Rugosuscandona, a New Genus of Candonidae (Crustacea: Ostracoda) from Groundwater Habitats in Texas, North America

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Rugosuscandona scharfi gen. nov. sp. nov. is described as a new genus of the family Candonidae from groundwaters of Texas, USA. The new genus differs from its congeners based on the presence of relatively long pore canals with sensory seta on the carapace surface, 6-segmented first antenna (A1), absence of bristles (t setae untransformed) and z setae on second antenna (A2), distinctly shaped male hemipenis and clasping organs, a simple claw-like uropod, and presence of 4+2 whorls on the Zenker’s organ. Additionally, reduction in the number of setae and segments of the other soft body parts can be used to differentiate between the new genus Rugosuscandona gen. nov. and its congeners. Therefore, the new genus is currently monotypic. Taxonomic status of the new genus is discussed and compared with living genera of the family.

Key Words: New genus, new species, taxonomy, diversity, distribution, phreatic groundwater, ecology, karst aquifer.

Introduction

From a biological perspective, groundwater (subterranean or hypogean) habitats are as important as surface (epigean) waters (Rouch and Danielopol 1997) because of (i) the prevalence of “living fossils” with interesting body shape and structure, (ii) the presence of narrowly specialized (stygobiontic) taxa with high sensitivity to environmental changes, and (iii) their value as laboratories to study the evolutionary role of changes in morphology, physiology, and ethology (Marmonier et al. 1993). Although our understanding of hypogean fauna and its ecology worldwide is restricted (Hutchins and Schwartz 2013), recent studies have highlighted the importance of subterranean animals as models for the study of ecology (Hutchins et al. 2016), evolution and developmental biology (Rohner et al. 2013), and emphasized priorities for their conservation (Asmyhr et al. 2014).

Ostracods are found in epigean habitats as important members but are also a poorly known component of hypogean habitats (Rouch and Danielopol 1997). Among the non-marine ostracods, Candonidae Kaufmann, 1900 has a worldwide distribution and is found in different types of water bodies (Martens and Savatenalinton 2011). Among the 3 subfamilies (Cyclocypridinae Kaufmann, 1900, and Paracypridinae Sars, 1923) of the family, Candoninae is the largest group with about 42 genera and more than 500 species distributed worldwide (Külköyloğlu et al. 2011; Martens and Savatenalinton 2011; Karanovic 2012). Although most species are known from epigean waters, studies have shown that hypogean candonid ostracods are unique and diverse (Schornikov 1969; Danielopol 1978; Karanovic and Pesce 2000; Danielopol et al. 2011; Smith 2011), and that their diversity is underestimated (Külköyloğlu et al. 2011, in review; Namiotko et al. 2014). Because groundwater ostracods show strong adaptive characteristics, some species and genera are also known to be groundwater endemics; for instance, Phreatocandona Danielopol, 1973 and Trajancandona Karanovic, 1999 were described from ground waters of Romania and Montenegro, respectively (Danielopol 1978; Karanovic 1999).

Additional genera of Candonidae include Baicalocandona Mazepova 1976, first reported from Lake Baikal (Mazepova 1976), Terrestricandona Danielopol and Betsch 1980 from Madagascar (Danielopol and Betsch 1980), Danielocandona Broodbakker 1983 and Caribecandona Broodbakker 1983 from the West Indies (Broodbakker 1983), Indocandona Gupta 1984 from India (Gupta 1984), Nambycpris Martens 1992 from Namibia (Martens 1992), and Bicorncandona Külköyloğlu et al., 2011 from North America (Külköyloğlu et al. 2011). Except for Baicalocandona, most
species in these genera have been reported from groundwater and/or related sites (e.g., aquifers, springs, artesian wells, and caves) where relatively endemic and/or rare species diversity are known (Krömmelbein 1975; Holsinger and Longley 1980; Ponder 2004; Culver and Pipan 2009; Külköylüoğlu 2009). In the subfamily Candoninae, there are 7 or 8 genera [Candona Baird, 1845; Typhlocypris Vejdovský, 1882 (or Pseudocandona Kaufmann, 1900, e.g., Meisch 2000; Gidó 2010), Paracandona Hartwig, 1899; Eucandona Daday, 1900; Nannocandona Ekman, 1914; Fabaeformiscandona Krstić, 1972; Bicornuscandona] with 42 formally described species known from North America (Karanovic 2006; Külköylüoğlu et al. 2011; Külköylüoğlu et al. in review). Twenty-seven of the 42 species are endemic of North America (Karanovic 2006; Külköylüoğlu et al. 2011). However, published and unpublished data suggest that these numbers underestimate true species diversity (see Stout 1976).

