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Author(s): Harlan T. Nichols and Timothy H. Bonner

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FIRST RECORD AND HABITAT ASSOCIATIONS OF *SPONGILLA CENOTA* (CLASS DEMOSPONGIAE) WITHIN STREAMS OF THE EDWARDS PLATEAU, TEXAS, USA

HARLAN T. NICHOLS* AND TIMOTHY H. BONNER

Department of Biology/Aquatic Station, Texas State University, San Marcos, TX 78666

**Correspondent: hn1035@txstate.edu*

ABSTRACT—We report the first record of *Spongilla cenota* occurrence among drainages of the Edwards Plateau, a large karst area within the western gulf slope drainages of central Texas, and provide the first quantitative habitat description for this species. *Spongilla cenota* was common in the two rivers of the Edwards Plateau, occurring within 23% of the quadrats surveyed in the Devils River and 31% of the quadrats surveyed in the Llano River. Among multivariate gradients, *S. cenota* was positively associated with moderate current velocities and coarser substrates and negatively associated with vegetation. The majority (74%) of the quadrats with *S. cenota* had boulder or bedrock substrates with the remaining sponges attached to aquatic macrophytes and cobble substrate. Among univariate gradients, *S. cenota* were observed at water depths from 0.5 to 2.5 m and current velocities from 0.1 to 0.6 m/s. Occurrence and abundance of *S. cenota* potentially provides a novel bioindicator of a sound ecological environment within streams of the Edwards Plateau.

RESUMEN—Nosotros reportamos el primer registro de la ocurrencia de *Spongilla cenota* entre los desagües de La Meseta de Edwards, un gran área karst en central Texas dentro de los desagües de la ladera oeste del Golfo, y proporcionamos la primera descripción cuantitativa del hábitat de esta especie. *Spongilla cenota* ocurrió con frecuencia en los dos ríos de La Meseta de Edwards, ocurriendo en 23% de los cuadrantes encuestados en Devils River y 31% de los cuadrantes encuestados en el Llano River. Entre las pendientes multi-variadas, *S. cenota* era asociada positivamente con mayores velocidades de corriente y los sustratos más ásperos, y asociada negativamente con la vegetación. En la mayoría (74%) de los cuadrantes en donde encontramos *S. cenota* había sustrato de roca o lecho de roca, con el resto de las esponjas creciendo en macrófitas acuáticas y adoquín. En las pendientes uni-variadas, observamos *S. cenota* en profundidades de agua desde 0.5 hasta 2.5 m y velocidades de corriente desde 0.1 hasta 0.6 m/s. Entre la región del Edwards Plateau, ocurrencia y frecuencia de *S. cenota* tiene el potencial de proveer indicación biológica nueva de un medio ambiente sano.

Species richness of freshwater sponges (Class Demospongiae) is greater in eastern than in western North America (Reiswig et al., 2010), which likely explains the paucity of information regarding freshwater sponge distribution and life-history information within the western gulf slope drainages of Louisiana, Texas, and New Mexico. At least six genera of freshwater sponges inhabit the western gulf slope drainages (Old, 1936; Sublette, 1957; Poirrier, 1972; Davis, 1980a, 1980b; Manconi and Pronzato, 2005), but only Davis (1980a, 1980b) documents occurrence of Class Demospongiae: Spongillidae in streams west of the Gulf Coastal Plain ecoregion of Texas. Except for descriptions of occurrences and morphologies, no information is available on freshwater sponge habitat associations from western gulf slope drainages and very few quantitative habitat assessments exist for sponges worldwide.

Globally, freshwater sponges inhabit a wide range of aquatic habitats (Manconi and Pronzato, 2008). Sponges

generally are successful only after settling on hard substrates, such as plants, woody debris, mollusk shells, mineral substrates, and artificial substrates (Manconi and Pronzato, 2008). Within floodplain habitats of a large European river, five species of sponges segregated between slack and swift waters (up to 0.25 m/s), chemical constituents of water (e.g., amount of Si), substrate type (e.g., wood or mineral substrates), and frequency of connectivity to the river mainstem (Dröscher and Waringer, 2007). Within smaller streams of Cuba, *Ephydatia facunda* (Weltner, 1895) is associated with gravel and boulder substrates in shallow (10 to 40 cm) and flowing waters shaded by dense riparian vegetation (Manconi and Pronzato, 2005).

