



Expanding the Known Ranges of the Phreatic Snails (Mollusca, Gastropoda, Cochliopidae) of Texas, USA

Authors: Alvear, Dominique, Diaz, Peter H., Gibson, J. Randy, Hutchins, Benjamin T., Schwartz, Benjamin, et al.

Source: Freshwater Mollusk Biology and Conservation, 23(1) : 1-17

Published By: Freshwater Mollusk Conservation Society

URL: <https://doi.org/10.31931/fmbc.v22i2.2020.1-17>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

REGULAR ARTICLE

EXPANDING THE KNOWN RANGES OF THE PHREATIC SNAILS (MOLLUSCA, GASTROPODA, COCHLIOPIDAE) OF TEXAS, USA

Dominique Alvear^{1#}, Peter H. Diaz², J. Randy Gibson³, Benjamin T. Hutchins⁴, Benjamin Schwartz^{4,5}, and Kathryn E. Perez^{1#*}

¹ Department of Biology, University of Texas Rio Grande Valley, Edinburg, TX 78542 USA

² Texas Fish and Wildlife Conservation Office, United States Fish and Wildlife Service, San Marcos, TX 78666 USA

³ Aquatic Resources Center, United States Fish and Wildlife Service, San Marcos, TX 78666 USA

⁴ Edwards Aquifer Research and Data Center, Texas State University, San Marcos, TX 78666 USA

⁵ Department of Biology, Texas State University, San Marcos, TX 78666 USA

ABSTRACT

The Edwards-Trinity Aquifer System of Texas, USA, one of the world's most ecologically diverse groundwater systems, contains 14 species (across seven genera) of small, poorly studied freshwater snails. Their underground habitat and microscopic size make them difficult to study and identify. Most published records are from original species descriptions, and some have not been seen since they were described more than 100 years ago. Here we use ~150 new collections, including spring and hyporheic zone sampling from across the Texas portions of the Edwards-Trinity Aquifer System, to update the ranges of these species. Two species were very uncommon, if encountered at all; individuals that might be *Phreatodrobia imitata* were seen at one sampling location, and a single individual of *P. punctata* was encountered once. The most frequently encountered snail, *P. nugax*, can be highly abundant and is found across a wide range. Other notable findings include the rediscovery and greatly expanded range of *Stygopyrgus bartonensis*, the Barton Cavesnail, as well as range extensions of 100 km or more for several species.

KEY WORDS: cavesnails, Edwards-Trinity Aquifer System, conservation, hyporheic, Bou-Rouch pump

INTRODUCTION

The Edwards-Trinity Aquifer System of Texas, USA, is home to 14 poorly known, minute snail species (Table 1), all now placed in the Cochliopidae (Clark 2019). A few species were described >100 years ago (Pilsbry and Ferriss 1906), with the remainder mostly described in the last 35 years (Hershler and Longley 1986a, 1986b). Little is known about most of these species beyond their original descriptions. Their underground habitat, microscopic size, and difficulty of sampling make them challenging to study and identify.

The Edwards-Trinity Aquifer System includes three hydrologically interconnected aquifers: the Edwards, Trinity,

and Edwards-Trinity aquifers (Miller 2000). These aquifers are made up entirely of Cretaceous-aged carbonates, with the Edwards Formation lying stratigraphically above the formations that make up the Trinity Aquifer. Their degree of hydrogeologic connectivity is spatially heterogeneous, but in some regions the Trinity and Edwards aquifers are well connected and, for the purposes of hydrogeology, treated as a single aquifer. These aquifers underlie a sweeping arc through the north, central, and western parts of the state of Texas, with surface landscapes ranging from rolling hills to desert (Fig. 1). Most snail species discussed here occur in all three aquifers, so we do not discuss each aquifer separately but provide some background from the Edwards Aquifer, which is the best-studied. A prolific karst aquifer and a recognized global hotspot of stygobitic (groundwater faunal) biodiversity, the

#The first and last authors contributed equally to this manuscript.

*Corresponding Author: perezke@gmail.com

Table 1. List of Texas's endemic, phreatic snail species examined in this study. Conservation status ranks as assigned by Hutchins (2018) using Vulnerable for S3, Threatened for S2, and Endangered for S1.

Habitat	Texas Endemic	Species	Authority	AFS Common Name	Conservation Rank Status
Phreatic, hyporheic	Yes	<i>Balconorbis uvaldensis</i>	Hershler and Longley, 1986	Balcones Ghostsnail	Vulnerable
Phreatic, surface, hyporheic?	No?	<i>Cochliopina riograndensis</i>	(Pilsbry and Ferris, 1906)	Spiral Pebblesnail	Threatened*
Phreatic, hyporheic	No?	<i>Phreatoceras taylora</i>	(Hershler and Longley, 1986)	Nymph Trumpet	Vulnerable
Phreatic	Yes	<i>Phreatodrobia conica</i>	Hershler and Longley, 1986	Hueco Cavesnail	Threatened
Phreatic	Yes	<i>Phreatodrobia coronae</i>	Hershler, 1987	Crowned Cavesnail	Threatened
Phreatic	Yes	<i>Phreatodrobia imitata</i>	Hershler and Longley, 1986	Mimic Cavesnail	Endangered
Phreatic, hyporheic	Yes	<i>Phreatodrobia micra</i>	(Pilsbry and Ferriss, 1906)	Flattened Cavesnail	Threatened
Phreatic, hyporheic	Yes	<i>Phreatodrobia nugax</i>	(Pilsbry and Ferriss, 1906)	Domed Cavesnail	Vulnerable
Phreatic	Yes	<i>Phreatodrobia plana</i>	Hershler and Longley, 1986	Disc Cavesnail	Threatened
Phreatic, hyporheic	Yes	<i>Phreatodrobia punctata</i>	Hershler and Longley, 1986	High-hat Cavesnail	Endangered
Phreatic	Yes	<i>Phreatodrobia rotunda</i>	Hershler and Longley, 1986	Beaked Cavesnail	Threatened
Phreatic, hyporheic	Yes	<i>Stygopyrgus bartonensis</i>	Hershler and Longley, 1986	Barton Cavesnail	Endangered
Phreatic	Yes	<i>Texapyrgus longleyi</i>	Thompson and Hershler, 1991	Striated Hydrobe	Endangered
Phreatic surface	Yes	<i>Tryonia diaboli</i>	Pilsbry and Ferriss, 1906	Devils Tryonia	Endangered*

**Tryonia diaboli* and *Cochliopina riograndensis* were unranked in Hutchins, therefore the rankings from Johnson et al. (2013) are used for these species.

Edwards Aquifer is home to more than 50 described vertebrate and invertebrate species (Longley 1981; Culver and Sket 2000). Meteoric water recharges the aquifer along its northern and western margins, where Edwards limestones are exposed

at the surface. South and east, a series of *en échelon* faults mark the transition between the recharge zone and the confined zone, where Edwards limestones are confined below nonpermeable strata and the aquifer is under artesian pressure.

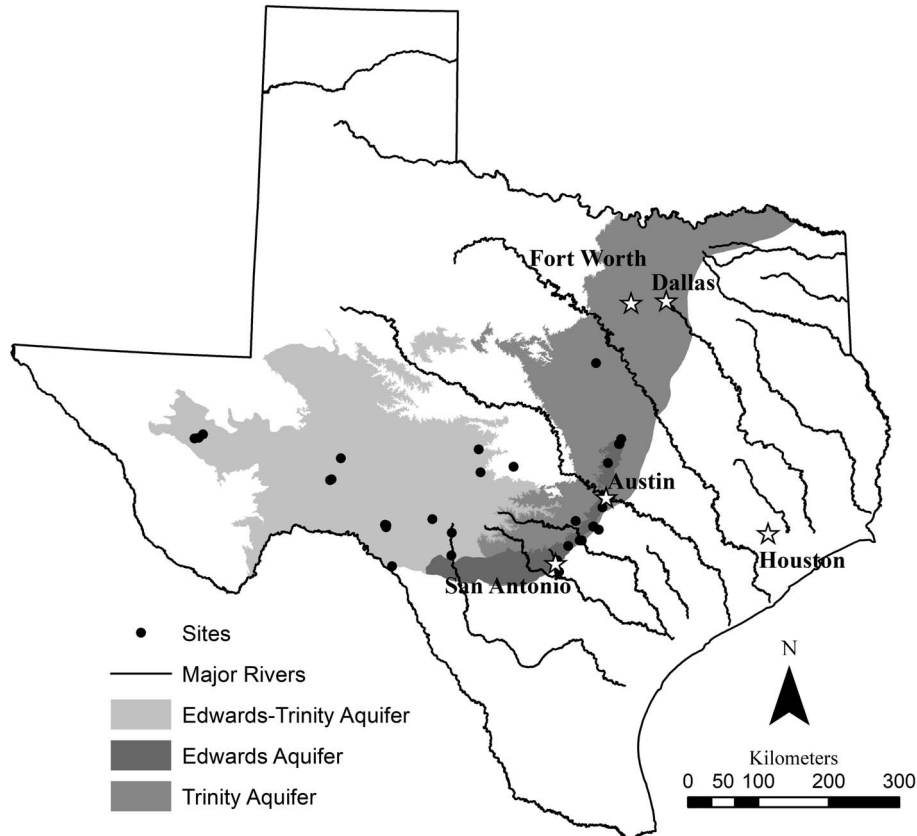


Figure 1. Map of Texas highlighting the three aquifers that comprise the Edwards-Trinity Aquifer System, major metropolitan areas, and streams. All localities drawn from taxonomic literature, and new sites are indicated.

Using stable isotope data, Hutchins et al. (2016) placed Edwards Aquifer *Phreatodrobia* spp. at the trophic level of primary consumer, presumably scraping and grazing on microbial mats and organic debris lining interconnected pores and conduits in the aquifer. In the phreatic (water-saturated zone, below the water table) portion of the Edwards Aquifer, invertebrate-dominated foodwebs are supported by (1) allochthonous (surface-derived photosynthetic) organic matter that enters the aquifer via surface connections in the recharge zone and (2) autochthonous (microbially derived chemolithoautotrophic) organic matter produced near a freshwater-saline water interface in the confined portion of the aquifer (Hutchins et al. 2016). Aquatic snails have been collected at both autochthonous- and allochthonous-dominated sites. They occur with a variety of other primary consumers (e.g., isopods and amphipods) as well as higher trophic level species that are potential predators (e.g., *Eurycea* salamanders, stygobitic catfish, cirolanid isopods, amphipods, and a flatworm *Sphalloplana* sp.). Species richness (and trophic complexity) decreases at sites where autochthonous organic matter is absent. Hyporheic zone (mixing zone of shallow groundwater and surface water along streams) ecology remains unstudied in Texas, but foodwebs are probably based on microbially processed particulates and dissolved organic carbon from downwelling surface waters (Vervier et al. 1992). As at phreatic aquifer sites, snails in hyporheic sites occur with a variety of potential predators, including flatworms, nematodes, salamanders, crustaceans, and aquatic insects (Hutchins et al. 2016), although none have been documented to make extensive use of snails as a food source. In some of the only available data, a gut-content analysis found 4% of the Salado salamander's (*Eurycea chisholmensis*) diet was *Phreatodrobia nugax* (Diaz and Warren 2018), but little other ecological information is known about these snails.

A recent conservation threat assessment (Hutchins 2018) ranked phreatic snails in Texas based on their reported range size and threats to their groundwater habitat. Researchers found that, due to a strong regulatory framework in place in much of the Edwards Aquifer, impacts of threats to species in the region are low. However, this was not the case in the western Edwards Plateau and Edwards-Trinity aquifers, where species face different anthropogenic stressors from industrial use rather than urban sprawl, and threats to many species were ranked medium. Hutchins (2018) and Johnson et al. (2013) assigned five of these phreatic snail taxa a conservation status of Endangered; six, Threatened; and three, Vulnerable. Several of these species were considered candidates for listing under the U.S. Endangered Species Act but were ultimately not listed due to insufficient information (USFWS 2009).

