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EDITOR'S NOTE

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

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INTERACTIONS BETWEEN TARANTULAS (*APHONOPELMA HENTZI*) AND NARROW-MOUTHED TOADS (*GASTROPHYRNE OLIVACEA*): SUPPORT FOR A SYMBIOTIC RELATIONSHIP

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TUBRI

Tulane University
NEW ORLEANS

Editor's Note

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The publication of this issue of Tulane Studies in Zoology and Botany (TSZB) marks the end of an era and the passing of a legendary figure in the biology of the southeast region of North America. This is final print issue of TSZB. The print version has finally succumbed to the challenges we have faced sustaining funding for printing and mailing this predominantly exchange-based periodical. With this issue, we are changing the format of TSZB to 'Open Access'. The contents will be available for download free-of-charge via the Internet. We will continue selling reprints and complete back issues to anyone wishing to have these until our supply runs out. Individuals and institutions interested in obtaining back issues should visit: http://www.museum.tulane.edu/publications/tszbback.shtml. PDF's of scanned back issues of Tulane Studies in Zoology and TSZB can also be obtained without cost from the Biodiversity Heritage Library (http://www.biodiversitylibrary.org/title/5361).

This issue of TSZB also contains what is very likely to be the final lead-authored publication of Dr. Royal D. Suttkus, who passed away on 28 December 2009, less than six months shy of his 90th birthday. Royal Suttkus, or "Sut", as he was affectionately known to family and friends, holds a special place in southeastern ichthyology, having described a significant component of the region's ichthyofauna. His insatiable appetite and great skill at field collecting are legendary. The collections he amassed over a professional career spanning 65 years - primarily fishes, but also important collections of plants, aquatic invertebrates, amphibians and reptiles, and mammals – constitute one of the most comprehensive records of regional biodiversity in existence and will serve organismal research for many decades to come. The following account of his remarkable life is excerpted from an obituary published in the journal *Copeia* in May 2010.

Suttkus was born 11 May 1920 in Ballville, Ohio, the third of four children of John Albright Suttkus and Myna Louise Schultz Suttkus. Royal, as he was called as a boy, developed a love for natural history in early childhood. He hunted rabbits and pheasant with Brother Merlin, and enjoyed birding, gathering wildflowers and collecting insects. He taught his friends about horned worms and hawk moths. He fished with his father below the hydrodam on the Sandusky River, catching white and black crappie. He caught small fish with his hands while searching for crayfish among slabs of rock. He recalls seeing redhorse suckers spawning along the Sandusky River and shooting an Egyptian goose with a bow and arrow along the Grand River in Michigan. He read Charles Darwin's *On the Origin of Species* while in high school.

Suttkus graduated from Fremont Ross High School in 1937 then worked in a celery garden for 2 years to earn money for college. In the fall of 1939, he enrolled in Michigan State University, eventually majoring in Wildlife Management. He joined the R.O.T.C. at Michigan State, where he trained in field artillery. After earning his bachelor's degree, he enrolled in Officer's Commission School. When he finished his training, he was promoted to Second Lieutenant and attached to the 686th Field Artillery, an all African American battalion. His battalion went to South Wales in 1944 then crossed the English Channel to France, where his training was put to immediate use in the Battle of the Bulge.

After his discharge from the Army in June 1946, he was accepted to the graduate program in the School of Agriculture at Cornell University, where he studied under Edward Raney. He met his bride to be, Jeanne Elizabeth Robinson, while working for New York Fish and Game on Saranac Lake. They were married in December 1947. Son, Jayson, the first of three children, was born in Ithaca, NY, two years later in January 1949 (Fig. 1).

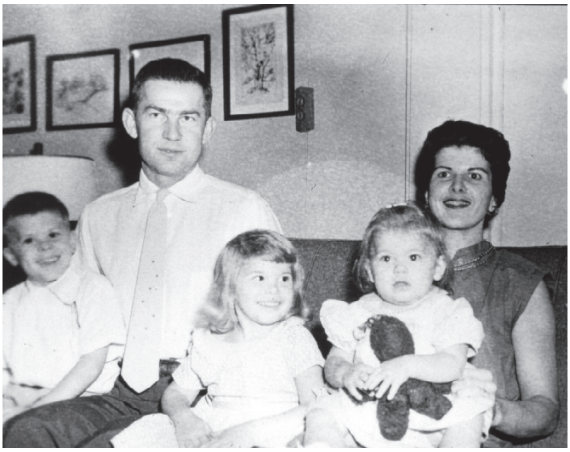

Figure 1. Suttkus pictured with wife Jeanne Robinson Suttkus, and kids Jayson (far left), Ramona (middle) and Jan (right.)

Suttkus accepted a faculty position in Zoology at Tulane University in the fall of 1950. Daughter, Ramona, was born in New Orleans in April 1951; Daughter, Jan, was born in September 1954. Suttkus devoted his career at Tulane to collection building and studies of the taxonomy and natural history of specimens he collected. From 1963 to 1968, he was Principal Investigator of the NIH-funded, Environmental Biology Training Program, a summer program in which students received lectures and training while in the field collecting and preparing specimens of plants, invertebrates, fishes, herps, birds, mammals, and fossils.

In 1963, Suttkus started a consulting business with his long-time Tulane colleague, the late Gerald E. Gunning. Their first contract was a survey of ten stations on the Pearl River near Bogalusa, Louisiana for a pulp and paper mill. The survey started with monthly samples in April 1963, then switched to quarterly (seasonal) collections a year later (Fig. 2). A quarterly survey of eight stations on the upper Pearl River was initiated in 1973. Suttkus continued both surveys until 2005. A survey of the lower Alabama River started in 1969 and continued until 2000. A survey of the Red River near Alexandria, LA was established in 1976 and ended in 2002. Shorter–term surveys were conducted on the Perdido Bay System, Sabine River, Mississippi River and Calcasieu River. All of the collecting on these surveys was supervised by Suttkus and involved standardized gear, technique and environmental sampling. Suttkus also collected marine organisms during oceanic cruises in the Gulf of Mexico, Indian Ocean, off the coasts of Peru and Venezuela, and around the Galapagos Islands. All of the specimens collected (fishes and any amphibians, reptiles, mussels, and decapods that happened to be collected) were preserved and ultimately cataloged into Tulane's natural history collections.