The aim of the present study is to propose Rugosuscandona scharfi gen. nov. sp. nov. as a new genus of Candonidae from a groundwater ecosystem, the Edwards Aquifer of Texas, USA.

Materials and Methods

The San Marcos Artesian Well (SMAW) is a site known for its stygobiontic diversity, which has been periodically sampled and studied since its construction in 1895. The well is completed in the confined zone in a relatively shallow portion of the San Antonio Pool of the Edwards Aquifer. At approximately 59.5 m depth, the well intersects a 1.5 m tall conduit (Holsinger and Longley 1980), from which most of the water and biological materials are presumed to discharge. Water quality is generally high at the site, which has been dye traced to San Marcos Springs (Fig. 1), less than 1 km to the northeast (Ogden et al. 1986). In November 2013, water temperature at the well averaged 22.3°C, dissolved oxygen averaged 5.3 mg/L, and electrical conductivity averaged 608 μS/cm (Külköylüoğlu et al. in review).

Individuals of a new species representing a new genus were sorted from composite invertebrate samples collected in a drift-net (100 μm aperture) over the well outflow pipe. Each sample integrated discharged biological materials for 24–96 hours, depending on the sample, and was sorted under a stereomicroscope at 10X magnification to separate all invertebrates from detritus; most of which is filamentous microbial growth.

Prior to dissection, similar ostracod specimens were grouped and individuals were measured. An adult male and a female were dissected in lactophenol solution under an Olympus SZX7 stereomicroscope. Valves were separated from soft body parts with fine needles and then stored on micropaleontological slides. Scanning Electron Microscope (SEM) photographs of the carapace were taken with a JEOL 6335F SEM at TÜBİTAK-MAM Institute (Gebze, Turkey).

Soft body parts were first drawn with the aid of camera lucida (Olympus U-DA model) attached to an Olympus BX-51 microscope. Measurements of the soft body parts were based on the mid length of the appendages. The number of segments refers to the total number of countable segments unless otherwise indicated. All drawings were digitized using Adobe Illustrator CS5. Species identification was based on relevant references (e.g., Broodbakker and Danielopol 1982; Martens 1987; Meisch 2000; Karanovic 2004, 2006, 2007, 2012, 2013). All specimens (catalog numbers OK-TX-AW016-008: 01–13) are stored at the Limnology Laboratory of the Biology Department, Abant İzzet Baysal University, Bolu, Turkey. They are available upon request from the corresponding author.

Abbreviations: a, outer lobe on hemipenis; A1, first antenna (antennula); A2, second antenna (antenna); b, inner lobe on hemipenis; β, seta on Md; d1–3 and dp, setae on the protopodite of the second (T2, walking leg) and third (T3, cleaning leg) thoracopods; G1–G3, GM, terminal claws of A2; y, seta on Md; H, height; h, medial lobe on hemipenis; L, length; LV, left valve; Md, mandibula; Mxl, maxillula; RV, right valve; S1 and S2, setae on Md; T1–T3, first 3 thoracopods; t1–4, setae on the penultimate segment of A2; UR, uropod; W, width; Y, ya, y1–y3, aesthetascs; z1–3, setae on the second segment of A2.

Diagnosis. Carapace sub-rectangular and ornamented with wrinkled hexagonal and/or pentagonal cells (Fig. 2A–J). Pore canals with sensory seta each elevated on sur-
face especially at anterior and posterior margins of valves (Fig. 2H, I). LV overlaps RV on all sides (Fig. 2A, B, E–G). LV with flange (protrusion) postero-dorsally, covering RV. Inner lamella wide at both ends (Fig. 3A). A1 6-segmented without Rome and Wouter’s organs (Fig. 4A). A2 4-segmented lacking γ1–2, z, t, and swimming setae (Figs 3B, 4B, C). Mandibular palp 4-segmented (Fig. 4D). First segment without alpha seta. Second segment with 3 smooth setae internally, and without setae externally. Penultimate (third) segment with 1 seta externo-distally and 1 interno-distally.