In this study, we address Issue no. 1 of the National Strategy for the Conservation of Freshwater Mollusks (FMCS 2016) by increasing the knowledge of the distribution of these species and providing information on collection methods. When possible, we also provide habitat information (Issue no. 4, FMCS 2016) for these poorly known, phreatic snail species.

METHODS

Sampling Methods

The new collections of snails examined in this study were from the hyporheic zone of spring-fed surface streams and from springs and other groundwater sites in the Edwards-Trinity Aquifer System (Fig. 1). Snail specimens were taken largely as a byproduct of sampling for other taxa, such as endangered salamanders or amphipods that occupy the same habitats, not as a result of randomized or directed sampling for snails. Sampling methods used in this study have been used in other studies of phreatic gastropods (Hershler and Longley 1986b). Depending on the type of site and access to the aquifer, a variety of sampling methods were used to collect specimens from springs, wells, streams, or the hyporheic zone. In streams, drift nets (0.45 by 0.30 m rectangular openings, 250 μm mesh) (Gibson et al. 2008) were deployed and checked periodically (Diaz and Warren 2018). Well samples were taken using (1) bottle traps (Nissen et al. 2018) that were baited with cotton substrate and pistachios or (2) drift nets placed on the outflow of flowing artesian wells. In some spring samples, the “mop head” technique (Hershler and Longley 1986b) was used. This method uses pieces of cotton mop heads placed in the spring orifice for several weeks, to allow bacteria and fungi to colonize, which in turn promotes colonization by snails. After the colonization period, the mop head is removed from the spring orifice and placed in a tray of water, allowing snails to be removed by hand. Additional detail on this sampling method can be found in Nissen et al. (2018). Stream, spring, and well samples were taken and preserved in 70–95% ethanol or isopropanol for identification. Hyporheic sites were sampled using a Bou-Rouch pump (Bou and Rouch 1967). The perforated interval of the pump spike was hammered into hyporheic sediments to a depth of 30–50 cm. A shallower interval was sampled only when tight sediments precluded reaching a depth of 30–50 cm. Approximately nine liters of hyporheic water was pumped from the hyporheic zone and filtered through a 200 μm -mesh net. Snails and sediments retained in the net were preserved in 95% ethanol in the field and sorted at 10 \times magnification in the lab.

In the records presented, we include new sample sites in the “new localities” category, as well as recollections from reported sites, because some large spring complexes have developed more detailed naming systems over time. For example, earlier collections from “Comal Springs” could be from several discrete spring orifices that are now individually named (e.g., Comal Springs Run 1). It is impossible to tell which spring orifices were sampled in those earlier collections, but it is important to distinguish between them as springs in a single complex often discharge water from different groundwater sources and have different faunal compositions. More generally, recollections confirm the continued presence of species in previously sampled sites—important information for conservation purposes.

Identifications

The source (literature, museum lot, or new collection) for each of these locality records, and a complete listing can be obtained from the corresponding author. New collections are vouchered at the Smithsonian Institution, USNM no. 1571271–1571310. To determine historic distributions, we included collection locality records ($n = 60$) and presented them on the distribution maps for each species, from the taxonomic literature describing these species (Pilsbry and Ferriss 1906; Hershler and Longley 1986a, 1986b; Thompson and Hershler 1991; Hershler 2001). Collection locality records for this study were not taken from unconfirmed museum lots, as identification in this group is difficult and other studies have shown misidentification rates of lots in museum collections to be a significant source of error in biodiversity studies (Shea et al. 2011; Goodwin et al. 2015). Below we include information on the diagnostic characteristics used to identify each species, but we also underwent an iterative training and identification process ourselves. For each locality record presented in this study that is from a new collection (hereafter “samples” or new collections, $n = 86$), the collector (coauthors: PD, RG, BH, or BS) assigned a preliminary identification, then the taxon experts (coauthors: KEP, DA) also assigned a preliminary identification. The taxon experts worked through the entire set of samples and assigned identifications based on the original species descriptions. At that point, we examined representatives of each species that had been identified by the species’ author, borrowed from the Smithsonian Institution, to refine our identifications; we then reidentified all samples. Identifications that were questionable required agreement from the two taxon experts (KEP, DA) for final identification. The final quality control step resulted in relatively few species reassignments (<1%), and all were juvenile *Phreatodrobia* spp. as detailed in the discussion below. Finally, 20 locality records are presented on the distribution maps from lots borrowed from the Smithsonian Institution, Zara Environmental Consulting, and the Texas Memorial Museum; as these are previously unpublished localities, they are presented here with the new collections.

RESULTS

We present 146 locality records of phreatic snails from the Edwards-Trinity Aquifer System. In the new collections presented in this study, we observed specimens matching the descriptions of 12 of the 14 described phreatic snails. We were unable to collect *Phreatodrobia imitata* specimens perfectly matching the species description, but we did find one population that was similar (additional details in species summary below). We refer to that population as *P. cf. imitata*. We collected a single individual attributable to *P. punctata* from near the type locality, but with some morphological differences from the species description and figures. We refer to that population as *P. cf. punctata*. Further work will be required to confirm the identification and full ranges of those two taxa. Below we present photographs of each species,

along with a map showing sites from the literature and new records from our sampling. We also include a summary of the key features used to distinguish each species from those that are similar and any notes about sampling or ecology that our data provide. If taxonomic concerns are apparent, comments are also included in each species summary. For drawings and definitions of snail morphological characters, we refer readers to Hershler and Ponder (1998) and Arnold (1965).

Cochliopidae

Balconorbis uvaldensis Hershler and Longley, 1986.—*Balconorbis uvaldensis* (Fig. 2) is distinguished from *Phreatodrobia* by having a pigmented shell, with a greater number of whorls, up to three, and pronounced growth lines on all whorls that follow the shape of the outer lip. At 0.90–1.22 mm width, *B. uvaldensis* is larger than *P. micra* at 1.00 mm or *P. plana* at 0.75–1.00 mm. *Balconorbis uvaldensis* can be distinguished from two *Phreatodrobia* (*P. nugax* and *P. micra*) species that have relatively circular aperture shapes and highly reflected and thickened lips by its elongate aperture (in the direction of the columellar axis) and only slightly reflected and thickened lip. This species is most likely to be confused with *P. plana*, as both have apertures that are elongate. However, the aperture in *P. plana* is enlarged to $\sim 1/3$ of the width of the shell, whereas the aperture of *B. uvaldensis* is $\sim 1/4$ of the width of the shell. If placed spire side down, *B. uvaldensis* is nearly flat, whereas *P. plana* is not, due to the enlargement of the aperture relative to the body whorl. The aperture shape also distinguishes *B. uvaldensis*; the outer edge of its aperture lip is slightly reflected and thickened, whereas the lip is not reflected or thickened in *P. plana*. *Balconorbis uvaldensis* has been observed in a relatively small region of the Edwards-Trinity Aquifer System; literature records were all from well sites, but hyporheic sampling added two sites on the Nueces River, and spring orifice sampling recovered this species from San Felipe Springs.

Cochliopina riograndensis (Pilsbry and Ferriss, 1906).—*Cochliopina riograndensis* (Fig. 3) is distinctive in shell morphology from the other phreatic and spring taxa described from the region; it is larger, average 2.23–2.80 mm width (Pilsbry and Ferriss 1906; Hershler 1985), globose, openly umbilicate, and usually with three to four brown pigmented bands around the body whorl. These pigmented bands usually mark distinctive spiral threads that extend the length of the shell. They are apparent in juveniles as well as adults, although they are not present in all individuals. Generally, the shell is slightly olive-colored, opaque, and shining; however, in some specimens collected from springs, the shell is nearly transparent, but it still retains faint pigment bands.

This species was described from river drift, with later workers describing it as epigeic; we also found it potentially occupying phreatic and hyporheic habitats. In Independence Creek (Terrell County), Leonard and Ho (1959) found this species alive “restricted to the edge of the stream, abundant

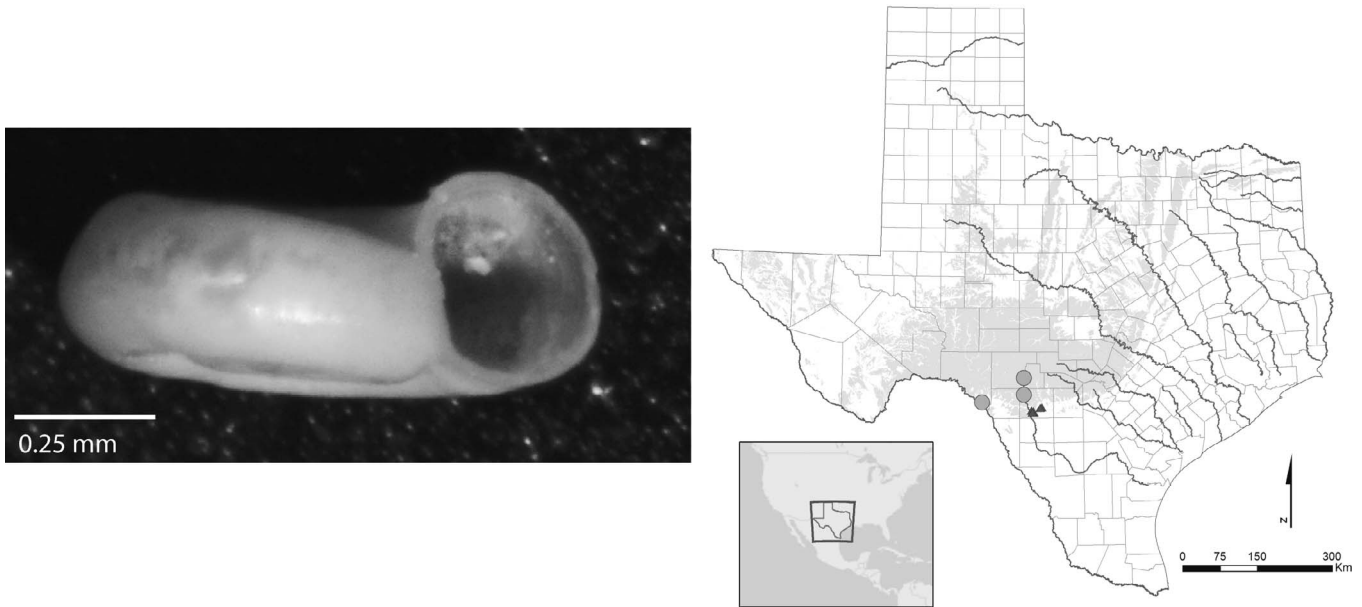
Balconorbis uvaldensis Hershler and Longley, 1986

Figure 2. *Balconorbis uvaldensis*, apertural view (0.95 mm width; Nueces at Barksdale, Edwards County, Texas). Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