Suttkus published an impressive body of scholarly work during his career. His most recent cv lists 125 papers, 54 of which deal directly with fish taxonomy and systematics, 41 report on various aspects of fish life history and/or distribution, and 27 are reports based on his fish monitoring surveys. As a sign of his taxonomic breadth, 11 of

Figure 2. Suttkus surveying the Pearl River in the 1960's.

his papers deal with mammals, three deal with crayfishes, and one deals with freshwater mussels. Among his systematic and taxonomic contributions are descriptions of 35 new fish species, 29 of which are freshwater species largely confined to the southeastern United States. It is in the southeastern U.S. that his contributions to knowledge of biology have been greatest. It is hard to collect anywhere in the southeast without encountering at least one of his species. Moreover, his taxonomic treatments are among the most thorough in the profession in terms of numbers of specimens examined.

Suttkus directed 24 graduate students during his career (10 M.S., 14 Ph.D.), including important contributors to ichthyology such as Rudolph J. Miller (M.S. 1958), John S. Ramsey (Ph.D. 1965), James E. Thomerson (Ph.D. 1965), Clyde D. Barbour (Ph.D. 1966), Michael D. Dahlberg (Ph.D. 1966), Kenneth Relyea (Ph.D. 1967), Roy J. Irwin (Ph.D. 1970), Glenn H. Clemmer (Ph.D. 1971), Anthony Laska (M.S. 1970; Ph.D. 1973), Robert C. Cashner (Ph.D. 1974), the late Salvador Contreras-Balderas (M.S., 1966; Ph.D. 1975), John H. Caruso (Ph.D. 1977), J. Van Connor (Ph.D. 1977), and the late Bruce A. Thompson (Ph.D. 1977).

Suttkus's greatest and most lasting contributions to southeastern biology are his collections. He built the Tulane fish collection on a foundation of just two mounted fish specimens left over from an early exhibit museum. By 1968, the fish collection had grown to a size of just over two million specimens, overfilling its space on the main Tulane campus. Later that year, the fish collection, along with birds, mammals and vertebrate fossil collections left over from the early exhibit museum, plus the thousands of specimens of plants, herps, mammals and fossils amassed by Suttkus and students in the Environmental Biology Training Program, were moved to a 500 acre parcel of land on the Mississippi River near Belle Chasse, LA, which Tulane had acquired from the U.S. Navy. The land, which had served as an ammunition storage depot during WWII, eventually became the F. Edward Hebert "Riverside" Research Laboratories. The collections became part of what was initially called the Systematics and Environmental Biology Laboratory. In 1976, Suttkus convinced the Tulane administration to formally recognize the collections at Riverside as the Tulane University Museum of Natural History, and to appoint him as the Museum's first Director.

In the years since the move to Riverside, the fish collection has grown to over 200,000 lots and more than seven million specimens (7,369,607 at this writing). Over a career spanning 45 years at Tulane, Suttkus made 12,060 collections. Remarkably, he had a hand in collecting 5,327,512 of the specimens in the fish collection. In addition to fishes, Suttkus collected over 5,000 mammals, 6,000 amphibians and reptiles, roughly 6,000 vascular plants (now in the Tulane Herbarium), and numerous aquatic mollusks, crustaceans, and fossils. Other biologists are now making valuable use of all of these specimens. One measure of this is the number of species that have been named in Suttkus's honor (six fishes, two decapods and one fossil oyster). Based on past and ongoing use of material from the Tulane fish collection, it is clear that Suttkus's collections will teach us much about taxonomy, distribution, and many other aspects of the biology of species he collected for many years to come.

In 1989, in anticipation of Suttkus's retirement, the Tulane Administration brought in a team of external reviewers to evaluate collections in the Museum and to make recommendations on their continued maintenance by Tulane. In their report to the administration, the reviewers described the fish collection as "a treasure of great national and international importance" and strongly recommended maintenance of the fish collection at Tulane. Suttkus officially retired from Tulane University in 1990. However, he continued to credit the university and the museum of natural history on papers published since this time.

Figure 3. A photo of Suttkus from the fall of 2000 in the fish collection that would soon be named in his honor.

In fall 2000, a jubilee celebration was held in New Orleans to honor Suttkus's 50 years of service to Tulane University and his contributions to southeastern biology (Fig. 3, http://www.museum.tulane.edu/sutjubilee/). The event was attended by most of his family, former students, and his closest professional colleagues and associates. A symposium was held in his honor, featuring talks on Suttkus's contributions to mammalogy, botany, malacology, invertebrate paleontology, training in all of biology, and, of course, ichthyology. Colleague, Dave Etnier, gave a talk entitled *Collecting caddisflies: how much is enough?* during which he introduced the term "*Suttkusian*" to describe the large collecting efforts that are required to collect sufficient numbers of male caddisflies needed for species descriptions. Colleague, Franklin "Buck" Snelson, wrote a song entitled "*Collecting Machine*", which was played with a special slide show at the Jubilee. The song and slide presentation can be viewed at http://www.museum.tulane.edu/sutjubilee/suttsong.html.

During a special closing ceremony held under a tent beside the fish collection, the Dean of Arts and Sciences read a proclamation from the President, Faculty and Administrators of Tulane University, officially renaming the Tulane Fish Collection, the

Royal D. Suttkus Fish Collection, and granting Suttkus the title of Emeritus Curator of Fishes.

Suttkus continued collecting and depositing specimens in the fish collection until Hurricane Katrina devastated the Gulf Coast in August 2005. The high winds and storm surge from the hurricane flooded and badly damaged Suttkus's home near the beach in Ocean Springs, Mississippi. He lost nearly all of his possessions, including his field notes and most of his library. What little remains is now part of the Royal D. Suttkus Fish Collection.

After the hurricane, Suttkus and Jeanne moved to an apartment in the Atlanta suburbs, where Suttkus continued to publish his research. In recent years, he had been publishing taxonomic treatments on *Menidia,* suckers of subfamily Ictiobinae, and species descriptions, including papers based on his dissertation research on *Pteronotropis.* He also had been battling prostate cancer. He died peacefully, surrounded by family. He is survived by his wife Jeanne, son Jayson, daughters Ramona and Jan and their families, Brother Hazen and numerous extended family members.

