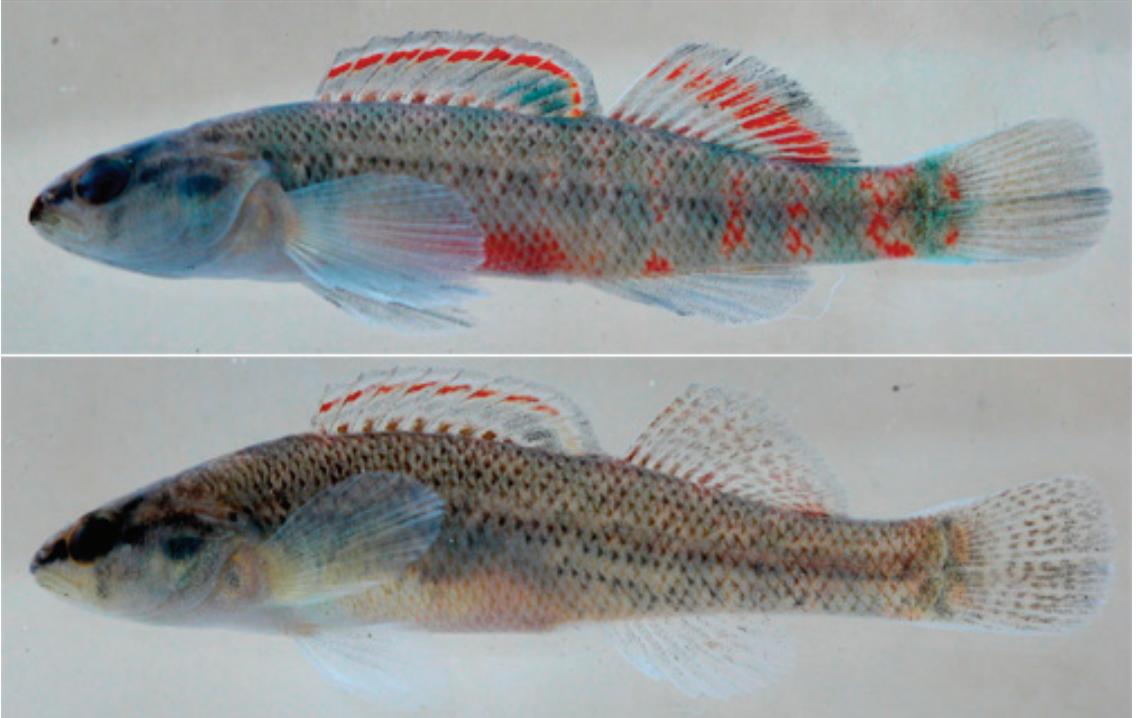


Figure 2. Recently collected (March 2008) paratypes of *E. thompsoni* showing nuptial coloration of male (top) and female (bottom).

Etheostoma thompsoni reaches a maximum size of 61 mm SL (a female). This single female specimen greatly exceeds the largest male (holotype, 53.7 mm SL). Frequency distributions of scale and fin ray counts are presented in Tables 1-6. Lateral line usually incomplete: total lateral-line scales range from 44-52 (42-54); pored lateral-line scales 34-45 (31-48); unpored lateral-line scales (0, 1 specimen), 4-13 (1-18). Caudal peduncle scale rows 20-22 (18-24). Transverse scale rows 14-17 (-18). Dorsal fin with 10-11 (9-12) spines and 12-14 (11-15) soft rays. Anal fin with 2 spines and 7-8 (6-9), modally 7 soft rays. Pectoral-fin rays 14-15 (12-16), modally 14 rays. Branchiostegal rays (all from Neches River system) number 6-6 (30), 6-7 (1), or 7-7 (1). Cephalic sensory canals (left side only, all from Neches River system) complete with 9 (1), 10 (77), or 11 (1) preoperculomandibular canal pores; 7 (1), 8 (65), 9 (12), or 10 (1) infraorbital canal pores; and 4 (46) or 5 (1) supraorbital canal pores. Gill rakers (Neches River system) 10(3), 11(11), 12(11), or 13(7). Branched caudal rays, scalation of cheek, opercle, nape, and prepectoral area, proportional measurements, and morphometrics discussed under "Comparisons".

The color description below is based primarily on a freshly preserved nuptial male, the holotype, (Fig. 1), collected 16 February 1979; air temperature 6°C, water temperature 11°C. The description is supplemented by information from two smaller males collected with the holotype and a recently collected spawning pair (Fig. 2) which did not appear to be at the peak of nuptial development.

The most striking body pattern is the five bright red bars that alternate with dark blue bars on posterior body and caudal peduncle. There are numerous small, red

blotches or flecks on side of body, above anal fin base. Anterior to the red flecks the body is pale olive-yellow. Lateral areas of the belly are bright red-orange. Between the prominent posterior dark blue bar and a smaller dark blue bar, centrally located at base of caudal fin, there are two vertically elongate, small, reddish spots. The remainder of the caudal fin is a mixture of blue-gray and brown, with more brownish basally and more blue-gray distally. The dorsum is brown between the dark saddles; the breast, cheeks, opercles, and gill membranes are dark gray. Two smaller males (51 and 43 mm SL) have less dark pigment; the breast, cheeks, opercles, and gill membranes are whitish cream to olive, not dusky gray. These same two males have five red bars on body and caudal peduncle, with the most posterior bar widest, just like the barred pattern described above for the larger male. The two smaller males also have similar bright red-orange sides of belly.

The anal fin of the large nuptial male is dark blue-gray, with two small red spots at mid-base of fin and a small brown spot near anterior end; pelvic fins are dark blue-gray, with a milky white anterior edge; pectoral fin bases are bright golden with some red, and the rest of the fin is essentially clear. The spinous dorsal fin has a narrow blue-gray margin, followed proximally by a narrow clear band, a narrow red band, and a broad blue-gray band (anterior) that shades to blue-black posteriorly. There are dark red to chocolate brown spots along the very base of the spinous dorsal fin. The soft dorsal fin also has a blue-gray marginal band, then a broad dark red band, a broad blue-gray band, and a narrow brown and russet basal band.

Distribution: *Etheostoma thompsoni* is rather widely distributed in the lower middle sections of the Neches, Sabine, and Calcasieu rivers in southeastern Texas and southwestern Louisiana (Figure 3). Five of the Sabine River records are preimpoundment collections from a section of the Sabine River now flooded by Toledo Bend Reservoir (Figure 3).

Bruce Thompson, just before his untimely death, was studying specimens from the Mermentau River drainage, tributary to the Grand-White lakes complex just east of the Calcasieu, that may ultimately prove to be *Etheostoma thompsoni*. However, the specimens have not, as yet, been located and studied by the authors.

Habitat and Biology: We have designated the Neches River just below Town Bluff dam at Town Bluff as the type locality (Fig. 3). The right (west) bank, where we collected our samples, is in Tyler County, Texas. The bank is very steep and covered with grasses, weeds, and low brush. The banks drop steeply just off the river's edge, with many exposed stems and roots revealed during low water. During January, February, and March the Gumbo Darter congregates and apparently spawns in vegetation along the drop-off area close to shore. The near (west) bank in the drop-off area, during moderately high water, was an excellent collecting place. Usually we could cast the seine out and pull it in toward the vertical drop-off bank. We did not discover any spawning areas in the Sabine River system; in fact nearly all specimens from that system were either small subadults or juveniles.

