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A new freshwater snail genus and species (Gastropoda: Caenogastropoda, Cochliopidae) with extremely spinous shells from sub-recent spring deposits in northeastern Mexico

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Abstract

A new monotypic genus of freshwater snail from late Holocene spring deposits in Viesca, Coahuila (Mexico), is described based on shell morphology. *Spinopyrgus luismaedai* **n. gen. et n. sp.** has two to three carinate shells with long and wide shovel-shaped spines, strong axial ridges and a pointed protoconch. All sculptural ornamentations on the teleoconch are part of the calcareous shell material and not projections of the periostracum. This combination of shell features and their almost "marine-like" appearance is unknown among North American recent and fossil freshwater snails. Because of its shell characteristics, we placed the new genus tentatively in the Cochliopidae. The springs of Viesca dried up in the second half of the 20th century so that any living occurrence of this species in neighboring areas is unlikely, rendering the new genus and species possibly extinct.

Key words: Gastropods, taxonomy, spring snails, Holocene, Mexico, Chihuahuan Desert

Introduction

The Chihuahuan Desert of northern Mexico is a hotspot of freshwater gastropod endemism and species richness (Hershler *et al*. 2011; Czaja *et al*. 2020). Both the fossil and recent molluscan faunas containing several new species and new genera of several of these sites were extensively described by our working group in the past years (Czaja *et al*. 2014a, 2014b, 2015, 2017, 2019, 2021, 2022; Czaja & Estrada-Rodríguez 2015). The family Cochliopidae is extraordinary diverse in the desert springs of Coahuila, México. One of the most famous sites in the region is the Cuatro Ciénegas Valley, from where several endemic species with ornamented shells were reported (Taylor 1966; Hershler 1985).

Sub-fossil gastropods are particularly diverse in sedimentary deposits near the town Viesca, Coahuila (Fig. 1), where more than 25 species of late Holocene freshwater gastropods (belonging mostly to Cochliopidae and Hydrobiidae) have been collected in recently dried up springs (personal observations of the first author). Although isolated desert springs are notable for high levels of speciation and endemism (Taylor 1966; Boss 1978; Hershler 1985; Hershler *et al*. 2011), this extremely high local diversity of freshwater gastropods has not been previously reported, either in extant or in fossil spring habitats of North America.

Historically, the springs consisted of 15 shallow pools that were up to 5 m deep and 30 to 80 m in diameter. The

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sediments consist of travertine, shells, shell fragments, plant debris, and clay. Remains of aquatic vegetation contain oogonia of *Chara*, seeds of *Nymphaea* and endocarps of sedges (*Cladium jamaicense* Crantz, *Schoenoplectus* sp.) (personal observations). Microbialites were observed in the Juan Guerra and El Molino springs (Fig. 1). The composition of these concretions is similar to those found in other nearby springs of Sobaco and Cuatro Ciénegas valleys (Winsborough 2000; Dinger *et al*. 2006; Czaja *et al*. 2014a).

The aim of the present paper is to describe a new freshwater gastropod genus and species from the Viesca deposits. We compare its unique aspects of shell morphology with shells of other spiny recent and fossil species from North and South America and discuss its family classification.

Materials and methods

Specimens of the new species were collected from present-day superficial sediments of three recently desiccated springs near the town of Viesca, Coahuila, Mexico (Juan Guerra spring: 25° 19' 17''N, 102° 49' 08''W; El Molino spring: 25°19'55''N, 102°55'49''W; Hacienda de Hornos y Carranza spring: 25° 20' 05''N, 102° 57' 39''W, Fig. 1). The springs are located at the foot of the Sierra la Cadena and were still active until 1959 (Blásquez 1959; Wolfe 2013). The late Holocene age of the superficial deposits is also confirmed by several reports and photographs that document the desiccation of the springs during the drought of 1958/59, while the area around the springs remained a partial wetland until the late 1990s (Czaja *et al*. 2015, 2019).