Tulane University is in the process of divesting itself of all of its natural history collections, except the Royal D. Suttkus Fish Collection and the Tulane Herbarium. The other collections are being donated to other institutions, but most will remain in the southeast region. The vertebrate collections (mammals, birds, reptiles, amphibians and vertebrate fossils) are being transferred to the Louisiana State University Museum of Natural Science. The invertebrate collections (decapods crustaceans and mollusks) are being transferred to the Mississippi Museum of Natural Science. Suttkus's plants were either incorporated into the Tulane University Herbarium, or distributed to other herbaria (duplicates) following tradition in botanical collections. The Royal D. Suttkus Fish Collection will remain at Tulane for the foreseeable future, where it will form the core of a new research facility – the Tulane University Biodiversity Research Institute (TUBRI).

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

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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. aprigene* 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

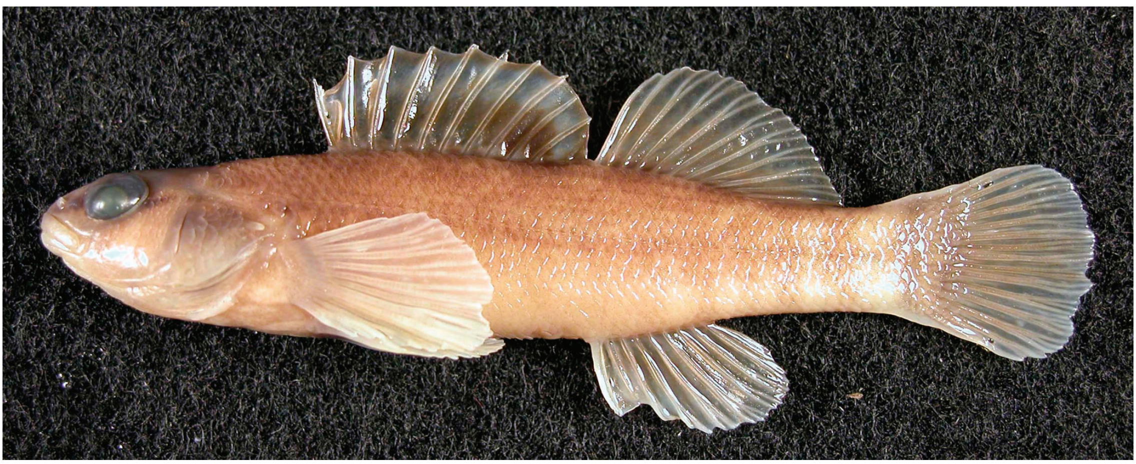

Figure 1. *Etheostoma thompsoni*, Holotype. TU 200366, Adult male 53.7 mm SL, Neches River, along right (west) bank just below Town Bluff dam, at Town Bluff, Tyler County, Texas, 16 February 1979.

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 in *E. asprigene* and other *Oligocephalus* compared) and the transpelvic width is distinctly narrower than in 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 anteriad and progressively widens posteriad 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.

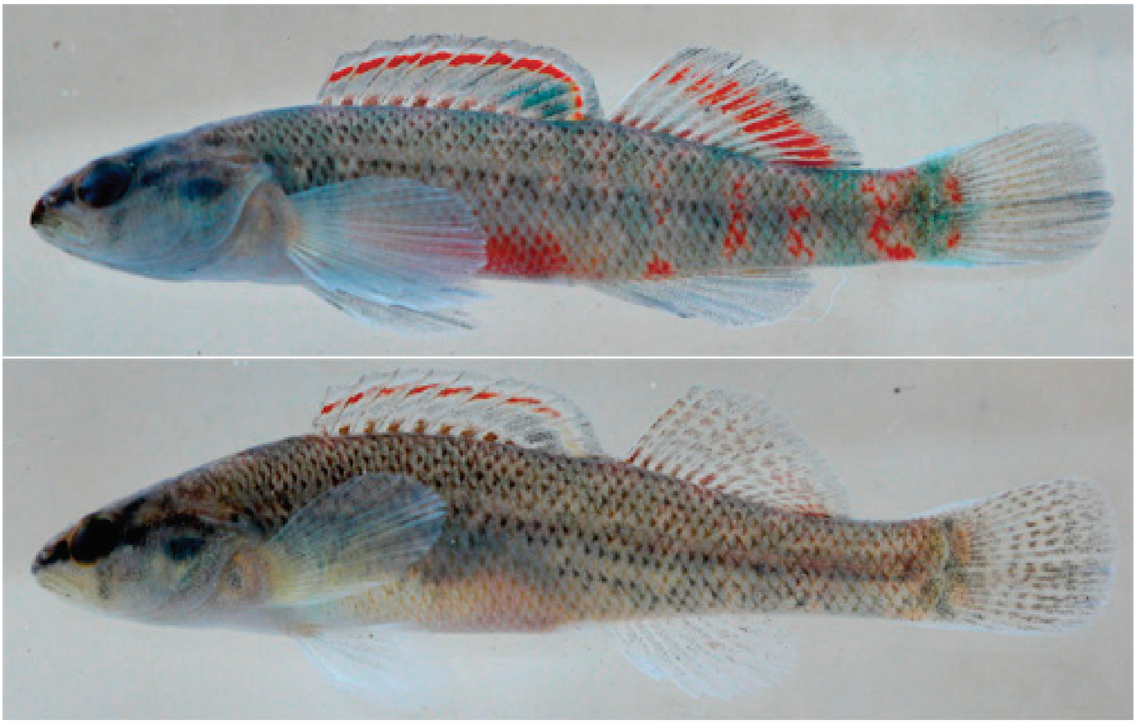

Figure 2. Recently collected (March 2008) paratypes of *E. thompsoni* showing nuptial coloration of male (top) and female (bottom).

