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A remarkable new genus and species of subterranean freshwater snail from a recently dried-up spring of Viesca, Coahuila, Northern Mexico

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Abstract

This paper describes a new genus and species of subterranean gastropod from a karstic region near Viesca, Coahuila in northern Mexico. Shells of *Phreatoviesca spinosa* **gen. nov. et sp. nov.** were found in spring-deposited sediments near the outlet of a cave that dried up in the late 20th century. The new genus can be primarily distinguished conchologically from other phreatic genera by three remarkable characteristics: (i) prominent open coiling of the last whorl, (ii) shovel-shaped spine ornamentations on the teleoconch, and (iii) a coarsely honeycomb-like pitted protoconch structure. Since only dry shells were found, the new species could already be extinct. However, in view of the relative recent drying up of the spring, we consider that *Phreatoviesca spinosa* is possibly extant in the aquifers in or adjacent to the Viesca region.

Keywords

Gastropods, interstitial habitat, new genus , North America, subterranean, systematics

Introduction

Owing to sampling difficulty associated with subterranean habitats, it is not surprising that stygobiotic (i.e., freshwater subterranean-obligate) gastropods are among the most understudied freshwater groups in the world (Prié 2019; Gladstone et al. 2021). Many stygobiotic gastropods inhabit a diversity of subterranean habitats that are near-to-completely inaccessible to humans, such as the hyporheic or phreatic zones of an aquifer system. In Mexico, the majority of the species have been discovered from these less accessible habitat types through opportunistic sampling of the groundwater saturated, interstitial spaces within the sediment of surface streams or from groundwater discharge in wells or small springs (Hershler 1985; Czaja et al. 2019a). This inaccessibility to extant populations and low probability of discovering stygobiotic gastropods *in vivo* has led to many taxonomic descriptions worldwide (whether later found extant or extinct) relying solely on empty shells (Georgiev 2013; Grego et al. 2017; Quiñonero-Salgado and Rolán 2017; Hofman et al. 2018; Czaja et al. 2019b).

Although mollusk shells generally have a high fossilization potential, there are few records of gastropod fossils that have been determined to be stygobionts worldwide. This fossil scarcity is likely owing to the usually narrow geographic distributions of stygobiotic gastropods, along with their extremely small size that does not typically exceed two millimeters (Gladstone et al. 2021). However, these small stygobiont fossils may be more likely obtained from sites that have gone through recent environmental change, such as the springs in Viesca, Mexico that dried up in the second half of the 20th century (Czaja et al. 2017, 2019a).

The aim of the present study is to describe a new subterranean genus and species from Coahuila, and to discuss unique aspects of the shell morphology compared to other stygobiotic gastropod species in North America. The new genus can be readily distinguished by three shell features: (i) prominent open coiling of the last whorl, (ii) shovel-shaped spine ornamentations on the teleoconch, and (iii) coarsely honeycomb-like pitted protoconch structure. Although the description of both genus and species based exclusively on shell morphology may appear erroneous, the shell features of the discovered specimens are so strikingly different from all known stygobiotic gastropods that we consider the erection justified. Nevertheless, in the absence of soft parts, the family designation is tentative until living specimens will be obtained for anatomical and molecular studies.

Materials and methods

The studied shells were collected during July 2015 and November 2019 in two sites within the spring "Túnel 7" (Fig. 1). Like most of the other 15 springs near Viesca, this spring began to dry up during the drought of 1958–59, but the area remained a partial wetland until the late 1990s (Czaja et al. 2015, 2019a). The shells were found in superficial spring deposits a few meters at the outlet of a cave. The area is now completely dry, but the outlines of the former water body are still clearly visible in satellite or drone