![Fig. 2. SEM photographs of carapace of *Rugosuscandona scharfi* gen. nov. sp. nov. A, C, D, H, I: paratype (OK-TX-AW016-008: 05) male. B, E, F, G, J: paratype (OK-TX-AW016-008: 06) female. A) right side view, B) dorsal view, C) posterior end of right side, D) anterior end of right side, E) dorsal view of anterior margin, F) dorsal view of posterior margin, G) pore canals on dorsal side, H) central muscle scars, I) pore canals on anterior end, J) pore canals and surface ornamentation. Scale bars: 100 µm for A, B; 10 µm for C–J. Arrows indicate forward.](image-url)
Gamma seta absent (but see discussion). Terminal segment fused with claw, and with 2 setae interno-distally and 1 seta externo-distally. L:W ratio of terminal segment less than 2:1. Maxillula (Fig. 4E) with 3 endites and 2-segmented palp. Claws on third endite smooth. Terminal segment of Mxl-palp trapezoidal to square. First thoracopod symmetrical in female (Fig. 5C) but asymmetrical (prehensile palps) in male (Fig. 6A, B), not segmented and without “a”, “c”, and “b” setae; only “d” seta present. Masticatory process of T1 with 7 setae. Walking leg (T2) 5-segmented with a “d1” seta on basal segment (Fig. 5A). Cleaning leg (T3) 4-segmented with “d1” and “d2” setae (d2≥d1) (Fig. 5B). Seta “e” not present.
present on third segment. Penultimate segment with “f” and “g” setae. Terminal segment with 2 long and 1 short setae (h3 > h2 > h1). Uropod (furca) uniramous, rod-like with claw (Figs 3C, 5D). Genital lobe almost round and without appendages (Fig. 5D). Labium with 4 + 4 small spines (Fig. 5E). Zenker’s organ with 4 + 2 whorls (Fig. 6C). Hemipenis large (largest of all other extremities) with square outer lobe (lobe a), large subtriangular inner lobe (lobe b), and small square to oval medial lobe (lobe h) (Fig. 6D).

Type species. *Rugosuscandona scharfi* sp. nov.

Etymology. A Latin word *rugosus*, meaning “wrinkled”, is combined with the genus name *Candona* (gender feminine) in reference to the wrinkled ornamentation on the carapace surface.
Rugosuscandona scharfi gen. nov. sp. nov. (Figs 2–6)

Material examined. Holotype: a male dissected with soft parts on one slide (OK-TX-AW016-008: 01). Collected from type locality on 07 March 2013 by Benjamin Hutchins and Benjamin Schwartz. Allotype: a female dissected with soft parts on one slide (OK-TX-AW016-008: 02). Collected 25 February 2013 by Benjamin Hutchins and Benjamin Schwartz. All soft body parts of holotype and allotype dissected in lactophenol solution and sealed with translucent nail polish; valves kept in micropalaeontological cavity slides (OK-TX-AW016-008: 03, 04). Non-dissected paratypes (OK-TX-AW016-008: 05–13): total of 12 adults and 3 juveniles (2 adults, 26 February 2013; 2 adults + 1 juvenile, 27 February 2013; 1 adult, 28 February 2013; 1 adult, 4 March 2013; 2 adults, 6 March 2013; 1 juvenile, 21 March 2013; 2 adults + 1 juvenile, 25 March 2013; 1 adult + 1 damaged adult individual, 27 March 2013) collected from the type locality by Benjamin Hutchins and Benjamin Schwartz, kept in 70% ethanol deposited at the Abant Izzet Baysal University, Department of Biology, Bolu Turkey.

Distribution. Known only from the type locality by Benjamin Hutchins and Benjamin Schwartz.

Description of male. Measurements (based on mid-length): L = 0.53–0.65 mm, H = 0.25–0.30 mm, W = 0.14–0.20 mm. Average: L = 0.62 mm, H = 0.28 mm, W = 0.18 mm (n = 7).