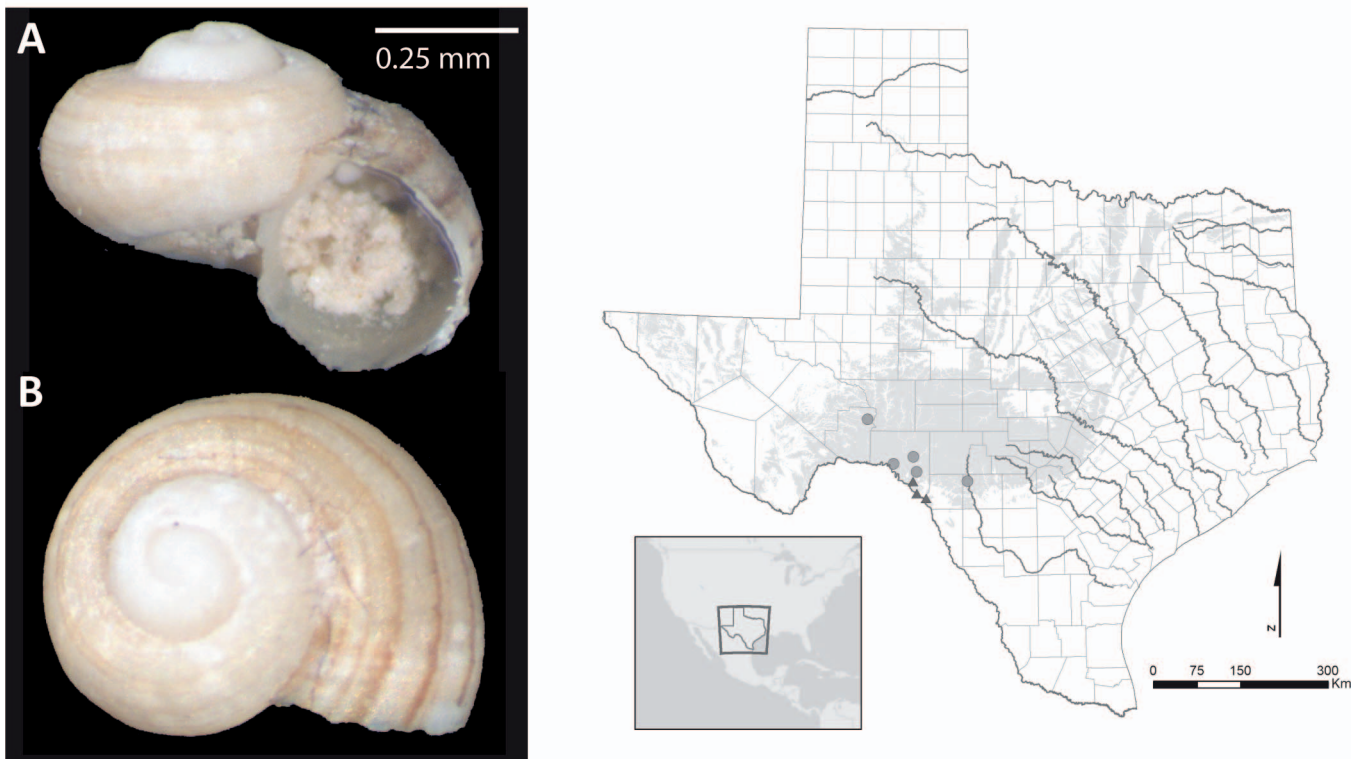
Cochliopina riograndensis Pilsbry and Ferriss, 1906

Figure 3. *Cochliopina riograndensis*, A: apertural view, B: spire view (1.31 mm wide; Caroline Springs, Independence Creek, Terrell County, Texas). Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

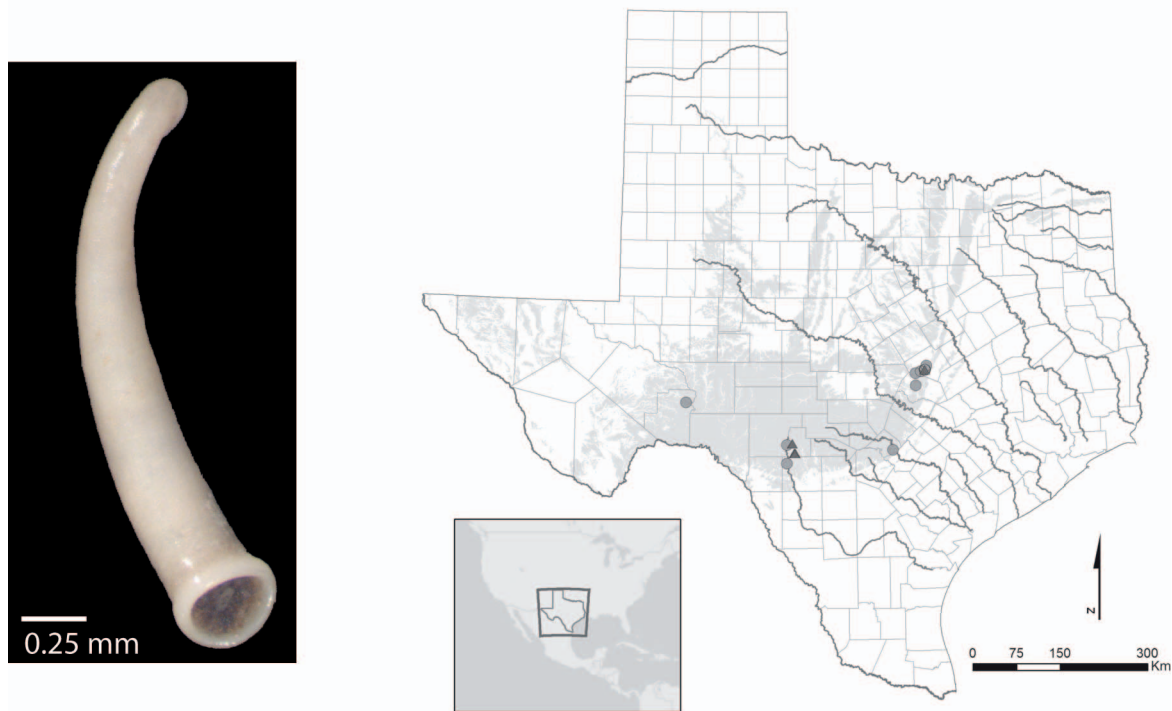
Phreatoceras taylori (Hershler and Longley, 1986)

Figure 4. *Phreatoceras taylori* (2.18 mm length; Tahuaya Springs, Bell County, Texas). Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

under cobbles, logs and in aquatic vegetation, and on fine mud on watercress.” In addition, sampling in Dolan and Finegan springs (Val Verde County) encountered live *C. riograndensis* ($N = 1,264$) in small numbers (2% of the individuals in the entire collection) from nets placed directly over water flowing from 19 spring orifices. These snails also were found in small numbers from riffles in Dolan Creek and the Devils River, but the greatest numbers by far were found in samples collected below the outflow of the orifice and in the transition zone between spring and spring run (89% of the individuals in the entire collection) (Diaz et al. 2018). Collections of live individuals from Snake Spring on Dolan Creek were found in nets placed over a spring orifice emerging directly from bedrock. All the shells of *C. riograndensis* from hyporheic sampling in our study were dead shells, so it is uncertain whether or not they were living in that habitat. We include this species here because, although it is found in spring runs, we hypothesize that it has a strong groundwater connection.

Cochliopina riograndensis also was reported from epigeal habitats on the surface of aquatic vegetation in a clear, cool, fast-flowing stream in the Cuatro Ciénegas basin in Coahuila, Mexico, and the Rio Salado de los Nadadores (20 km east of Cuatro Ciénegas), 290 km to the southwest of the nearest locality in Texas (Taylor 1966; Hershler 1985). It is worth noting, however, that there are morphological differences between shells figured from these locations, with the populations from Mexico having a more elevated, conical

shell, a solid pigmented band, and coarser striae (Hershler 1985).

Phreatoceras taylori (Hershler and Longley, 1986a).—*Phreatoceras taylori* (Fig. 4) is distinguished by its uncoiled trumpet-like shell. It has a round aperture and usually is slightly curved. This species was previously known only from the type locality and spring sites nearby, all in Real County (Hershler and Longley 1986a, 1986b). We expand its range to include spring and hyporheic samples as much as 240 km to the west at Independence Creek, Terrell County, and fill in sites within the documented range. A similar snail was reported from epigeal habitats in the Cuatro Ciénegas basin of Coahuila, Mexico, 380 km to the southwest (Hershler 1985) and fossils in other sites in Coahuila (Czaja et al. 2017); however, there are morphological differences between shells figured from these locations and those found in Texas.

Phreatodrobia conica Hershler and Longley, 1986.—*Phreatodrobia conica* (Fig. 5) is distinctive among phreatic hydrobiids of the Texas aquifers because it has a smooth, conical shell. It has a circular aperture with a thickened lip around the entire aperture. It can be distinguished from the surface-dwelling *Marstonia comalensis* by that species’ tear-drop shaped aperture. It is distinguished from *P. punctata* and *P. imitata* by their characteristic shell sculpture and apertural lip. This species was previously known from well, cave, and spring samples in Bexar and Comal counties, and we report a

Phreatodrobia conica Hershler and Longley, 1986

Figure 5. *Phreatodrobia conica*, apertural view (0.75 mm width; Creek Springs, Robertson Springs, Bell County, TX). Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

140-km range extension to the northeast at Tahuaya Springs, Bell County.

Phreatodrobia coronae Hershler, 1987.—*Phreatodrobia coronae* (Fig. 6) is similar in shape to *P. nugax* and *P. micra* in that it has a trochoid shape that is less (Fig. 6A) or more (Fig. 6B) depressed. This shape varies from nearly planar to trochoid in some individuals. However, the species is recognized by its distinctive uncoiled, hornlike protoconch. In other *Phreatodrobia* species, the protoconch is rounded and appressed to the other whorls, not free. In addition, *P. coronae* has unique sculpture in some populations, with distinct spiral lines on all whorls (except the protoconch) and large lamelliform costae in some individuals. The costae are highly variable with some individuals having just a hint of the structure (Fig. 6B) and others with costae extending nearly 1/3 the width of the whorl (Fig. 6A). The aperture is always attached to the body whorl in adult shells. We illustrated individuals with and without costae as well as more or less depressed for comparison. The range of this species is relatively restricted, with all known sites within 60 km of each other in Val Verde County, Texas. These additional samples expand the range to include further upstream in the Devils River at Snake, Dolan, and Finegan springs, and we confirm the population at San Felipe Springs is still extant. The Devils River groundwater region was considered by Hutchins (2018) as having high vulnerability due to proposed, unregulated groundwater extraction.

Phreatodrobia imitata Hershler and Longley, 1986.—*Phreatodrobia imitata* (Fig. 7) is distinguished by its tall, conical shape and distinctive shell sculpture. It has a smooth embryonic whorl followed by ribs that run in the direction of the apertural lip (collabral costae) and spiral lines on the remaining whorls. The aperture is round with a lip that is flared all around, with the greatest expansion in the low-outermost portion of the lip. This species has been recorded from Bexar County well sites in the literature, and we provide one potential new record of a population that might be *P. imitata*. *Phreatodrobia imitata* is described as variable in sculpture pattern with some individuals lacking the costae and with the lip sometimes not touching the body whorl. The individuals from Hidden Spring no. 2 in Bell County, Texas, may represent a large range extension and unusual sculpture pattern for *P. imitata*, or they may not be the same species. We figure them and refer to them as *P. cf. imitata*, as they are similar to *P. imitata*, but there is uncertainty in this identification. Soft tissues were not present in our sample, so we could not compare internal anatomical features to those described for *P. imitata*.

