

Description of the first anchialine gastropod from a Yucatán cenote, *Teinostoma brankovitsi* n. sp. (Caenogastropoda: Tornidae), including an emended generic diagnosis

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ABSTRACT

A new species of *Teinostoma* (Tornidae) is described from an under-investigated section of the anchialine cave system Cenote Crustacea, situated on the northeastern coast of the Yucatán Peninsula. *Teinostoma brankovitsi* n. sp. is the first anchialine gastropod reported from the Yucatán Peninsula and the first record of the family from an anchialine cave. Specimens were found in chalky sediments riddled with orange bacterial patches, c. 450 m from the inland entrance pool, in complete darkness. *Teinostoma brankovitsi* has a circular, multispiral operculum with a central nucleus and does not have tentacles on the foot or opercular lobe. Specimens possess a taenioglossate radula with a central tooth broadly V-shaped and a serrated cutting area with two basal denticles. The diagnosis of *Teinostoma* is emended based on these new findings.

INTRODUCTION

The Yucatán Peninsula is an immense and geologically stable platform comprised of Mesozoic limestone (Gabriel *et al.*, 2009), which projects from the southeastern coast of Mexico and separates the Gulf of Mexico from the Caribbean Sea. Numerous epigeal and subterranean aquatic systems are present throughout this large karstic network (Mercado-Salas *et al.*, 2013), which also harbours the highest density of anchialine caves in the world. Anchialine caves occur worldwide, but are especially numerous in the Caribbean and Mediterranean basins (Stock, Iliffe & Williams, 1986). In the Yucatán Peninsula these caves usually open at the surface as large circular pools, locally known as cenotes, which extend into maze-like networks throughout the vast subterranean realm of the region. Holthuis (1973) coined the term ‘anchialine’ for tidally influenced brackish or marine pools that lack a surface connection to the surrounding marine water and harbour unusual faunal assemblages.

Crustaceans dominate the fauna of anchialine cenotes on the Yucatán Peninsula, with more than 45 stygobitic crustacean species recognized (Alvarez *et al.*, 2015). To date, few investigations have documented macrofaunal noncrustacean lineages in these habitats (Gonzalez *et al.*, 2012) and even fewer have focused on the microscopic biota of the water column and sediments (Gabriel *et al.*, 2009). In other anchialine environments the endemic crustacean diversity also exceeds that of any other animal group. However, recent sampling has revealed a previously unrecognized diversity of endemic annelids and molluscs

in anchialine caves of the Canary Islands (Martínez *et al.*, 2009; Núñez, Martínez & Brito, 2009; Wilkens *et al.*, 2009; Worsaae, Martínez & Núñez, 2009; Martínez, Di Domenico & Worsaae, 2013; Schmidt-Rhaesa, Rothe & Martínez, 2013), the Bahamas (Palmer, 1985; Gonzalez *et al.*, 2015), Bermuda (Moolenbeek, Faber & Iliffe, 1988; Worsaae, Sterrer & Iliffe, 2004) and the Mediterranean (Iliffe & Bishop, 2007; Curini-Galletti *et al.*, 2012).

The subterranean diversity of molluscs is quite high, with over 600 gastropods currently recognized, primarily within Hydrobiidae *s. l.* (Strong *et al.*, 2008). However, there are few records of molluscs from the marine waters of anchialine caves (Moolenbeek *et al.*, 1988; Kano & Kase, 2008; Espinosa & Ortea, 2009). Neritiliidae is the most diverse gastropod family found in marine and anchialine caves, and includes a remarkable radiation in the Indo-Pacific and several species in the Caribbean and north-west Africa (Kano & Kase, 2004, 2008; Pérez-Dionis, Espinosa & Ortea, 2011). Moolenbeek *et al.* (1988) described two species of *Caecum* from anchialine caves on Bermuda based on shells. Similarly, the Globocornidae, a new family in the Neritopsoidae, was erected for a few, mostly damaged, shell specimens from anchialine caves of the Pinar del Río and Ciénaga de Zapata regions of Cuba (Espinosa & Ortea, 2009). Alvarez *et al.* (2015) mentioned an undescribed gastropod from an anchialine cave in Yucatán, but gave no details of this discovery. This record may refer to material from Cenote Aerolito, Isla Cozumel, which opens directly into the Caribbean Sea and contains marine fauna

in several portions of its passageways (Frontana-Uribe & Solis-Weiss, 2011; Bribiesca-Contreras *et al.*, 2013). Subterranean gastropods often have troglomorphic features similar to those of crustaceans and annelids, including depigmentation, reduction or absence of eyes and other anatomical structures, and a thin subhyaline shell (Graening & Brown, 2003; Romero, 2011).