LV overlaps RV from all sides (Fig. 2A, C, D). In lateral view, carapace subrectangular in shape, with elevated pore canal openings. Dorsal margin flat, LV almost rounded in all parts, RV slightly sloping posteriorly. Both margins equally rounded anteriorly. LV with flange (protrusion) postero-dorsally in both sexes. Greatest height approximately at center. Valve surface ornamented with wrinkles forming almost hexagonal and/or pentagonal cells. Pore canals long with sensory setae on valve surface and dense around marginal zones of both valves in both sexes and juveniles (Fig. 2H, I). Muscle scars located closer to center but not visible on valve surface. Calcified inner lamella wide at both ends, outer lamella wide. In dorsal view, carapace narrow, hinge adont, both ends thin and almost blunt. In ventral view, valves

Fig. 5. Rugosuscandona scharfi gen. nov. sp. nov. A, B, E: holotype male (OK-TX-AW016-008: 01), C, D: allotype female (OK-TX-AW016-008: 02). A) T2, B) T3, C) T1, D) UR with genital organ and furcal attachment, E) labium. Scale bar: 100 µm.
A new genus of Candonidae

Rugosuscandona scharfi gen. nov. sp. nov. holotype male (OK-TX-AW016-008: 01). A) left clasping organ, B) right clasping organ, C) Zenker’s organ, D) hemipenis. Scale bar: 100 µm.

Slightly concave, LV strongly encompasses RV. Color translucent or opaque to pale white.

A1 (Fig. 4A) 6-segmented. First segment with 2 long smooth anterior and posterodistal setae; former reaching about end of second segment, latter extending almost to end of terminal segment. Wouter’s and Rome organs absent. Second segment with medium-sized smooth antero medial seta reaching about to end of third segment. Both third and fourth segments without setae. Penultimate segment anterodorsally with 3 long setae subequal in length to all segments. Terminal segment with 3 subequally long setae and shorter ya aesthetasc.

A2 (Fig. 4B) 4-segmented including protopodite. First segment with smooth posterodistal seta reaching about end of penultimate segment. Exopod and exopodial setae not apparent: absent or rudimentary. Second segment with long L-shaped medio-ventral aesthetasc Y and long smooth seta, both extending to tips of terminal segment. y1 seta absent. Natatory (swimming) setae absent. Third (penultimate) segment without y2, z, or t setae. G2 and G3 claws slightly plumose and subequal in size. G1 claw absent. Medium-sized smooth antero-medial seta present on same segment. Terminal segment with GM and Gm claws and y3 aesthetasc. GM claw equal in size with G2 and G3 claws. Gm claw short, about 2/3 length of GM. Aesthetasc y3 longer than Gm by about 1/3 of its length.

Md (Fig. 4D) composed of coxa and Md-palp. Coxa well developed with 6 + 1 teeth and medium-sized smooth seta internally. Md-palp 4-segmented. First segment internally with slightly plumose S1 and S2. Alpha seta absent. Vibratory plate with 7 + 1 setae. Second segment with cluster of 3 equally long smooth setae internally. Beta seta short, about 1/3 length of S1 seta. Penultimate segment with 2 internodistal smooth setae exceeding length of terminal segment and externomedial seta reaching to about middle of terminal claw. Short seta on penultimate segment present externodistally, extending to about middle of terminal segment. Gamma seta not seen well. Terminal segment with fused and distally pappose claw, long and smooth external seta, and 2 setae internally (1 thin and small, another robust and slightly plumose). L ratios of 4 segments measured in middle: 1.5: 1.1: 2:1.

Mxl (Fig. 4E) composed of three endites and Mxl-palp. First and second endites bearing 6 and 5 short setae, respectively. Third endite with 2 long bristles and with 2 smooth short setae. Base of first endite with medium-sized plumose seta. Mxl-palp 2-segmented. First segment with 3 smooth claw-like setae, second (terminal) segment subrectangular and short (L: W ratio 1.2 : 1) with 3 long (2 smooth claw-like and 1 somewhat shorter), and 2 small setae. Vibratory plate with 13 plumose long setae.

Hemipenis (Fig. 6D) largest organ with well-developed subtriangular medial lobe “b”, small rounded distal lobe “h”, and lateral lobe “a” square in shape. M-process complex with distal part (g2) pointed. Sperm type helicoidalized, filamentous, and aflagellate. M-process comprising about half length of T1, ending with about 6 + 1 fine setae. Right palp with ventral projection with short spine-like claw and longer smooth claw. Same palp ending with short and thin claw. Left palp slightly longer and wider, without ventral projection. Only short d seta present, other setae (a, b, c setae) and vibratory plate not seen.

T2 (Fig. 5A) 5-segmented with plumose d1 seta on first segment (protopodite). Setae dp and d2 not observed. Next 3 segments (second, third and penultimate segments) with smooth and relatively short sub-apical seta (e, f, g) each, posteriorly. Terminal segment with very long, smooth claw (h2), extending about 2/3 length of second segment, and short external (h3) seta.