Unlike the habitat described in the literature for *E. asprigene*, *E. thompsoni* invariably was taken along the bank, sometimes under cuts, where there were exposed roots with accumulated vegetational debris, and sand to mixed sand and gravel substrate with very little silt. We had a total of 40 sampling sites in the three river

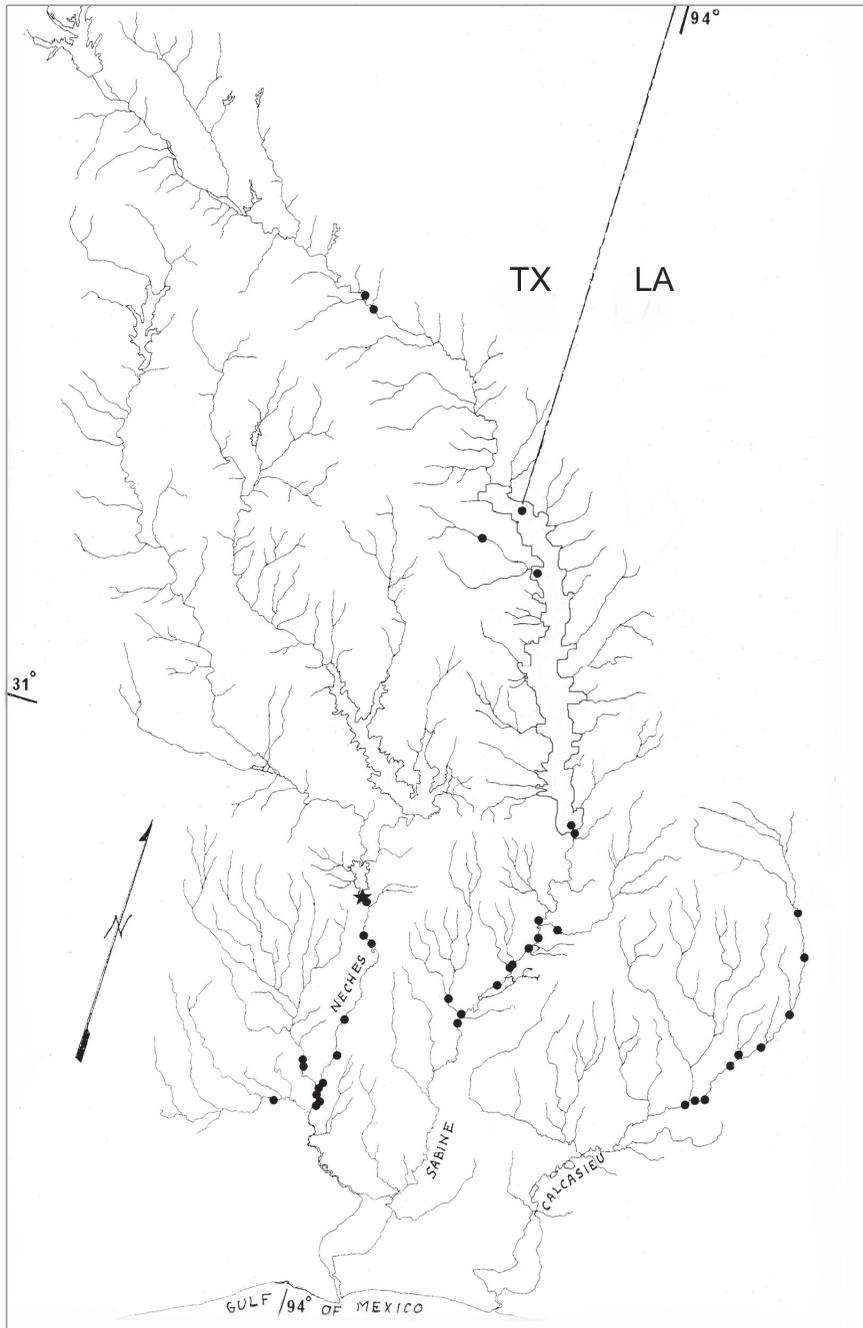


Figure 3. Map of southwestern Louisiana and southeastern Texas showing the distribution of *E. thompsoni* in the Calcasieu, Sabine and Neches rivers.

systems. There were only eight sites in tributaries and these sites were only a short distance from the confluence with the main river. There were 32 collecting sites along the main channels (11 in Neches River, 13 in Sabine River, and 8 in Calcasieu River). Two samples from spawning aggregations were taken from Calcasieu River, Allen Parish, Louisiana. One sample was taken from below a dam, 3.0 mi W Kinder; the other sample was taken from Calcasieu River, 2.0 mi W Oakdale.

Males outnumbered females in the two samples from spawning aggregations in the Calcasieu River drainage. One sample of 33 specimens, collected on 15-16 February 1967 from Calcasieu River 2.0 mi W Oakdale, and the other sample for 52 specimens, collected on 18 February 1981 from Calcasieu River, 3.0 mi NW Kinder, LA. The two samples resulted in 85 specimens, 50 males and 35 females. Males ranged from 26.3-47.1 mm SL and females ranged from 27.5-47.1 mm SL; males averaged 33.4 mm SL and females averaged 34.3 mm SL.

The fish species associates of *E. thompsoni* at the type locality, based on eight collections taken between 16 February 1979 and 1 March 1981 are as follows: *Ichthyomyzon castaneus*, *Atractosteus spatula*, *Lepisosteus oculatus*, *L. osseus*, *Amia calva*, *Anguilla rostrata*, *Dorosoma cepedianum*, *D. petenense*, *Cyprinella lutrensis*, *C. venusta*, *Hybognathus nuchalis*, *Hybopsis amnis*, *Lythrurus fumeus*, *Macrhybopsis hyostoma*, *Notemigonus crysoleucas*, *Notropis atherinoides*, *N. atrocaudalis*, *N. sabiniae*, *N. texanus*, *N. volucellus*, *Phenacobius mirabilis*, *Pimephales vigilax*, *Erimyzon succetta*, *Moxostoma poecilurum*, *Ameiurus melas*, *Ictalurus furcatus*, *I. punctatus*, *Esox americanus*, *Labidesthes sicculus*, *Fundulus notatus*, *F. olivaceus*, *Morone chrysops*, *Centrarchus macropterus*, *Lepomis macrochirus*, *L. megalotis*, *L. microlophus*, *L. miniatus*, *Micropterus punctulatus*, *M. salmoides*, *Pomoxis annularis*, *P. nigromaculatus*, *Ammocrypta vivax*, *Etheostoma chlorosoma*, *E. histrio*, *Percina macrolepida*, *P. sciera*, *P. shumardi*, and *Aplodinotus grunniens*. One mile below the type locality, on 2 March 1981, three specimens of *E. thompsoni* plus two additional species, *Notropis buchani* and *Opsopoeodus emiliae*, were obtained.

Etymology: We take pleasure in naming this darter, *Etheostoma thompsoni*, in honor of our good friend and colleague, the late Bruce Allen Thompson, in recognition of his intense interest in the systematics and biology of darters. His detailed studies of the log perches, wherein he described four new species, were exemplary. His leadership in two extensive papers on Percophidae, *A review of Western North Atlantic species of Bembrops*, and *A revision of Indo-Pacific Bembrops*, was commendable.