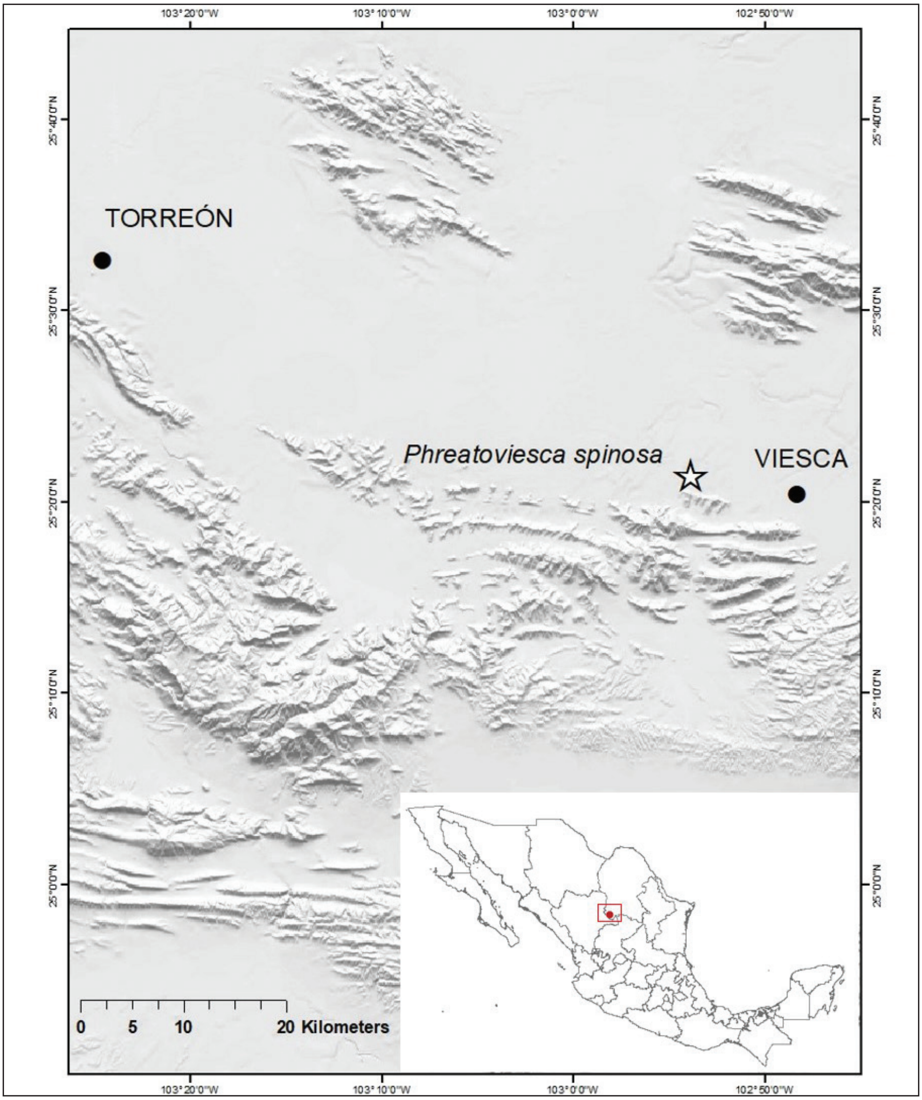


Figure 1. Map of the study area with localization of the sampling site near the town of Viesca, Coahuila, Mexico.

imagery. Moreover, the presence of remaining moisture in the subsoil is indicated by sparse vegetation within the original spring. The possible anthropogenic causes for the drying up of all 15 springs of Viesca were presented in detail by Czaja et al. (2019a).

The collected material was screened through two sieves with a mesh size of 0.5 mm and 0.3 mm. For the morphological analysis, the shells were photographed and measured with a Zeiss AxioCamERc 5s camera attached to a Zeiss Stemi 2000-C microscope. Some specimens, particularly their protoconchs, were examined in the Laboratory of Biotechnology, Universidad Autónoma de Coahuila (UAC) in Torreon, Coahuila, using a HITACHI high performance FlexSEM 1000 scanning electron microscope (SEM).