The Tornidae are a diverse family of microscopic gastropods having depressed rounded shells that range widely from the Arctic to Southern Atlantic Ocean, with the greatest diversity of taxa in the Caribbean. The tornids were early classified within the superfamily Rissooidea based on limited shell and morphological characters (Ponder, 1988). More recently the family was transferred to the Truncatelloidea based on molecular phylogenetic evidence (Criscione & Ponder, 2013). Tornid monophyly is supported only by a combination of shell characters. Only seven species in the family have been studied in anatomical detail: *Circulus striatus* Jeffreys, 1865, *C. texanus* Moore, 1965 and *C. mortoni* Ponder, 1994; *Cochliolepis parasitica* Stimpson, 1858; *Tornus subcarinatus* Montagu, 1803; *Cyclostremiscus beaui* (Fischer, 1857) and *Sigaretornus plana* Adams, 1850 (Fretter, 1956; Moore, 1972; Graham, 1982; Bieler & Mikkelsen, 1988; Ponder, 1994). This is unfortunate since shell morphology is highly convergent among microscopic Caenogastropoda (e.g. Hershler & Ponder, 1998).

Teinostoma is a diverse tornid genus containing about 72 described species, most of which are distributed in the tropics. In their revision of the tornids of the Caribbean basin, Rubio, Fernández-Garcés & Rolán (2011) recognized 27 species belonging to *Teinostoma*. In addition to describing eight new species, Rubio *et al.* (2011) provided the first description of the *Teinostoma* radula (from *T. parvicallum* Pilsbry & McGinty, 1945 and *T. expansum* Rubio *et al.*, 2011). The only published anatomical data for *Teinostoma* consists of schematic drawings of living specimens of *T. lerema* Pilsbry & McGinty, 1945, *T. parvicallum* and *T. carinicalus* Pilsbry & McGinty, 1946, which show the morphology of the foot and the number and arrangement of the cephalic and pallial tentacles (Pilsbry & McGinty, 1945).

Herein we report the discovery of a new species of *Teinostoma* from an anchialine cave along the Caribbean coast of the Yucatán Peninsula that was collected during two cave diving expeditions. This paper provides new data on the diversity of anchialine molluscs in these poorly known but highly specialized anchialine habitats and on the morphology (including operculum and radula), behaviour and ecology of this diverse but poorly known genus.

MATERIAL AND METHODS

This new species was collected during scientific cave diving expeditions in July 2013 and June 2014 from Cenote Crustacea, located south of Puerto Morelos, Quintana Roo, Mexico. Examination of sediment from an artificial substrate experiment during the first expedition yielded five specimens. Specimens obtained in June 2014 were collected in the same passageway, c. 2–4 m from the 2013 collections, using three, 1-l plastic screw-cap containers. Fourteen specimens were preserved for molecular and morphological examination.

Live animals were examined, photographed and video-recorded using a digital camera mounted on a SZX16 Olympus stereoscope. Specimens were relaxed in the field using an isotonic MgCl₂ solution and fixed in 3% trialdehyde in 0.1 M cacodylate buffer over 24 h or preserved in 100% ethanol. All samples were transported back to the University of Copenhagen, Denmark, for laboratory study.

Specimens utilized for scanning electron microscopy (SEM) were postfixed for 60 min in 1% osmium tetroxide buffered in 0.1 M cacodylate solution and rinsed in distilled water. The shell was removed by soaking in 3% hydrochloric acid

(in MgCl₂) prior to postfixation to help facilitate the study of soft-bodied external morphology and radula extraction. All specimens were dehydrated using an ethanol series (10, 25, 50, 75 and 100%), followed by an ethanol:acetone series (2:1, 1:1, 1:2) before transfer and storage in 100% acetone. Critical-point dried specimens were mounted on aluminium stubs and sputter-coated with platinum/palladium using a high-resolution fine coater (JFC-2300HR) and examined using a JEOL JSM-6335F field emission SEM at the Natural History Museum of Denmark. Imaging of the radula, operculum and shell was conducted at the University of Vigo, using a Quanta 200 SEM. Measurements were taken from scaled SEM or LM pictures using ImageJ (Schneider, Rasband & Eliceiri, 2012).

SYSTEMATIC DESCRIPTION

Family TORNIDAE Sacco, 1896 Subfamily TEINOSTOMATINAE Cossmann, 1917 Genus *Teinostoma* Adams & Adams, 1853

Teinostoma Adams & Adams, 1853: 122.

Type species: *Teinostoma politum* Adams & Adams, 1853 (by monotypy).

Diagnosis: Shell minute, depressed, thin, glossy. Protoconch of about 1.3 convex whorls, sometimes covered by the last whorl. Teleoconch with convex whorls, smooth or covered by spiral cords, may contain small pits. Umbilical region covered by large and smooth callus. Operculum circular, multispiral, chitinous. Radula taenioglossate; central tooth V-shaped, cutting edge serrated with 2 basal denticles; ventral process U-shaped. Lateral tooth angulated; inner third serrated, with 8 pointed elongated cusps along outer margin. Inner marginal tooth comb-like, with numerous small cusps. Outer marginal tooth narrow, with few elongated cusps.