Comparisons: There is considerable overlap in meristic characters among *E. thompsoni*, *E. collettei*, *E. asprigene*, and *E. swaini*. *Etheostoma swaini* has the lowest number of lateral-line scales (Table 1); *E. thompsoni* and *E. collettei* have a slightly higher number, and *E. asprigene* has the highest number for the four species. *Etheostoma swaini* from the type locality area (Pearl River drainage) have strikingly lower counts than those from eastern tributaries to the Mississippi River.

The four species are slightly more distinct in numbers of unpored lateral-line scales than in pored and total number of lateral-line scales (Table 2). *Etheostoma swaini* has the lowest number of unpored scales, with *E. thompsoni*, *E. asprigene*, and *E. collettei*, respectively, each having successively higher counts.

Etheostoma collettei has the lowest number of pored lateral-line scales (Table 3), with *E. thompsoni*, *E. asprigene*, and *E. swaini* averaging about the same number of pored lateral-line scales, but a somewhat higher number than in *E. collettei*. Again, *E. swaini* from the Pearl River drainage have much lower counts than *E. swaini* from eastern Mississippi River tributaries, and a mean count slightly lower than that of *E. collettei*. There is little difference in vertical scale counts between the four species (Table 4). In number of scale rows around caudal peduncle, *E. collettei* and *E. swaini* have the lowest counts, *E. thompsoni* is intermediate in number, and *E. asprigene* has the highest number. The three species are essentially the same in number of transverse scale rows. In both of these counts, *E. swaini* from the Pearl River drainage have strikingly lower counts than populations of *E. swaini* from eastern tributaries to the lower Mississippi River and those of the other three species.

Etheostoma thompsoni and *E. swaini* (except in the Pearl River drainage) have a mode of 11 dorsal spines (Table 5), whereas *E. collettei*, *E. asprigene*, and Pearl River *E. swaini* have a mode of 10 dorsal spines. The number of dorsal soft rays is essentially the same in *E. thompsoni* and *E. collettei* (12 or 13 rays). *Etheostoma swaini* populations counted all have a strong mode of 12 rays. Variation in dorsal soft rays is considerable in *E. asprigene*, with a mode of 11 in the Mississippi River basin above the mouth of the Ohio River (mostly from Kaskaskia River, IL); bimodal at 11 or 12 in the Green River system of the Ohio River basin, and with modes of 13 or even 14 in the remainder of the Ohio basin and in the lower Mississippi River basin (Table 5).

Anal soft rays are higher (modally 7 or 8) in *E. thompsoni* and *E. asprigene*, but tend to be lower (modally 6 or 7) in *E. collettei* and *E. swaini* (Table 6). Pectoral-fin rays (Table 6) also tend to be higher (modally 14) in *E. thompsoni* and *E. asprigene* than in *E. collettei* and *E. swaini* (modally 13). Our pectoral ray counts for *E. collettei* and *E. asprigene* agree with those reported by Birdsong and Knapp (1969).

Branched caudal fin rays have a strong modal number of 15 for *E. asprigene* (except for Mississippi River tributaries above the Ohio River), *E. swaini* (except for the Pearl River drainage), and *E. thompsoni* (all populations examined), with over 90% of counts in the range 14-16, and means of 14.5-15.3. Counts are slightly lower in the upper Mississippi (mostly from Kaskaskia River, IL) varying from 13(2), 14(10), and 15(8) with mean = 14.3. In the Pearl River *E. swaini* has modally 13 branched caudal rays with counts of 11(1), 12(3), 13(26), and 14(7), mean = 13.1. In 20 specimens of *E. collettei* examined (10 from Red River system, 10 from Ouachita River system) counts were 13(3), 14(9), and 15(8), mean = 14.3.

Branchiostegal ray counts were 6-6 in all populations of all four species, with deviations of 5 or 7 rays representing about 10% of the counts. Gill rakers counts were very similar for the four species, with modal values of 11 or 12, means of 10.8 (Pearl River drainage *E. swaini*) to 12.2 (Ohio River basin *E. asprigene*); well over 90% of counts were between 10 and 13 except for Pearl River *E. swaini*, where 5 of 33 specimens had only 9 gill rakers.

Variation in the cephalic lateralis system is conservative in the four species, with preoperculo-mandibular canal complete with modally 10 pores; deviants of 9 or 11 pores typically occurred in 10% or fewer specimens. Counts were 9(1), 10(77), 11(1) in *E. thompsoni*, all from the Neches River system; 10(18), 11(2) in *E. collettei*; 9(9),

10(152), 11(17) in *E. asprigene*; and 9(2), 10(101), 11(2) in *E. swaini* from eastern tributaries to the lower Mississippi River. In Pearl River *E. swaini* counts were 8(3), 9(6), 10(20), and 11(1) in 30 specimens. The infraorbital canal was complete with modally 8 pores in all 4 species. Counts were 7(1), 8(65), 9(12), 10(1) in Neches River *E. thompsoni*; 7(4), 8(15), and 9(1) in *E. collettei*; 7(6), 8(96), 9(13) in *E. asprigene*; and 7(3), 8(120); 9(10) in *E. swaini*. Supraoccipital canal complete with modally 4 pores. Counts were 4(46), 5(1) in *E. thompsoni* from Neches River; 3(1), 4(19) in *E. collettei*; 3(6), 4(86); 5(13) in *E. asprigene*; and 3(5), 4(99), 5(1) in *E. swaini* from eastern tributaries to the lower Mississippi River. In the Pearl River drainage 6 of 14 specimens had 3 pores. The supratemporal canal (pores not counted) of *E. thompsoni* is complete; authors discussing the cephalic lateralis system of the other three species consistently report a complete supratemporal canal. We find the supratemporal canal to be narrowly to widely interrupted in many specimens of *E. asprigene* (see "Discussion") from several populations within its range.

Invariably, *E. thompsoni*, *E. asprigene*, and *E. swaini* have fully scaled cheeks and opercles, whereas only about 65% of *E. collettei* have these areas fully scaled. There is a striking difference in nape scalation: 74% of 280 *E. thompsoni* have a naked nape and only one specimen of the 280 has a fully scaled nape; 87% of 84 *E. collettei* have a fully scaled nape and none of the 84 has a naked nape; 98% of 109 *E. asprigene* have a fully scaled nape, and of the two specimens that do not have a fully scaled nape, one is 3/4 scaled and the other is 2/3 scaled. Nape scalation is variable in *E. swaini*, but it is rarely fully scaled in populations we examined. In eastern tributaries to the Mississippi river the nape was scored as completely scaled in only 13 of 123 specimens; 42 of these were scored as being 1/2 or 3/4 scaled, and 68 were scored as being naked to 1/4 scaled. In 34 Pearl River system *E. swaini* the nape was naked to 1/4 scaled in 18, 1/2 to 3/4 scaled in 12, and fully scaled in 4. All four species have the breast naked. The prepectoral area is variably scaled in *E. thompsoni*, with 13 scored as naked and 16 with 1 or more (up to about 7) scales. In *E. collettei* 18 of 18 specimens were scored as naked. In *E. swaini* from eastern tributaries to the lower Mississippi River and in *E. asprigene* the prepectoral area was variably scaled, with the former having 22 of 110 scored as naked, and the latter with 48 of 172 scored as naked; all 33 specimens of *E. swaini* from the Pearl River drainage were scored as naked.