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 sale 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 (anteriad) that shades to blue-black posteriad. 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

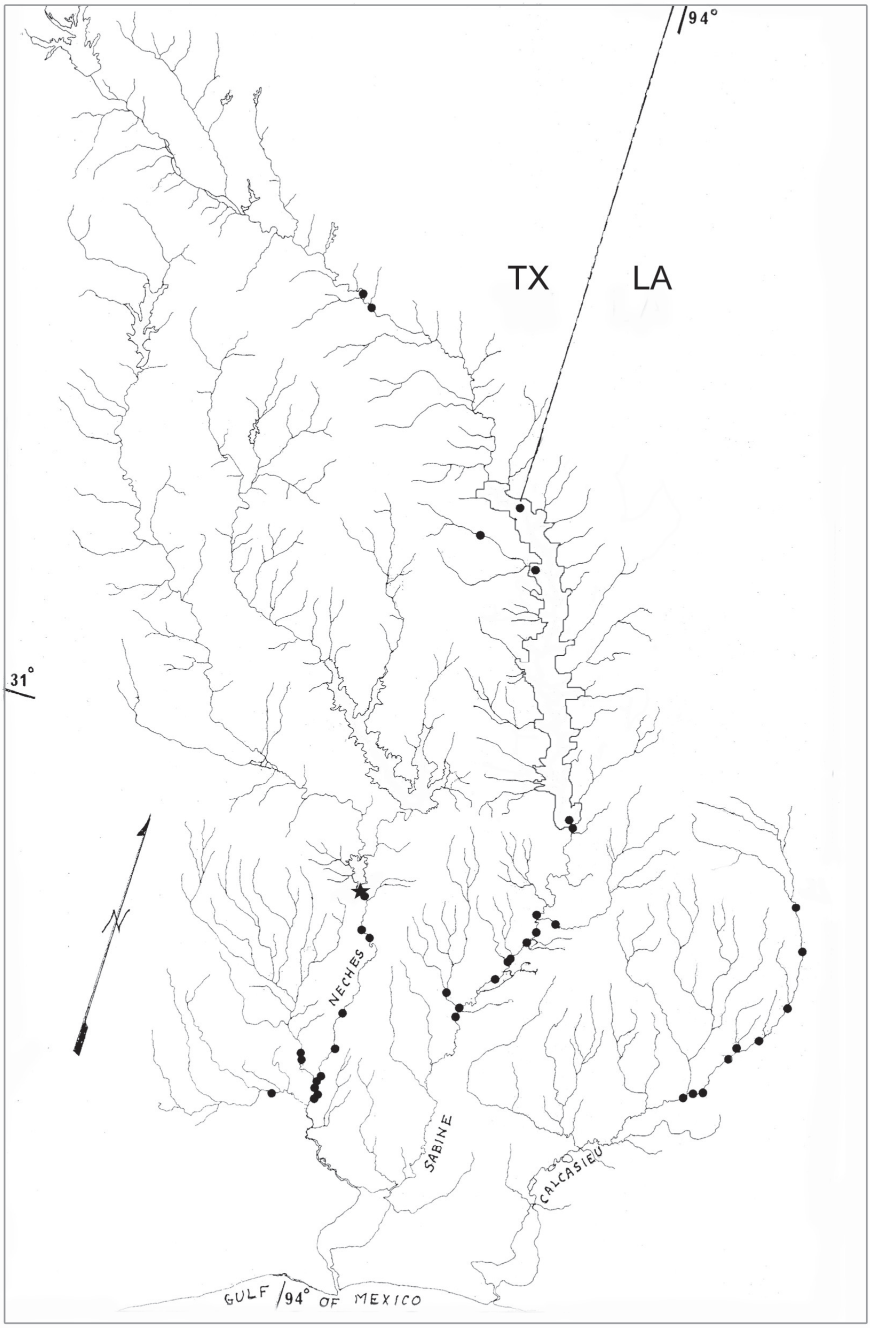

Figure 3. Map of southwestern Louisiana and southeastern Texas showing the distribution of *E. thompsoni* in the Calcasieu, Sabine and Neches rivers.

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. sabinae, N. texanus, N. volucellus, Phenacobius mirabilis, Pimephales vigilax, Erimyzon sucetta, 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 buchanani* 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 or7) 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 preoperculomandibular 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*.