Objectives of this study were to determine the sponge species present and to quantify their habitat associations within streams and rivers of the Edwards Plateau, the largest karst geographic area among the western gulf slope drainages. We predict that habitat associations of

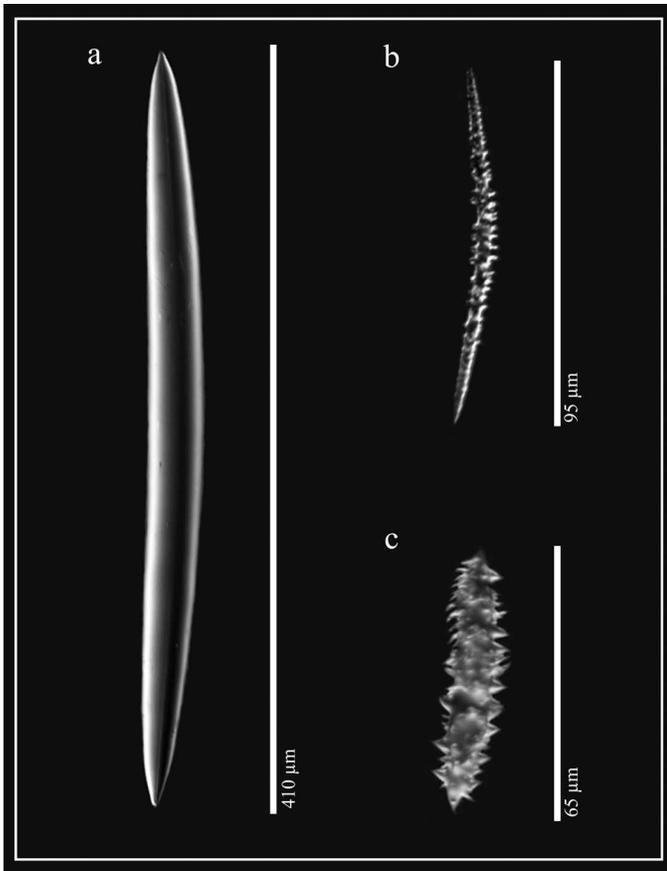


FIG. 1—*Spongilla cenota* spicules: a) megasclere, b) microscelere, and c) gemmosclere.

sponges within the Edwards Plateau region will be similar to that of *E. facunda*, given that streams and rivers of the Edwards Plateau seldom form floodplain aquatic habitats.

METHODS—We initially surveyed sponges in the Llano River (Colorado River drainage; Mason County, U.S. Hwy 87 crossing, 30°39'38.21"N, 99°06'48.04"W), James River (Colorado River drainage, Mason County; James River Road crossing near Bar None River Ranch, 30°33'55.58"N, 99°19'47.43"W), Devils River (Rio Grande drainage, Val Verde County, near the Devils River State Natural Area, 29°54'02.95"N, 100°59'56.61"W), Independence Creek (Rio Grande drainage, Terrell County, The Nature Conservancy of Texas-Independence Creek Preserve, 30°28'07.77"N, 101°48'07.98"W), and lower Pecos River (Rio Grande drainage, Val Verde County, Pandale Road crossing, 30°07'48.65"N, 101°34'26.13"W). We removed several 25-mm² sections of sponge from plant material, cobble, boulder, and bedrock with knives while using snorkel or SCUBA equipment. In the laboratory, sections were dried and placed in a heated, concentrated sulfuric acid bath (98%) to isolate the siliceous spicules similarly to Poirrier (1972). The acid solution was diluted and filtered through acid-safe paper in a buchner funnel to collect the spicules. Permanent mounts of spicules were made using balsam mounting media. High-resolution images were taken using a FV1000 confocal microscope with differential interference contrast filter and a 20× water immersion lens. Species identification was determined from spicule morphology

of megascleres, microscleres, and gemmoscleres (Penney and Racek, 1968) and independently confirmed by M. Poirrier (pers. comm.). Specimens from Independence Creek, lower Pecos River, and James River were identified as the cosmopolitan *Ephydatia fluviatilis* and were different from the sponge species taken from the Llano and Devils rivers. We chose not to conduct habitat associations for *E. fluviatilis*, instead concentrating this study on habitat associations of a regional species.