Body Proportions and Morphometrics: Means and standard deviations of 19 body measurements for samples of females and males of *E. thompsoni*, *E. asprigene*, *E. collettei*, and *E. swaini* are reported as proportions (thousandths) of standard length in Table 7. However, univariate and multivariate statistical comparisons are based on residuals from regressions of data for each of the measurements on standard length.

Etheostoma thompsoni differs significantly from *E. asprigene*, *E. collettei* and *E. swaini* in having a longer spinous dorsal fin base and narrower transpelvic width (males and females), a narrower body width, and a shorter snout and caudal peduncle (especially in males, Table 7). Males and females of *E. asprigene* have significantly taller spinous dorsal fins and longer anal and pelvic fins than *E. thompsoni*, *E. collettei* and *E. swaini*. Males and females of *E. collettei* have significantly narrower caudal peduncles and shorter caudal fins than *E. thompsoni*, *E. asprigene*, and *E. swaini*.

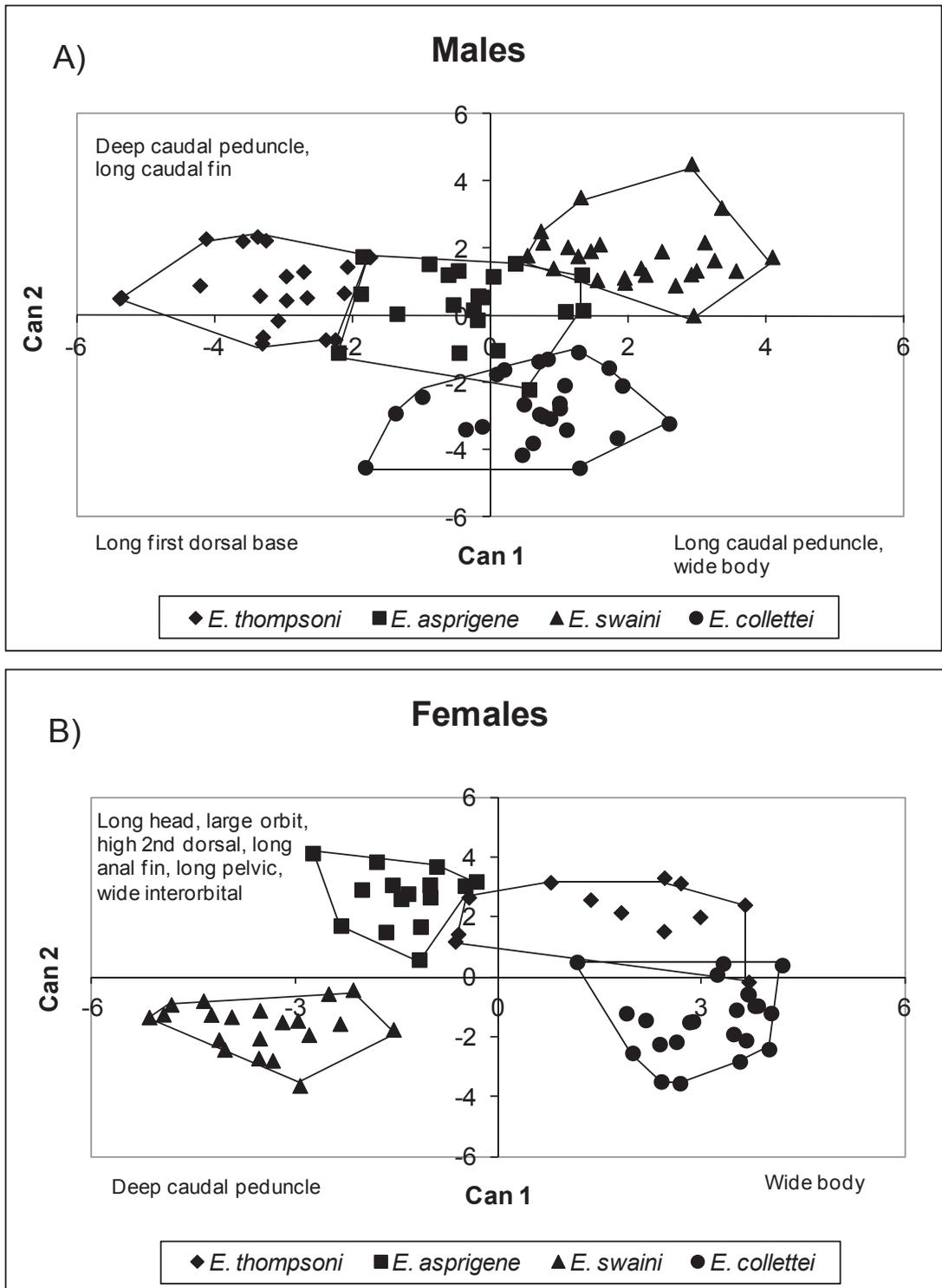


Figure 4. Results of Canonical Discriminant Analysis showing variation in body proportions of males (A) and females (B) of *E. thompsoni* and three species of *Oligocephalus*.

Males and females of *E. swaini* have significantly shorter heads and pelvic fins, smaller orbits and deeper caudal peduncles than *E. thompsoni*, *E. asprigene* and *E. collettei*.

Results of multivariate canonical discriminant analysis (CDA) show reasonably good separation among species clusters and generally confirm body proportion differences described above based on univariate comparisons (Figs. 4). *Etheostoma thompsoni* males separate mainly along CAN 1 and cluster in the region of the plot corresponding to long spinous dorsal fin base, narrow body, and short caudal peduncle (Fig. 4). Females of *E. thompsoni* separate mainly along CAN 1, clustering in the region corresponding to a narrow caudal peduncle and wide body (the latter probably reflecting the gravid condition of specimens). *Etheostoma collettei* males separate mainly along CAN 2 and cluster in the region of the plot corresponding to a narrow caudal peduncle and short caudal fin. Females of *E. collettei* separate mainly along CAN1, clustering in a region of the plot corresponding to a narrow caudal peduncle and relatively wide body. *Etheostoma swaini* males separate along CAN 1 and 2 and cluster in the region corresponding to long and deep caudal peduncle, relatively long caudal fin, and wide body. Females of *E. swaini* also separate along CAN 1 and 2, clustering in a region of the plot corresponding to a short head, small orbit, and short pelvic fins. *Etheostoma asprigene* males cluster in the center of the CDA plot, corresponding to intermediate states of the above body proportion characters. Females cluster in the region of the plot corresponding to high dorsal fin, long anal and pelvic fins, and deep caudal peduncle.

DISCUSSION

Of the species of *Oligocephalus* compared in this study, *E. thompsoni* is most similar to *E. asprigene*, and may be a recent Western Gulf Slope derivative of that species based on shared similarities in general body pigmentation, nuptial male coloration, and body morphometrics. *Etheostoma asprigene* occurs throughout the Mississippi River Valley, from Minnesota/Wisconsin southward to Louisiana, including the lower Ouachita and Red rivers of Louisiana. *Etheostoma thompsoni* occurs just to the west of the Mississippi River Basin in the Calcasieu, Sabine, Neches, and possibly the Mermentau river systems. Such a vicariant event is unusual among currently recognized darter species. Nevertheless, this appears to represent peripheral isolation west of the Mississippi River.