T3 (Fig. 5B) 4-segmented. First segment with medium d1 and longer d2 setae. Second segment without “e” seta. Penultimate segment not divided, f and g setae present. Terminal segment almost square and short with 3 setae (length: h3 > h2 > h1). L ratios of setae h1: h2: h3 = 1.1: 2.5: 6. Setae h1 and h2 slightly curved, seta h3 almost straight. UR thin and with spine-like or rod-like claw with ramus. Other claws absent. Both anterior and posterior setae absent. Uropodal attachment slightly curved with branch.

Rake-like organ not observed.

Zenker’s organ (Fig. 6C) with 4 + 2 rings of spines ending with sperm canal.

Hemipenis (Fig. 6D) largest organ with well-developed subtriangular medial lobe “b”, small rounded distal lobe “h”, and lateral lobe “a” square in shape. M-process complex with distal part (g2) pointed. Sperm type helicoidalized, filamentous, and aflagellate (Fig. 3D, E).

Description of female. Carapace similar in shape but slightly longer than that of male (Figs 2B, E–G, 3A). Female L = 0.56–0.65 mm, H = 0.25–0.30 mm, W = 0.16–0.20 mm.
Rugosuscandona gen. nov. possesses several unique morphological characteristics in both carapace and soft body parts but also exhibits similarities with other genera of the tribe Candonopsini. The new genus has interesting carapace ornamentation consisting of hexagonal and pentagonal wrinkled cells on the surface of the carapace (Fig. 2). Pore canals with sensory setae are dense on the surface, and radial pore canals are located along both margins of the valves (Fig. 2H, I). While the other 7 genera (Candonopsis Vavra, 1891, Cubacandona Brookbakker, 1983, Marocandona Karanovic, 2005, Marocandona Boulou, and Idmbenner, 2005, Newrocinandona, 2003, Humphreyscandona gen. nov. differs from 1 other groundwater genus of the tribe Candonopsini, only Caribeandona seems to bear 6-segmented A1 (III and IV segments fused) (Broodbakker 1983; Marmonier et al. 2005). According to Karanovic (2012), Marocandona Marmonier, Boulou and Idmbenner, 2005 has 6-segmented A1, but this seems to be in error as the species was described as having 5 segmented A1 (see Marmonier et al. 2005: figs 5A, 7A). Smith (2011) and Smith and Kamiya (2015) described Undulacandona Smith, 2011 with 2 species stating that A1 bears 6 segments where the first 2 segments were partially fused together.

Therefore, aside from Rugosuscandona gen. nov., Caribeandona seems to be the only known genus with 6-segmented A1. However, these 2 genera are not closely related, on the basis of the terminal segment of the cleaning leg bearing 2 short and 1 long setae in Caribeandona, and 2 long and 1 short setae in Rugosuscandona gen. nov. Furthermore, despite the similarity in the numbers of A1 segments, Caribeandona and Rugosuscandona gen. nov. differs from 1 another in number and position of A1 setae. For example, in Caribeandona, there are 2 medium setae on the first segment of A1 (Broodbakker 1983), but 1 long seta is present anteriorly in the new genus. In addition, while no setae are present on the third and fourth segments of the new genus, Caribeandona bears 2 long setae on each segment. The terminal segment ends with 1 medium and 2 long setae in the latter genus but there are 3 long setae on the new genus.

A2 of Rugosuscandona gen. nov. has unusual characteristics including a rudimentary or missing exopod, and absence of t and z setae (as diagnostic characteristics). Species of some genera (e.g., Paracandona) and tribes (e.g., Humphreyscandondini Karanovic, 2005) do not have bristles on the male A2, but mostly bear z-setae. Also, some genera have 2 short setae (e.g., Danieloandona) or 3 short setae (e.g., Trajecandona and Undulacandona) on the exopod (see Karanovic 1999; Smith and Kamiya 2015), while a majority of genera of Candoniniae have 2 short and 1 long seta. The absence of an exopod and t-setae are only known in 1 other groundwater genus of the tribe Candonopsini (Kükköylüoğlu et al. in review). As far as we know, such reductions are not known in the family Candonidae. Loss of the exopod may indicate that the new genus may not even belong to the subclass Podocopa (Dan Danielopol pers. comm.). According to Kornicker (2003), a reduced exopodial lobe on the sixth limb of halocyprid ostracods (Myodocopa) is only found on species from deep sea and anhialine caves and the absence of an exopod or exopodial lobe, bristles, and exopod muscles suggest a more derived state. In other words, absence of such organs and features may be derived in individual taxa as autapomorphies. The reduction or loss of A2 organs and features exhibited by Rugosuscandona gen. nov. and other species inhabiting deep sea...
or anchialine environments may suggest similar selective pressures resulting from similar environmental conditions. However, at the moment, because of a lack of representative species in the new genus, this idea needs further investigation.

