Species Diversity **22**: 175–185
25 November 2017
DOI: 10.12782/sd.22_175

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

Okan Külköylüoğlu[1,6], Derya Akdemir[2], Mehmet Yavuzatmaca[1], Benjamin F. Schwartz[3,4], and Benjamin T. Hutchins[5]

[1] *Department of Biology, Faculty of Arts and Science, Abant İzzet Baysal University, Bolu 14280, Turkey*
E-mail: kulkoyluoglu_o@ibu.edu.tr
[2] *Merdivenköy Mahallesi, Şair Arşi Caddesi. No:16/14, Kadıköy, Istanbul 34732, Turkey*
[3] *Edwards Aquifer Research and Data Center, Texas State University, San Marcos, Texas 78666, USA*
[4] *Department of Biology, Texas State University, San Marcos, Texas 78666, USA*
[5] *Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, Texas 78744, USA*
[6] *Corresponding author*

(Received 5 August 2016; Accepted 9 May 2017)

http://zoobank.org/CD308AA8-CCA0-4831-B7CB-3052E946588F

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, Candoninae 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 (Külköylüoğlu *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 (Külköylüoğlu *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), *Namibcypris* Martens 1992 from Namibia (Martens 1992), and *Bicornucandona* Külköylüoğlu *et al.*, 2011 from North America (Külköylüoğlu *et al.* 2011). Except for *Baicalocandona*, most

© 2017 The Japanese Society of Systematic Zoology

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; *Bicornucandona*] 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.



Fig. 1. Type locality indicated as a closed circle of the new genus and species, from San Marcos, 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 10× 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 6335 F 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, GM, terminal claws of A2; *γ*, 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.

Class **Ostracoda** Latreille, 1802
Order **Podocopida** Sars, 1866
Suborder **Cypridocopina** Baird, 1845
Superfamily **Cypridoidea** Baird, 1845
Family **Candonidae** Kaufmann, 1900
Subfamily **Candoninae** Kaufmann, 1900
Genus ***Rugosuscandona*** gen. nov.
(Figs 2–6)