A recent molecular phylogenetic analysis involving mitochondrial and nuclear gene regions consistently resolved *Etheostoma asprigene*, *E. collettei* and *E. swaini* as part of a monophyletic group of *Oligocephalus* darters – referred to as the *E. asprigene* group – that included *E. nuchale*, *E. ditrema* and *E. caerulueum* (Lang and Mayden 2007). *Etheostoma collettei* was always sister to *E. swaini* in nuclear (S7 intron) and mitochondrial (cytb) gene trees, and in a combined data analysis. These species were sister either to *E. nuchale* and *E. ditrema*, or to *E. asprigene*. The analysis did not include *E. thompsoni*.

From our results, it would appear that species-level recognition may be justified for populations currently identified as *Etheostoma swaini* from eastern tributaries to the Mississippi River. They differ markedly from specimens from the Pearl River drainage

(type locality) in lateral-line scales, pored lateral-line scales, scales around caudal peduncle, pectoral fin rays, and branched caudal fin rays. The most southerly Mississippi River system tributary from which we examined specimens identified as *E. swaini* was the Homochitto River. In this system, counts of transverse scale rows, dorsal soft rays, and anal soft rays appear to be somewhat intermediate between counts for the Pearl River drainage and more northerly eastern tributaries to the Mississippi River. Specimens from Bayou Pierre, geographically intermediate between the Homochitto and Big Black rivers might provide additional insights into the status of populations of *E. swaini* from eastern Mississippi River tributaries.

We also noted interesting variation in the cephalic lateralis system of *E. asprigene*. The supratemporal canal is interrupted on the mid-line in 29 of 31 specimens of *Etheostoma asprigene* from the Kaskaskia River, IL; whereas the canal is complete in both specimens from the upper Mississippi River. In the Ohio River basin, the canal was interrupted in only two of 15 specimens from Wabash River Mile 181 and 183.7 (Sullivan Co.) but interrupted in five of nine specimens from the lower Wabash (Knox and Posey counties); three of 10 from the Green River, 0 of 11 from the Cumberland River, and three of 16 from the Tennessee River had interrupted supratemporal canals. In the lower Mississippi River the canal was interrupted in five of 28 specimens, but four of the five with interrupted canals were from the extreme lower portion of the river in Louisiana. In large western tributaries to the lower Mississippi river the canal was interrupted in two of 20 from the White River, one of 10 from the Arkansas, and three of four from the Red.

While this may merely be the result of regional intraspecific variation, we wonder if this phenomenon is similar to that discussed by Bauer et al. (1995, p 11). They found that only five of 68 specimens of *Etheostoma (Ulocentra) scotti* collected in 1990 from Butler Creek, tributary to Allatoona Creek, Cobb County, GA, north of Atlanta, had complete supratemporal canals. Specimens of *E. scotti* from this same creek had 13 of 29 canals complete in specimens collected from 1984-1987, and complete in 14 of 15 specimens collected in 1950. They attributed this rapid and drastic change in the canal to be "perhaps caused by chemical pollutants entering the system", and to possibly be ". . . an early warning of the imminent demise of that population."

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ADDITIONAL MATERIAL EXAMINED

For systems that are consolidated into a single row in Tables 1-6, we provide below, means, number of specimens, and range of values for the following characters: total lateral-line scales (**LLS**), unpored LLS (**LLU**), pored LLS (**LLP**), scales around caudal peduncle (**SACP**), transverse scale rows (**TR**), dorsal fin spines (**D1**), dorsal fin soft rays (**D2**), anal fin soft rays (**A**), and left pectoral fin rays (**P**).

***Etheostoma asprigene*. Mississippi River and tributaries above mouth of Ohio River:** SU 2201, USNM 34415, UT 91.134, UT 91.6545, INHS 12594, INHS 87621, INHS 25597, INHS 87622; **LLS**, 49.5, 54, 46-55; **LLU**, 10.1, 57, 6-13; **LLP**, 39.2, 55, 34-45; **SACP**, 19.8, 42, 18-22; **TR**, 13.8, 43, 13-16; **D1**, 10.3, 51, 9-11; **D2**, 11.5, 51, 10-14; **A**, 7.3, 52, 6-9; **P**, 13.7, 36, 12-15. **Ohio River Basin, Green River system:** UT 91.5437, UT 91.6100; **LLS**, 45.4, 22, 42-49; **LLU**, 9.6, 20, 7-15; **LLP**, 35.9, 21, 33-40; **SACP**, 21.2, 11, 20-22; **TR**, 14.5, 13, 13-16; **D1**, 10.2, 23, 9-11; **D2**, 11.4, 23, 10-12; **A**, 7.8, 23, 7-9; **P**, 13.4, 23, 12-15. **Wabash River system:** USNM66960, US 91.1711, UT 91.1714, UT 91.3142, UT 91.3183, TU 19290, TU 19329, TU 101164; **LLS**, 49.1, 56, 43-55; **LLU**, 11.7, 37, 7-16; **LLP**, 36.8, 40, 29-43; **SACP**, 21.1, 33, 19.24; **TR**, 14.9, 30, 13-17; **D1**, 10.3, 41, 9-11; **D2**, 12.9, 41, 11-15; **A**, 7.8, 41, 6-9; **P**, X 13.8, 41, 13-16. **Cumberland River drainage:** UT 91.1107, UT 91.3722, UT 91.5234; **LLS**, 47.8, 11, 44-52; **LLU**, 8.6, 11, 4-12; **LLP**, 39.6, 12, 32-46; **SACP**, 21.7, 8, 21-23; **TR**, 16.0, 9, 15-17; **D1**, 9.4, 10, 9-10; **D2**, 12.9, 10, 12-14; **A**, 7.8, 10, 7.9; **P**, 13.8, 10, 13-15. **Tennessee River drainage:** UT 91.2842, UT 91.2843, UT 91.4643, UT 91.5234, TU 89447; **LLS**, 47.4, 31, 42-52; **LLU**, 9.9, 26, 5-13; **LLP**, 37.6, 30, 32-42; **SACP**, 21.7, 33, 19-24; **TR**, 14.6, 31, 13-16; **D1**, 10.3, 32, 9-11; **D2**, 13.2, 43, 12-14; **A**, 8.0, 32, 7-9; **P**, 13.9, 32, 13-15. **Mississippi River and smaller tributaries below mouth of Ohio River:** MMNS 30684, UAFS 1400 UAFS 1696, UAFS 1848, UAFS 1894, UAFS 1898, UT 91.138, UT 91.553, UT 91.564, UT 91.599, UT 91.1286, UT 91.2632, UT 91.3040, UT 91.3410, UT 91.4079, UT 91.5424, TU 99565, TU 108113; **LLS**, 50.0, 143, 40-57; **LLU**, 9.6, 118, 5-17; **LLP**, 39.9, 135, 30-48; **SACP**, 21.5, 47, 20-24; **TR**, 15.3, 60, 13-19; **D1**, 10.3, 93, 9-12; **D2**, 13.3, 91, 12-15; **A**, 7.9, 89, 6-10; **P**, 14.0, 92, 13-15. **White River system:** UAFS0895, UAFS0892, UAFS 0898, UAFS 0899, UAFS 0902, UAFS 0903, UAFS 0904, UAFS 1593, UAFS 1667; **LLS**, 47.6, 33, 44-52; **LLU**, 8.5, 28, 3-13; **LLP**, 38.8, 28, 33-43; **SACP**, 20.9, 25, 19-23; **TR**, 15.7, 25, 14-17; **D1**, 10.3, 43, 9-11; **D2**, 13.2, 43, 12-15; **A**, 7.6, 43, 7-8; **P**, 13.9, 43, 13-15. **Arkansas River system:** UAFS 0894, UAFS 0900, UAFS 1847; **LLS**, 47.0, 34, 43-53; **LLU**, 8.5, 28, 4-13; **LLP**, 38.3, 32, 34-43; **SACP**, 24.4, 20, 20-22; **TR**, 15.5, 25, 14-17; **D1**, 10.4, 36, 10-12; **D2**, 12.4, N 36, 12-15; **A**, 7.8, 35, 6-9; **P**, 13.8, 35, 13-15. **Red River system:** AR: UAFS 1345, UAFS 1356, UAFS 1697, UAFS 1849; **LLS**, 48.7, 4, 46-51; **LLU**, 5.0, 2, 2-8; **LLP**, 43.5, 2, 43-44; **SACP**, 21.5, 4, 21-22; **TR**, 16.5, 4, 16-17; **D1**, 10.0, 4, 10; **D2**, 12.3, 4, 11-13; **A**, 7.8, 4, 7-8; **P**, 14.0, 3, 14. LA: USNM 173058; **LLS**, 50.1, 9, 48-53; **LLU**, 9.8, 9, 8-12; **LLP**, 37, 37-43. ***Etheostoma collettei* Red River system, LA:** TU 55133; **LLS**, 50.3, 28, 46-55; **LLU**, 11.6, 28, 8-16; **LLP**, 38.6, 28, 36-42; **SACP**, 21.7, 28, 20-24; **TR**, 16.1, 28, 14-18; **D1**, 10.8, 28, 10-12; **D2**, 12.6, 28, 12-14; **A**, 7.1, 28, 6-8; **P**, 13.0, 28, 12-13. **Ouachita River system, AR:** USNM 165915, TU 100993; **LLS**, 49.7, 18, 46-54; **LLU**, 13.8, 18,