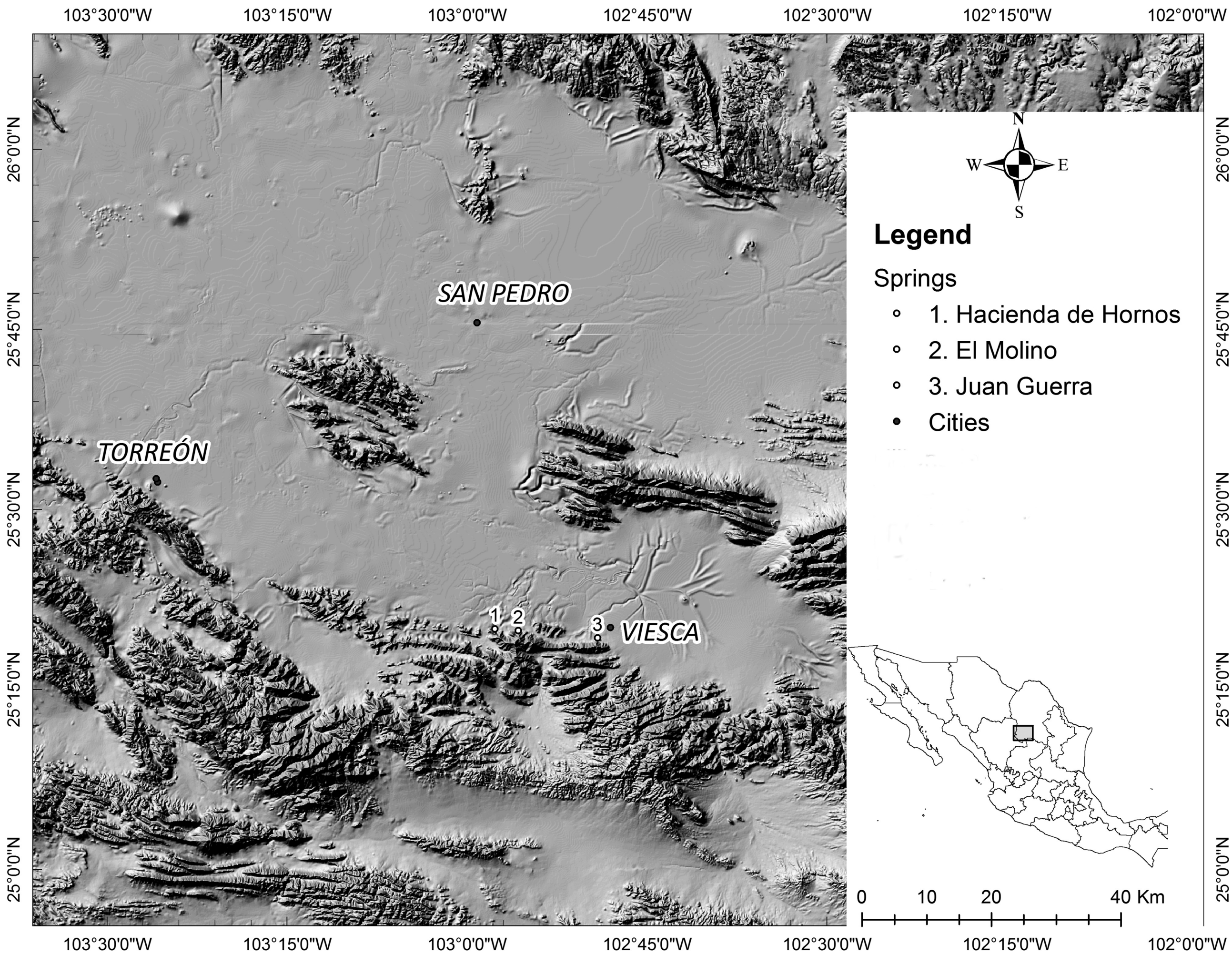

FIGURE 1. Study area showing the locations of the Viesca springs. The scale bar refers to the map with the springs marked. The topography is illustrated using HillShade in ArcGIS.

Sediments were screened through 0.5 mm and 0.3 mm sieves to collect the sub-fossil shells. Some specimens (especially their apertures) were cleaned of sediments using hydrogen peroxide. Shells were photographed and measured with a Zeiss AxioCamERc5s camera attached to a Zeiss Stemi 2000-C microscope. Some specimens, especially their teleoconch details and the protoconchs, were examined in the Centro de Investigaciones Biológicas del Noroeste S.C. (CIBNOR) in Baja California, Mexico using a Hitachi S-300N scanning electron microscope (SEM). Shell whorls were counted according to the method of Pilsbry (1939). 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; AH/SH ratio of aperture height to height of the shell. The shell collections are maintained at the malacological collection of the Faculty of Biological Science of the Juarez State University of Durango (UJMC=University Juarez Malacological Collection).