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-

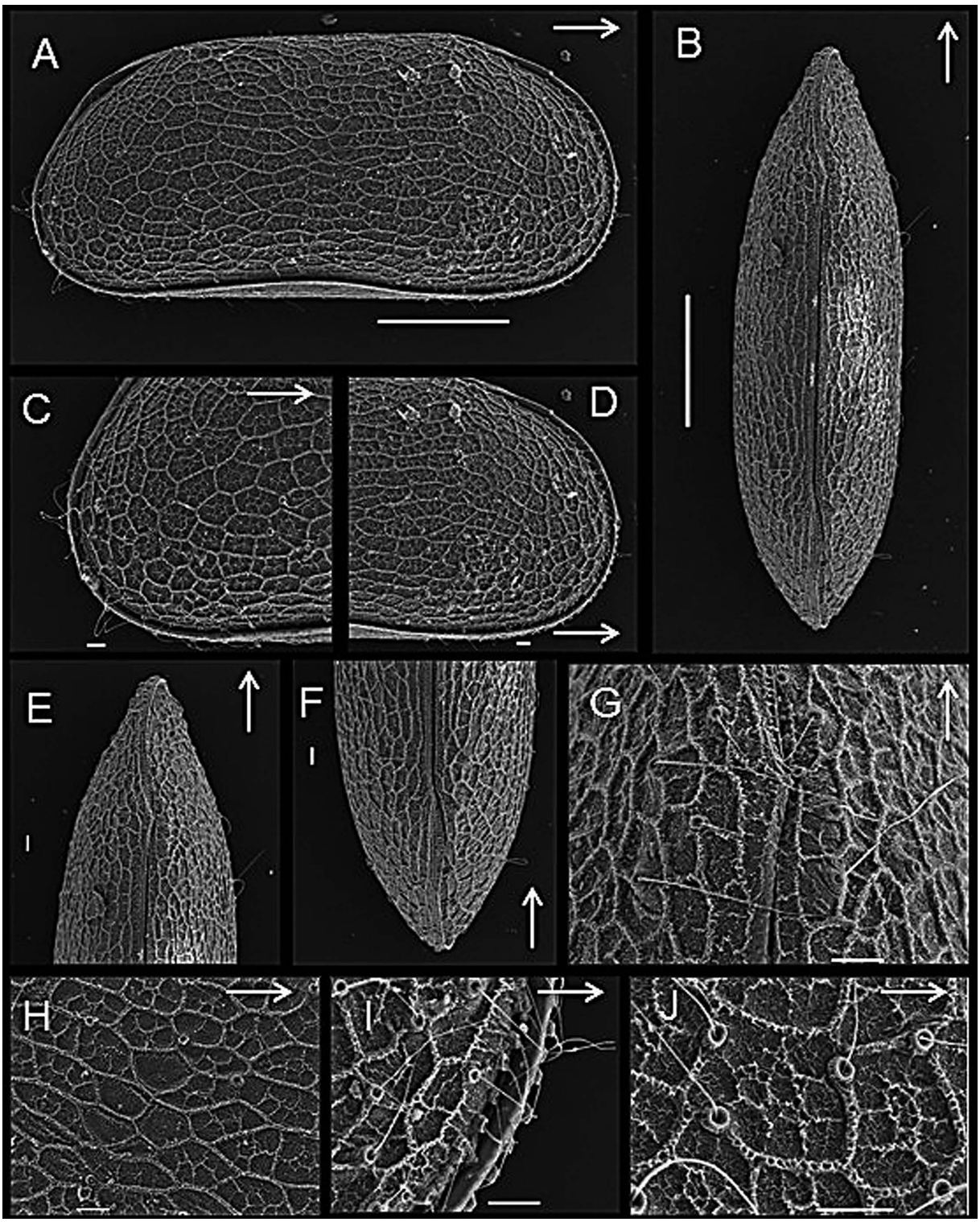


Fig. 2. SEM photographs of carapace of *Rugosuscandona scharfi* gen. nov. sp. nov. A, C, D, H, I: paratype (OK-TX-AW016-008: 05) male. B, E, F, G, J: paratype (OK-TX-AW016-008: 06) female. A) right side view, B) dorsal view, C) posterior end of right side, D) anterior end of right side, E) dorsal view 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.

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 y1–2, 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.