7-25; **LLP**, 35.9, 18, 27-41; **SACP**, 20.6, 8, 17-23; **TR**, 15.7, 8, 15-17; **D1**, 10.4, 8, 10-11; **D2**, 12.2, 8, 15-17; **A**, 6.9, 8, 6-7; **P**, 13.0, 8, 13, LA: TU 76092; **LLS**, 49.5, 48; 44-56; **LLU**, 15.0, 48, 10-26; **LLP**, 34.5, 48, 24-40; **SACP**, 20.2, 48, 18-23; **TR**, 15.1, 48, 13-17; **D1**, 10.2, 48, 9-12; **D2**, 12.6, 48, 11-14; **A**, 7.0, 48, 6-8; **P**, 13.0, 48, 12-14.

***Etheostoma swaini*. Obion River system:** UT 91.306, UT 91.963, UT 91.1608, UT 91.2292, UT 91.2756; **LLS**, 46.8, 35, 43-51; **LLU**, 6.2, 38, 1-10; **LLP**, 40.3, 38, 35-46; **SACP**, 20.1, 23, 19-22; **TR**, 14.9, 23, 13-17; **D1**, 10.7, 42, 9-12; **D2**, 11.7, 42, 10-13; **A**, 7.3, 42, 7-8; **P**, 12.9, 42, 12-14. **Forked Deer River system:** UT 91.84, UT 91.1268, UT 91.1276, UT 91.1279, UT 91.1350, UT 91.1355; **LLS**, 46.8, 50, 41-54; **LLU**, 7.2, 49, 1-12; **LLP**, 39.7, 48, 32-48; **SACP**, 20.6, 25, 19-22; **TR**, 14.8, 24, 13-16; **D1**, 10.3, 50, 10-12; **D2**, 11.7, 50, 11-13; **A**, 7.4, 50, 6-8; **P**, 12.9, 49, 12-14; **Hatchie River system:** UT 91.275, UT 91.533, UT 91.534, UT 91.915, UT 91.918, UT 91.928, UT 91.6061, UT 91.6088, UT 91.6668; **LLS**, 47.1, 45, 43-52; **LLU**, 7.9, 44, 3-16; **LLP**, 39.1, 44, 31-47; **SACP**, 20.5, 17, 19-22; **TR**, 15.0, 17, 13-16; **D1**, 10.6, 48, 10-11; **D2**, 11.6, 48, 9-13; **A**, 7.2, 40, 6-8; **P**, 12.8, 45, 12-14; **Wolf River system:** UT 91.2934, UT 91.5907; **LLS**, 47.6, 29, 44-52; **LLU**, 5.1, 29, 1-11; **LLP**, 42.5, 29, 35-49; **SACP**, 20.2, 26, 19-22; **TR**, 15.2, 27, 14-17; **D1**, 10.8, 35, 10-12; **D2**, 11.7, 35, 11-13; **A**, 7.2, 35, 6-8; **P**, 13.2, 35, 11-15; **Yazoo River system:** TU 158073, TU 162800, TU 163328, UT 91.2171 UT 91.3541; **LLS**, 46.0, 1, 41-50; **LLU**, 4.4, 17, 0-7; **LLP**, 41.5, 17, 35-48; **SACP**, 19.9, 17, 18-21; **TR**, 15.2, 17, 14-17; **D1**, 10.6, 16, 8-12; **D2**, 12.5, 17, 11-13; **A**, 7.2, 17, 6-8; **P**, 13.2, 17, 12-14; **Big Black River system:** TU 79980, TU 133582, UT 91.2476, UT 91.3401; **LLS**, 46.7, 51, 38-52; **LLU**, 6.3, 51, 1-13; **LLP**, 40.4, 51, 32-46; **SACP**, 19.5, 41, 18-21; **TR**, 15.4, 42, 13-18; **D1**, 11.0, 43, 10-12; **D2**, 12.2, 43, 11-14; **A**, 7.3, 34, 7-8; **P**, 13.3, 34, 12-14; **Homochitto River system:** TU 55431, TU 66983, UT 91.3406; **LLS**, 46.3, 68, 40-52; **LLU**, 3.3, 68, 0-9; **LLP**, 43.0, 68, 37-52; **SACP**, 19.2, 33, 18-21; **TR**, 14.3, 33, 12-16; **D1**, 10.9, 33, 10-12; **D2**, 11.6, 33, 11-13; **A**, 6.8, 33, 6-8; **P**, 13.3, 33, 12-14. **Mississippi River:** TU 55398, 66841, TU 99565, TU 108113, **Pearl River system:** USNM 35308, TU 43119, UT 91.3424, UT 91.306, UT 91.1922; **LLS**, 39.9, 62, 36-44; **LLU**, 5.0, 6.2, 0.9; **LLP**, 35.0, 62, 30-43; **SACP**, 16.7, 40, 14-19; **TR**, 12.2, 40, 10-14; **D1**, 10.4, 45, 9-11; **D2**, 11.6, 44, 10-13; **A**, 6.5, 48, 5.8; **P**, 12.5, 46, 12-14.