Animal: Head with rounded snout bilobed distally. Long cephalic tentacles with motile cilia and stiff compound cilia. One pair of pallial tentacles. Ctenidium finger-shaped, protruding from pallial cavity along mantle edge. Anterior end of the foot expanded into small lateral projections. Metapodial tentacle absent.

Remarks: According to Pilsbry (1953) the species included in the genus *Teinostoma* are known from the Upper Cretaceous to Recent and very common in Tertiary deposits. Since the type species *T. politum* is only known by its shell, we have augmented the diagnosis of the genus with radular and opercular data from *T. parvicallum* and *T. expansum* (Rubio *et al.*, 2011) and anatomical data from schematic drawings of live specimens of *T. lerema*, *T. parvicallum* and *T. carinicalus* (Pilsbry & McGinty, 1945). The morphological details obtained from study of live specimens and scanning electron micrographs of *T. brankovitsi* n. sp. conform to the emended diagnosis.

Teinostoma brankovitsi n. sp. (Figs 1–4)

Type material: Holotype (ZMUC-GAS 531), complete spec. on SEM stub. Paratypes: 2 complete SEM specs (ZMUC-GAS 532–533), 2 SEM specs with shells removed (ZMUC-GAS 534–535), all deposited in Natural History Museum of Denmark (ZMUC). Two specs preserved in ethanol deposited in Colección Nacional de Moluscos, Instituto de Biología, Universidad Nacional Autónoma de México (CNMO 5709, 5710). Several complete specs in ethanol (MNCN 15.05/60155)