In other ways, A2 of Rugosuscandona gen. nov. is similar to other members of the Candonidae. For example, sexual dimorphism that is common in the family Candonidae is also evident in the new genus where all G-claws are present in females but only G2 and G3 claws are developed in males.

Rugosuscandona gen. nov. exhibits unique setation of the Md-palp which bears S1 and S2 setae on the first segment (alpha seta absent) and 3 smooth setae (and beta seta) internally on the second segment. In other family members, the numbers of these setae vary from 5+2 [e.g., Candonina candida (Müller, 1776) and species of Pseudocandona compressa-group] to 2+2 (e.g., Trajancandona) (Meisch 2000; Karanovic 2012). There are a few genera [e.g., Nannocandona, Mixtacandona Klie 1938, and Danielocandona] and several additional species [e.g., Pseudocandona eremita (Vejdosky, 1882), P. zschokkei (Wolf, 1920), P. rostrata (Brady and Norman, 1889), and Candonopsis kinglei (Brady and Robertson, 1870)] have been reported with 3 setae on the second segment (see Namiotko et al. 2014). Presently, it seems that Rugosuscandona gen. nov. is the only genus with 3 setae on the second segment of the Md-palp in the tribe Candonopsini. Gamma (γ) and accompanying setae are not well expressed in the penultimate segment. The reduction of this seta is an important feature because the presence of gamma seta is common in the tribe.

The large vibratory plate of Mxl is characteristic of the tribe as is the case in Rugosuscandona gen. nov. but differences in setal parts are important for discussion. For example, the maxillula of the new genus has 3 long apical setae on the outer corner of the first segment, which is different from other genera of the tribe Candonopsini in which most genera (e.g., Pioneercandonopsis and Marococandona) have 4 smooth or plumosed setae. Unlike these genera, some other genera (Meischcandona, Namibcypris, Danielocandona, and Trajancandona) in other tribes of the subfamily Candoninae exhibit 3 setae (Karanovic 2001). In Rugosuscandona gen. nov., the terminal segment consists of 3 long claw-like and 2 short smooth setae but other congeneres have total 6 on the same segment (e.g., Undulacandona) (Smith and Kamiya 2015). Reduction of the setae may be considered as convergent with those of other species with similar niches (Mayr and Ashlock 1991), but this needs further investigation.

Male of the new genus display asymmetrical prehensile palps without “a”, “b”, and “c” setae and vibratory plate. Such a reduction in these setae is not known in any species of the family. Asymmetrical palps are known in 4 genera (Candonopsis, Marococandona, Cubacandona, and Caribecandona). Two genera (Latinopsis and Pioneercandonopsis) of the tribe have symmetrical palps. Karanovic (2005a) stated that 2 genera (Cubacandona and Caribecandona) had almost symmetrical prehensile palps may not be correct. The absence of “a”, “b”, and “c” setae and vibratory plate is currently unique to Rugosuscandona gen. nov. This corresponds to the reduction noted above on A2 and further supports the hypothesis that the genus may exhibit derived characters.

The number of basal setae in T2 and T3 distinguishes Rugosuscandona gen. nov. from other members of the tribe Candonopsini. While Rugosuscandona gen. nov. has only 1 “d1” seta on T2 and 2 setae (d1, d2) on T3, other genera possess 0 (e.g., Abcandonopsis, Marococandona, and Pioneercandonopsis) or 1 seta (e.g., Candonopsis, Caribecandona, Cubacandona, and Latinopsis) on T2 and 3 setae on T3 (except Marococandona which bears 2 setae on T3 protopodite). However, several genera of the tribe exhibit similar numbers of segments of this limb. For example, Rugosuscandona gen. nov. and Marococandona both have 5 and 4 segments on T2 and T3, although as shown above, several other characteristics differentiate these 2 genera.