Table 1. Frequency distributions of total lateral-line scales in *Etheostoma thompsoni*, *E. collettei*, *E. asprigene*, and *E. swaini*

	Total Lateral-line Scales																			N	\bar{x}	S.D.								
	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54				55	56	57	58	59			
<u><i>E. thompsoni</i></u>																														
Neches River						1	1	1	10	10	15	21	15	10	12	10	4	1										111	48.5	2.5
Sabine River							1	1	2	2	4	6	5	6	3	5	4											39	49.1	2.6
Calcasieu River						2	4	7	11	27	13	20	16	13	7	6	3											129	47.5	2.5
Totals						3	6	9	23	39	32	47	36	29	22	21	11	1										279	48.1	2.5
<u><i>E. collettei</i></u>																														
								1		5	10	9	15	19	15	13	4	1	1	1								94	49.8	2.2
<u><i>E. asprigene</i></u>																														
Mississippi R. above Ohio R.										2	4	15	8	10	7	3	1	2	2									54	49.5	2.1
Ohio River basin						3	4	9	13	16	10	17	13	11	7	6	6	4	1									120	47.9	3.0
Mississippi R. & tribs. below Ohio R. Western tribs.				1		1	3	1	2	10	12	12	17	21	18	14	11	9	6	1	4							143	50.0	3.2
lower Mississippi R. IL, IN, TN, LA							1	7	10	10	11	11	8	10	6	3	3											80	47.7	2.5
Totals				1		4	8	17	25	38	36	53	44	48	37	25	17	14	9	1	4							397	48.8	2.7
<u><i>E. swaini</i></u>																														
Eastern tribs. to lower Mississippi R.				1		1	3	6	10	19	48	48	45	48	36	13	11	5		1								295	46.8	2.3
Pearl	2	2	12	12	13	7	8	3	3																			62	39.9	1.9

Table 2. Frequency distributions of unpored lateral-line scales in *Etheostoma thompsoni*, *E. collettei*, *E. asprigene*, and *E. swaini*

	Unpored Lateral-line Scales																										N	\bar{x}	S.D.	
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25				26
<i>E. thompsoni</i>																														
Neches River	1	2	3	4	4	13	21	12	26	10	8	5	1			1												111	6.9	2.5
Sabine River			1	1	1		2	3	9	5	6	2	1	5	1				1	1								39	9.4	3.3
Calcasieu River						3	9	19	31	13	23	15	7	5	4		1											130	9.1	2.2
Totals	1	2	4	5	5	16	32	34	66	28	37	22	9	10	5	1	1	1	1									280	8.3	
<i>E. collettei</i>																														
								1	2	1	6	7	16	13	13	15	8	8			1	1				1	1	94	13.7	3.0
<i>E. asprigene</i>																														
Mississippi R. above Ohio R.							3	3	7	8	10	11	9	6														57	10.1	1.9
Ohio River basin				1	1	3	5	11	15	12	20	12	9	7	4	1												101	10.5	2.4
Mississippi R. & tribs. below Ohio R. Western tribs.						3	4	10	25	19	20	15	11	6	3	1				1								118	9.6	2.2
lower Mississippi R.			1	1	3	1	1	8	17	15	16	4	3	3														73	8.7	2.1
Totals			1	1	4	5	11	26	60	57	58	50	35	24	10	5	1	1										349		
<i>E. swaini</i>																														
Eastern tribs. to lower Mississippi R.	10	18	18	18	23	35	54	47	28	22	10	3	7	2						1								296	5.8	2.8
Pearl	2	2	2	8	8	14	13	6	6	1																		62	5.0	2.0

Table 3. Frequency distributions of pored lateral-line scales in *Etheostoma thompsoni*, *E. collettei*, *E. asprigene*, and *E. swaini*

		Pored Lateral-line Scales																												N	\bar{x}	S.D.		
		24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52				
<u><i>E. thompsoni</i></u>																																		
Neches River										1				2	8	6	6	18	11	16	16	13	3	6	3	2						111	41.6	2.8
Sabine River									1	1	1	2	3	2	2	4	3		6	3	1	5	3		2							39	39.7	4.2
Calcasieu River										2	3	8	8	6	17	21	16	17	11	9	8	1	1	1								129	38.5	2.8
Totals									1	3	5	10	11	10	27	31	25	35	28	28	25	19	7	7	5	2						279		
<u><i>E. collettei</i></u>		1	1		2		1		2	5	4	12	5	16	13	10	10	5	4	3												94	36.0	3.5
<u><i>E. asprigene</i></u>																																		
Mississippi R. above Ohio R.												1	1	10	4	6	5	14	6	1	3	2	2									55	39.0	2.6
Ohio River basin Mississippi R. & tribs. below Ohio R. Western tribs.					1	1	2	2	6	7	11	18	10	13	8	13	7	6	2	2				1								110	37.0	4.8
lower Mississippi R. Totals						1	1	1	2	3		2	11	11	15	18	19	16	13	8	5	5	1	3							135	39.9	5.6	
									1	1	4	5	11	11	9	10	6	5	5	3												71	38.9	2.6
					1	2	3	3	9	12	16	35	36	41	37	55	38	28	23	15	7	6	1	3								371		
<u><i>E. swaini</i></u>																																		
Eastern tribs. to lower Mississippi R. Pearl										1	2	1	5	5	12	20	22	30	35	32	37	26	22	17	15	4	4	3	1		1	295	40.8	4.1
										1	4	2	9	16	8	7	6	4	2		2		1									62	35	2.5

Table 5. Frequency distributions of dorsal fin rays in *Etheostoma thompsoni*, *E. collettei*, *E. asprigene*, and *E. swaini*

	Dorsal Spines							Dorsal Soft Rays												
	8	9	10	11	12	N	\bar{x}	S.D.	9	10	11	12	13	14	15	N	\bar{x}	S.D.		
<i>E. thompsoni</i>																				
Neches R.		1	23	84	3	111	10.8	0.5					6	60	41	4	111	12.4	0.6	
Sabine R.			5	29	5	39	11.0	0.5					13	20	6		39	12.8	0.7	
Calcasieu R.			38	85	7	130	10.8	0.5					5	59	56	9	1	130	12.5	0.7
Totals		1	66	198	15	280							11	132	117	19	1	280		
<i>E. collettei</i>																				
		4	44	34	2	84	10.3	1.2					2	39	35	8	84	12.5	1.2	
<i>E. asprigene</i>																				
Mississippi R. above Ohio R.		4	29	18		51	10.3	0.6		5	20	23	2	1			51	11.5	0.8	
Ohio River basin		12	64	30		106	10.2	0.6		1	14	34	36	31	1		117	12.7	1.0	
Mississippi R. & tribs. below Ohio R. Western tribs.		9	48	33	3	93	10.3	0.7					15	42	28	6	91	13.3	0.8	
lower Mississippi R.		1	51	30	1	83	10.4	0.5			1	11	43	24	4		83	13.1	1.6	
Totals		26	192	111	4	333				6	35	83	123	84	11		342			
<i>E. swaini</i>																				
Eastern tribs. to lower Mississippi R. Pearl	1	1	54	197	14	267	10.8	0.8	1	1	77	151	37	1			268	11.8	0.7	
		2	22	21		44	10.4	0.6		2	15	24	3				44	11.6	0.7	

Table 6. Frequency distributions of anal and pectoral fin ray counts in *Etheostoma thompsoni*, *E. collettei*, *E. asprigene*, and *E. swaini*