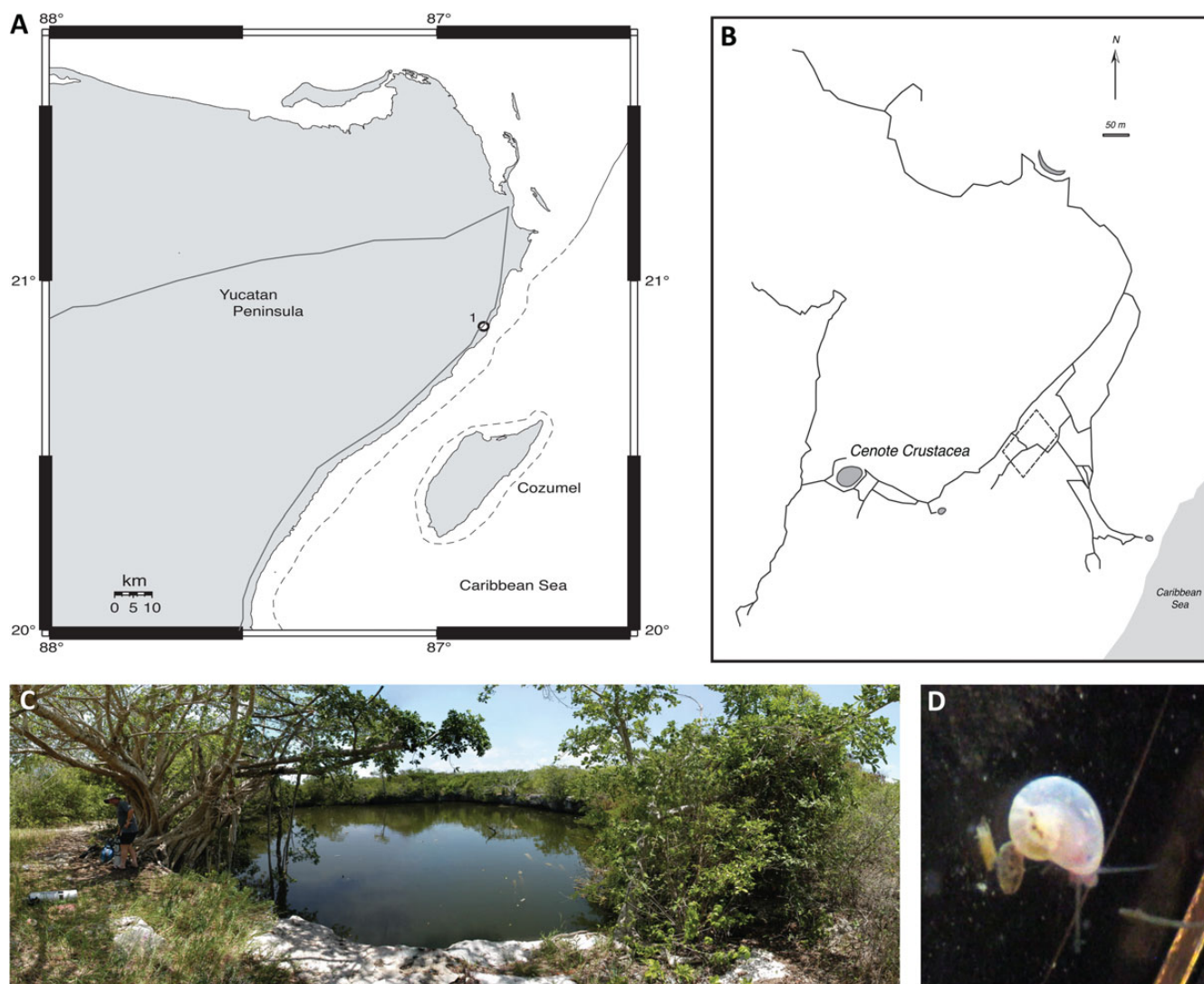


Figure 1. *Teinostoma brankovitsi* n. sp. **A.** Location (1) of Cenote Crustacea on the Caribbean Coast of the Yucatán Peninsula, Mexico. **B.** Cenote Crustacea line map; dashed box represent collection location. **C.** Surface pool of Cenote Crustacea (photo T. Thomsen). **D.** Live images of *T. brankovitsi*.

deposited in Museo Nacional de Ciencias Naturales, Madrid, Spain. Type locality (Fig. 1A–C): Cenote Crustacea, a submerged cave south of Puerto Morelos, Quintana Roo, Mexico (20°46'N, 86°56'W); substrate of chalky fine-grained silt with orange bacterial patches, c. 450 m from entrance pool, northeast direction, 17–20 m depth, below halocline.

ZooBank registration: urn:lsid:zoobank.org:act:D2B51EE3-79EA-447D-8717-8579990DD29F

Etymology: Named after our research colleague Dávid Brankovits, who assisted with fieldwork and specimen collection.

Description (Figs 1D, 2A–G): Shell minute, width 1.49 mm, height 0.85 mm (holotype), depressed, planispiral, dorsally and peripherally convex, slightly concave basally; umbilicus covered by thick callus; translucent. Protoconch, spire and sutures covered by body whorl. Teleoconch c. 1.5 whorls. Sculpture of >45 fine spiral cords, present on entire teleoconch; individual cords slightly wider than spaces separating them, more defined than growth lines. Aperture rounded, prosocline; external lip

smooth, simple. Parietal area covered by thick callus covering umbilicus; columella arched and reflected towards umbilicus.

External morphology (Figs 1D, 3C–F, 4A–F): Head bearing elongate, extendable snout, rounded and bilobed distally; mouth vertical, slit-shaped; cephalic tentacles long, finely ciliated, with short motile cilia and numerous stiff compound cilia along distal end. Eyes absent. One pair of pallial tentacles arising from edge of mantle at rear corner of aperture; anterior tentacle rounded, shovel-shaped, dorsally and ventrally flattened; margin profusely covered by cilia arranged in bands. Posterior pallial tentacles rounded in section; conical, distal margin with fine cilia and compound cilia. Ctenidium finger-shaped, protruding from pallial cavity along mantle edge; comprising 5 conical units, deep longitudinal grooves between right cephalic and pallial tentacles, each covered by dense tufts of long cilia. Foot wide, posterior margin bilobed. Sole ciliated. Opercular lobe simple, extending just past margin of sole. Propodium densely ciliated on outer margin. No tentacles associated with foot or opercular lobe. Metapodial tentacle absent. Operculum circular, chitinous, multispiral, with central