Phreatodrobia micra (Pilsbry and Ferriss, 1906).—*Phreatodrobia micra* (Fig. 8) has a very small, flattened (but not planispiral) shell. Other flat taxa, such as *P. plana* and *P. rotunda*, are distinguished by their distinctive aperture shapes while the aperture of *P. micra* is round. It is most similar to *P. nugax* and co-occurs with that species. *Phreatodrobia micra* is

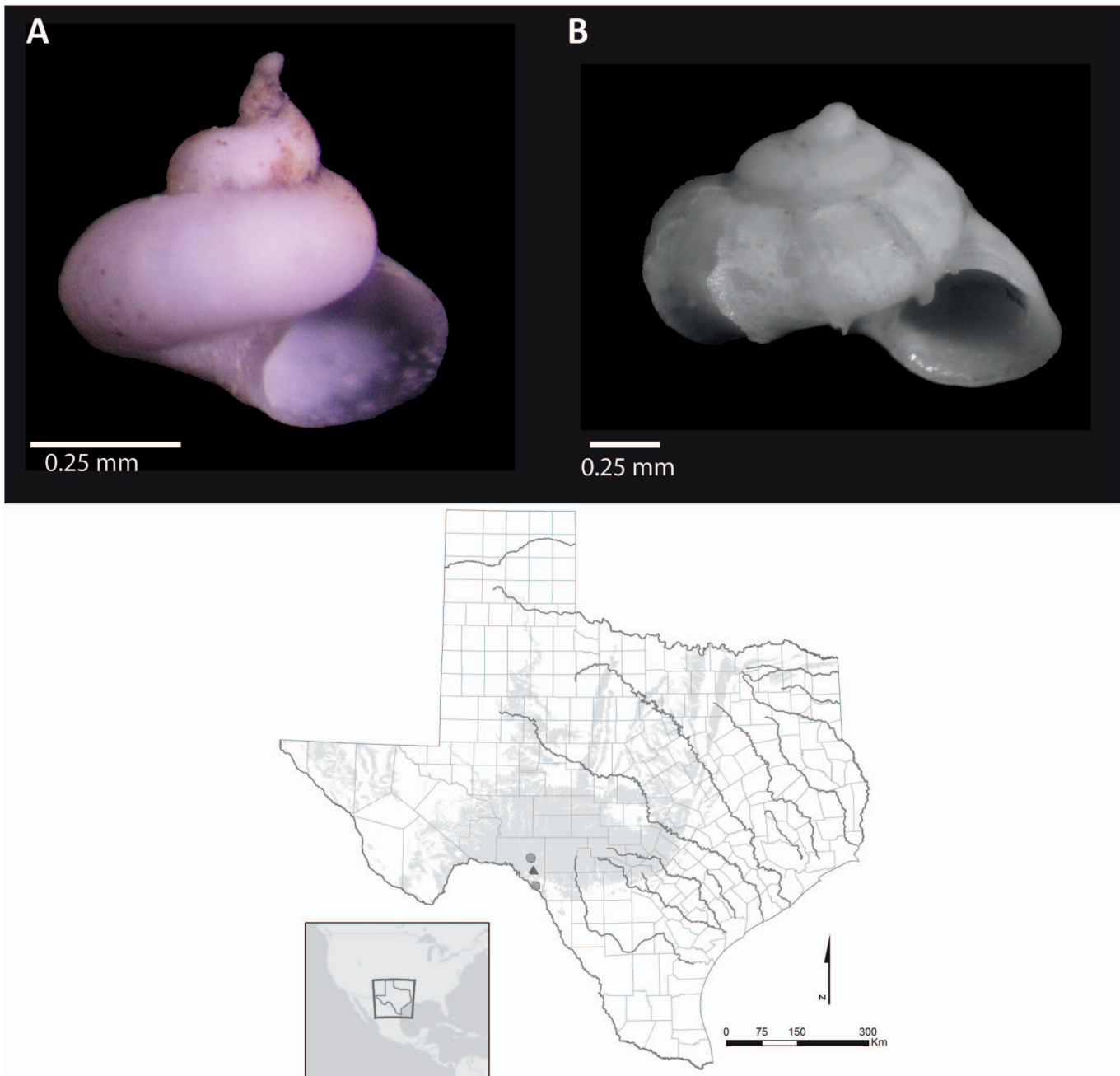
Phreatodrobia corona Hershler 1987

Figure 6. A. *Phreatodrobia corona*, apertural view (0.64 mm width; Blue Springs, Dolan Falls Preserve, Val Verde County, Texas); B. *Phreatodrobia corona*, apertural view (1.51 mm width; Finegan Springs, Devils River, Val Verde County, Texas) lamellate individual. Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

distinguished from *P. nugax* by a smaller adult size and even whorl expansion rate; moreover, the aperture is always attached to the body whorl. Additionally, in the redescription of *P. micra* and *P. nugax*, Hershler and Longley (1986b) included shells of *P. micra* with an average shell height of 0.41 mm and width of 0.95 mm for a h/w ratio of 0.43; shells of *P. nugax* had an average shell height of 1.02, width of 1.14, and a h/w ratio of 0.89.

Great care as well as observation of a size series is necessary to reliably distinguish *P. micra* morphologically from the juveniles of other flattened *Phreatodrobia* spp. Juvenile snails can be difficult or impossible to identify, and in the case of the flat *Phreatodrobia* species, they are positively misleading. In our final round of quality control, some individuals that were initially identified as *Phreatodrobia micra* were reidentified as juveniles of *P. plana*, *P. rotunda*,

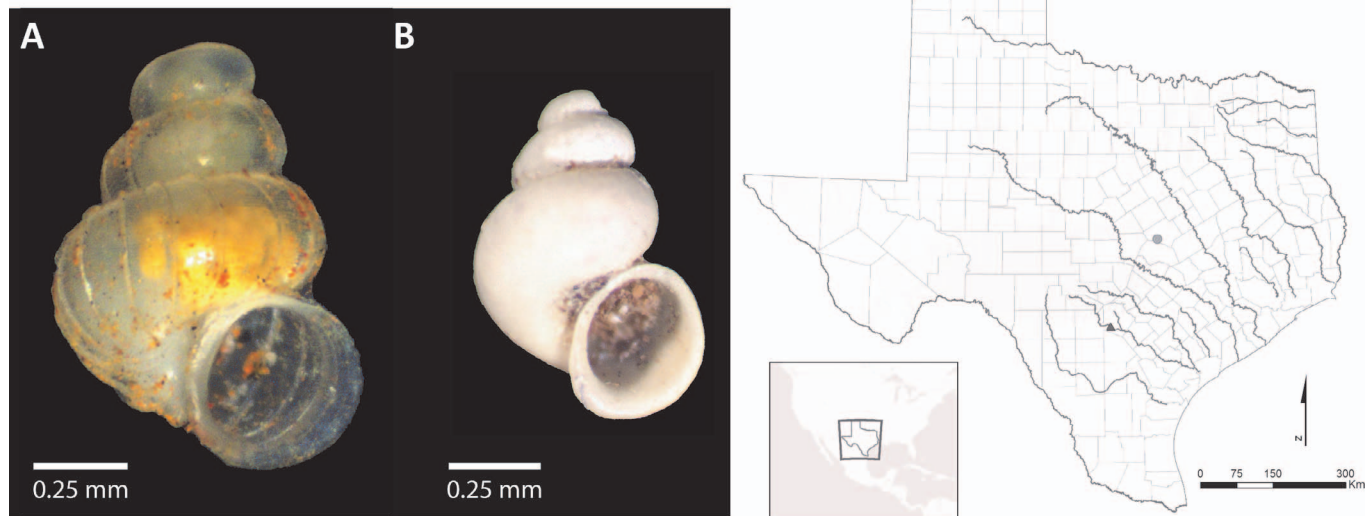
Phreatodrobia imitata Hershler and Longley, 1986

Figure 7. A: *Phreatodrobia imitata*, apertural view (1.13 mm length; Verstraeten well, Bexar County, Texas). B: *Phreatodrobia cf imitata*, apertural view (0.88 mm length; Hidden Spring no. 2, Bell County, Texas). Figured with relative sizes preserved to allow comparison. Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

and *P. nugax*, all of which may co-occur at some sites. This reidentification occurred when the individuals were small and possessed just the embryonic whorl and half a whorl of additional growth. *Phreatodrobia plana*, *P. rotunda*, and *P. nugax* are similar in shape, sculpture, and size; all have

apertures that are detached from the body whorl as adults, but the aperture is attached during growth, making them look similar to *P. micra*. To distinguish juveniles of these other species from adult *P. micra*, we observed that if the shell near the aperture is very translucent, it is juvenile, and it becomes

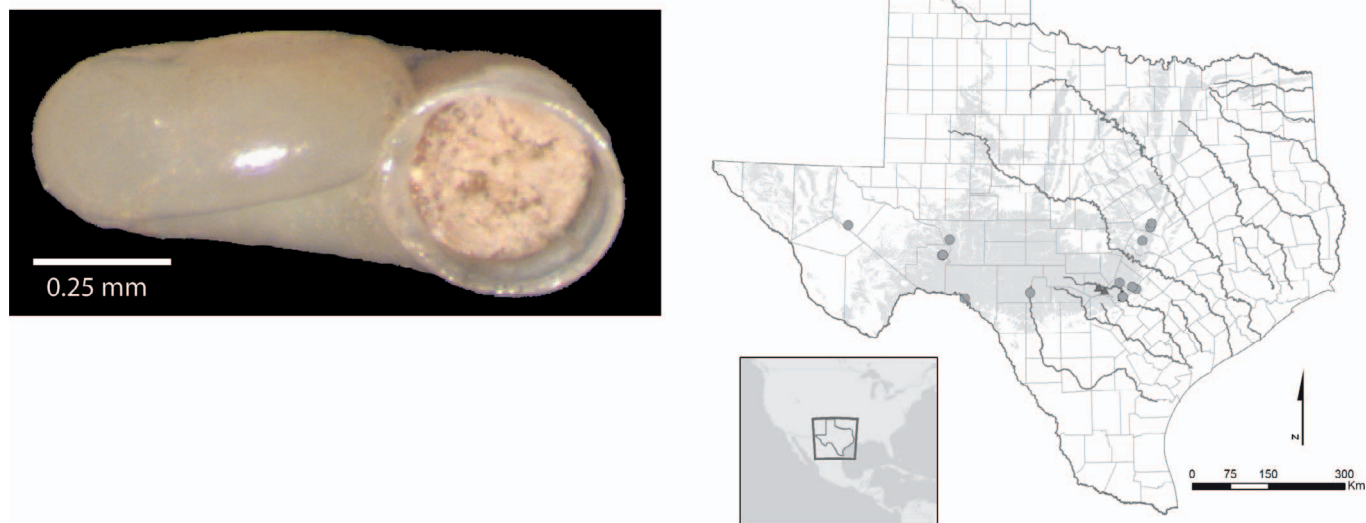
Phreatodrobia micra Hershler and Longley, 1986

Figure 8. *Phreatodrobia micra*, apertural view (1.08 mm width; Scull Rd. Crossing San Marcos River, Hays County, Texas). Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