We conducted a second sponge survey and habitat assessments within the Devils River (November 2012) and Llano River (January 2013). At each location, seven transects were established perpendicular to the river margin and spaced up to 150 m apart. For each transect, five 1-m² quadrats (polyvinyl chloride pipe) were spaced equidistant from each other across the length of the transect. When necessary, quadrats were adjusted to ensure that depth and current velocity were homogenous within the quadrat or to capture a unique habitat type (i.e., vegetated areas). Within each quadrat, divers surveyed a defined area and noted whether sponges were absent or present. Numbers and sizes were not quantified because of the difficulty of distinguishing individual colonies. Voucher samples (25-mm² section) were taken from each quadrat and identified to species as previously described. Gemmoscleres and microscleres were used to determine species (Poirrier, 1972). After the completion of the survey, current velocity (m/s at 60% of measured depth), water depth (m), dissolved oxygen (mg/L), specific conductance (µS/cm), and temperature (°C) were taken for each quadrat. Percent substrate composition and percent coverage of vegetation (algae and macrophytes) were visually estimated. Substrate sizes were categorized using a modified Wentworth scale (silt: <0.06 mm, sand: 0.06–1.99 mm, gravel: 2–63 mm, cobble: 64–255 mm, boulder: ≥256 mm, and bedrock).

Habitat associations were quantified with multivariate and univariate analyses. Principal component (PC) analysis (Proc Princomp; SAS 9.3; SAS Institute Inc., Cary, North Carolina) was used to ordinate quadrats among linear combinations of habitat variables. Habitat variables were *z*-transformed before being used in the model (Krebs, 1999). Quadrat PC 1 and 2 scores were plotted and represented habitat available. Distributions along PC 1 and 2 axes were compared between all quadrats (habitat available) and quadrats with sponges, using a Student's *t*-test ($\alpha = 0.05$). Distributions along univariate gradients (current velocity and depth) were compared between available and sponge use with Kolmogorov–Smirnov (KS) goodness-of-fit tests.

RESULTS—Specimens from the Llano River and Devils River were identified as *Spongilla cenota* (Penney and Racek, 1968) (Class Demospongiae) on the basis of the following distinguishing characteristics of spicules: megascleres (400–480 µm) consisted of large and smooth oxoas without noticeable projecting spines; microscleres (85–95 µm) consisted of long and slender oxoas that terminated in pointed tips with projecting spines concentrated in the center; and gemmoscleres were short (65–70 µm), stout, and spiny (Fig. 1). Colonies were encrusted and predominantly small (<150 mm in greatest linear diameter) in size but with a few up to 0.75 m in diameter. White and green sponges were observed in both rivers and contained numerous basal gemmules near attach-