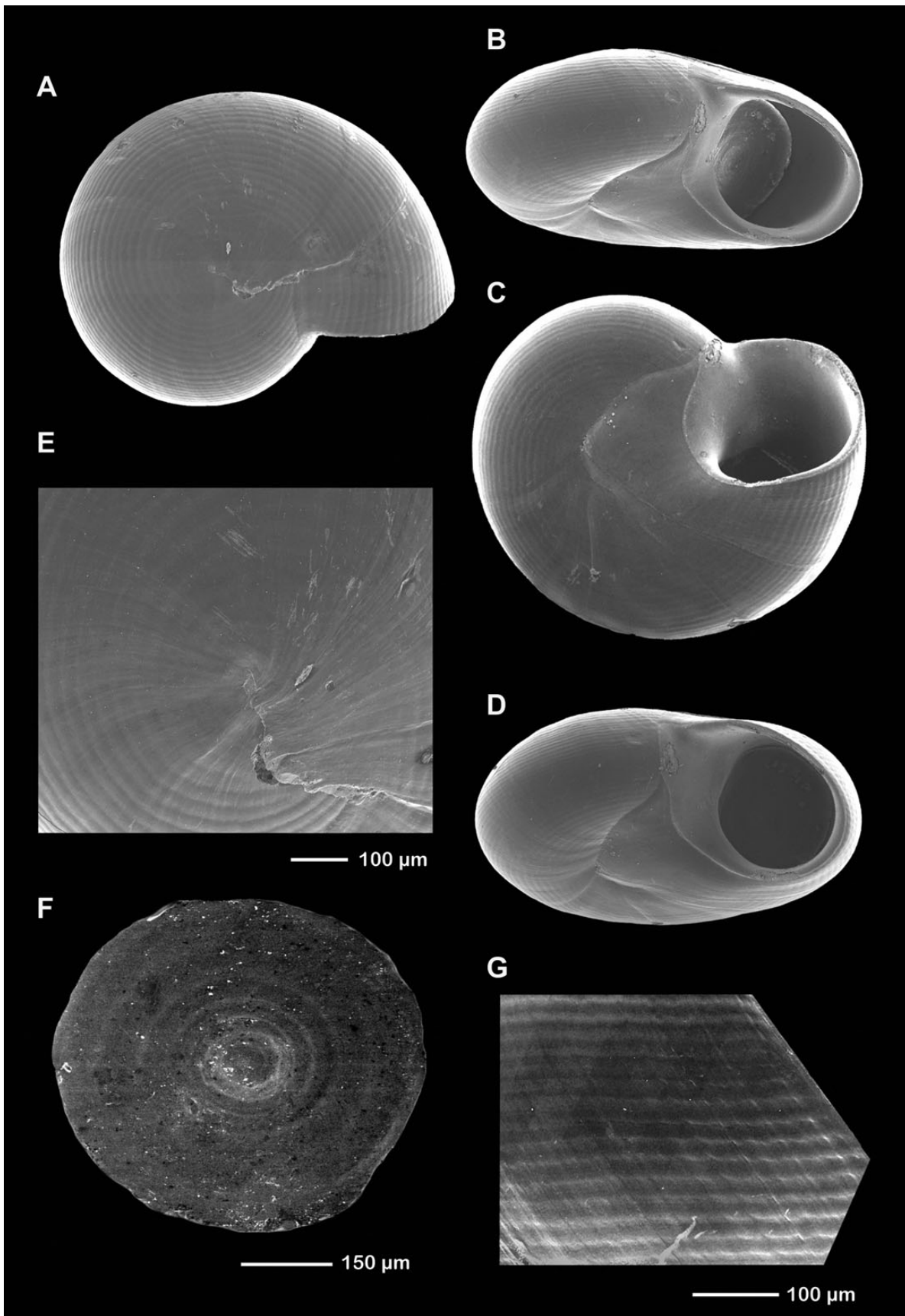


Figure 2. *Teinostoma brankovitsi* n. sp., holotype (ZMUC-GAS 531). **A–D.** Views of whole shell, 1.49 mm diameter. **E.** Apex. **F.** Outer surface of operculum. **G.** Shell microsculpture.