We obtained the following shell morphometrics for each specimen collected (excluding ratios): total number of whorls, shell height, shell width, aperture height, and aperture width. The mean, standard deviation and sample size are given in text (shell measurements). Shell whorls were counted according to the method of Pilsbry (1939). The studied material was deposited in the Malacological Collection of the Faculty of Biological Science of the Juarez State University of Durango.

Abbreviations used for shell morphometrics are as follows: WN, total number of whorls; SH, shell height; SW, shell width; AH, aperture height; AW, aperture width; HBW, height of body whorl; UJMC = University Juárez Malacological Collection.

Systematics

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Superfamily Truncatelloidea Gray, 1840
Family Cochliopidae Tryon, 1866

***Phreatoviesca* Czaja & Gladstone, gen. nov.**
http://zoobank.org/517E4E3B-915D-4056-A65C-312806C6DB02

Type species. *Phreatoviesca spinosa* by present designation.

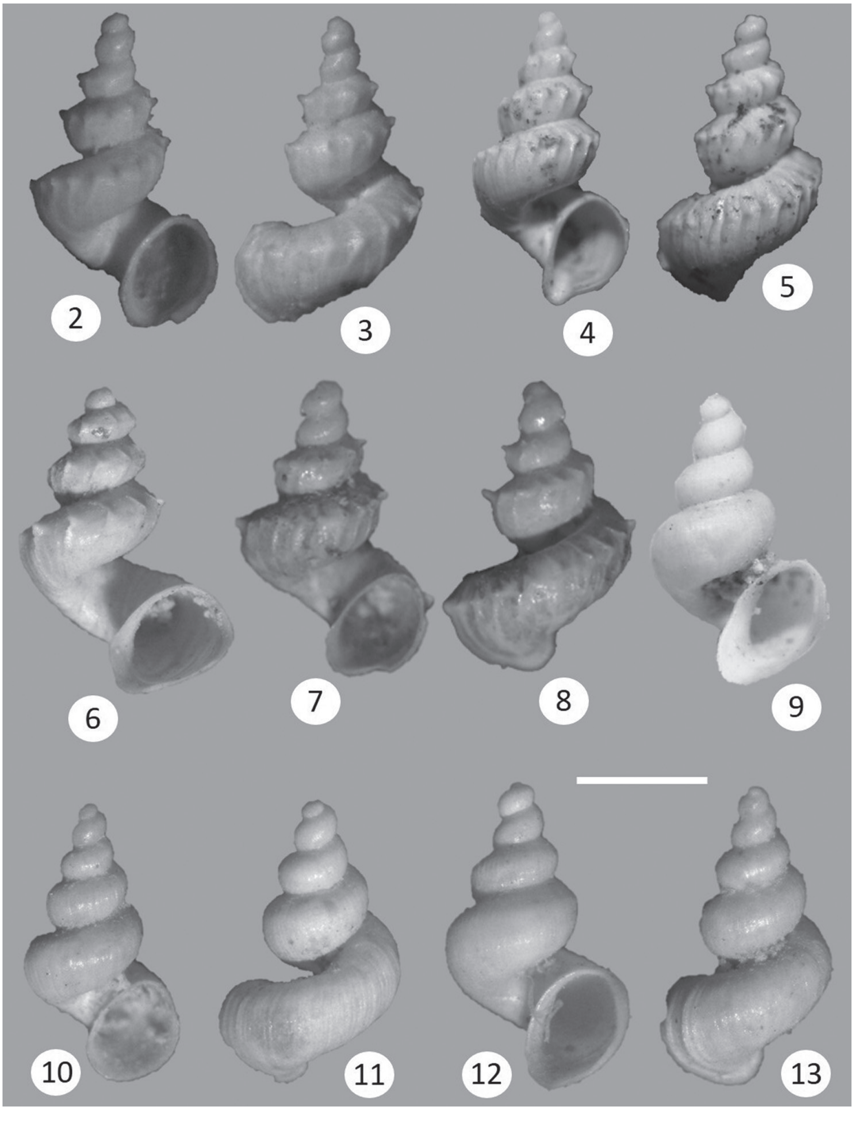
Diagnosis. Shell small, conical in form, protoconch sculptured with coarsely honeycomb-like pits, teleoconch with curved ribs which are at the carina modified into regularly spaced shovel-shaped spines (Figs 14, 24), body whorl always open-coiled, some specimens with a corkscrew morphology, apertures large, ovate, rarely rounded, often trumpet-like.