Karanovic (2005b) cited the presence of a spine on the uropodal claws as a synapomorphic character in almost all the clades of African, the only Central American, and Australian species of Candonopsis s. str. Later, she associated this character with zoogeographical groupings of almost all species from the subtopics and tropics (see Klie 1932). In contrast, except for a few species, European species lack a spine on the uropodal claws. In Rugosuscandona gen. nov., the uropod is strongly reduced into a single rod-like claw without spines. Although in other parts of the world, only several species in the tribe (e.g., Marococandona nicolae Marmonier et al. 2005, Caribecandona trapezoidea Broodbakker 1983, C. anea Broodbakker 1983, C. auricularia Broodbakker 1983, and Danielocandona lieshoutae Broodbakker, 1983) show the similar character (see Broodbakker, 1983; Marmonier et al. 2005), this is only the second genus with such a rod-like or whip-like uropod that has been described in North America (Külköylüoğlu et al. 2011). Moreover, the members of the tribe Candonopsini do not have posterior seta on the uropod. On the other hand, the uropod of a few genera in different tribes is characterized by 1 claw (e.g., Indocandona) (Gupta 1984). That is either fused or less developed with the ramus (Meisch 2000; Karanovic 2001; Karanovic and Lee 2012; Külköylüoğlu et al. in review).

Differences in shape and size other than those described above are found in the hemipenis and Zenker’s organ in males, and in the genital lobe in the female. For males, a square lobe “a” is most distinctively different relative to the other parts of the hemipenis, along with the small distal lobe “h” and a large subtriangular inner lobe “b”. With the exception of D. lieshoutae, 4 + 2 whorls in Zenker’s organ are also unique to Rugosuscandona gen. nov.

As discussed above, we described Rugosuscandona gen. nov. as a member of Candoninae. However, several morphological differences strongly support that the new genus is included in the tribe Candonopsini. Rugosuscandona gen. nov. exhibits reductions in several different body parts (see discussion above). We hypothesize that these reductions (i.e., in chaetotaxy) might represent derived adaptations to groundwater ecosystems, but since we do not know fossil forms of the genus yet, general conclusion of its evolutionary history cannot be made at the moment. This is also the case indicated for Undulacandona from Japan by Smith and
Kamiya (2015). Up to now, the only fossil form of the tribe is known from the genus Candonopsis from the Miocene (Danielopol 1980). Therefore, until clear evidence of fossil species of the new genus is found, we recommend additional studies to resolve this problem.

Rugosuscandona scharfi gen. nov. sp. nov. is known only from the type locality although groundwater ostracods in Texas remain largely unassessed. At the type locality, R. scharfi gen. nov. sp. nov. occurs with >25 other described species of stygobionts, including 1 planarian, 1 hirudinean, 3 species of gastropods, 1 thermostbanacean, 1 cyclopoid copepod, 2 species of isopods, 2 species of decapods, other undescribed genus and 2 species of ostracods, 1 dytiscid beetle, 1 plethodontid salamander, and 10 species of amphipods with additional descriptions in review. However, the stygobiont fauna from this locality is still poorly understood. Since it was implied that the San Marcos artesian well is one of the most biologically diverse groundwater sites on Earth (Longley 1981; Culver and Pipan 2009), additional undescribed species of ostracods, cyclopoid and harpacticoid copepods, aquatic mites, bathynellid, isopods, and other amphipods have been found (Küköylüoğlu, Hutchins, and Schwartz pers. obs.).

Species at the San Marcos artesian well utilize diverse carbon sources derived in part from chemolithoautotrophic production occurring along a freshwater-saline water interface along the down-dip edge of the Edwards Aquifer (Hutchins et al. 2016). Primary productivity has played an important role in the evolution and maintenance of the longest subterranean food chain currently known (Hutchins and Schwartz 2013), and species partition food resources (Hutchins et al. 2014, 2016). Furthermore, invertebrates from the San Marcos artesian well display a diversity of body morphologies, and the relative abundance of species varies substantially in response to precipitation and aquifer levels (Hutchins and Schwartz pers. obs.). These data suggest a heterogeneous environment comprised of a mosaic of microhabitats. Lack of pigment, relatively thin carapace, and eyelessness suggests that R. scharfi gen. nov. sp. nov. is a stygobiont but there is currently no detailed information about habitat preference or trophic ecology for the new species. However, lack of natatory setae suggests that the species may be benthic or associated with conduit walls. Of the nearly 12,000 ostracod specimens collected from this site, far less than 1% are R. scharfi gen. nov. sp. nov. This may be due to relative rarity in the aquifer of the new species or the new species may be rarely expelled from the well.

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