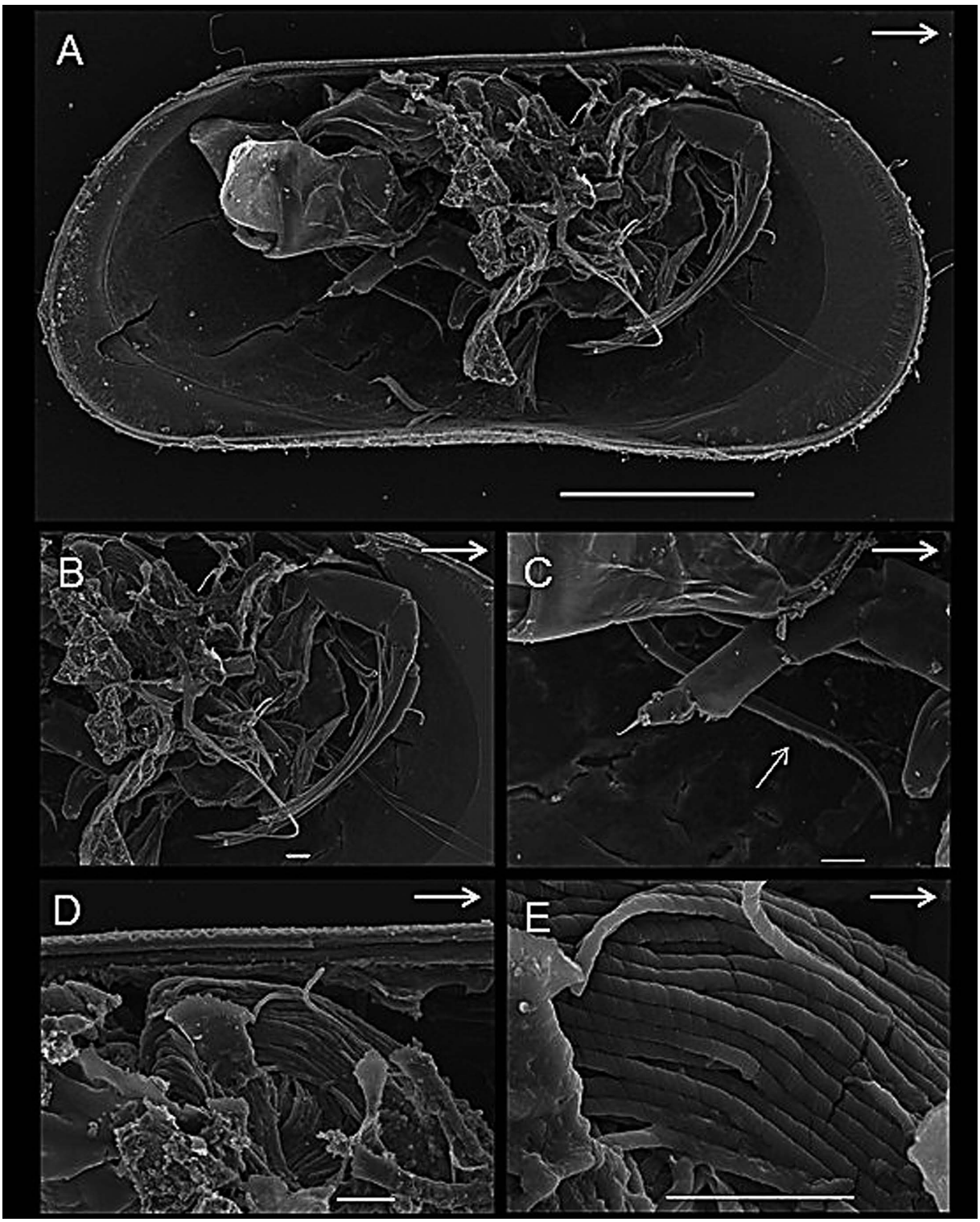


Fig. 3. SEM photographs of *Rugosuscandona scharfi* gen. nov. sp. nov. removed RV, paratype (OK-TX-AW016-008: 07) female. A) LV, interior view, B) right pair of A2, C) UR shown with thin arrow, D) sperm packs, E) close view of sperm packs. Scale bars: 100 µm for A; 10 µm for B–E. Arrows indicate forward.

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

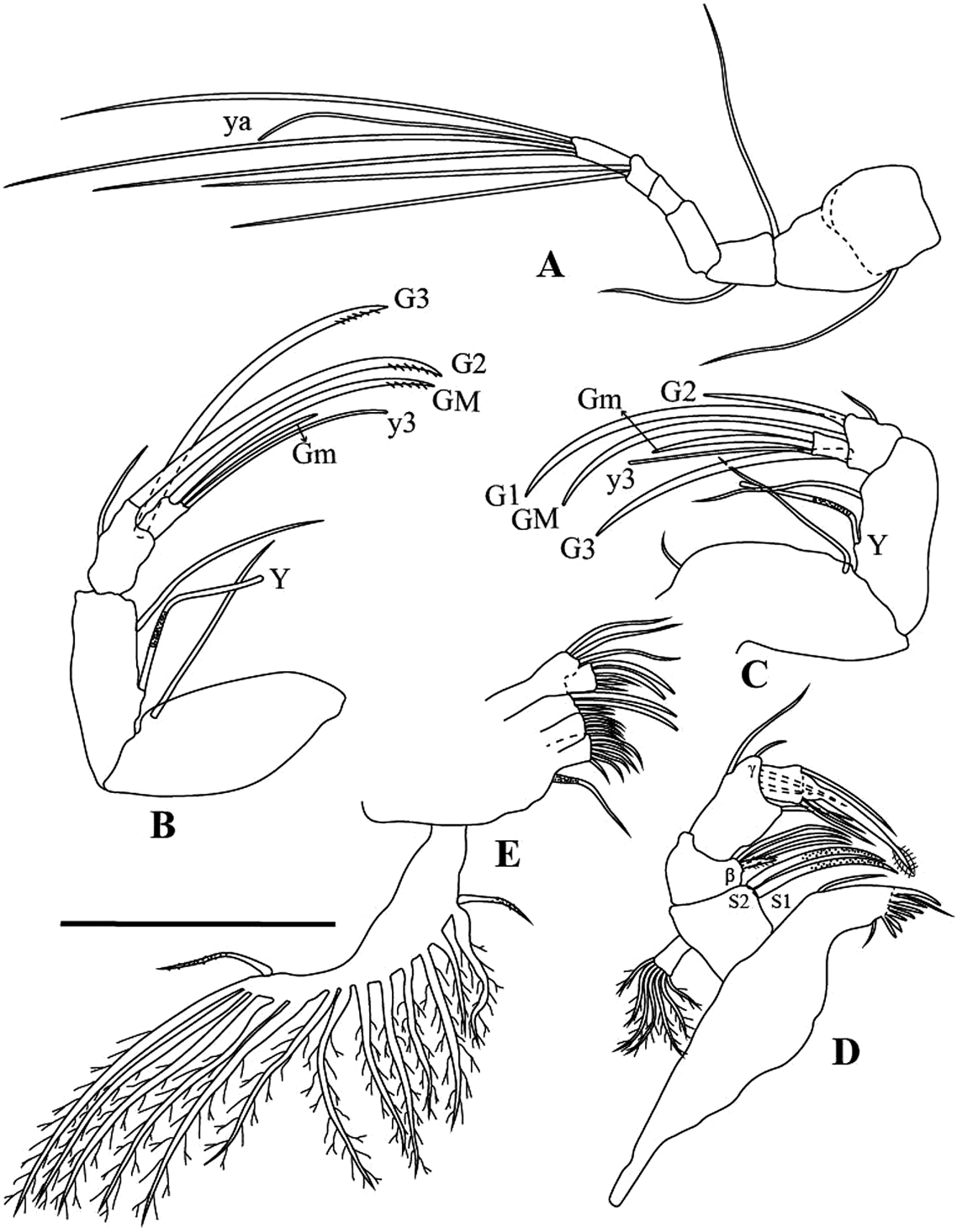


Fig. 4. *Rugosuscandona scharfi* gen. nov. sp. nov. A, B, D, E: holotype male (OK-TX-AW016-008: 01), C: allotype female (OK-TX-AW016-008: 02). A) A1, B) A2, C) A2, D) Md, E) Mxl with vibratory plate. Scale bar: 100 µm.