Results

Systematics

The higher classification follows Bouchet *et al*. (2017).

Class Gastropoda Cuvier, 1795

Subclass Caenogastropoda Cox, 1960

Superfamily Truncatelloidea Gray, 1840

Family Cochliopidae Troschel, 1857

Genus *Spinopyrgus* Czaja, Covich, Neubauer & Estrada-Rodríguez gen. nov.
ZooBank registration number: urn:lsid:zoobank.org:act:14D420DC-E8E7-4E6B-8E34-A6A31BEC9FB8

Type species. *Spinopyrgus luismaedai* **sp. nov.**, by present designation.

Diagnosis. See diagnosis of the type species (monotypic).

Etymology. The generic name is derived from the combination of two words from Latin and Greek language: *spino*, referring to the strong spines, and *pyrgus*, related to the tower-like shape.

***Spinopyrgus luismaedai* Czaja, Covich, Neubauer & Estrada-Rodríguez n. gen. et n. sp.**
(Figures 2A to 3P)
ZooBank registration number: urn:lsid:zoobank.org:act:385187F6-986B-4200-84D1-91147F22F4D1

Etymology. The new species is named in honor of Dr. Luis Maeda Villalobos, Torreón, Coahuila, who was the first collector of fossil snails at Viesca.

Holotype. Specimen UJMC-250 (Fig. 2A, B).

Type locality. Superficial sediments in the desiccated Juan Guerra spring, ca. 1 km south of Viesca, Coahuila, Mexico. Collected by Alexander Czaja and José Luis Estrada-Rodríguez, 2014 (Figure 1).

Type material. Holotype (Fig. 2A, B), UJMC-250 from Juan Guerra spring, Viesca, 25° 19’ 17’’N, 102° 49’ 08’’W, paratypes (Figs. 2C–F), UJMC 251, UJMC 252, UJMC 252a. Paratypes 1, 2 and 3 from the same lot as the holotype.

Type horizon. Holocene (sub-fossil).

Studied material. 154 specimens from the type locality (UJMC 250-252b, 254), 45 specimens from El Molino spring (UJMC 253-253c) and 50 specimens from Hacienda de Hornos y Carranza spring (UJMC 257-257c).

Occurrence. Endemic to Juan Guerra, Hacienda de Hornos y Carranza and El Molino springs near Viesca, Coahuila, Mexico.

Diagnosis. Shell medium-sized, usually light brown or (when blanched) white, narrow-conic, variably umbilicate to imperforate. Aperture round polygonal, inner lip adnate. Teleoconch whorls having one to three distinct keels sculptured with broad, strong, conical spines.