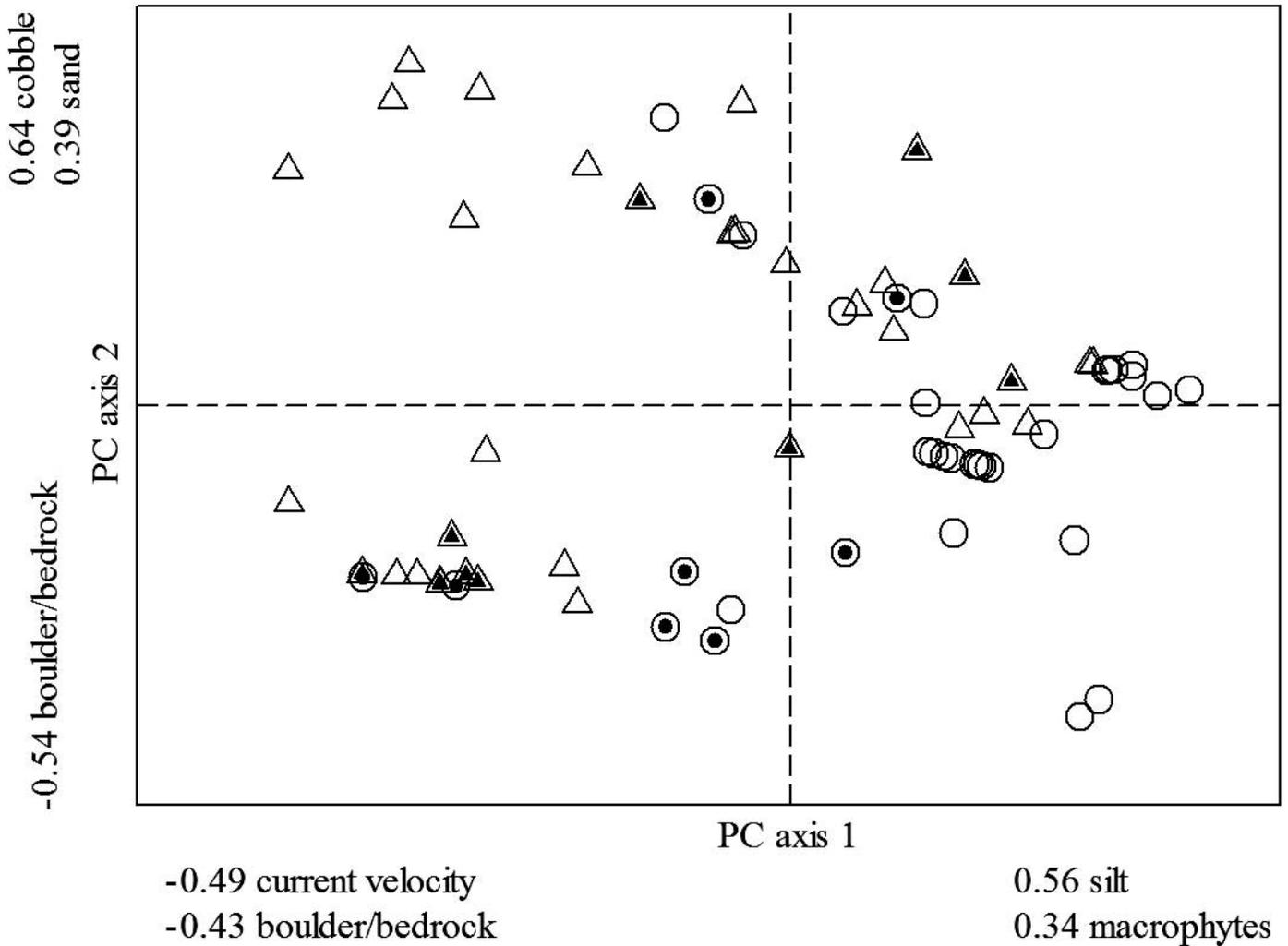


FIG. 2—Scatter plot of quadrats taken from the Devils River (circle) and the Llano River (triangle) along principal component axes 1 and 2. All *Spongilla cenota*-positive quadrats are noted with black filled triangles or circles.

ment with substrate. The white variety was associated with areas without direct exposure to sunlight (i.e., under boulders), whereas the green variety with symbiotic algae (Williamson, 1979; Sand-Jensen and Pedersen, 1994) was associated with areas in direct sunlight.

Within the Llano River and Devils River, habitat quadrats ($N = 70$) ranged from shallow (0.07 m) to moderately deep (2.3 m) water with sluggish (0.00–0.01 m/s) to swift (0.76 m/s) current velocities, predominantly silt, cobble, or bedrock substrates, and low amounts of aquatic macrophytes. Principal component axes 1 and 2 explained 44% of total variation in habitat variables among quadrats (Fig. 2). Axis 1 explained 29% of the total variation and described a current velocity and substrate gradient. Quadrats with positive PC scores along axis 1 consisted of sluggish current velocities, silt substrates, and dense percent vegetation, whereas quadrats with negative PC scores along axis 1 consisted of swifter current velocities, coarser substrate size, and zero to low percent vegeta-

tion. Axis 2 explained 15% of total variation and described a substrate size gradient. Quadrats with positive PC scores along axis 2 consisted of smaller substrate sizes (i.e., sand and cobble), whereas quadrats with negative PC consisted of larger substrate sizes (i.e., boulder and bedrock).