Differential diagnosis. The characteristic combination of three aforementioned shell features (open coiling of the last whorl, shovel-shaped spines, and protoconch with coarsely honeycomb-like pits) separate the new genus clearly from shells of all other subterranean (and epigean) genera. Some members of *Phreatodrobia* Hershler & Longley 1986 and *Paludiscala* Taylor 1966, genera which include exclusively subterranean species, also have conical shells, but these are not uncoiled (except the slightly uncoiled *Phreatodrobia nugax* (Pilsbry & Ferriss, 1906) to this extent do not possess prominent spine ornamentations.

Etymology. The name is derived from Greek *phreato* = groundwater environment, and *Viesca* (referring to the town of Viesca where the shells were found).

***Phreatoviesca spinosa* Czaja & Gladstone, sp. nov.**
http://zoobank.org/C72889DC-5B7A-4366-B703-964353942786
Figs 2–24

Type locality. Mexico, Coahuila state, Viesca, spring “Túnel 7” (25°20'38"N, 102°54'19"W, 1102 m a.s.l.) (Fig. 1).

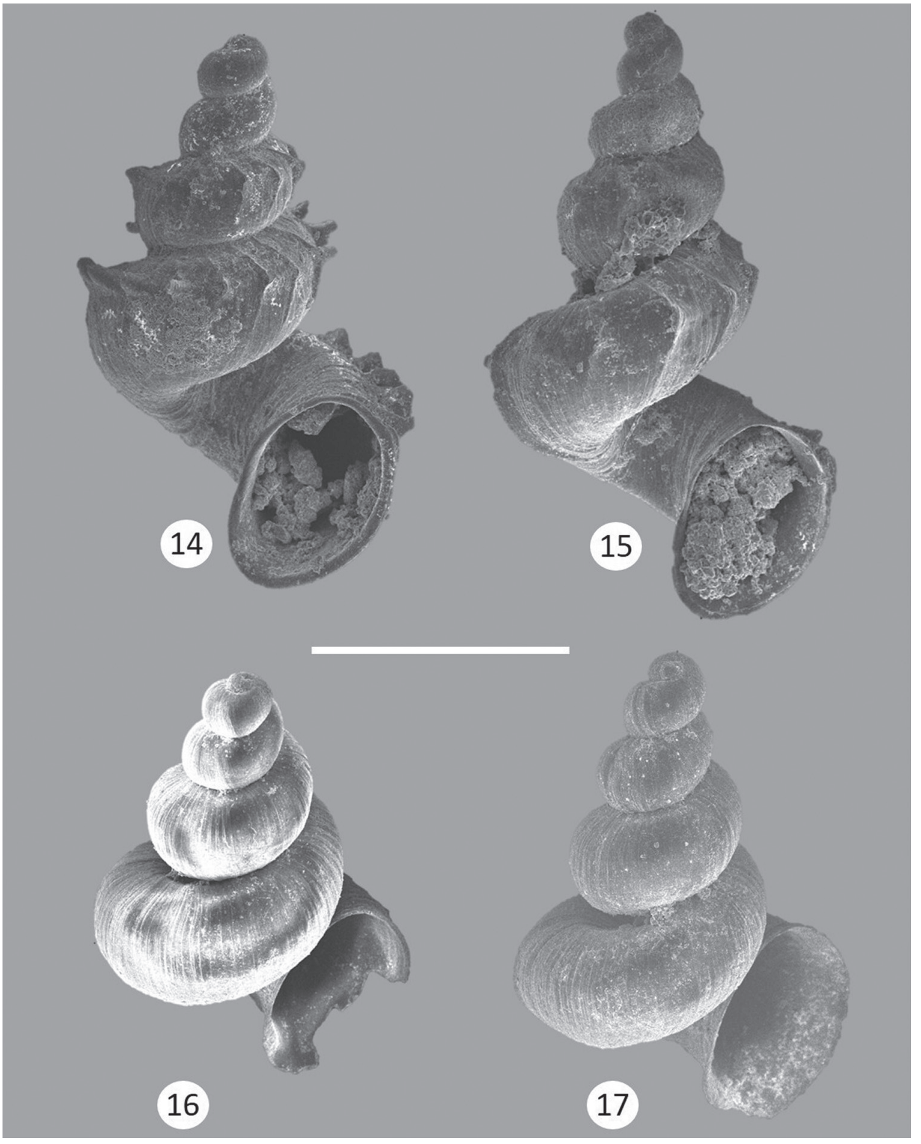