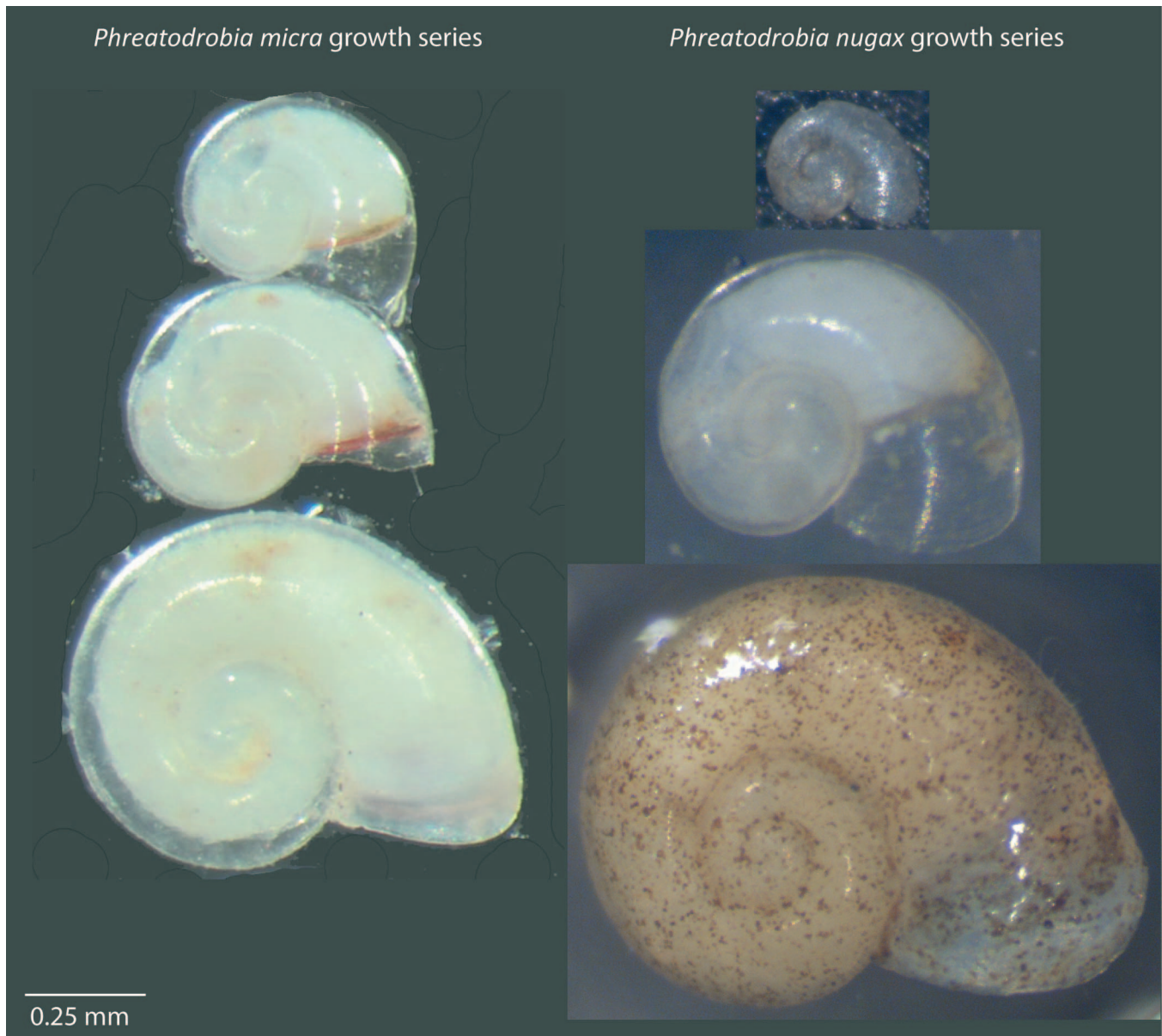


Figure 9. Comparison of a range of sizes of *P. micra* and *P. nugax* (adult *P. nugax* = 1.34 mm wide; San Antonio River, Bexar County, Texas). Relative sizes preserved to allow comparison.

less translucent with age (Fig. 9); a fully grown *P. micra* shell, while small, is not translucent and has a flared or thickened lip.

Phreatodrobia micra was known from cave, well, and spring sites from a restricted range in the central Edwards-Trinity Aquifer System (Comal, Kendall, and Hays counties). Our sampling expands the range 360 km to the west at San Solomon Springs, Reeves County, and 130 km to the northeast at Robertson Springs, Bell County, and it documents new occurrences from both hyporheic and spring samples.

Phreatodrobia nugax (Pilsbry and Ferriss, 1906).—*Phreatodrobia nugax* (Fig. 10), as currently understood, is highly variable in phenotype and includes shells that are variously flattened, elevated, conical, with and without ribbed sculpture, and with free or attached whorls. This species is characterized

by a rounded aperture that is often (not always) free from the previous whorl. The apertural lip is thickened and flared. The flare is most pronounced in adult individuals. It is most similar to *P. micra* but can be distinguished by its larger adult size (~1.75 mm adult width vs. 0.99 mm adult width), height/width ratio (detailed above in *P. micra* summary), and whorl expansion rate. In *P. micra*, when examining a view from the embryonic whorl, the whorl expansion rate is relatively even, so each whorl seems slightly wider than the previous whorl, whereas in *P. nugax* the whorl expansion rate is uneven, with the body whorl nearly twice as wide as the previous whorl. Finally, the aperture is always attached in *P. micra*, whereas in *P. nugax* adults it is often free. *Phreatodrobia nugax* is the most commonly encountered and broadly distributed phreatic

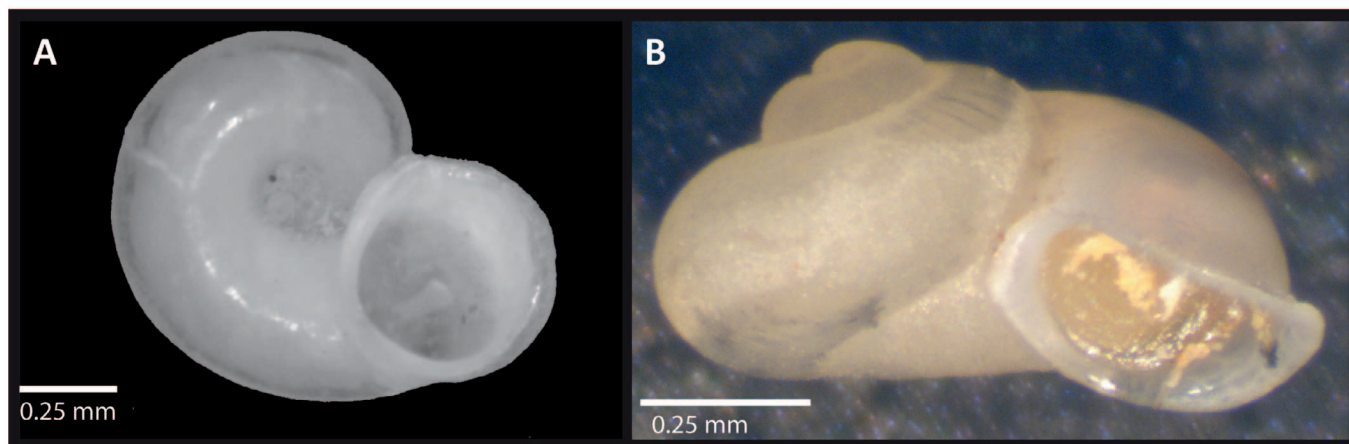
Phreatodrobia nugax Hershler and Longley, 1986

Figure 10. *Phreatodrobia nugax*, A: umbilical view, 1.09 mm width; and B: apertural view (1.02 mm width; San Marcos Artesian Well, Hays County, Texas). Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

snail in the region and was known from well, drift, and spring samples in Uvalde, Kendall, Bexar, Comal, Hays, and Travis counties. This species's range, as currently understood, is extended by 280 km west (Independence Creek, Terrell County) and 80 km east (Tahuaya Springs, Bell County) and now includes the hyporheic zone.

Phreatodrobia plana Hershler and Longley, 1986b.—*Phreatodrobia plana* is recognized from the apertural view (Fig. 11). It has a flat shell aspect, depressed in both embryonic and umbilical aspects. The aperture is elongate, longest in width along the columellar axis. The aperture also extends above the spire where the lip is flared. In the flared portion, the apertural lip is thicker in larger (adult) individuals. This species has a very restricted range that was not extended by the few localities added in this study; all were within the

previously documented range and habitat in Hays and Comal counties.

Phreatodrobia punctata Hershler and Longley, 1986.—*Phreatodrobia punctata* has a rounded, conical shell, with a thick reflected aperture (Fig. 12). This species has similar morphology to the other relatively conical, minute, snail taxa such as *P. conica*, some *P. nugax*, and *M. comalensis*. It can be distinguished from *P. conica* by that species' round aperture and an apertural lip that is not reflected or flared. *Phreatodrobia punctata* can be distinguished from very conical individuals of *P. nugax* (e.g., Hershler and Longley 1986b; Fig. 4, individuals M and Y) by having an apertural lip that is appressed to the body whorl; the lip is usually not fused to the body whorl in *P. nugax*. It can be distinguished from *M. comalensis* by having a flared apertural lip, whereas the lip in *M. comalensis* is not flared or thickened.

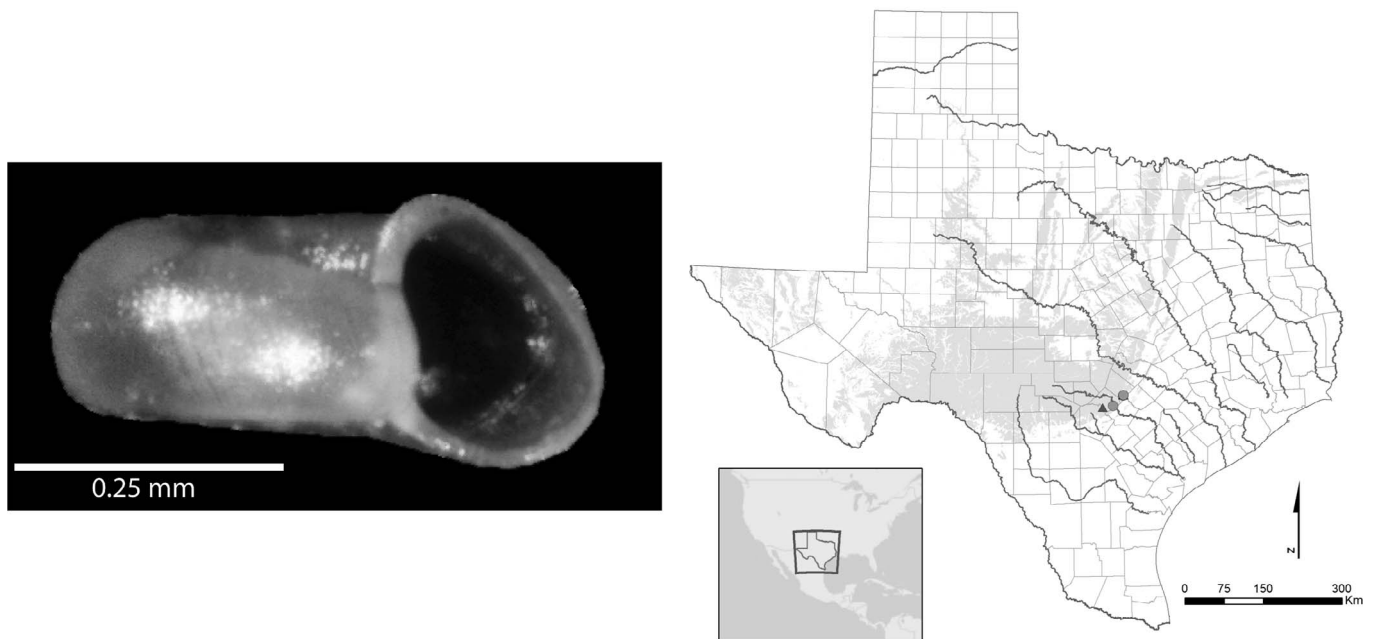
Phreatodrobia plana Hershler and Longley, 1986

Figure 11. *Phreatodrobia plana*, apertural view (0.51 mm width; Comal Springs Run 3, Comal County, Texas). Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

The single individual of *P. cf. punctata* that we encountered was from a hyporheic sample in Sessom Creek, relatively close to the type locality (San Marcos Springs). The individual we encountered (Fig. 12) appears to be slightly juvenile, but it also differs from the species description by having a smoother shell, a pyriform (not rounded) lower apertural lip, and reflection where the lip meets the body whorl. This species' documented range is narrow, with all localities within 50 km of each other.