Spongilla cenota colonies were observed in 31% ($N = 11$) of the quadrats from the Llano River and 23% ($N = 8$) of the quadrats from the Devils River. Mean (± 1 SE) PC scores of quadrats with *S. cenota* were negative on PC axes 1 (-0.87 ± 0.30) and 2 (-0.49 ± 0.28) and differed from quadrats without *S. cenota* along PC axis 1 (t -statistic: 2.95; $P < 0.01$) and axis 2 (t -statistic: 2.11; $P = 0.04$). Specifically, 74% of quadrats with *S. cenota* contained $\geq 25\%$ boulder and bedrock substrates. *Spongilla cenota* was less common in quadrats without boulder or bedrock substrates, occurring once on cobble and four times on stems of aquatic macrophytes with substrates of silt (20–100%), cobble (0–80%) and with 10–100% macrophyte coverage. Among depth and current velocity gradients, *S.*

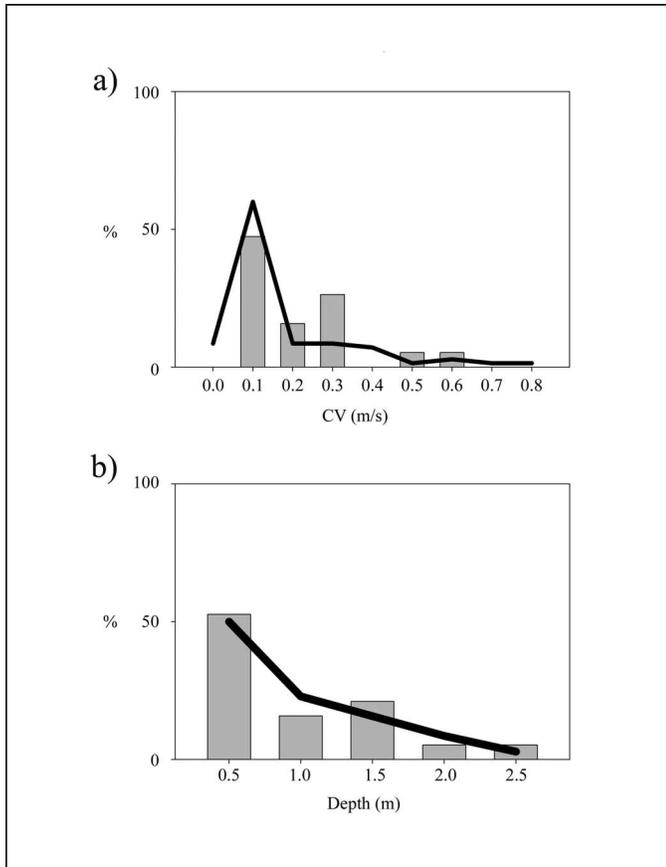


FIG. 3.—Percent occurrence of *Spongilla cenota* (observed values; gray bars) along a) current velocity and b) depth intervals taken among available habitats (line) from sites on the Devils River and the Llano River.

cenota was observed at depths ranging from 0.5 to 2.5 m in similar proportion as available (KS goodness-of-fit test, $D_{19} = 0.033$, $P > 0.05$) and at current velocities ranging from 0.1 to 0.6 m/s in similar proportion as available (KS goodness-of-fit test, $D_{19} = 0.044$, $P > 0.05$; Fig. 3).

DISCUSSION—We report the first record of *S. cenota* occurrence among drainages of the Edwards Plateau. This observation extends the known northernmost range of *S. cenota* within North America, from Florida (Poirrier et al., 1987) and south within the Yucatan Peninsula of Mexico (Penney and Racek, 1968; Poirrier et al., 1987) and Costa Rica (Roush, 1999). To date, *S. cenota* distribution is associated with alkaline waters (Volkmer-Ribeiro and Machado, 2009) of karst geographic regions, except in the Cuajiniquil River (Guanacaste Conservation Area) of Costa Rica. Preferences for various chemical constituents of water differ among sponge species (Jewell, 1935, 1939; Poirrier, 1972; Barton and Addis, 1997; Dröscher and Waringer, 2007; Volkmer-Ribeiro and Machado, 2009). As such, preferences for alkaline waters might partially explain the occurrence of *S. cenota* within karst geographic regions. However, *S. cenota* was not

found in Independence Creek, the lower Pecos River, or the James River, which are within the karst geographic region and have similar water quality to the Devils River and Llano River. Conversely, *E. fluviatilis* occurred within Independence Creek, the lower Pecos River, and the James River but were not found in the Devils River and the Llano River. It is unclear as to why *S. cenota* and *E. fluviatilis* do not overlap, especially within the Llano River basin where the Llano River site with *S. cenota* is 32 km downstream from the James River site with *E. fluviatilis*.