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.

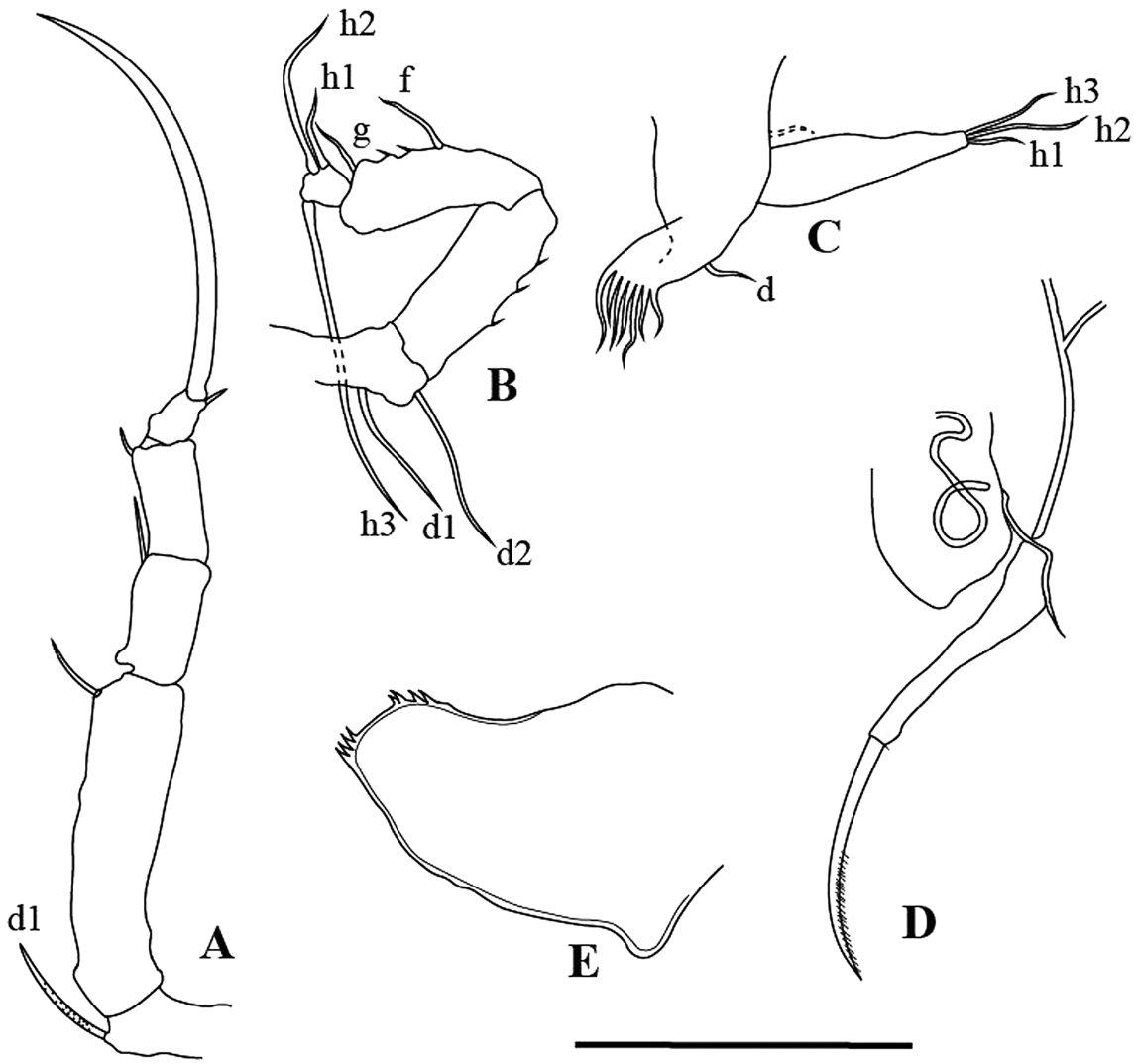


Fig. 5. *Rugosuscandona scharfi* gen. nov. sp. nov. A, B, E: holotype male (OK-TX-AW016-008: 01), C, D: allotype female (OK-TX-AW016-008: 02). A) T2, B) T3, C) T1, D) UR with genital organ and furcal attachment, E) labium. Scale bar: 100 µm.