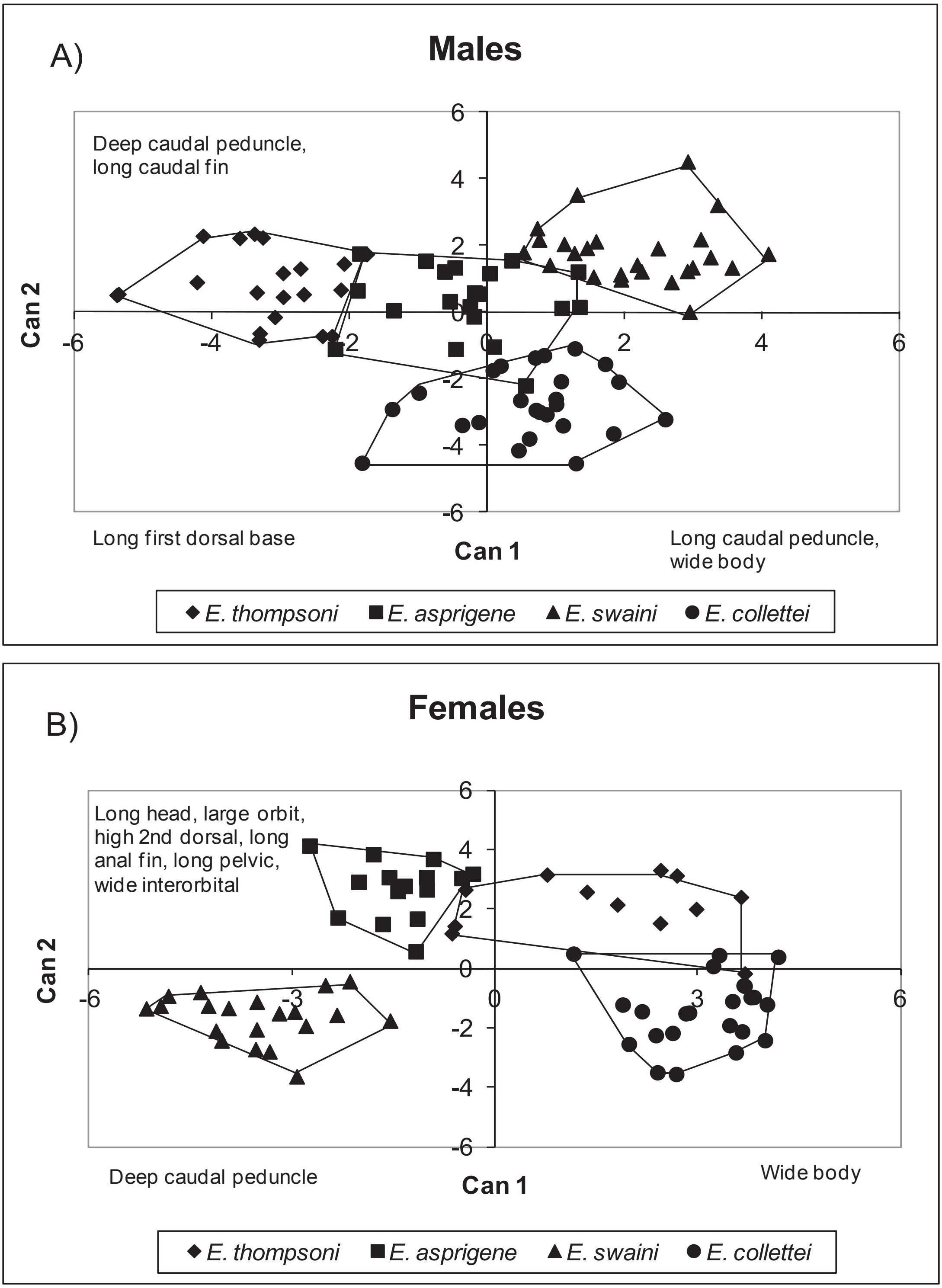

Figure 4. Results of Canonical Discriminant Analysis showing variation in body proportions of males (A) and females (B) of *E. thompsoni* and three species of *Oligocephalus*.

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."

Acknowledgments

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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; DI, 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																										
	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	N	$\bar{x}$	S.D.
E. thompsoni																											
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
E. collettei									1		5	10	9	15	19	15	13	4	1	1	1				94	49.8	2.2
E. asprigene																											
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.					1		1	3	1	2	10	12	12	17	21	18	14	11	9	6	1	4			143	50.0	3.2
Western tribs. lower Mississippi R.								1	7	10	10	11	11	8	10	6	3	3							80	47.7	2.5
IL, IN, TN, LA								1		3	4	2	4	4	4	6	3	1	2						34	49.0	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
E. swaini																											
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																													
	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	N	$\bar{x}$	S.D.
E. thompsoni																														
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	
E. collettei								1	2	1	6	7	16	13	13	15	8	8			1	1				1	1	94	13.7	3.0
E. asprigene																														
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.						3	4	10	25	19	20	15	11	6	3	1		1										118	9.6	2.2
Western tribs. 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		
E. swaini																														
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																															
	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	N	$\bar{x}$	S.D.
E. thompsoni																																
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		
E. collettei	1	1		2		1		2	5	4	12	5	16	13	10	10	5	4	3											94	36.0	3.5
E. asprigene																																
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						1	1	2	2	6	7	11	18	10	13	8	13	7	6	2	2		1							110	37.0	4.8
Mississippi R. & tribs. below Ohio R.							1	1	1	2	3		2	11	11	15	18	19	16	13	8	5	5	1	3					135	39.9	5.6
Western tribs. lower Mississippi R.										1	1	4	5	11	11	9	10	6	5	5	3									71	38.9	2.6
Totals						1	2	3	3	9	12	16	35	36	41	37	55	38	28	23	15	7	6	1	3					371		
E. swaini																																
Eastern tribs. to lower Mississippi R.								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
Pearl							1	4	2	9	16	8	7	6	4	2		2		1										62	35	2.5

Table 4. Frequency distributions of scale counts in *Etheostoma thompsoni, E. collettei, E. asprigene, and E. swaini*

	Scales around caudal peduncle																	Transverse scale rows												
	14	15	16	17	18	19	20	21	22	23	24	25	26	27	N	$\bar{x}$	S.D.	10	11	12	13	14	15	16	17	18	19	N	$\bar{x}$	S.D.
<u>*E. thompsoni*</u>																														
Neches R.						3	16	26	55	11					111	21.5	0.9					4	33	47	21	6		111	15.9	0.9
Sabine R.						1	2	12	11	6					32	21.6	1.0					4	14	7	4	3		32	15.6	1.1
Calcasieu R.						8	18	48	38	15	3				130	21.3	1.1				3	21	45	41	18	2		130	15.4	1.0
Totals						12	36	86	104	32	3				273	21.4					3	29	92	95	43	11		273	15.6	
<u>*E. collettei*</u>					2	11	28	17	20	5	1				84	20.7	1.3				3	9	30	27	14	1		84	15.5	1.0
<u>*E. asprigene*</u>																														
Mississippi R. above Ohio R.					3	15	14	8	2						42	19.5	1.0				15	23	4	1				43	13.8	0.7
Ohio River basin						3	13	25	34	8	2				85	21.2	1.0			3	26	28	15	11				83	14.8	1.1
Mississippi R. & tribs. below Ohio R.							7	16	19	4	1				47	21.4	1.0				3	10	22	16	7	1	1	60	15.3	1.2
Western tribs. lower Mississippi R.						2	8	19	19	1					49	21.2	0.9					9	10	19	11			49	15.6	1.0
Totals					3	20	42	68	74	13	3				223					3	44	70	51	47	18	1	1	235		
<u>*E. swaini*</u>																														
Eastern tribs. to lower Mississippi R.					11	51	64	50	6						182	19.9	1.0			1	10	42	82	37	10	1		183	15.0	1.0
Pearl	2	4	7	22	2	3									40	16.7		1	6	17	14	2						40	12.2	0.9

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.
E. thompsoni																		
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		
E. collettei		4	44	34	2	84	10.3	1.2			2	39	35	8		84	12.5	1.2
E. asprigene																		
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.		9	48	33	3	93	10.3	0.7				15	42	28	6	91	13.3	0.8
Western tribs. 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		
E. swaini																		
Eastern tribs. to lower Mississippi R.	1	1	54	197	14	267	10.8	0.8	1	1	77	151	37	1		268	11.8	0.7
Pearl		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									Left Pectoral Fin Rays								
	5	6	7	8	9		N	$\bar{x}$	S.D.	11	12	13	14	15	16	N	$\bar{x}$	S.D.
E. thompsoni																		
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		
E. collettei		7	65	12			84	7.1	0.5		4	76	4			84	13.0	0.5
E. asprigene																		
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		
E. swaini																		
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.