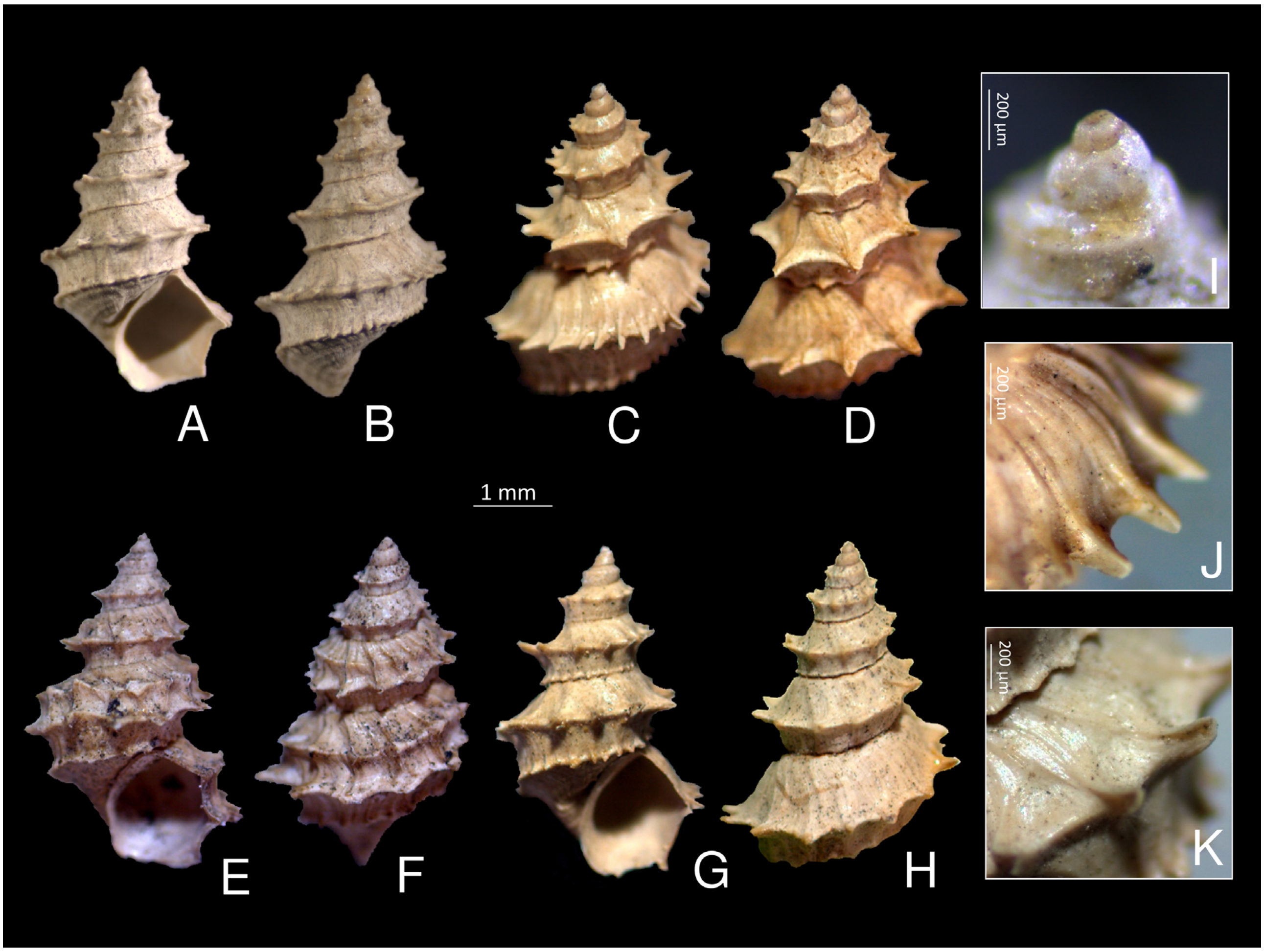

FIGURE 2. *Spinopyrgus luismaedai* **n. gen.** et **n. sp.** (**A–K**). **A–B.** Holotype (UJMC-250) from Juan Guerra spring. **C.** Paratype 1 (UJMC-251) from Juan Guerra spring. **D.** Paratype 2 (UJMC-252) from Juan Guerra spring. **E, F.** Paratype 3 (UJMC-252a) from Juan Guerra spring, specimen with three keels. **G**. Specimen (UJMC-253) from El Molino spring. **H.** Specimen (UJMC-254) from Juan Guerra spring. **I.** Specimen (UJMC-253) from El Molino spring, protoconch view. **J.** Paratype 3 (UJMC-251), details of the carina with spines. **K.** Specimen (UJMC-253b) from El Molino spring, details of the carina with shovel-shaped spines.

Description. Shell medium-sized, thickened, imperforate, and conical, up to 7.25 whorls, the holotype has 6.25 whorls, first two rounded. The apex is acute and inclined, protoconch consisting of about one whorl, smooth or slightly wrinkled, measuring 160–180 µm in diameter. A shoulder frequently develops on early teleoconch whorls. The slightly corrugate nucleus is narrow and immersed and has 40–50 µm in diameter. Protoconch-teleoconch boundary is clearly discernable, characterized by the onset of fine, axial growth lines, which are prosocline on first whorls and later become almost orthocline. Teleoconch whorls have fine or often more pronounced irregular axial ribs (Fig. 2J, 3O), as well as two to three spiral carinae. Because of the strong carinae the whorls appear more angular than rounded (Fig. 2A–H, 3L). Along the central carina, many axial ribs extend into strong spines on the periphery. The spines are regularly spaced and always in the middle part of the whorl. The last three or four whorls are geniculate, angled at location of carina. Body whorl large, almost always having a second carina with spines on the lower side, sometimes with a third carina (Fig. 2E, F). Whorls mostly with very pointed, shovel-shaped spines, with up to 30 spines on the body whorls, spines very pointed. The spines like all other shell ornamentations are part of the calcareous shell material. Suture slightly impressed. Many shells conserve still their thin light-brown periostracal layer (Figs. 2C–J). Aperture polygonal, mostly pentagonal in shape (Figs. 2A, E, G), slightly longer than wide. Parietal lip adnate, the basal and outer lip rounded and thin. Opercula were not preserved.