Rugosuscandona scharfi 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 İzzet 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) posterodorsally 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

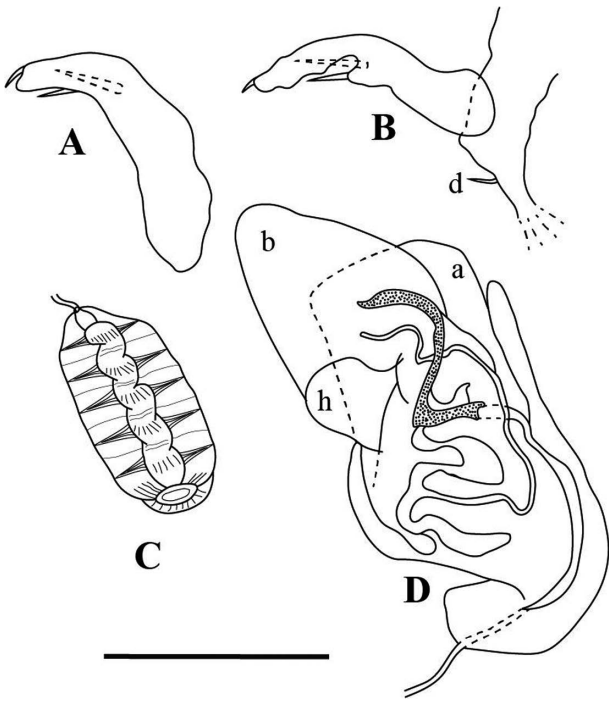


Fig. 6. *Rugosuscandona scharfi* gen. nov. sp. nov. holotype male (OK-TX-AW016-008: 01). A) left clasping organ, B) right clasping organ, C) Zenker's organ, D) hemipenis. Scale bar: 100 µm.

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 postero-distal 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 antero-dorsally 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 postero-distal 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 interno-distal smooth setae exceeding length of terminal segment and externo-medial seta reaching to about middle of terminal claw. Short seta on penultimate segment present externo-distally, 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 plumosed 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.

Rake-like organ not observed.

Labium wide with 4+4 spine-like teeth on both sides (Fig. 5E).

T1 (Fig. 6A, B). Prehensile palps not divided, almost equal in size (left being slightly longer) and modified into clasping organs. Masticatory 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.

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.

Average: L=0.63 mm, H=0.28, W=0.182 mm (n=7). T1 normally developed, smaller than male clasping organs, with 3 relatively short subequal h1–3 setae (Fig. 5C) (h2>h3>h1). h2 seta twice long of h1. G claws (G1–G3, GM, Gm) present (Figs 3B, 4C). G2 claw shortest, about ½ long of G1 and G3 claws. GM claw long reaching tip of G1 claw and slightly longer than G3 claw (compare with male G1 absent, G2≈G3≈GM>Gm). All claws smooth. y3 longer than Gm claw. Uropod same to that of male with genital part large, rounded and without appendages (Figs 3C, 5D). All other soft parts same to that of male.

Etymology. The species is named after Dr Burkhard W. Scharf (Germany) for his invaluable contribution to the ecology and taxonomy of the species of Ostracoda.

Discussion

The new genus, *Rugosuscandona* gen. nov., with its type species is described based on several diagnostic characteristics that differentiate it from its congeners. Therefore, we propose *Rugosuscandona* gen. nov. as a new genus of Candoninae from an artesian well in the Edwards Aquifer of Texas, USA. With the inclusion of this new genus, there are now 10 genera containing 44 species in the family that are found in USA, where the number of endemic species has increased to 30.

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 seta 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, *Marococandona* Marmonier, Boulal, and Idbennacer, 2005, *Caribecandona*, *Pioneercandonopsis* Karanovic, 2005, *Latinopsis* Karanovic and Datry, 2009, and *Candobrasilopsis* Higuti and Martens, 2012) of the tribe have normal pore canals with sensory setae (Karanovic 2004; Higuti and Martens 2012, 2014), the new genus can be differentiated by its high, elevated pore canals (0.25–0.30 µm in height).

In addition, the presence of a postero-dorsal flange on the LV has never been found in another genera of the tribe Candonopsini. Although ornamentation of the carapace is known in some species in different tribes of the subfamily Candoninae (*e.g.*, *Kencandona verrucosa* Karanovic, 2007, *Meridiescandona facies* Karanovic, 2003, *M. lucerna* Karanovic, 2003, *Areacandona korallion* Karanovic, 2007, and *Humphreyscandona ventosa* Karanovic, 2007) (see Karanovic 2003, 2007), the unique carapace ornamentation of *Rugosuscandona* gen. nov. is one of the most prominent characteristics of the new genus that can be used to distinguish it from all other genera, including fossil forms. According to previous studies (Krstić 1972; Krstić and Guan 2000), carapace ornamentation may be more common in Tertiary genera than in recent forms. This may have implications for understanding the historical background of *Rugosuscandona* gen. nov.