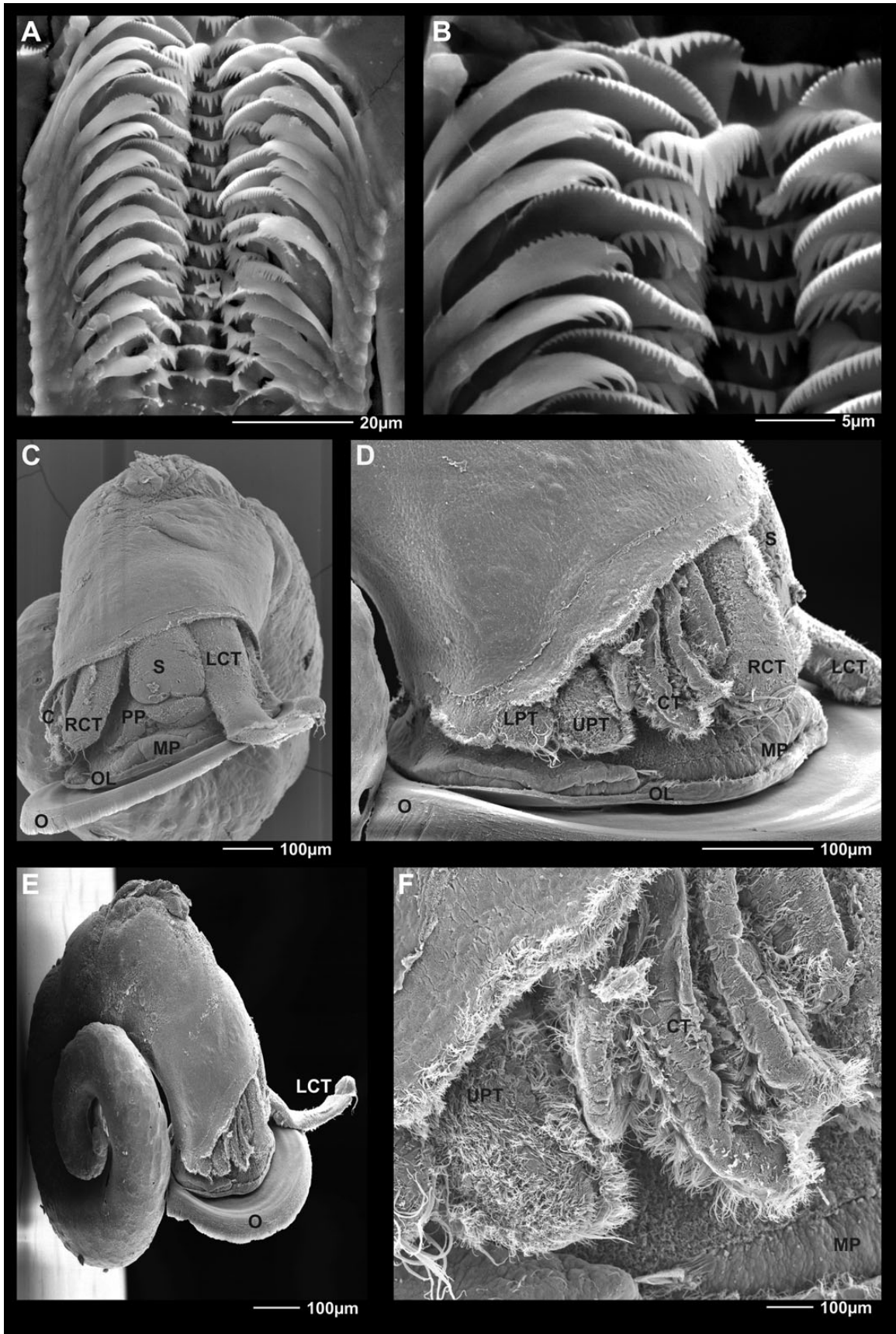


Figure 3. *Teinostoma brankovitsi* n. sp.: SEM images. **A, B.** Radula. **C–F.** External morphology of headfoot (paratype ZMUC-GAS 532). **C.** Frontal view. **D.** Lateral view, right cephalic tentacle, pallial tentacles and ctenidium. **E.** Frontal view, detail. **F.** Detail of the pallial tentacles and ctenidium. Abbreviations: CT, ctenidium; LPT, lower pallial tentacle; UPT, upper pallial tentacle; RCT, right cephalic tentacle; LCT, left cephalic tentacle; S, snout; O, operculum; OL, opercular lobe; PP, propodium; MP, metapodium; FC, fine cilia.