Phreatodrobia rotunda Hershler and Longley, 1986.—*Phreatodrobia rotunda* (Fig. 13) has a larger-sized (1.83–2.16 mm), planispiral shell. Individuals examined from Comal Springs have a more declined aperture (angled downward) than those from San Marcos Springs figured in the original description (Hershler and Longley 1986b). This species is diagnosed by the shape of the aperture, which is wide rather than elongate along the columellar axis (as found in *P. plana*) and which is always attached to the body whorl. The expansion rate of the whorls is relatively even, but in some individuals, the body whorl a quarter turn before the aperture has a pronounced “pinch” or dent where the whorl is slimmer for a fraction of the whorl. *Phreatodrobia rotunda* can be distinguished from *P. nugax* by the latter species' round aperture and flare on the outer lip only; in *P. rotunda* the aperture is wide and flares on both the inner and outer lip. This species has a narrow range, and we extended it by only 30 km to include Comal Springs and the San Marcos artesian well, near San Marcos Springs.

Stygopyrgus bartonensis Hershler and Longley, 1986.—*Stygopyrgus bartonensis* (Fig. 14) has an elongate shell, ~4× taller than it is wide with strong spiral lines throughout the

shell. *Stygopyrgus bartonensis* is most similar to *Texapyrgus longleyi* but differs by having the following characteristics: a slightly thickened lip that does not flare, more prominent and regular spiral lines and no collabral growth lines, fewer whorls (maximum of 4.6 vs. 5–5.5), sutures that are slightly impressed, whorls that are rounded, and a shell that is cylindrical. *Stygopyrgus bartonensis* was described from a few shells collected near the Barton Springs concession stand spring (Hershler and Longley 1986b). It was declined for listing consideration by USFWS due to insufficient information (USFWS 2009). We add two new localities (Mormon and Treadwell Springs) near the type locality and one from a 150 km distant hyporheic sample on the Llano River, greatly expanding the range occupied by this species.

Texapyrgus longleyi Thompson and Hershler, 1991.—*Texapyrgus longleyi* (Fig. 15) is distinguished from most of the other Texas phreatic species by being much (~4×) taller than it is wide and by usually having striations. The species most similar in shape are *Tryonia diaboli* and *Stygopyrgus bartonensis*. *Tryonia diaboli* is described as smooth-shelled, with rounded, deeply incised whorls and a lip that is barely touching the body whorl at the upper end. *Texapyrgus longleyi* usually has raised spiral and longitudinal lines resulting in a “crosshatched” sculpture pattern. *Stygopyrgus bartonensis* and *Te. longleyi* are similar in adult shell height (~1.3 mm); however, at adult height *Te. longleyi* has 5.5 whorls and *S. bartonensis* has 4.0–4.6 whorls. Both species have spiral striation, but they are weaker on the adapical shell of *S. bartonensis*. *Texapyrgus longleyi* has strong collabral striae that are not present in *S. bartonensis*. Finally, *Te. longleyi* has

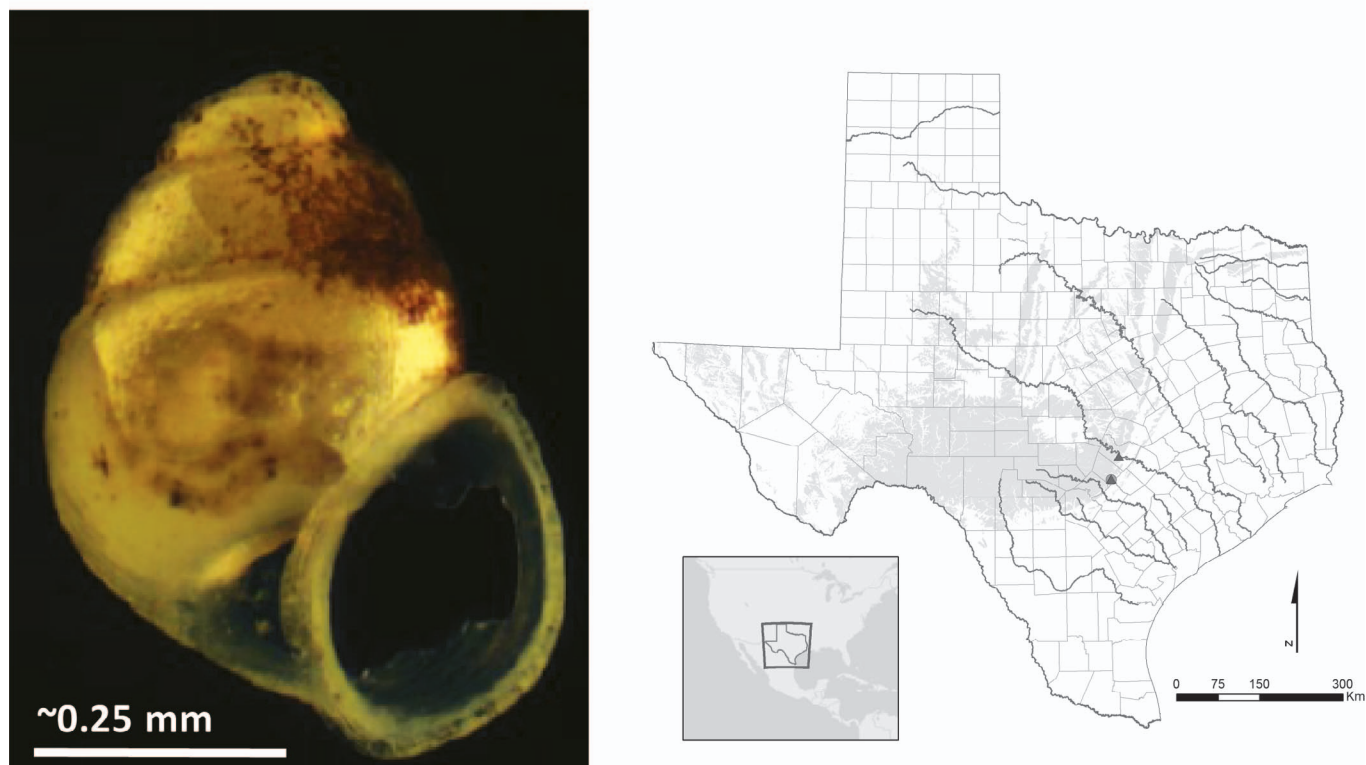
Phreatodrobia punctata Hershler and Longley, 1986

Figure 12. *Phreatodrobia punctata*, apertural view (average length of species 1.1 mm; Sessom Springs, Hays County, Texas). Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

a prominent protoconch, which is less prominent in *S. bartonensis*. *Texapyrgus longleyi* was described from drift net sampling of the spring orifice feeding a small rheocrene just downflow from Slaughter Bend on the Devils River; we expand the known localities to include Dolan and Finegan springs, ~30 km upstream.

Tryonia diaboli Pilsbry and Ferriss, 1906.—*Tryonia diaboli* (Fig. 16) is most similar in overall shape to *Texapyrgus longleyi* and *Stygopyrgus bartonensis*. It is distinguished from *Te. longleyi* by the original description of a completely smooth shell, while *Te. longleyi* is highly sculptured. It is also distinguished from *S. bartonensis* by smooth sculpture, but that species is more columnar in shape while *T. diaboli* is distinctly tapered.

Tryonia diaboli was described from Devils River drift in 1906 (Pilsbry and Ferriss 1906), and we have not been able to find additional references to this species in the published literature, except for a ranking by Johnson et al. (2013). Along with *Te. longleyi* and *P. coronae*, it was encountered during a recent survey of the Devils River (Diaz et al. 2018).

DISCUSSION

The records presented here advance our understanding of the distributions of the phreatic snail fauna of the U.S. portion

of the Edwards-Trinity Aquifer System; however, there are still large regions of the aquifer that are not sampled or only incompletely. Our sampling, and that of prior investigators, has been primarily in the Balcones Fault region where there are concentrations of springs and artesian wells. The Edwards-Trinity Aquifer System extends 300 km north of our sampling, and there are large gaps in records throughout the northern and western portions of the aquifer. Sampling in those areas would likely extend the described species' ranges and reveal undescribed species.

An important consequence of this study was numerous new records for seven snail species from hyporheic samples in surface streams (indicated in Table 1). Previously, these snails had been recorded only from caves, springs and wells, and as river drift of uncertain provenance. Documentation of species from this new habitat has several implications for species conservation. First, surface streams can be an important target for conservation of groundwater species, particularly if hyporheic populations are a distinct ecological phenotype that could uniquely contribute to the species' evolutionary potential. Second, occurrence in the hyporheic zone potentially increases the area and connectivity of habitat that species occupy. Finally, the hyporheic zone is much more accessible and productive for research compared to efforts to study or sample fauna that can be accessed only via deep wells.

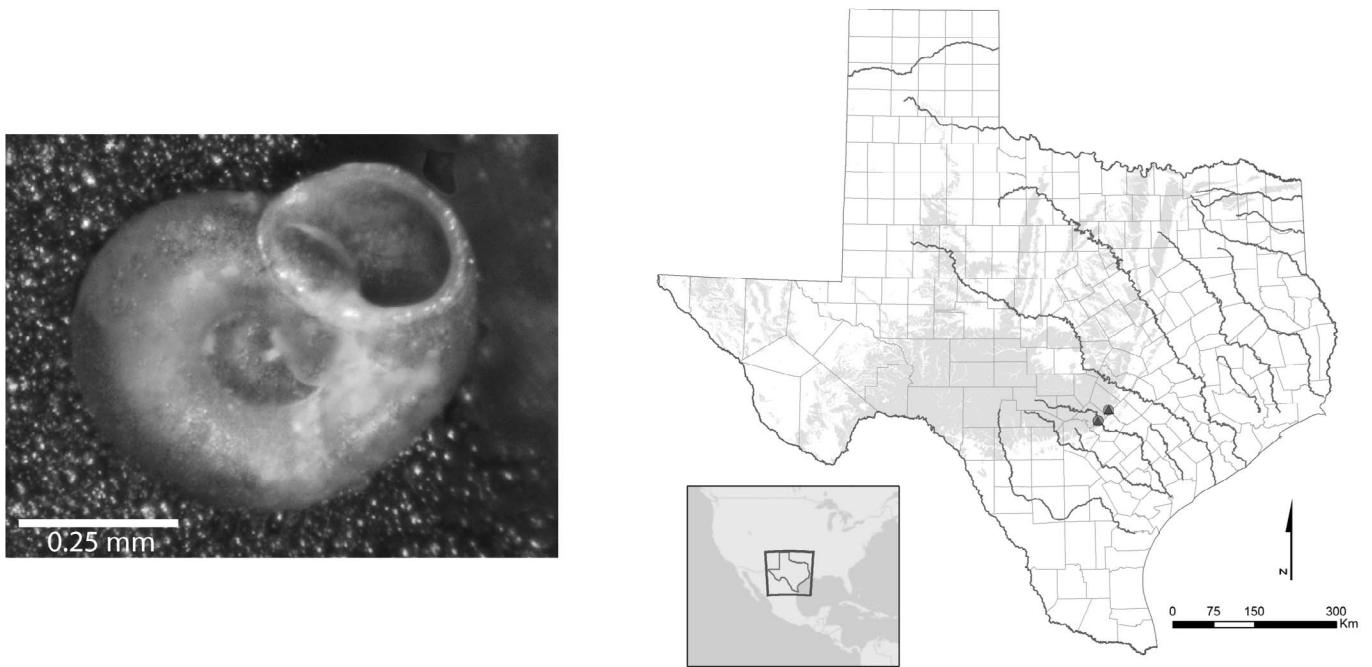
Phreatodrobia rotunda Hershler and Longley, 1986