The new genus has a 6-segmented A1 without Rome and Wouter's organs. Among the 7 genera (*Candonopsis*, *Cubacandona*, *Marococandona*, *Caribecandona*, *Pioneercandonopsis*, *Latinopsis*, and *Candobrasilopsis*) of the tribe Candonopsini, only *Caribecandona* seems to bear 6-segmented A1 (III and IV segments fused) (Broodbakker 1983; Marmonier *et al.* 2005). According to Karanovic (2012), *Marococandona nicolae* Marmonier, Boulal and Idbennacer, 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., *Caribecandona* 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 *Caribecandona*, and 2 long and 1 short setae in *Rugosuscandona* gen. nov. Furthermore, despite the similarity in the numbers of A1 segments, *Caribecandona* and *Rugosuscandona* gen. nov. differs from 1 another in number and position of A1 setae. For example, in *Caribecandona,* 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, *Caribecandona* 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.*, *Humphreyscandonini* Karanovic, 2005) do not have bristles on the male A2, but mostly bear z-setae. Also, some genera have 2 short setae (*e.g.*, *Danielocandona*) or 3 short setae (*e.g.*, *Trajancandona* and *Undulacandona*) on the exopod (see Karanovic 1999; Smith and Kamiya 2015), while a majority of genera of Candoninae 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 (Külköylüoğlu *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 anchialine 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.*, *Candona 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* (Vejdovsky, 1882), *P. zschokkei* (Wolf, 1920), *P. rostrata* (Brady and Norman, 1889), and *Candonopsis kingsleii* (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 congeners 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 subtropics 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. ansa* 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 thermosbanacean, 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 (Külköylüoğlu, 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.

Acknowledgments

We thank Prof. Dan Danielopol (Karl-Franzens-Universität Graz), Prof. Dietmar Keyser (Universität Hamburg), and Prof. Ivana Karanovic (Hanyang University) for sharing their ideas about the new genus. Cem Berk (TÜBİTAK-MAM) helped on SEM photography. Weston Nowlin, Zachary Schwartz, Jonny Scalise, and Aaron P. Swink (Texas State University) assisted with sorting raw samples and counting ostracods.

References

Asmyhr, M. G., Linke, S., Hose, G., and Nipperess, D. A. 2014. Systematic conservation planning for groundwater ecosystems using phylogenetic diversity. PLOS ONE 9: e115132.

Baird, W. 1845. Arrangement of the British Entomostraca, with a list of species, particularly noticing those which have as yet been discovered within the bounds of the Club. History of the Berwickshire Naturalists' Club 2: 145–158.

Broodbakker, N. W. 1983. The subfamily Candoninae (Crustacea, Ostracoda) in the West Indies. Bijdragen tot de Dierkunde 53: 287–326.

Broodbakker, N. W. and Danielopol D. L. 1982. The chaetotaxy of Cypridacea (Crustacea, Ostracoda) limbs: proposals for a descriptive model. Bijdragen tot de Dierkunde 52: 103–120.

Culver, D. C. and Pipan, T. 2009. *The biology of caves and other subterranean habitats.* Oxford University Press, Oxford, 272 pp.

Danielopol, D. L. 1978. Über Herkunft und Morphologie der Süsswasser-hypogaïschen Candoninae (Crustacea, Ostracoda). Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Abt. I 187: 1–162.

Danielopol, D. L. 1980. An essay to assess the age of the freshwater interstitial ostracods of Europe. Bijdragen tot de Dierkunde 50: 243–291.

Danielopol, D. L., Baltanás, A., Morocutti, U., and Österreicher F. 2011. On the need to renew the taxonomic system of the Candoninae (Non-Marine Ostracoda, Crustacea). Reflexions from an analysis of data using the Yule Process. Geo-Eco-Marina 17: 195–210.

Danielopol, D. L. and Betsch, J. M. 1980. Ostracodes terrestres de Madagascar: Systématique, origine, adaptations. Revue d'Ecologie et de Biologie du Sol 17: 87–123.

Gidó, Z. 2010. Description of *Pseudocandona serfozoi* n. sp. (Crustacea, Ostracoda, Candonidae) from Romania. Bulletin de la Société des naturalistes Luxembourgeois 111: 131–143.

Gupta L. P. 1984. *Indocandona krishnakanti* gen. et sp. nov. (Crustacea: Ostracoda: Candonidae) from subterranean water of Bihar. Records of the Zoological Survey of India 8: 291–298.

Higuti, J. and Martens, K. 2012. Description of a new genus and species of Candonopsini (Crustacea, Ostracoda, Candoninae) from the alluvial valley of the Upper Paraná River (Brazil, South America). European Journal of Taxonomy 33: 1–31.