Figures 2–13. Shells of *Phreatoviesca spinosa* gen. nov. et sp. nov. **2, 3** holotype, specimen from both sides, UJMC 500 **4, 5** paratype 1, specimen from both sides, UJMC 501 **6** paratype 2, specimen with a 'corkscrew'-like morphology, UJMC 502 **7, 8** paratype 3, specimen from both sides, UJMC 503 **9** paratype 4, specimen with smooth whorls and a trumpet-like aperture, UJMC 504 **10, 11** paratype 5, specimen with smooth whorls, UJMC 505. Opercula **12, 13** paratype 5, specimen with smooth whorls, UJMC 505. Scale bar: 1 mm.

Types. Holotype (Figs 2, 3), UJMC 500, from type locality, leg. A. Czaja, 15/v/2019. Paratypes, UJMC 501-511, from same lot, >100 dry shells.

Etymology. Name is derived from the Latin word *spinosa* = having spines.

Referred material. Coahuila. Viesca, Spring "Túnel 7", UJMC 500-511, A. Czaja, J. L. Estrada-Rodríguez 10/vi/2015 and 15/v/2019.



Figures 14–17. SEM images of *Phreatoviesca spinosa* gen. nov. et sp. nov. **14** specimen with strong spines, UJMC 506 **15** specimen with ribs, UJMC 507 **16** specimen with smooth whorls, UJMC 508 **17** specimen with smooth whorls, UJMC 509. Scale bar: 1 mm.

Diagnosis. Like for the genus.