	E. thompsoni				*E. asprigene*				*E. collettei*				*E. swaini*			
	Females (12)		Males (20)		Females (15)		Males (20)		Females (23)		Males (25)		Females (20)		Males (25)	
Proportion	$\overline{X}$	STD	$\overline{X}$	STD	$\overline{X}$	STD	$\overline{X}$	STD	$\overline{X}$	STD	$\overline{X}$	STD	$\overline{X}$	STD	$\overline{X}$	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

INTERACTIONS BETWEEN TARANTULAS *(APHONOPELMA HENTZI)* AND NARROW-MOUTHED TOADS *(GASTROPHYRNE OLIVACEA)*: SUPPORT FOR A SYMBIOTIC RELATIONSHIP

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ABSTRACT

The Great Plains narrow-mouthed toad, *Gastrophryne olivacea* often shares burrows with other vertebrates (lizards) and invertebrates (spiders and insects). The association with large tarantulas (*Aphonopelma hentzi*) is particularly interesting because these spiders are opportunistic feeders that readily attack and consume vertebrate prey including anurans. We show that *A. hentzi* will attack and consume the cricket frog (*Acris crepitans*) which is similar in size to *G. olivacea*. In trials where *G. olivacea* and more palatable A. *crepitans* and invertebrates were presented simultaneously to tarantulas, the presence of *G. olivacea* did not appear to affect the predatory response of the tarantulas. However, when placed in a confined space with *G. olivacea* or *G. carolinensis*, the tarantulas never initiated a predatory response. Because we were using wild caught, adult tarantulas, this may be a learned response towards *G. olivacea*. We have no field records that tarantulas share burrows with *G. carolinensis*. The laboratory experiments suggest that tarantulas are sensitized to *Gastrophryne* spp. and may be able to detect chemicals secreted by the toads.

Key words: *Gastrophryne olivacea*, *Gastrophryne carolinensis*, tarantulas, *Aphonopelma hentzi*, burrow-commensals, toxic skin secretions, predatory response

INTRODUCTION

Spiders are important predators of amphibians (Sharma and Sharma, 1977; Groves and Groves, 1978; Littlejohn and Wainer, 1978; Formanowicz et al., 1981). However, certain anurans are capable of avoiding this predation (Szelistowiski, 1985). Three theraphosid spiders (tarantulas) have been shown to have commensal relationships with specific anurans (Blair, 1939), which may protect both associates from predators (Hunt, 1980; Mulvany, 1983). In these associations, anurans are not only tolerated around the burrow, but also take refuge within the burrow. Blair (1936) found up to nine *Gastrophryne olivacea* with a single tarantula burrow under a stone and Dundee (1999) found 22 *G. olivacea* with a tarantula in a burrow under a stone. Although tarantulas are opportunistic feeders capable of subduing and consuming large prey items, including vertebrates, certain amphibians probably are immune from predatory attacks because their toxic skin secretions (Garton and Mushinsky, 1979) make them unpalatable. The presence of myrmecophagous anurans such as *G. olivacea* may benefit tarantulas by reducing ant predation on the spiders' eggs (Hunt, 1980). In return, anurans may benefit from a microenvironment which reduces the risk of desiccation (Cocroft and Hambler, 1989; Hunt, 1980) and/or provides protection from predators (Hunt, 1980; Mulvany, 1983).

This paper explores the association of the Great Plains narrow-mouthed toad *Gastrophryne olivacea* and the tarantula, *Aphonopelma hentzi* which are sympatric from Kansas to Texas and small areas of Missouri to northeastern Louisiana. In particular, we observed the predatory feeding responses of tarantulas towards vertebrate and invertebrate prey and compared this with the behavior that tarantulas exhibit towards *G. olivacea*.

Aphonpelma hentzi are fossorial tarantulas which live in a silk-lined burrow. They are sedentary, sit-and-wait predators that emerge at dusk and wait near the burrow entrance for suitable prey to pass by. Females may remain in the same burrow for most of their lifetime whereas males abandon their burrows once they reach sexual maturity. Tarantulas, in general, have poorly developed eyesight and are more dependent on tactile and chemical cues for prey recognition (Foelix, 1996). As with other spiders, they have numerous contact ("taste") and airborne ("smell") chemoreceptors which are capable of determining chemical properties of substrates and substances (Foelix, 1970, Drews and Barnard, 1976; Foelix, 1996). The taste or contact chemoreceptors are located on the distal segments of the legs and palps but the exact location of the olfactory receptors is still uncertain (Foelix, 1996).

Gastrophryne olivacea is a small, myrmecophagus narrow-mouthed toad that, because it is an inefficient digger (Freiburg, 1951; Fitch, 1956), often shelters in burrows of lizards, insects, or spiders (Freiburg, 1951). Garton and Mushinsky (1979) examined the distribution of skin secretory glands in *G. olivacea* and the closely related *G. carolinensis*. The two *Gastrophryne* species are partially sympatric and hybrids are not infrequent (Nelson, 1972). Both species have numerous secretory glands and poison glands in all regions of the skin and copious skin secretions that may form an effective antipredator defense (Garton and Mushinsky, 1979). Predators include garter snakes *Thamnophis sirtalis* (Wright, 1932), short-tailed shrews (*Blarina brevicauda*) (Freiburg, 1951), and copperheads (*Agkistrodon contortix*) (Anderson, 1942, Freiburg, 1951). In the laboratory, Gorton and Mushinsky (1979) found that *G. carolinensis* were eaten by *Thamnophis sirtalis*. However, snapping turtles (*Chelydra sepentina*) that they used ate *G. carolinensis* but often regurgitated them. They also noted that black-crowned herons (*Nycticorax nycticorax*) would bite *G. carolinensis*, but would then release them. In addition, these toads are primarily myremecophagous so their skin secretions may also protect them from counterattacks by ants (Wood, 1948; Freiburg, 1951; Fitch, 1956; Garton and Mushinsky, 1979).