Higuti, J. and Martens, K. 2014. Five new species of Candoninae (Crustacea, Ostracoda) from the alluvial valley of the Upper Paraná River (Brazil, South America). European Journal of Taxonomy 106: 1–36.

Holsinger, J. R. and Longley, G. 1980. The subterranean amphipod crustacean fauna of an artesian well in Texas. Smithsonian Contributions to Zoology 308: 1–62.

Hutchins, B. T. and Schwartz, B. F. 2013. Food chain length in groundwater: patterns in δ15N range. Proceedings of the 16th International Congress of Speleology 403–409.

Hutchins, B. T., Schwartz, B. F., and Nowlin, W. H. 2014. Morphological and trophic specialization in a subterranean amphipod assemblage. Freshwater Biology 59: 2447–2461.

Hutchins, B. T., Engel, A. S., Nowlin, W. H., and Schwartz, B. F. 2016. Chemolithoautotrophy supports macroinvertebrate food webs and affects diversity and stability in groundwater communities. Ecology 97: 1530–1542.

Karanovic, I. 1999. Two interesting species of Candoninae (Crustacea, Ostracoda) from Montenegro (SE Europe). Biologie 69: 47–56.

Karanovic, I. 2001. *Meischcandona* gen. nov. from Africa, with a key to the genera of the subfamily Candoninae (Crustacea, Ostracoda). Biologie 71: 93–99.

Karanovic, I. 2003. Towards a revision of Candoninae (Crustacea: Ostracoda): description of two new genera from Australian ground waters. Species Diversity 8: 353–383.

Karanovic, I. 2004. Towards a revision of Candoninae (Crustacea, Ostracoda): on the genus *Candonopsis* Vávra, with descriptions of new taxa. Subterranean Biology 2: 91–108.

Karanovic, I. 2005a. A new Candoninae genus (Crustacea: Ostracoda) from subterranean waters of Queensland, with a cladistics analysis of the tribe Candonopsini. Memoirs of the Queensland Museum 50: 303–319.

Karanovic, I. 2005b. Towards a revision of Candoninae (Crustacea: Ostracoda): Australian representatives of the subfamily, with descriptions of three new genera and seven new species. New Zealand Journal of Marine and Freshwater Research 39: 29–75.

Karanovic, I. 2006. Recent Candoninae (Crustacea, Ostracoda, Candonidae) of North America. Records of the Western Australian Museum 71: 1–75.

Karanovic, I. 2007. *Candoninae* (*Ostracoda*) *from the Pilbara region in Western Australia*. Crustaceana Monographs, 7, Brill, Leiden, Boston, 442 pp.

Karanovic, I. 2012. *Recent freshwater Ostracods of the world: Crustacea, Ostracoda, Podocopida.* Springer Publishing, Heidelberg, Germany, 605 pp.

Karanovic, I. 2013. *Earicandona*, new genus and the first record of *Typhlocypris pratensis* (Crustacea, Ostracoda) from South Korea. Journal of Species Research 2: 145–158.

Karanovic, I. and Lee, W. 2012. A review of candonid ostracods (Crustacea: Ostracoda: Podocopida) from East Asia, with descriptions of five new species from South Korea. Zootaxa 3368: 7–49.

Karanovic, I. and Pesce, L. 2000. *Trapezicandona italica* n. sp. from the underground waters of Southern Italy (Crustacea, Ostracoda). Fragmenta Entomologica 32: 213–224.

Kaufmann, A. 1900. Über zwei neue Candona-Arten aus der Schweiz. Zoologischer Anzeiger 23: 108–110.

Klie, W. 1932. Die Ostracoden der Deutschen Limnologischen Sunda-Expedition. Archiv für Hydrobiologie 11: 447–502.

Kornicker, L. S. 2003. Morphology and Musculature of the Fifth and Sixth Limbs of Halocyprida (Ostracoda: Myodocopa). Journal of Crustacean Biology 23: 765–776.

Krömmelbein, K. 1975. Ostracoden aus der Kreide des Great Artesian Basin, Queensland, Australien. Senckenbergiana Lethaea 55: 455–483.

Krstić, N. 1972. Rod *Candon*a (Ostracoda) iz Kongerijskikh Slojeva juzhnog dela Panonskog basena (Genus *Candona* (Ostracoda) from Congeria beds of Southern Pannonian Basin). The Serbian Academy of Sciences and Arts, Section of Natural and Mathematical Sciences, Monographs CDL 39: 1–145. [In Serbian with English summary]

Krstić, N. and Guan, S. Z. 2000. A proposal for the systematics of the subfamily Candoninae (Ostracoda) with the description of the *Macedocandona*, new genus. Geologica Macedonica 14: 25–48.

Külköylüoğlu, O. 2009. Ecological Succession of Freshwater Ostracoda (Crustacea) in a newly developed rheocrene spring (Bolu, Turkey). Turkish Journal of Zoology 33: 115–123.