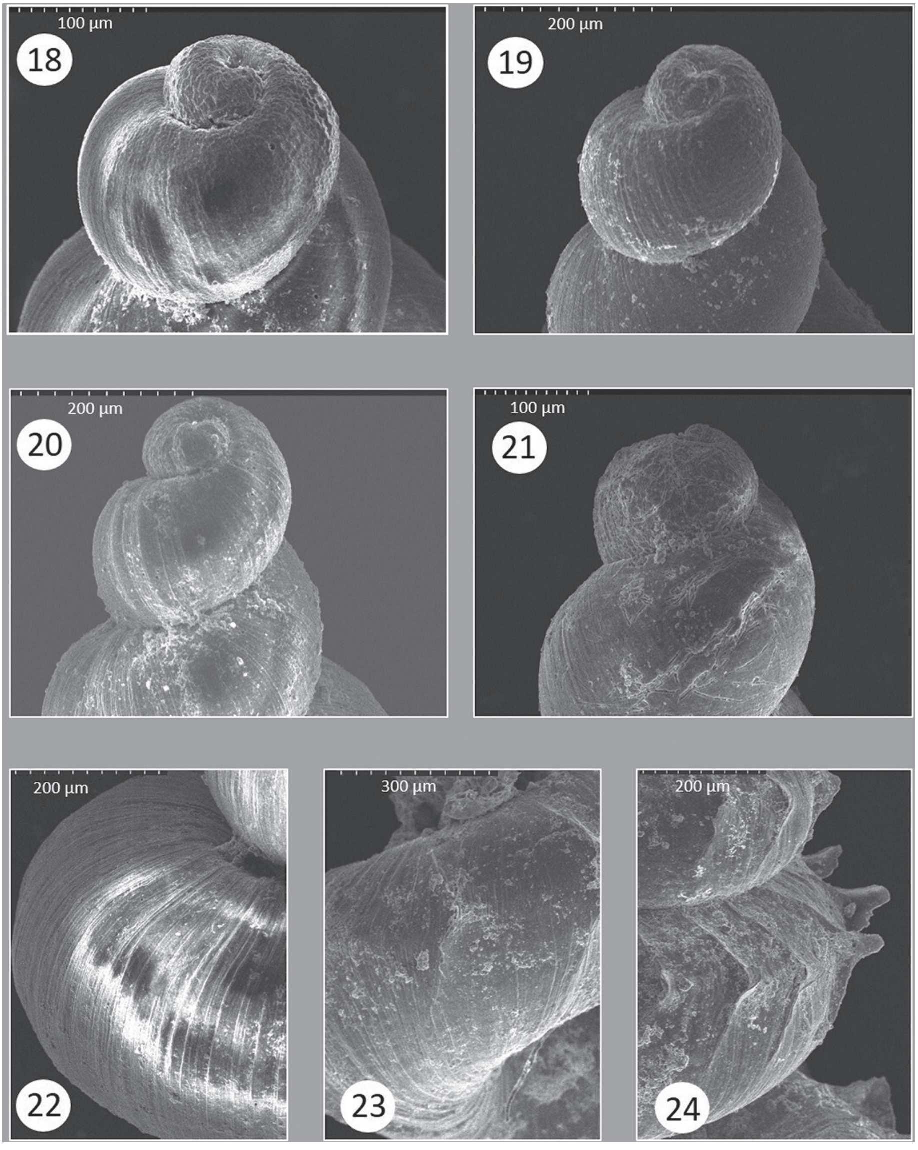
Description. Shell small, conical, white or colorless, sometime with rests of light brown periostracum, yielding diversity in shell form, with 4–5½ rounded whorls (usually 5), whorls increasing in radius, the first three whorls never uncoiled, subsequent whorls open coiled, body whorl always uncoiled, some specimens show a 'corkscrew'-like morphology (Figs 3, 6), suture deep; teleoconch sculptured with irregular, strong marked growth lines and with ribs (Figs 4, 5), spiny shells with whorls with a peripheral slightly pronounced carinae, ribs at the carina are modified into regularly spaced shovel-shaped spines (Figs 14, 24), transition protoconch/teleoconch distinct, marked by a change in surface texture from pitted to axial growth lines, whorls rapidly increasing in diameter, first two whorls smooth, without carina or spines, the last three whorls with increasing number spines (up to 40 on the body whorl, but usually less than 30), spiral lines beginning at the end of protoconch, a few specimens with smooth whorls without any sculpture but with thickened axial growth lines, some (smooth) specimens with a varix just behind the aperture (Fig. 13), body whorl large, apertures large, ovate to subrounded, often trumpet-like (Fig. 9). Protoconch with coarsely honeycomb-like pits, the basal and outer lip rounded and thin, some smooth specimens with trumpet-like peristome, umbiculus deep or, in corkscrew-like specimens, almost without umbiculus; Opercula not preserved. ***Shell measurements*** (mean ± standard deviation in parentheses; $n = 17$): SH 2.08 (0.31) mm, SW 1.24 (0.17) mm, AH 0.79 (0.09) mm, AW 0.61 (0.08) mm, WN 4.93 (0.44) whorls; HBW 1.23 (0.21) mm. Paratypes from the type locality.

Measurements of holotype. WN 5¼ whorls; SH 2.26 mm; SW 1.41 mm; AH 0.86 mm; AW 0.67 mm, HBW 1.46 mm.

Habitat. The new species was found exclusively in one spring near Viesca, Coahuila. The original habitat was probably the outlet of a cave, were the species likely inhabited interstitial waters.