Although anuran-arachnid associations have been reported for several different species of both spiders and anurans, little information exists on interactions between these unusual burrow-commensals. The objectives of this study were: 1) to observe narrow-mouth toads in tarantula burrows in the field, 2) to observe behavior of *A. hentzi* towards potential prey items including invertebrates (cockroaches, grasshoppers, and crickets) and anurans (*Acris crepitans* and *G. olivacea*) and, 3) to determine if the presence of *G. olivacea* affects the predatory behavior of *A. hentzi* towards other prey. Because adult, wild-caught tarantulas were used in these experiments, it is possible that the lack of a predatory response towards *G. olivacea* is a learned behavior as a result of previous contact. Thus, the final objective 4) was to observe and compare interactions between *A. hentzi* and *G. carolinensis*. *G. carolinensis* is closely related to *G. olivacea*; it is similar in size and also has toxic skin secretions. However, although *G. carolinensis* occurs within the same habitant as *A. hentzi* no report of tarantulas sharing a burrow with *G. carolinensis* is known.

Materials and Methods

Field Observations: The field site encompassed approximately 1.62 ha of savanna type habitat on an upland limestone outcrop adjacent to Red Bud Valley Nature Preserve, approximately 5 km west of Catoosa in Rogers County, Oklahoma. This area has abundant flat stones. Woody vegetation included many small persimmon trees (*Diopyros virginiana*), aromatic sumac (*Rhus aromatica*), and hawthorn (*Crategus reverchonii*). Observations of tarantulas and narrow-mouthed toads were made at this site from June-August 1977. Tarantulas from a site in McCurtain County, Oklahoma were checked for several years and no *Gastrophryne* were discovered there, nor were breeding choruses of the toad ever heard.

Laboratory Trials: *A. hentzi*, *G. olivacea*, and the hylid species *A. crepitans* were collected from several counties in Oklahoma (Delaware, Okmulgee, Payne, Rogers, and Tulsa) and Texas (Dimmit and La Salle). *G. carolinensis* were collected from the vicinity of Spavinaw Creek, in Delaware County, Oklahoma. All tarantulas used in this study were mature females. They were maintained in individual containers and were fed a diet of cockroaches, grasshoppers, and crickets. The anurans were housed in groups but separated by species. They were fed pinhead crickets for the duration of the study.

To observe the behavior of *A. hentzi* towards potential prey, three species of orthopterans (cockroaches, crickets, and grasshoppers) were placed individually in a covered glass finger-bowl with tarantulas. The finger-bowls were approximately 6.5 cm deep and 21 cm in diameter. Interactions between tarantula and prey were recorded. These interactions were compared with observations of either *G. olivacea* or *G. carolinensis* together with *A. hentzi* under similar conditions.

To demonstrate that tarantulas eat anurans, but were choosing not to eat *G. olivacea*, tarantulas were placed into one gallon plastic shoe-box containers with either *A. crepitans* or *G. olivacea* for three days. *A. crepit*ans is similar in size to *G. olivacea* but is not reported to have toxic skin secretions although they do have a warty skin (pers. comm.. R. Kazmaier). Two experimental groups of tarantulas were established.

Tarantulas in group 1 were first exposed to *A. crepitans*, while those in group 2 were exposed to *G. olivacea* first. Containers were checked daily to determine if the anurans had been consumed by the tarantulas. After three days, live anurans were removed from the containers and new frogs and toads were introduced but in reverse order (i.e., group 1 now received *A. crepitans* and group 2 received *G. olivacea*).

Finally, to determine if the presence of *G. olivacea* affects predation by tarantulas on other potential prey, tarantulas were again divided into two groups. Those in group 1 were placed in a finger-bowl with *G. olivacea* together with either *A. crepitans* or a cricket while those in group 2 were placed in finger-bowls with the prey species but without *G. olivacea*. The predatory response of tarantulas in each group was recorded. Chi square tests were performed to test for differences in the predatory responses of tarantulas toward potential anuran prey.

Tarantulas from the McCurtain County, Oklahoma site, where no *Gastrophryne* were discovered, could be presumed to be naive. They also were placed into containers with *Gastrophryne* to determine their reactions.

Results

Field Observations: On 23 trips to the Red Bud Valley area, 137 *G. olivacea* were observed under stones with occupied tarantula burrows. An additional 28 were found under stones with no burrows. No toad was found without a stone covering it. Fifteen of the 28 sighted in the absence of burrows were found on visits after substantial rain. Toads were not marked or removed during these observations, so the same individuals could have been observed during each visit. The majority of *G. olivacea* were discovered under seven stones, each with a tarantula burrow. Under one stone with a large burrow, 11 toads were found during one visit. By flooding these seven tarantula burrows with water, additional *G. olivacea* were recovered from five of the seven burrows.

Laboratory Trials: Tarantulas (n=22) displayed four responses to contact with prey species; (1) quick, predatory response, (2) charging towards prey species but without grabbing the prey item, (3) rising to a defensive posture and possibly backing away, and (4) no response. Cockroaches were eaten most frequently and incidental contact between tarantulas and cockroaches in the finger-bowls usually resulted in a predatory response by the tarantula. Cockroaches that survived up to a day with the tarantula were usually found on the opposite side of the finger-bowl from the tarantula. Crickets and grasshoppers on the other hand, often wandered into the tarantula without effect.