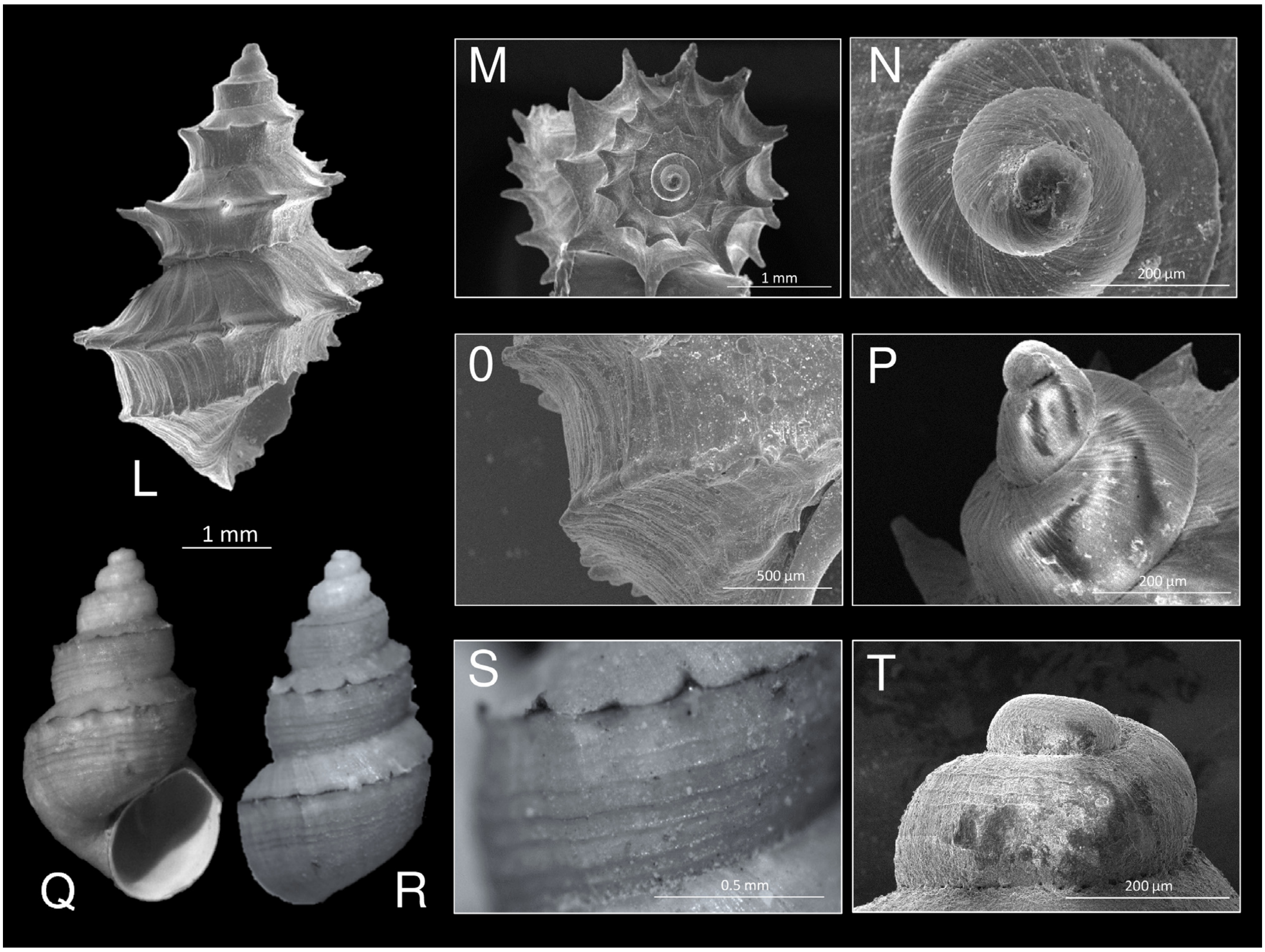

FIGURE 3. SEM images of *Spinopyrgus luismaedai* **n. gen.** et **n. sp.** (**L–P**). **L.** Specimen (UJMC-255) from El Molino spring with strong spines. **M.** Specimen (UJMC-255) apical view. **N**. Specimen (UJMC-256), protoconch. **O.** Specimen (UJMC-255), details of the strong axial elements of the body whorl. **P.** Specimen (UJMC-256) from Juan Guerra spring, protoconch. **Q-T.** *Pyrgophorus parvulus* (Guilding) from Río Sabinas, Coahuila, Mexico (from Czaja *et al*. 2022, Fig. 5A). **Q, R.** Specimen (UJMC 460a) from Río Sabinas from both sides. **S.** Same specimen with details of the spiral elements of the body whorl. **T.** Same specimen (UJMC 460a), protoconch.

Shell measurements (mean ± standard deviation in parentheses; n = 20). SH 4.64 (0.46) mm, SW 2.19 (0.31) mm, WN 6.05 (0.49) whorls (shells from Juan Guerra spring).

Measurements of Holotype. SH 4.91 mm, SW 2.72 mm, AH 1.89 mm, AW 1.83 mm, AH/SH 0.39, WN 6.25 whorls.

Remarks. The prominent spine ornamentations of *S. luismaedai* with extremely long and almost "marine-like" spines are not seen in any other North American gastropod species. All spines are built completely of shell material and are not made of a combination of shell material and periostracal projections, like in some other spiny *Pyrgophorus* Ancey (Cochliopidae) or *Potamopyrgus* Stimpson (Tateidae) species. The variability of the shell ornamentations is remarkable especially regarding the number and form of the spines (Fig. 2C–K). Most of the shells are turriform with 5–7 elongated whorls (Fig. 2A–H), but there are also in all springs a sub-population with a more rounded general form and less than 5 whorls. This variability could be an indication of different ecophenotypes within the *S. luismaedai* populations.

Discussion

Comparison of *Spinopyrgus luismaedai* n. gen. et n. sp. with other spiny species. Unlike marine snails, only relatively few freshwater gastropods develop strong spines on their teleoconch (Covich 2010, Davis *et al*. 