Figure 13. *Phreatodrobia rotunda*, umbilical view (1.6 mm width; Comal Springs Run 3, Comal County, Texas). Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

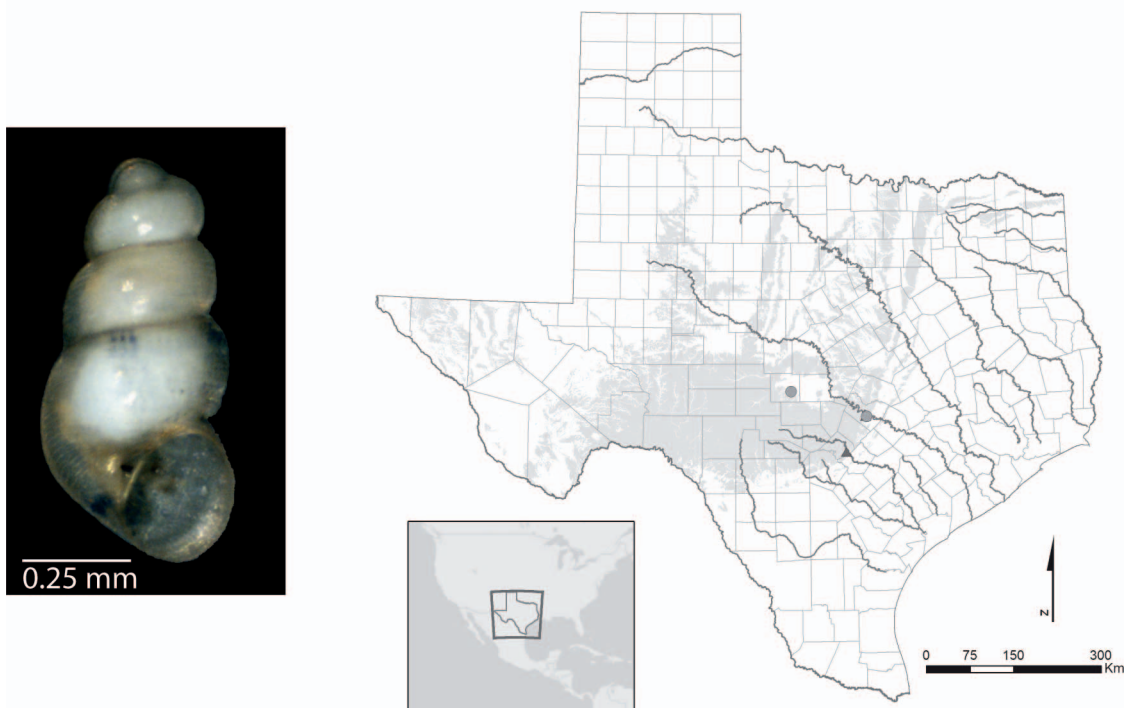
Stygopyrgus bartonensis Hershler and Longley, 1986

Figure 14. *Stygopyrgus bartonensis*, apertural view (1.08 mm length; Mormon Spring no. 3, Travis County, Texas). Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

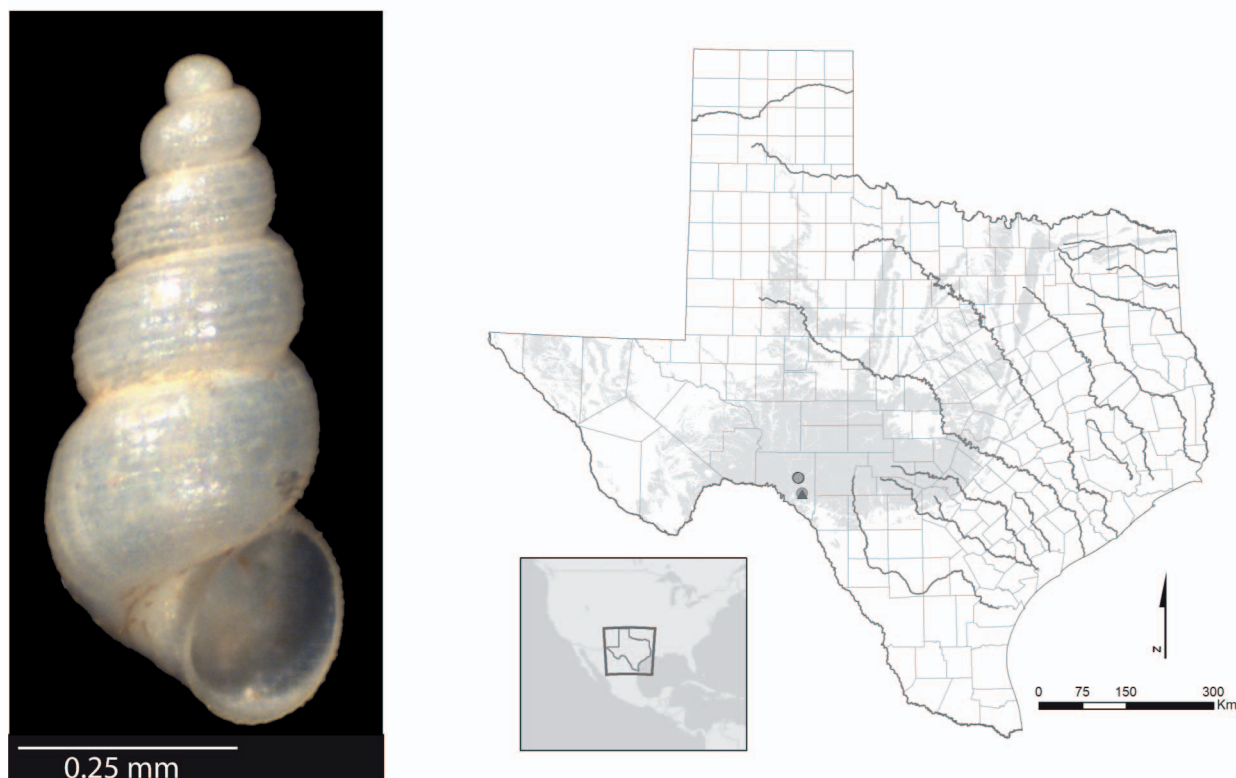
Texapyrgus longleyi Thompson and Hershler, 1991

Figure 15. *Texapyrgus longleyi*, apertural view (1.31 mm length; Finegan Springs, Devils River, Val Verde County, Texas). Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

The hyporheic zone of rivers provides much larger cross sections of landscapes than is possible to sample with wells. However, it is worth considering that portions of deep aquifer habitats that are hydrologically isolated from surface recharge points might be less susceptible to environmental variability and point-source pollution if they are outside the recharge zone. Indeed, Hutchins et al. (2016) suggested that deep-aquifer habitats with foodwebs supported by *in-situ* primary production may serve as refugia for groundwater species during periods of increased aridification. Unfortunately, across much of Texas, hydraulic connectivity between the surface and subsurface is not well understood, and even confined aquifers are susceptible to contamination (Hutchins 2018).

Although it is possible for widespread species to be threatened, the phreatic snails of the greatest immediate conservation concern are those with narrow ranges and low abundances that occur in regions with great potential for modification and withdrawal of groundwater. *Phreatodrobia plana* and *P. rotunda* have very narrow ranges, but they are relatively frequent in samples from Comal and San Marcos Springs. Both spring systems have multiple federally protected endangered species and a local water regulatory framework in place for protection of the springs. Therefore, snails in these systems have a higher level of protection than some of the

other phreatic snail species. For example, *Tryonia diaboli*, *Texapyrgus longleyi*, and *Phreatodrobia coronae* are restricted to the Devils River region, described by Hutchins (2018) as having high vulnerability due to the lack of a regulatory framework for groundwater conservation and water extraction for oil and gas as well as human consumption. The species that are restricted to that region may face a much higher risk of extinction. In contrast to *P. plana* and *P. rotunda*, *P. punctata* is reported only from San Marcos and Barton Springs. However, we found only a single shell of this species in a sample from Sessom Creek. A similar situation occurs for *P. imitata*, reported from the Verstraeten well (Bexar County). We encountered individuals that loosely resemble this species only in a Bell County spring. Resampling Verstraeten and nearby wells and hyporheic sites is needed to confirm whether this species still occurs at historic sites, as well as to undertake taxonomic work to determine if the Bell county population is *P. imitata*. Finally, with these samples, we report the rediscovery of *Stygopyrgus bartonensis*, previously known from only a few shells from one heavily human-impacted site. This species appears to persist in Austin-area springs and hyporheic zones, and additional hyporheic sampling in the region could greatly expand its known range.

Groundwater fauna typically have narrow ranges, often

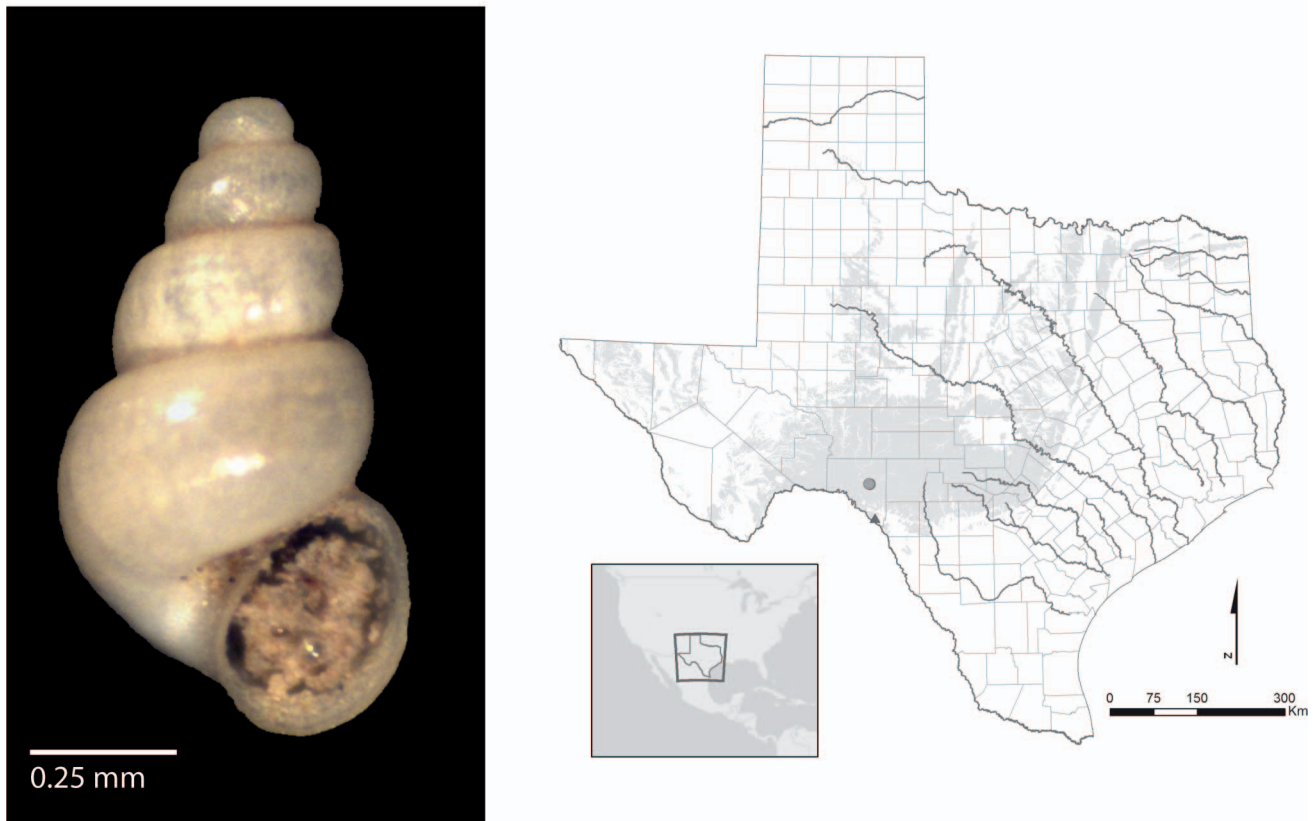
Tryonia diaboli Pilsbry and Ferriss 1906