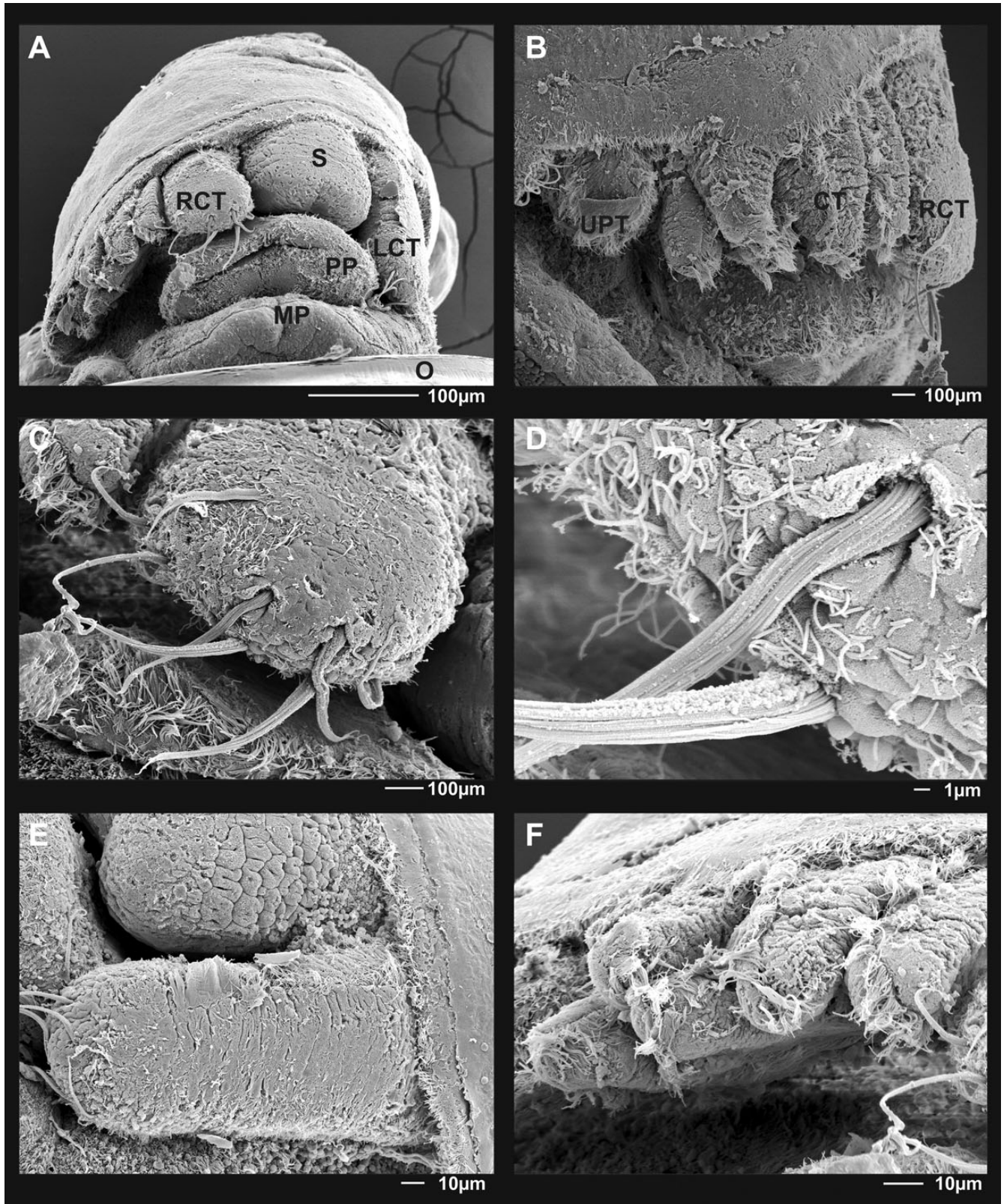


Figure 4. *Teinostoma brankovitsi* n. sp. SEM images of headfoot (paratype ZMUC-GAS 532-533). **A.** Frontal view of headfoot. **B.** Lateral view of pallial tentacles and ctenidium. **C.** Detail of distal end of right cephalic tentacle showing bristle-like compound cilia and fine cilia. **D.** Compound cilia and fine cilia of right cephalic tentacle. **E.** Dorsal view of left cephalic tentacle. **F.** Ctenidium in basal view. Abbreviations as in Figure 3.

nucleus. Colouration (Fig. 1D): headfoot translucent; snout, gills and foot pale pink; epipodial and pallial tentacles translucent; digestive gland yellow-brown.

Radula (Fig. 3A, B): Taenioglossate, formula 2 + 1 + 1 + 1 + 2. Central tooth wide basally; ventral margin with two denticles. Cutting edge with large, pointed central cusp; 5 smaller denticles on each side. Lateral teeth similar to central tooth. Cutting edge with large sharp cusp; flanked by 8 internal and 5–6 external denticles. Inner marginal teeth elongate, comb-like, with >40 small denticles. Outer marginal teeth hook-shaped, 4–5 internal cusps, 20–22 small denticles on upper end.

Distribution (Fig. 1A–C): Known only from type locality.

Live observations (Fig. 1D): Animals crawl quickly, leaving shallow grooved tracks on the sediment. Locomotion is by ciliary action. The long, thin cephalic tentacles appear to be quite smooth with little ciliation. The snout continuously extended and contracted while the snails moved along the substrate.

Ecology: All specimens were found in fully marine water in complete darkness on the surface of mud and silt in the northeast passages of Cenote Crustacea. The main passage of Cenote Crustacea parallels the Caribbean coastline; specimens were concentrated in a perpendicular offshoot of the main passage (Fig. 1B). Cenote Crustacea has no direct openings to the Caribbean Sea although marine algae occasionally are found in its passages after storms, indicating that crevicular exchange occurs. The sediment in Cenote Crustacea is extremely fine. A patchy distribution of orange bacterial growth is found only in sediments below the halocline. Cenote Crustacea differs from other surrounding cenotes in having two distinct haloclines below the freshwater entrance pool. *Teinostoma brankovitsi* was collected from sediments in or adjacent to bacterial growths with an overlying salinity of 35.7 ppt (see Neiber *et al.*, 2012). The temperature (26.3 °C) of the surrounding water is slightly cooler than the entrance pool, but with a higher concentration of dissolved oxygen (5.2 mg/l), which may reflect a horizontal flow of water through the surrounding limestone platform.

Teinostoma brankovitsi was the only mollusc found in samples collected during the 2013 and 2014 investigations. Five annelid taxa were found in association with *T. brankovitsi*, including a species of Acrocirridae (Gonzalez *et al.*, 2012), of Flabelligeridae (Gonzalez *et al.*, 2012), of Sabellidae, of Cirratulidae and a marine oligochaete. These newly discovered annelids, with the exception of the acrocirrid, were restricted to the same location and passages in Cenote Crustacea as the tornid. *Teinostoma brankovitsi* was absent from sediment samples collected in adjacent sections of Cenote Crustacea, including those with brackish and fresh water. Samples from surrounding cenotes and calcareous intertidal and deeper reef sands between Puerto Morelos and Tulum (Mexico) did not contain tornids.

