

DESCRIPTION OF A NEW TRIBE *CABRALCANDONINI* (CANDONIDAE, OSTRACODA) FROM KARST AQUIFERS IN CENTRAL TEXAS, U.S.A.

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ABSTRACT

Cabralcandonini tribe n., with the type genus *Cabralcandona* gen. n. from an artesian well in the San Marcos, Texas (U.S.A.) and six other genera from karst aquifers in Texas, is proposed as a new tribe of the subfamily Candoninae (Candonidae) (Crustacea, Ostracoda). The new tribe and genus have morphological features that distinguish them from other members of the subfamily. The most diagnostic characteristics of the type genus are (1) two horn-like structures developed on the antero- and postero-dorsal margins of the left valve, (2) numbers of central muscle scars, (3) hexagonal or pentagonal (honeycomb-like) ornamentation on the subrectangular shaped carapace, (4) four segmented second antenna in both sexes, (5) absence of an exopod on A2, (6) shape and size of Y aesthetasc, (7) absence of e, f and g setae on cleaning leg, (8) flagellum (whip-like) uropod morphology, (9) shape of hemipenis, and (10) reduction in number of segments and setae on other limbs. Taxonomic keys for the tribes of the subfamily Candoninae including *Cabralcandonini* tribe n. are presented.

Introduction

Artesian wells are windows into otherwise inaccessible deep aquifer systems, and flowing artesian wells bring groundwater directly from the aquifer to the land surface. The name “artesian” traces its origins to the Province of Artois, France (Carpenter, 1891), where artesian groundwaters have been tapped for centuries. Natural and man-made artesian systems can support human usage, hypogean organisms, and many ecosystems including lentic and lotic aquatic habitats (Danielopol, 1978; Holsinger and Longley, 1980; Ponder, 2004; Külköylüoğlu, 2009; Culver and Pipan, 2009; Garza et al., 2015).

Artesian wells often discharge hypogean organisms, and some wells have a long history of intensive biological monitoring and sampling. Because of these efforts, and the fact that they allow access into an otherwise-inaccessible ecosystem, some artesian wells are associated with unique and high species diversity. Increasing our knowledge of groundwater species abundance and diversity, along with the biogeographic and ecologic processes that have contributed to observed diversity patterns, can support sound conservation activities and policies (Lopez et al., 2017).

Ostracods are small (adult freshwater forms range from 0.3 to 5.4 mm in length) aquatic invertebrates and are one of the most abundant and diverse groups of Crustacea. They can be found in almost all marine to freshwater habitats in natural (springs, creeks, rivers, pools, lakes, ditches etc.) and artificial settings (e.g., troughs, wells, canals, dams, ponds, etc.). Ostracods have a pair of valves (a carapace) composed of low magnesium / calcium ratio calcite (Chivas et al., 1986). Because of this calcified carapace, ostracods can be fossilized in sediments and are known from at least the Silurian period, about 425 Ma (Siveter, 2008; Williams et al., 2008). Individual species prefer certain environmental conditions (Külköylüoğlu, 1998), therefore, ostracods are excellent model organisms for evolutionary (Cohen and Johnston, 1987; Chaplin and Ayre, 1997), ecological (De Deckker, 1981; Külköylüoğlu, 2009), biological (Kesling and Crafts, 1962; Lopez et al., 2002) and paleontological studies (Tunoğlu, 2002; Tuncer and Tunoğlu, 2015). In addition, they are useful as indicators of water quality (Hoff, 1942; Wise, 1961; Bromley and Por, 1975; Benson, 1990; Mezquita et al., 1999; Külköylüoğlu and Vinyard, 2000).

The family, Candonidae, known for its worldwide distribution (Danielopol, 1978; Danielopol et al., 2011; Smith, 2011), contains at least 515 species (Martens and Savatentalinton, 2011; Külköylüoğlu et al., 2017a-e). Karanovic (2018) stated that no species of Candonopsini have ever been recorded from North America due to a lack of freshwater ostracod studies on the continent, failing to recognize the several genera and species (e.g., *Comalcandona*, *Lacrimacandona*, *Ufocandona*, *Rugosuscandona*) reported from Texas groundwaters (Külköylüoğlu et al., 2011; 2017a-d; 2018). Although there is debate about the taxonomic position of some species (see. e.g., Higuti and Martens, 2012; 2014), there are more than 46 genera described in the subfamily Candoninae (Karanovic, 2001; Külköylüoğlu et al., 2011; Külköylüoğlu et al., 2017a-e; Külköylüoğlu and Gibson, 2018). Most recently, descriptions of 5 new species from Texas (Külköylüoğlu

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et al., 2017a-e) increased the number of known species in the subfamily to 47 with 10 genera in North America. Of these, there are now more than 33 species endemic to North America (Karanovic, 2006; Külköylüoğlu et al., 2017a-e). Because of known undescribed taxa and a lack of studies in the area, these numbers are believed to be underestimated for the subfamily.