When *G. olivacea* were introduced into finger-bowls with tarantulas, the anurans usually initiated contact within a few minutes. If the toad made sudden, forceful contact with the tarantula (i.e., hopping/jumping in the fingerbowl), tarantulas usually rose into a defensive position. If less forceful contact was made, this resulted in only minor postural adjustments by the tarantula. Usually introduction of tarantula and toad resulted in an initial period in which familiarization between the two species seemed to occur. After initial contact, the tarantula might slowly retreat a few steps, or walk slowly over the toad. After repeated, seemingly random contacts of this nature, the two animals came to rest with the toad positioned under or slightly anterior to the cephalothorax of the tarantula. This occurred approximately 50% of the time. This positioning would usually occur within 20 minutes of introduction and lasted for a few minutes to several hours. Through the observation period, the two species were often found in this "hovering" position. On rare occasions, tarantulas rested the tips of their pedipalps on *G. olivacea*. In general, however, tarantulas avoided contact with the toad (e.g., if a tarantula came into contact with *G. olivacea* while walking around the finger-bowl, the tarantula would stop or recoil or adjust course to avoid the toad). Several times a tarantula was observed holding one leg aloft for several hours, which if lowered, would contact the anuran. No qualitative difference was noted between the interactions of *G. carlinensis* and *A. hentzi* and those of *G. olivacea* and *A. hentzi*. Resting of pedipalps on *G. carolinensis* was observed and instances of "hovering" occurred frequently.

When presented with either *G. olivacea* and *A. crepitans*, 72% of tarantulas (n = 16) ate *A. crepitans*, but none (0%) ate *G. olivacea*. Although both anurans are similar in size, *A. crepitans* had a significantly greater chance of being eaten by tarantulas compared with *G. olivacea* ($\chi^2 = 10.78$, df = 1, P < 0.05).

Finally, no difference in the predatory response of tarantulas towards crickets was noted (n = 6, ($\chi^2 = 1.33$, df = 1, P < 0.05) or *A. crepitans* (n = 8, ($\chi^2 = 2.5$, df = 1, P < 0.05) in the presence or absence of *G. olivacea*. Tarantulas were overall less likely to eat *A. crepitans* (50% of trials) compared with crickets (67% of trials), but sample size of tarantulas was small and no statistically significant difference was evident between either group ($\chi^2 = 0.89$, df = 1, P < 0.05).

Discussion

The first published account of the cohabitation of tarantulas and anurans was reported by Blair (1936) who examined over 100 occupied tarantula burrows. Of these, 75% included one to three toads living in the same burrow with the tarantula. In this study, we also observed numerous tarantula burrows and found up to 22 toads sharing the same burrow with the tarantula. The association may occur throughout the range of co-occurrence of *G. olivacea* and *A. hentzi* and the number of narrow-mouthed toads in any burrow apparently varies substantially.

We observed typical predatory response of tarantulas to invertebrate prey and also showed that tarantulas will eat some anurans but not *G. olivacea* and *G. carolinensis*. They readily attacked and consumed *A. crepitans*, but did not harm the similarly sized *G. olivacea* and *G. carolinensis*. Surprisingly, no initial attack was made by tarantulas towards either *Gastrophryne* species. Both Cocroft and Hamber (1989) and Szelistowiski (1985) reported that spiders attacked and quickly released toxic anurans that were introduced. The attack response occurred even though it was probable that the tarantulas had previously come into contact with other individuals of the same species. Thus these tarantulas are apparently relying on substrate vibrations or airborne pressure waves to initially locate prey (Foelix, 1996; Cocroft and Hamber, 1989; Szelistowiski, 1985). After the initial attack, contact chemoreceptors on the distal portions of the legs and palps (Foelix, 1996) were important to determine the toxicity of potential prey. Our observations of *A. hentzi* with *Gastrophryne* species did not follow this pattern; *A. hentzi* never initiated an attack towards any of the narrow-mouthed toads. Although this could be a learned response towards *G. olivacea*, the same is not true for *G. carolinesis*. *G. carolinesis* are not known to share tarantula burrows even though the two species are sympatric. That the supposedly naive tarantulas from McCurtain County reacted similarly to those from Red Bud Nature Preserve suggests that the tarantulas react instinctively or that some form of chemical communication indicated that the toad was toxic. One reason that may explain the different responses of arachnids in our study compared with other studies, is the experimental setup. Both Cocroft and Hambler (1989) and Szelistowiski(1985) conducted experiments with spiders in their natural environment, whereas our observations took place in small, glass bowls. Within this restricted, artificial environment, *A hentzi* may have been able to determine the toxicity of the narrow-mouthed toads very quickly without physical contact via olfactory cues. Although *A. hentzi* ate *A. crepitans* in these experiments, more tarantulas attacked and ate invertebrate prey. Prior to the laboratory experiments, tarantulas were fed only invertebrate prey and this may have biased their initial response to introduced prey items. The reduced predatory response towards *A. crepitans* may simply be due to its novelty as a prey item rather than indicating a preference for invertebrate prey. In addition, because of a small sample size, determining if the predatory response of *A. hentzi* is influenced by the presence of *G. olivacea* is impossible. Rödel and Braun (1999) reported that skin toxins of one species of anuran can be transferred onto another less toxic species and provide protection for the latter from ants. This, however, involved physically rubbing the skins of the two anurans together. *A. crepitans* and *G. olivacea* were never in such close contact and under natural conditions the presence of *G. olivacea* in tarantula burrows probably has little impact on the tarantulas' feeding behavior.

The association between *G. olivacea* and *A. hentzi* appears to be a relationship of mutual benefit, although both species thrive outside the range of the other, and *G. olivacea* inhabits burrows of other animal species besides tarantulas. A potential benefit to the tarantula is the elimination of predatory ants by *G. olivacea* and consequently increased survival rates of young tarantulas. Hunt's (1980) observations on a captive *A. hentzi* showed that the tarantula tolerated *G. olivacea* around its egg case and the toads did not prey on small, newly hatched tarantulas. Baerg (1958) stated that the tarantula is "powerless to cope with ants, which are predators on the eggs and young with the cocoon. When ants tear open a cocoon of young, the female retreats to the far corner of her residence …. and later departs to seek a safer place to live." For *G. olivacea*, the tarantula burrow provides a favorable microenvironment that reduces the risk of desiccation (Blair, 1936; Powel et al., 1984). In addition, adult tarantulas may prevent potential anuran predators from entering the burrow, thus providing a safe retreat for the narrow-mouthed toads (Hunt, 1980). Thus, although this association is not critical for survival, it may be advantageous to both species.

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