2020). Some of them, like *Phreatodrobia spica* Perez & Alvear, 2020 from central Texas, and *Phreatoviesca spinosa* Czaja & Gladstone, 2021 from Viesca, Coahuila, indeed have spines, but as members of subterranean genera their shells are morphologically completely different and much smaller in shell height (< 2 mm). Of the living epigean freshwater snails, *Io fluvialis* (Say) (Pleuroceridae) possess shells with strong spines (Adams, 1915), but this species is not comparable with our material because of its general form, large size (3–5 cm, *Spinopyrgus*: 4–6 mm) and long, prolonged aperture.

Of the extinct species, only *Mexipyrgus viescaensis* Czaja, Estrada-Rodríguez & Romero-Méndez (Cochliopidae) from the late Holocene of Viesca, Coahuila shows spiny shells. However, its shells differ from those of *Spinopyrgus* by having knobbed and wave-like axial ribs, spiral subsutural cords and an elongate aperture (Czaja *et al*. 2015).

More than 30 nominal species of the genus *Pyrgophorus* were described from North, Central and South America based on shell-morphology. Hershler & Thompson (1992) considered it likely that all belong to one polymorphic and widely distributed species. We agreed and previously we found (at least morphologically) no significant differences comparing shells of some *Pyrgophorus* populations from north and south Mexico (Czaja *et al*. 2022). The oldest name for such smooth to spinose shells is *Pyrgophorus parvulus* (Guilding, 1828). The only living species which differs from *P. parvulus* in shell morphology is *P. cenoticus* Grego, Angyal & Beltrán, 2019, a stygobiont snail endemic to the Cenote Xoch in Yucatán, Mexico (Grego *et al*. 2019).

Our material from Viesca shares most of the morphological shell characters with those of recent and fossil members of the genus *Pyrgophorus*. In comparing the possible similarities between shells of *S. luismaedai* **n. gen.** et **n. sp.** and the living *Pyrgophorus* species in detail, we found no less than ten morphological shell differences which are listed in Table 1.

TABLE 1. Morphological shell differences between *Pyrgophorus* and *Spinopyrgus* **n. gen.** Data of *Pyrgophorus* spp. shell morphology derived from Harrison (1984), Hershler & Thompson (1992), Wesselingh (2006), Nava Ferrer & Severyn Valbuena (2011), Grego, Angyal & Beltrán, (2019), Coote *et al*. (2021) and own observations.