Remarks: *Teinostoma brankovitsi* resembles *T. biscaynense* Pilsbry & McGinty, 1945, *T. obtectum* Pilsbry & McGinty, 1945 and *T. expansum* in having a depressed, planispiral shell that is dorsally and peripherally convex while slightly concave at the base. Furthermore, these species share an umbilicus covered by a strong callus. However, the species described herein differs from the above in having spiral cords covering the entire teleoconch. *Teinostoma nesaeum* Pilsbry & McGinty, 1945 and *T. semistriatum* d'Orbigny, 1842 have similar teleoconch sculpture. The teleoconch is covered by a callous layer in *T. semistriatum*, while the spiral cords do not extend along the entire teleoconch in *T. nesaeum*.

Woodringilla glyptylus Pilsbry & Olsson, 1951 and *W. solida* (Laseron, 1954) resemble *T. brankovitsi* in having a solid shell with the teleoconch surface completely covered by spiral cords, but differ from it in the shape and ornamentation of the umbilical callus (Fukuda, 1993; Hasegawa, 2000). Pilsbry & Olsson (1951) distinguished *Woodringilla* from *Teinostoma* by the conspicuous spiral sculpture along the teleoconch, as well as the presence of a heavy umbilical callus deeply engraved by parallel grooves along the anterior edge. The thick, deeply grooved umbilical callus is a unique feature of the two species of *Woodringilla*, although the shells of these taxa otherwise are closely similar to more compact species of *Teinostoma*.

DISCUSSION

Morphology of Teinostoma

Our light and SEM studies of *Teinostoma brankovitsi* enable a morphological comparison with previously studied *Circulus texanus*, *C. mortoni* and *Cyclostremiscus beau* (Bieler & Mikkelsen, 1988). These genera share a distally bilobed snout, cephalic tentacles having bands of short motile cilia and numerous stiff compound cilia along the distal end, two pallial tentacles (the anterior having few cilia and posterior having sparse cilia and compound cilia on the distal margin) and a posteriorly-bilobed margin of the foot.

The absence of eyes and body pigmentation in *T. brankovitsi* may reflect a secondary loss associated with its anchialine cave habitat. Numerous hypogean gastropods are characterized by some degree of loss or reduction in eye pigmentation and structure (e.g. *Potamolithus karsticus* described by Desimone & Moraccholin, 1994; Romero, 2009), a common characteristic of other stygobitic anchialine fauna. However, lack of eyes and pigmentation is also an adaptation to interstitial environments, where many species of *Teinostoma* are found. Therefore, phylogenetic analyses and additional morphological studies of more tornids will be needed to determine whether the absence of eyes and pigmentation is a plesiomorphy of the genus or an adaptation of *T. brankovitsi* to the anchialine environment.

Other structures in *T. brankovitsi* do not seem to present any particular adaptations to the cave environment. The radula, for example, shows the same formula as that of *T. expansum* and *T. parvicallum* (Rubio *et al.*, 2011) and the tentidium is very similar to that of other species in the family.

Diversity of gastropods in anchialine caves

Teinostoma brankovitsi is the first anchialine Tornidae and the first endemic mollusc described from anchialine caves in the Yucatán Peninsula. Molluscs have the fourth highest diversity in anchialine cave systems after arthropods, annelids and teleost fish (Martínez *et al.*, 2015). However, most of the molluscs found in caves are marine species inhabiting areas enriched by trophic resources, of which the majority are not considered to be exclusive to caves. Interstitial representatives of the families Caecidae, Skeneidae and Cimidae have been recorded from caves with accumulations of marine sediments in the Canary Islands, Bermuda and the Bahamas (Moolenbeek *et al.*, 1988; Martínez *et al.*, 2004, 2009). Among these records, only two caecids (from Bermuda) are considered to be exclusive to anchialine caves (Moolenbeek *et al.*, 1988).

Quintana Roo has the highest anchialine diversity in the Yucatan Peninsula with 45 recognized crustaceans, seven undescribed annelids, one or two echinoderms and two species of fish (Romero, 2009; Alvarez *et al.*, 2015). Alvarez *et al.* (2015) reported an undescribed gastropod, but no additional information could be obtained regarding collection location or for

comparison. Additionally, 14 anchialine taxa are found elsewhere throughout the Yucatán Peninsula or Isla Cozumel, increasing the recognized records of anchialine diversity in the Yucatán Peninsula to more than 60 species, with several records awaiting description.

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