Külköylüoğlu, O., Gibson, R., Diaz, P. H., and Colin, J. P. 2011. *Bicornucandona* gen. nov., sp. nov. (Crustacea, Ostracoda) from Finegan Springs (Texas, U.S.A.). Zootaxa 3059: 47–58.

Latreille, P. A. 1802. Histoire Naturelle Genrale et Particulière, des Crustacés et des Insectes. 413 pp.

Longley, G. 1981. The Edwards Aquifer: Earth's Most Diverse Groundwater Ecosystem? International Journal of Speleology 11: 123–128.

Marmonier, P., Vervier, P., Gibert, J., and Dole-Olivier, M. J. 1993. Biodiversity in ground waters. Trends in Ecology & Evolution 8: 392–395.

Marmonier, P., Boulal, M., and Idbennacer, B. 2005. *Marococandona*, a new genus of Candonidae (Crustacea, Ostracoda) from southern Morocco: morphological characteristics and ecological requirements. International Journal of Limnology 41: 57–71.

Martens, K. 1987. Homology and functional morphology of the sexual dimorphism in the antenna of *Sclerocypris* Sars, 1924 (Crustacea, Ostracoda, Megalocypridinae), Bijdragen tot de Dierkunde 57: 183–190.

Martens, K. 1992. On *Namibcypris costata* n. gen., n. sp. (Crustacea, Ostracoda, Candoninae) from a spring in northern Namibia, with the description of a new tribe and a discussion on the classification of the Podocopina. Stygologia 7: 27–42.

Martens, K. and Savatenalinton, S. 2011. A subjective checklist of the Recent, free-living, non-marine Ostracoda (Crustacea). Zootaxa 2855: 1–79.

Mayr, E. and Ashlock, P. D. 1991. *Principles of systematic zoology*. McGraw-Hill, Inc. New York. 475 pp.

Mazepova, G. F. 1976. A new genus of Ostracoda from the fauna of Lake Baikal, and its relationship with the cave-dwelling *Candona taurica* from the Crimea. Trudy Limnologicheskogo Instituta 182: 54–79. [In Russian]

Meisch, C. 2000. *Freshwater Ostracoda of Western and Central Europe-Süsswasserfauna von Mitteleuropa* 8/3. Spektrum Akad. Verlag/ Gustav Fischer, Heidelberg, 522 pp.

Namiotko, T., Danielopol, D. L., Meisch, C., Gross, M., and Mori, N. 2014. Redefinition of the genus *Typhlocypris* Vejdovský, 1882 (Crustacea, Ostracoda, Candonidae). Crustaceana 87: 952–984.

Ogden, A. E., Quick, R. A., and Rothermel, S. R. 1986. Hydrochemistry of the Comal, Hueco, and San Marcos Springs, Edwards Aquifer, Texas. Pp. 115–131. *In*: Abbott, P. L. and Woodruff, C. M. Jr. (Eds) *The Balcones Escarpment: Geology, Hydrology, Ecology and Social Development in Central Texas*. Geological Society of America, San Antonio, Texas.

Ponder, W. F. 2004. Endemic aquatic macroinvertebrates of artesian springs of the Great Artesian Basin–progress and future directions. Records of the South Australian Museum Monograph Series 7: 101–110.

Rohner, N., Jarosz, D. F., Taipale, M., Kowalko, J., Yoshizawa, M., Jeffery, W. R., Borowsky, R. L., Lindquist, S., and Tabin, C. J. 2013. Cryptic variation in morphological evolution: HSP90 as a capacitor for the adaptive loss of eyes in cavefish. Science 342: 1372–1375.

Rouch, R. and Danielopol, D. L. 1997. Species richness of microcrustacea in subterranean freshwater habitats. Comparative analysis and approximative evaluation. Internationale Revue der gesamten Hydrobiologie und Hydrographie 82: 121–145.

Sars, G. O. 1866. Oversigt af Norges marine ostracoder. Forh Videnskab-Selsk Christiania 1865: 1–130.

Schornikov, E. I. 1969. A new subgenus of ostracods of the genus *Candona* from underground waters in Crimea. Zoologicheskii Zhurnal 4: 927–929.

Smith, R. J. 2011. Groundwater, spring and interstitial Ostracoda (Crustacea) from Shiga Prefecture, Japan, including descriptions of three new species and one new genus. Zootaxa 3140: 15–37.

Smith, R. J. and Kamiya, T. 2015. Four new species of the subfamily Candoninae (Crustacea, Ostracoda) from freshwater habitats in Japan. European Journal of Taxonomy 136: 1–34.

Stout, L. N. 1976. *Review and index through 1975 of Genus Candona (Ostracoda) in North America (Exclusive of Pre-Quaternary Species)*. The Geological Society of America, Inc. Microform Publication 6, Colorado, 82 pp.