Shell Character	***Spinopyrgus***	***Pyrgophorus***
Apex	pointed	blunt
Nucleus	narrow (35-50µm)	broad (80-100µm)
Carinae/last body whorl	2-3	1
Aperture	roundly (pentagonal)	oval
Spines	strong (always present)	weak (sometimes present)
Spines position on the whorls	centrally	upper third
Shovel-shaped spine	yes	no
Tips of the spines	calcareous	periostracal
Smooth forms	no	yes (mostly smooth)
Axial elements (ridges)	yes (strong, irregular)	no

While the whorls of *Pyrgophorus* species show only spiral elements such as lines, ridges and cords (Fig. 3Q–S; Grego *et al*. 2019, Figs. 11–19; Wesselingh 2006, p. 126, Fig. 157a–c), *Spinopyrgus* have almost exclusively axial elements (except the keels), which are often strong and irregularly developed (Fig. 2J, K, Fig. 3L, O). In addition, *Pyrgophorus* has a blunt apex with a flat and broad protoconch and spiral elements such as lirae or strong cords (Fig. 3S; Grego *et al*. 2019, Figs. 17–19; Wesselingh 2006, p. 123), whereas *Spinopyrgus* has an acuminate apex and a thin protoconch (Fig. 3N, P).

The position of the carinae (keels) on the whorls is another criterion for differentiation. The single carina with the spine-wreath is in *Pyrgophorus* always on the shoulder in the upper third of the respective whorl, while in shells from Viesca it is located in all specimens in the center of the whorls (Figs. 2A–H, 3L). Unlike *Pyrgophorus*, shells of *Spinopyrgus* **n. gen.** et **n. sp.** have always two, sometimes even three keels (Fig. 2E, F). Another difference is the strikingly dimorphic shells of *Pyrgophorus* species, which usually occur in two clearly different morphotypes with smooth or spiny shells (Hershler & Thompson 1992; Nava Ferrer & Severyn Valbuena 2011; Grego *et al*. 2019; Wesselingh 2006; Coote *et al*. 2021; own observations). The vast majority of living and fossil *Pyrgophorus* populations have smooth shells, the spinous forms are usually rare, not exceeding 30% (Harrison 1984; Wesselingh 2006; Nava Ferrer & Severyn Valbuena 2011; Grego *et al*. 2019; Coote *et al*. 2021; own observations). In contrast, all shells of *Spinopyrgus* occurring in all three sites have strong spinous shells without any smooth variants. However, whether this is possible sexual dimorphism, cannot be determined from empty shells. Finally, the spines themselves are different in structure. Spines formed by *Pyrgophorus* are calcareous, mostly short, triangular and always with a dark periostracal layer on the top of their hollow, often blunt spines (Harrison 1984). The spines of *Spinopyrgus* **n. gen.**, on the other hand, are strong, extended in length (more than 300 µm), shovel-shaped and are composed entirely of calcareous shell material with generally acute tips (Fig. 2I–K).

Family affiliation of the new genus. Because of its shell characteristics and general similarity to *Pyrgophorus*, we placed the new genus tentatively in the Cochliopidae. Especially the protoconch structure is indicative of Cochliopidae, many of which have an inclined, often tilted protoconch and a narrow nucleus (Wesselingh 2006). Also, the morphological variability and ornamentational variability is particularly high in cochliopids such as *Phreatoviesca* Czaja & Gladstone, *Mexipyrgus* Taylor, *Tryonia* Stimpson, *Dyris* Conrad (Wesselingh 2006; Hershler 1985; Czaja *et al*. 2021) and *Pyrgophorus* as discussed in detail above. However, the assignment to Cochliopidae is tentative, since the new species exhibits similarities with species of other families as well. This concerns particularly the Hydrobiidae, where sculptured shells also occur (Radoman 1983; Hershler & Thompson 1987; Czaja *et al*. 2017). However, the classification of extant hydrobioid snails (both Cochliopidae and Hydrobiidae) is mostly based on soft-part anatomy (Hershler & Thompson 1992) and molecular data (Wilke *et al*. 2013; Delicado *et al*. 2019), which has thrown into question the taxonomic utility of shell characters for particular groups (Boulaassafer *et al*. 2018; Delicado *et al*. 2019). Therefore, the proposed familial placement of the new genus must be interpreted with caution.

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