Distribution. A microendemic species, only in spring "Túnel 7", near the town of Viesca.

Remarks. The open coiled last whorl, shovel-shaped spines and a protoconch with coarsely honeycomb-like pits are the most evident characteristics which differentiated the shells of *Phreatoviesca* gen. nov. et. sp. nov. from shells of all other described stygobiotic gastropods in North America. We considered these shell features as derived characters (apomorphy) of a new clade, most likely within the family Cochliopidae. The SEM imagines of the two different morphotypes (smooth and spinous) from Viesca show that both have identical coarsely honeycomb-like pitted protoconchs (Figs 18, 19) and also the details of the shell wall microstructure with fine growth lines are similar (Figs 22, 23). Therefore, we consider these two morphotypes as belonging to the same species. There is no significant difference in shells measurements between smooth and spiny morphotypes and therefore sexual dimorphism is unlikely. Moreover, most of the shells have strong spines and only less than 5% of the morphotypes collected are smooth. Two morphotypes (one smooth and other with lamelliform costae) not associated with sexual dimorphism, were reported also from shells of the subterranean genus *Paludiscala* Taylor, 1966, described from the neighboring Cuatro Ciénegas Basin (Hershler, 1985). Interestingly, our material is conchologically similar to members of the stygobiotic and stygophilic genus *Pyrgophorus* Ancey, 1888 in Mexico, which show similar shovel-shaped spines (Grego et al. 2019). This resemblance is surely an evolutionary convergence and result from living in subterranean habitats.



Figures 18–24. SEM images of *Phreatoviesca spinosa* gen. nov. et sp. nov. **18** shell apex with protoconch, UJMC 508 **19** paratype 3, shell apex with protoconch, UJMC 503 **20** shell apex with protoconch, UJMC 510 **21** paratype 1, apex with protoconch, UJMC 501 **22** smooth specimen with body whorl shows irregular, strong marked growth lines, UJMC 508 **23** paratype 1, body whorl shows irregular, strong marked growth lines, UJMC 501 **24** paratype 2, body whorl shows regularly spaced shovel-shaped spines, UJMC 502.

Discussion

Comparison with other North American stygobiotic gastropods

The general turriform shell shape of *Phreatoviesca spinosa* is common among other stygobiotic cochliopids that occupy hyporheic and phreatic habitats in the Edwards Aquifer (e.g., *Stygopyrgus bartonensis* Hershler & Longley, 1986; *Texapyrgus longleyi* Thompson & Hershler, 1991) or cave streams in the Appalachians (e.g., *Holsingeria unthanksensis* Hershler, 1989). Moreover, the large aperture and widely-reflected lip is also seen among hyporheic and phreatic taxa (e.g., *Phreatodrobia* species). However, the two primary structural differences not shared among any other stygobiotic gastropods in North America is the highly separated, uncoiled body whorl and the large spines on the teleoconch.

Regarding the open-coiling shell morphology, it seems as though *Phreatoviesca spinosa* is of an intermediate form compared to other open-coiling cochliopid stygobionts. In one case of minute open-coiling, Hershler and Longley describes the aperture of *Phreatodrobia nugax nugax* as "often free from [the] penultimate whorl", and several specimen photos from their study show *P. nugax nugax* with an open-coiled body whorl with accompanying lamelliform costae. However, *Phreatodrobia nugax nugax* shells can also appear trochoid to low conical and without costae (Hershler and Longley 1986). On the opposite side of the spectrum, *Phreatoceras taylori* (Hershler and Longley 1986) is completely uncoiled (trumpet-shaped). This suggests that an open-coiled shell morphology may be more common that previously understood for stygobiotic gastropods, and we may potentially discover more species with this feature through additional sampling efforts.