	Anal Soft Rays					N	\bar{x}	S.D.	Left Pectoral Fin Rays						N	\bar{x}	S.D.
	5	6	7	8	9				11	12	13	14	15	16			
<i>E. thompsoni</i>																	
Neches R.		6	63	39	3	111	7.3	0.6		1	8	89	13		111	14.0	0.5
Sabine R.			13	24	2	39	7.7	0.5			3	30	6		39	14.1	0.5
Calcasieu R.		7	68	53	2	130	7.4	0.6			9	97	23	1	130	14.1	0.5
Totals		13	144	116	7	280				1	20	216	42	1	280		
<i>E. collettei</i>																	
		7	65	12		84	7.1	0.5		4	76	4			84	13.0	0.5
<i>E. asprigene</i>																	
Mississippi R. above Ohio R.		5	32	11	4	52	7.3	0.7		1	11	23	1		36	13.7	0.6
Ohio River basin		1	27	63	15	106	7.9	0.6		1	29	71	4	1	106	13.8	0.6
Mississippi R. & tribs. below Ohio R.		1	20	51	16	1	89	7.9	0.7			9	70	13	92	14.0	0.5
Western tribs. lower Mississippi R.		3	22	51	6	82	7.7	0.6			14	62	5		81	13.9	0.5
Totals		10	101	176	41	1	329			2	63	226	23	1	315		
<i>E. swaini</i>																	
Eastern tribs. to lower Mississippi R.			15	154	82	251	7.3	0.6		1	23	180	50	1	255	13.0	0.9
Pearl		2	20	25	1	48	6.5	0.6			23	21	2		46	12.5	0.6

Table 7. Comparison of 19 body measurements expressed as proportions of standard length for males and females of four species of *Oligocephalus*. Superscripted letters are SNK groupings based on ANOVA comparison within sexes (proportions with the same letter are not significantly different).

Proportion	<i>E. thompsoni</i>				<i>E. asprigene</i>				<i>E. collettei</i>				<i>E. swaini</i>			
	Females (12)		Males (20)		Females (15)		Males (20)		Females (23)		Males (25)		Females (20)		Males (25)	
	\bar{X}	STD	\bar{X}	STD	\bar{X}	STD	\bar{X}	STD	\bar{X}	STD	\bar{X}	STD	\bar{X}	STD	\bar{X}	STD
Head length	0.269 ^a	0.012	0.274 ^{ab}	0.010	0.277 ^a	0.011	0.283 ^a	0.010	0.269 ^a	0.010	0.269 ^b	0.011	0.252 ^b	0.005	0.259 ^c	0.008
Body depth	0.202 ^a	0.009	0.192 ^b	0.010	0.198 ^a	0.013	0.197 ^a	0.010	0.204 ^a	0.013	0.194 ^b	0.008	0.196 ^a	0.010	0.203 ^a	0.009
Snout length	0.059 ^{ab}	0.005	0.059 ^b	0.005	0.064 ^a	0.005	0.064 ^a	0.007	0.060 ^{ab}	0.005	0.063 ^a	0.005	0.055 ^b	0.009	0.063 ^a	0.005
Orbit length	0.067 ^b	0.006	0.067 ^b	0.006	0.076 ^a	0.006	0.077 ^a	0.006	0.067 ^b	0.005	0.067 ^b	0.006	0.055 ^c	0.005	0.056 ^c	0.005
Spinous dorsal fin base length	0.308 ^a	0.021	0.311 ^a	0.013	0.278 ^b	0.011	0.282 ^c	0.017	0.287 ^b	0.010	0.299 ^b	0.013	0.285 ^b	0.014	0.289 ^c	0.016
Longest dorsal spine	0.130 ^a	0.011	0.135 ^a	0.010	0.130 ^a	0.015	0.137 ^a	0.011	0.116 ^b	0.010	0.131 ^a	0.011	0.119 ^b	0.013	0.128 ^a	0.015
Soft dorsal fin base length	0.263 ^b	0.011	0.281 ^a	0.017	0.282 ^a	0.011	0.289 ^a	0.016	0.264 ^b	0.015	0.281 ^a	0.015	0.254 ^b	0.018	0.279 ^a	0.017
Longest dorsal ray	0.141 ^b	0.006	0.153 ^b	0.013	0.157 ^a	0.012	0.166 ^a	0.012	0.134 ^{bc}	0.013	0.146 ^b	0.010	0.131 ^c	0.010	0.144 ^b	0.015
Caudal peduncle length	0.241 ^b	0.012	0.227 ^b	0.012	0.237 ^b	0.011	0.238 ^a	0.016	0.26 ^a	0.014	0.247 ^a	0.012	0.246 ^b	0.013	0.246 ^a	0.009
Caudal peduncle depth	0.104 ^b	0.006	0.109 ^c	0.005	0.114 ^a	0.006	0.116 ^b	0.007	0.094 ^c	0.007	0.097 ^d	0.009	0.116 ^a	0.007	0.125 ^a	0.016
Anal fin length	0.224 ^b	0.014	0.247 ^b	0.015	0.251 ^a	0.016	0.266 ^a	0.011	0.215 ^b	0.013	0.237 ^c	0.012	0.212 ^b	0.019	0.231 ^c	0.016
First anal spine length	0.098 ^a	0.016	0.095 ^b	0.011	0.096 ^a	0.012	0.106 ^a	0.008	0.091 ^a	0.011	0.092 ^b	0.009	0.094 ^a	0.007	0.101 ^a	0.010
Longest anal ray length	0.132 ^{ab}	0.018	0.142 ^a	0.011	0.144 ^a	0.014	0.149 ^a	0.011	0.133 ^{ab}	0.010	0.140 ^a	0.012	0.129 ^b	0.012	0.129 ^b	0.015
Caudal fin length	0.205 ^a	0.013	0.205 ^a	0.010	0.212 ^a	0.014	0.209 ^a	0.012	0.186 ^b	0.013	0.187 ^b	0.013	0.201 ^a	0.012	0.199 ^a	0.011
Pectoral fin length	0.233 ^a	0.019	0.238 ^b	0.014	0.248 ^a	0.015	0.256 ^a	0.014	0.239 ^a	0.017	0.240 ^b	0.011	0.232 ^a	0.013	0.237 ^b	0.013
Pelvic fin length	0.206 ^{ab}	0.010	0.212 ^{ab}	0.013	0.219 ^a	0.012	0.225 ^a	0.013	0.204 ^b	0.011	0.204 ^b	0.011	0.179 ^c	0.012	0.190 ^c	0.016
Trans-pelvic width	0.057 ^c	0.005	0.062 ^b	0.005	0.065 ^a	0.006	0.067 ^a	0.007	0.062 ^b	0.007	0.067 ^a	0.009	0.068 ^a	0.005	0.072 ^a	0.006
Maximum body width	0.141 ^{ab}	0.010	0.121 ^b	0.010	0.134 ^b	0.012	0.132 ^a	0.006	0.148 ^a	0.010	0.131 ^a	0.008	0.135 ^b	0.010	0.136 ^a	0.010
Interorbital width	0.046 ^a	0.004	0.046 ^a	0.004	0.049 ^a	0.005	0.048 ^a	0.004	0.037 ^b	0.006	0.040 ^b	0.005	0.038 ^b	0.005	0.042 ^b	0.005