Within the Llano River and Devils River, *S. cenota* colonies attached primarily to limestone boulder and bedrock substrates and were ubiquitously distributed among available depths and current velocities. Association with larger substrates likely is related to substrate permanency, with larger substrates being more immobile during high flow pulses and, therefore, providing a stable substrate for colonies to grow and expand. Association with larger substrates likely is related to substrate permanency, with larger substrates being more immobile during high flow pulses and, therefore, providing a stable substrate for colonies to grow and expand. *Spongilla cenota* was not observed in soft sediments and rarely on substrates and macrophytes surrounded by soft sediments. *Spongilla cenota* has a somewhat flat amorphous form, which likely limits its ability to inhabit soft sediments. Heavy deposits of sediment can cause mortality in unbranched-gemmulated colonies of *Spongilla lacustris* in lentic systems (Frost et al., 1982). As such, *S. lacustris* produces a branching form in soft sediments to minimize the effects of sediment accumulation. Branching forms of *S. cenota* have not been reported. *Spongilla cenota* distribution along current velocity and depth gradients is similar to those reported for other freshwater sponges (Dröscher and Waringer, 2007; Manconi and Pronzato, 2008), especially those of small, flowing streams (Manconi and Pronzato, 2005). Colony size is directly related to current velocity gradient, with larger colonies of some freshwater sponges occurring in current velocities >0.20 m/s (Dröscher and Waringer, 2007). Although not quantified, we did not observe a colony size and current velocity relationship, but we did observe that larger colonies of *S. cenota* (0.2–0.75 m in diameter) were in deeper waters (0.7–2.2 m) of the Devils River. Freshwater sponges are recorded at depths of 500 m in Lake Baikal (Manconi and Pronzato, 2002), so depth likely has little physiological influence on sponge distributions. Instead, greater depths, along with attaching to large substrates, might protect sponge colonies from erosive current velocities in riverine habitats. Greater depths in riverine habitats might also protect colonies from seasonal fluctuations in water levels and consequently desiccation.

Ecosystem services of *S. cenota* in waters of the Edwards Plateau are not known but likely are similar to freshwater sponges elsewhere. Freshwater sponges filter and consume organic matter, bacteria, fungi, and zooplankton (Frost, 1978; Reisinger et al., 2010) at rates ranging from 0.01 to 0.03 mL/s per milliliter of sponge tissue (Frost, 1976). Depending on colony sizes and densities, benefits

of filtration are detectable and quantifiable (Frost, 1978). As such, freshwater sponges transfer nutrients and energy from pelagic zones to the benthos (Skelton and Strand, 2013). In addition, spongivorous aquatic insects, such as Trichoptera (Leptoceridae), Neuroptera (Sisyridae), and Diptera (Chironomidae), associate with and consume freshwater sponges (Skelton and Strand, 2013). Within the Devils River and the Llano River, we observed larvae of the family Chironomidae often associated with colonies of *S. cenota*.

Freshwater sponges are sensitive to perturbations and are used as bioindicators of water quality because of their preferences for chemical constituencies of water and substrates, limited mobility, and feeding from the water column (Poirrier, 1974; Mysing-Gubala and Poirrier, 1981; Poirrier and Trabanino, 1989; Richelle et al., 1995; Dröscher and Waringer, 2007; Anakina, 2010). The value of *S. cenota* as a bioindicator of alkaline streams within the Edwards Plateau has yet to be explored, but the potential exists for *S. cenota* to be a bioindicator of both water quantity and quality. Concerns with reductions of spring outflows and river base flows by groundwater extraction or surface flow diversions are widespread throughout the Edwards Plateau region (Bowles and Arsuffi, 1993). Alterations in water quantity and related or unrelated changes in water quality could collectively limit distributions of *S. cenota* within a river basin. With greater understanding of *S. cenota* spatial and temporal relationships with water quantity and quality gradients, then occurrence, distribution, and colony size of *S. cenota* could offer a novel and additional approach to biomonitoring within the region.

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