Figure 16. *Tryonia diaboli*, apertural view (1.09 mm length; Dolan Springs, Val Verde County, Texas). Map of Texas with Edwards-Trinity Aquifer System highlighted in gray. Counties and major river drainages are also illustrated. Literature records are indicated with triangles and new records with circles.

known from one or a few sites (Falniowski et al. 2008), and it is expected that different groundwater units or catchments form hydrological barriers to gene flow (Barr and Holsinger 1985). A review of genetic connectivity among stygobitic animals found that 94% of the species examined had ranges <200 km in length (Trontel et al. 2009). Regional groundwater flow paths, the relative permeability and connectedness of karst systems, and whether there are stratigraphic and/or structural barriers separating groundwater units could all affect the frequency of gene flow (Barr and Holsinger 1985). Species that occupy both the hyporheic zone and connected aquifer habitats would be expected to have more opportunities for gene flow, thus resulting in potentially wider species ranges with sufficient mixing to preserve a more-or-less connected gene pool (Ward and Palmer 1994; Finston and Johnson 2004). In subterranean amphipods, for example, unique sets of species were found to occur in distinct catchment areas and show significant genetic differentiation over short geographical distances (Finston and Johnson 2004), and similar patterns have been observed in numerous groundwater-dependent gastropods (Perez et al. 2005; Trontel et al. 2009; but see Richling et al. 2017). In this study, assigning new collections of phreatic snails to species based on shell morphological characters, we find that some taxa (particularly *Phreatodrobia*

nugax, *P. micra*, and *Ph. taylori*) have surprisingly extensive ranges compared to our expectations for phreatic taxa. Based on findings in other groups (Stoch 1995; Trontel et al. 2009), and the observed morphological variability of these species, it is likely that these taxa include multiple cryptic lineages.

ACKNOWLEDGMENTS

This work was supported by a UTRGV Engaged Scholars grant to DA, the UTRGV College of Sciences, and the UTRGV COS High Scholars Program. Alison Schofield assisted with sample curation and Scott Gunn and Zen Faulkes with microscopy. We appreciate the assistance of Dr. Robert Hershler for reviewing early specimens and his time over the years with other samples. Peter Sprouse, Zara Environmental, the Smithsonian Institution, and James Reddell at the University of Texas Biodiversity Center contributed additional samples. We appreciate the support from Bell County, the Village of Salado, and Clearwater Underground Water Conservation District for funding work in Bell and Williamson counties and The Nature Conservancy for funding the work in Val Verde County. The views expressed in this paper are those of the authors and do not necessarily reflect the view of the

U.S. Fish and Wildlife Service. We appreciate the contributions of reviewers and the editor to improve this manuscript.

LITERATURE CITED

- Arnold, W. H. 1965. A glossary of a thousand-and-one terms used in conchology. *Veliger* 7 (Supplement):1–54.
- Barr, T. C., and J. R. Holsinger. 1985. Speciation in cave faunas. *Annual Review of Ecology and Systematics* 16:313–337.
- Bou, C., and R. Rouch. 1967. Un nouveau champ de recherches sur la faune aquatique souterraine. *Compte Rendus de l'Académie des Sciences de Paris* 265:369–370.
- Clark, S. A. 2019. Cochliopidae Tryon, 1866. Pages 104–108 in C. Lydeard and K. S. Cummings, editors. *Freshwater Mollusks of the World: A Distribution Atlas*. Johns Hopkins University Press, Baltimore, Maryland.
- Culver, D. C., and B. Sket. 2000. Hotspots of subterranean biodiversity in caves and wells. *Journal of Cave and Karst Studies* 62:11–17.
- Czaja, A., J. L. Estrada-Rodríguez, U. Romero-Méndez, V. Ávila-Rodríguez, I. G. Meza-Sánchez, and A. P. Covich. 2017. New species and records of phreatic snails (Caenogastropoda: Cochliopidae) from the Holocene of Coahuila, Mexico. *Archiv für Molluskenkunde* 146:227–232.
- Diaz, P., M. Montagne, C. Norris, K. Aziz, and J. Gibson. 2018. Final Report for The Nature Conservancy in fulfillment of Dolan Springs assessment. Texas Fish and Wildlife Conservation Office. U.S. Fish and Wildlife Service, San Marcos, Texas. Available at https://www.researchgate.net/publication/323994933_Final_Report_for_the_Nature_Conservancy_in_Fulfillment_of_Dolan_Springs_Assessment (accessed March 25, 2019).
- Diaz, P., and J. B. Warren. 2018. Salado Salamander Monitoring Final Report 2018. Texas Fish and Wildlife Conservation Office. U.S. Fish and Wildlife Service, San Marcos, Texas. Available at https://www.researchgate.net/publication/331429960_Salado_Salamander_Monitoring_Final_Report_2018 (accessed March 25, 2019).
- Falniowski, A., M. Szarowska, I. Sîrbu, A. Hillebrand-Voiculescu, and M. Baci. 2008. *Heleobia dobrogica* (Grossu and Negrea, 1989) (Gastropoda: Rissooidea: Cochliopidae) and the estimated time of its isolation in a continental analogue of hydrothermal vents. *Molluscan Research* 28:165–170.
- Finston, T. L., and M. S. Johnson. 2004. Geographic patterns of genetic diversity in subterranean amphipods of the Pilbara, Western Australia. *Marine and Freshwater Research* 55:619–628.
- FMCS (Freshwater Mollusk Conservation Society). 2016. A national strategy for the conservation of native freshwater mollusks. *Freshwater Mollusk Biology and Conservation* 19:1–21.
- Gibson, J. R., S. J. Harden, and J. N. Fries. 2008. Survey and distribution of invertebrates from selected springs of the Edwards Aquifer in Comal and Hays counties, Texas. *Southwestern Naturalist* 53:74–84.
- Goodwin, Z. A., D. J. Harris, D. Filer, J. R. I. Wood, and R. W. Scotland. 2015. Widespread mistaken identity in tropical plant collections. *Current Biology* 25:R1057–R1069.
- Hershler, R. 1985. Systematic revision of the Hydrobiidae (Gastropoda: Rissooidea) of the Cuatro Ciénegas Basin, Coahuila, Mexico. *Malacologia* 26:31–123.
- Hershler, R. 2001. Systematics of the North and Central American aquatic snail genus *Tryonia* (Rissooidea: Hydrobiidae). *Smithsonian Contributions to Zoology* 612:1–64.
- Hershler, R., and G. Longley. 1986a. *Hadoceras taylori*, a new genus and species of phreatic Hydrobiidae (Gastropoda: Rissooidea) from South-Central Texas. *Proceedings of the Biological Society of Washington* 99:121–136.
- Hershler, R., and G. Longley. 1986b. Phreatic hydrobiids (Gastropoda: Prosobranchia) from the Edwards (Balcones Fault Zone) Aquifer region, South-Central Texas. *Malacologia* 27:127–172.
- Hershler, R., and W. F. Ponder. 1998. A review of morphological characters of hydrobioid snails. *Smithsonian Contributions to Zoology* 600:1–55.
- Hutchins, B. T. 2018. The conservation status of Texas groundwater invertebrates. *Biodiversity and Conservation* 27:475–501.
- Hutchins, B. T., A. S. Engel, W. H. Nowlin, and B. F. Schwartz. 2016. Chemolithoautotrophy supports macroinvertebrate food webs and affects diversity and stability in groundwater communities. *Ecology* 97:1530–1542.
- Johnson, P. D., A. E. Bogan, K. M. Brown, N. M. Burkhead, J. R. Cordeiro, J. T. Garner, P. D. Hartfield, D. A. W. Lepitzki, G. L. Mackie, E. Pip, T. A. Tarpley, J. S. Tiemann, N. V. Whelan, and E. E. Strong. 2013. Conservation status of freshwater gastropods of Canada and the United States. *Fisheries* 38:247–282.
- Leonard, A. B., and T. Ho. 1959. New *Calipyrgula* from Pleistocene of Texas and notes on *Cochliopa riograndensis*. *The Nautilus* 73:125–129.
- Longley, G. 1981. The Edwards Aquifer: Earth's most diverse groundwater ecosystem? *International Journal of Speleology* 11:123–128.
- Miller, J. A., editor. 2000. *Ground Water Atlas of the United States*. United States Geological Survey, Reston, Virginia. 300 pp.
- Nissen, B. D., T. J. Devitt, N. F. Bendik, A. G. Gluesenkamp, and J. R. Gibson. 2018. New occurrence records for stygobiontic invertebrates from the Edwards and Trinity aquifers in west-central Texas, USA. *Subterranean Biology* 28:1–13.
- Perez, K. E., W. Ponder, D. J. Colgan, S. A. Clark, and C. Lydeard. 2005. Molecular phylogeny and biogeography of spring-associated hydrobiid snails of the Great Artesian Basin, Australia. *Molecular Phylogenetics and Evolution* 34:545–556.
- Pilsbry, H. A., and J. H. Ferriss. 1906. Mollusca of the Southwestern states, II (plates V–IX). *Proceedings of the Academy of Natural Sciences of Philadelphia* 58:123–175.
- Richling, I., Y. Malkowsky, J. Kuhn, H.-J. Niederhofer, and H. D. Boeters. 2017. A vanishing hotspot—The impact of molecular insights on the diversity of Central European *Bythiospeum* Bourguignat, 1882 (Mollusca: Gastropoda: Truncatelloidea). *Organismal Diversity and Evolution* 17:67–85.
- Shea, C. P., J. T. Peterson, J. M. Wisniewski, and N. A. Johnson. 2011. Misidentification of freshwater mussel species (Bivalvia: Unionidae): Contributing factors, management implications, and potential solutions. *Journal of the North American Benthological Society* 30:446–458.
- Stoch, F. 1995. The ecological and historical determinants of crustacean diversity in groundwaters, or: why are there so many species? *Mémoires de Biospéologie* 22:139–160.
- Taylor, D. W. 1966. A remarkable snail fauna from Coahuila, Mexico. *Veliger* 9:152–228.
- Thompson, F. G., and R. Hershler. 1991. New hydrobiid snails (Mollusca: Gastropoda: Prosobranchia: Truncatelloidea) from North America. *Proceedings of the Biological Society of Washington* 104:669–683.
- Trontel, J. P., C. J. Douady, C. Fišer, J. Gibert, Š. Gorički, T. Lefébure, B. Sket, and V. Zakšek. 2009. A molecular test for cryptic diversity in ground water: How large are the ranges of macro-stygobionts? *Freshwater Biology* 54:727–744.
- USFWS (United States Fish and Wildlife Service). 2009. Endangered and threatened wildlife and plants; partial 90-day finding on a petition to list 475 species in the southwestern United States as threatened or endangered with critical habitat. FWS-R2-ES-2008-0130 MO 9221050083. United States Fish and Wildlife Service, Washington, D.C. Available at <https://www.federalregister.gov/d/2011-24633> (accessed March 25, 2019).
- Vervier, P., J. Gibert, P. Marmonier, and M.-J. Dole-Olivier. 1992. A perspective on the permeability of the surface freshwater-groundwater ecotone. *Journal of the North American Benthological Society* 11:93–102.
- Ward, J. V., and M. A. Palmer. 1994. Distribution patterns of interstitial freshwater meiofauna over a range of spatial scales, with emphasis on alluvial river-aquifer systems. *Hydrobiologia* 287:147–156.