The prominent spine ornamentations of *Phreatoviesca spinosa* is not seen in any other North American stygobiotic gastropod species. The recently described species *Phreatodrobia spica* Perez & Alvear, 2020 is the only other stygobiotic gastropod species to have a 'spiny' teleoconch, but the spines on the shells of *Phreatodrobia spica* are considerably smaller and sporadically distributed across the shell (Alvear et al. 2020). The spine ornamentations of some *Pyrgophorus* species (e.g., *Pyrgophorus coronatus* (L. Pfeiffer, 1840)) show some similarities to *Phreatoviesca spinosa* regarding the structure and placement of spines along the whorls (Grego et al. 2019). However, there are still considerable differences of the spines among these two genera.

Open coiling

An openly coiled shell is a rather atypical character among gastropods, but occurs in both marine and continental (freshwater and terrestrial) groups across many independent lineages since the earlier Paleozoic (Rex and Boss 1976; Bandel & Frýda, 2004). Though far less prevalent compared to now extinct gastropod groups, open coiling is still seen among extant species (for a review of select extant species with open coiling, see Rex and Boss 1976). Many hypotheses have been generated regarding the adaptive significance of this open coiling, including that it is (but not limited to) a response to predator release (since the shell is structurally weaker and movement is more difficult; Vermeij 1987; Scholz and Glaubrecht 2010), high chemical stress (Nützel and Bandel 1993), sessility (Gould 1968), gerontic conditions (Yochelson 1971), or increased hybridization (Woodruff and Gould 1987). Notably, Rex and Boss (1976) also hypothesized that open coiling of shells that have spine ornamentations (such as the terrestrial species *Blaesospira echina* (Pfeiffer, 1864)) is a predator avoidance adaptation owing to the increased difficulty of any predator consuming the effectively larger, spiny shell. However, the predator release hypothesis is seemingly the most widely held throughout the literature (Vermeij and Covich 1978).

Several of these hypotheses were discussed in detail by Clements et al. (2008) when detailing the significance of the exaggerated open coiling of the terrestrial microgastropod *Opisthostoma vermiculum* (Architaenioglossa: Diplommatinidae), but none could be verified without further *in vivo* study. Liew and Schilthuizen (2014) performed *in vivo* predator-prey interaction studies for the terrestrial microgastropod genus *Plectostoma* (Diplommatinidae), and found their results suggested that open coiling may be an anti-predation adaptation that provides a less direct predation path when compared to a typical, tightly coiled gastropod (which counters predator release hypothesis).

Clearly the wide range of potential mechanisms that may drive open coiling makes narrowing down on any one a difficult task, and all of these hypotheses require much additional study (particularly *in vivo*) in order to be applied to a specific lineage. However, not all of these hypotheses seem plausible, and we believe that defining uncoiling or open coiling *a priori* as maladaptive (e.g., in response to chemical stress) should not be favored. It would be equally unfavorable to assume that it is a pathological phenomenon (Baynes et al. 2019) that occurs in few individuals within a population, or the sole product of ecophenotypic plasticity (e.g., Scholz and Glaubrecht 2010; Clewing et al. 2015). On the contrary, most of the uncoiled fossil and recent forms have been described as independent species with a robust number of collected specimens (Kase 1986; Scholz and Glaubrecht 2010; Alba et al. 2012).

Although we cannot validate any hypothesis with certainty for *Phreatoviesca spinosa*, we can confirm that open coiling seems to be a prevalent strategy among stygobiotic or stygophilic gastropods (Hershler 1985; Hershler and Longley 1986; Falniowski et al. 2021). Through additional sampling of the Viesca springs, we were able to successfully uncover a new openly coiled species, and we hope that these findings encourage additional sampling.

Conclusion

Phreatoviesca spinosa gen. nov. et sp. nov. is a new phreatic snail with remarkable shell characteristics such as prominent open coiling of the last whorl, shovel-shaped spine ornamentations on the teleoconch, and a coarsely honeycomb-like pitted protoconch structure. These morphological features are strikingly different compared to all known recent and fossil stygobiotic gastropods from North America. This newly described subterranean snail from Coahuila demonstrates that there continues to be great potential for discovering more stygobiont gastropods in these large unexplored karst regions in northern Mexico.

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