Here, we propose *Cabralcandonini* tribe n. and *Cabralcandona* gen. n. with the type species (*Cabralcandona mixoni* sp. n.) from the San Marcos Artesian Well, San Marcos, Texas, U.S.A.: the sixth genus found and described from this well. Six genera (*Ufocandona*, *Rugosuscandona*, *Lacrimacandona*, *Schornikovdona*, *Comalcandona*, *Bicornucandona*) previously included in other tribes are also transferred into the new tribe due to shared characteristics in carapace and soft body parts (see Külköylüoğlu et al., 2017a,b).

Methods

Site Description

The San Marcos Artesian Well (SMAW) (Fig. 1) is known for its exceptional biodiversity (Longley, 1981; Culver and Sket, 2000; Hutchins et al., 2014, 2016; Külköylüoğlu et al., 2017a-e; Külköylüoğlu and Gibson, 2018). It was completed in a relatively shallow portion of the confined zone of the San Antonio Pool in the Edwards Aquifer of Texas in 1895 (Stejneger, 1896). At 59.5 m deep, the well intersects a 1.5 m tall conduit (Holsinger and Longley, 1980) from which the water and biological materials are presumed to discharge. Excluding the new species proposed herein, 36 stygobiont species are known from the well (Hutchins 2018), and the number is rapidly increasing as renewed efforts describe undocumented diversity. Ten of these species (an undescribed erpobdellid leech, the cyclopoid copepod *Cyclops cavernarum* Ulrich, 1902, the asellid isopod *Lirceolus smithii* (Ulrich 1902), the helminth parasites *Amphibiocapillaria texensis* Moravec & Huffman 2000 and *Dendronucleata americana* Moravec & Huffman 2000, and five ostracods (Külköylüoğlu et al., 2017a-e)) are only known from the single site or the nearby San Marcos Spring (Chippindale, 2000; Hutchins et al., 2014, 2016; Külköylüoğlu et al., 2017a-e). More than 50 % of the 51 described stygobiont species known from this central Texas region are endemic to the Edwards Aquifer (Hutchins, 2018). However, considering the number of documented undescribed taxa and lack of in-depth studies in the region, the actual diversity of the well and aquifers are unknown, and higher species richness certainly exists (Schwartz et al., 2018).

Water quality is generally high at the site, which has been dye traced to San Marcos Springs, less than 1 km to the northeast (see details in Ogden et al., 1986). In November 2013, water temperature at the well averaged 22.3 °C (SD \pm 0.01), dissolved oxygen averaged 5.3 mg/l (SD \pm 0.01) and electrical conductivity averaged 608 μ S/cm (SD \pm 0.50).

Sample Collection and Description

All materials were collected from the type locality (Fig. 1) with a drift-net (100 μ m mesh size) placed on the outflow pipe. Sample collection intervals ranged from 24 to 72 hours, and each sample was sorted under a dissecting microscope to count and identify all invertebrates to lowest taxonomic level (species, for most organisms). All organisms were stored in 95 % ethanol in glass vials with poly-seal caps.

Ostracods were dissected in lactophenol solution using fine needles under a stereomicroscope, and soft body parts were mounted on glass slides, covered with coverslips, and sealed with clear fingernail polish. Each slide was labeled with a unique catalog number. Valves were kept in micropaleontological slides whenever possible. External views of carapace and valves were acquired by Scanning Electron Microscope (JEOL 6335 F SEM) after ostracods were prepared with hexamethyldisilazane (HMDS) as a drying agent at the TÜBİTAK-MAM Institute (Gebze, Turkey). SEM images of the internal views of the valves were also taken with Scanning Electron Microscope at the Research Service Center, Texas State University (U.S.A.). Line drawings of the soft body parts of holotype and allotype specimens were made with a camera lucida (Olympus U-DA) attached to an Olympus BX-51 microscope before the drawings were digitized in Adobe Illustrator CS5 (ADOBE). The following literature was used during species description: Broodbakker and Danielopol, 1982; Martens, 1987; Meisch, 2000, and Karanovic, 2004, 2005a-c, 2006, 2007, 2011, 2012, 2013, 2018. Methodological details can be found in Külköylüoğlu et al. (2017a-e). Materials and slides prepared for identification (catalog numbers OK-TX-AW036-055: 07-12) are stored at the Limnology Laboratory of the Biology Department, Abant İzzet Baysal University (Bolu, Turkey), and are available upon request.

Clustering Analyses

WinClada, version 1.00.08 (Nixon, 2002) along with the NONA program was used to elucidate best clustering relationships among 49 genera of the subfamily Candoninae. Two outgroup genera, *Cypria* and *Cyclocypris*, were chosen due to their distinct morphological characteristics compared to genera of the subfamily (for details see Karanovic, 2007). All of the 31 morphological characters (Table 1) and taxa used in the reduced model of Karanovic (2007) were included. We added 5 more characters and 10 genera published since 2007 to this data matrix (Table 1). Additional characters were chosen based on their importance for identification and prevalence in current taxonomic keys (e.g., see Meisch, 2000; Karanovic, 2007, 2012; Higuti and Martens, 2012, 2014). For example, there were no character states of Mx1 in the origi-

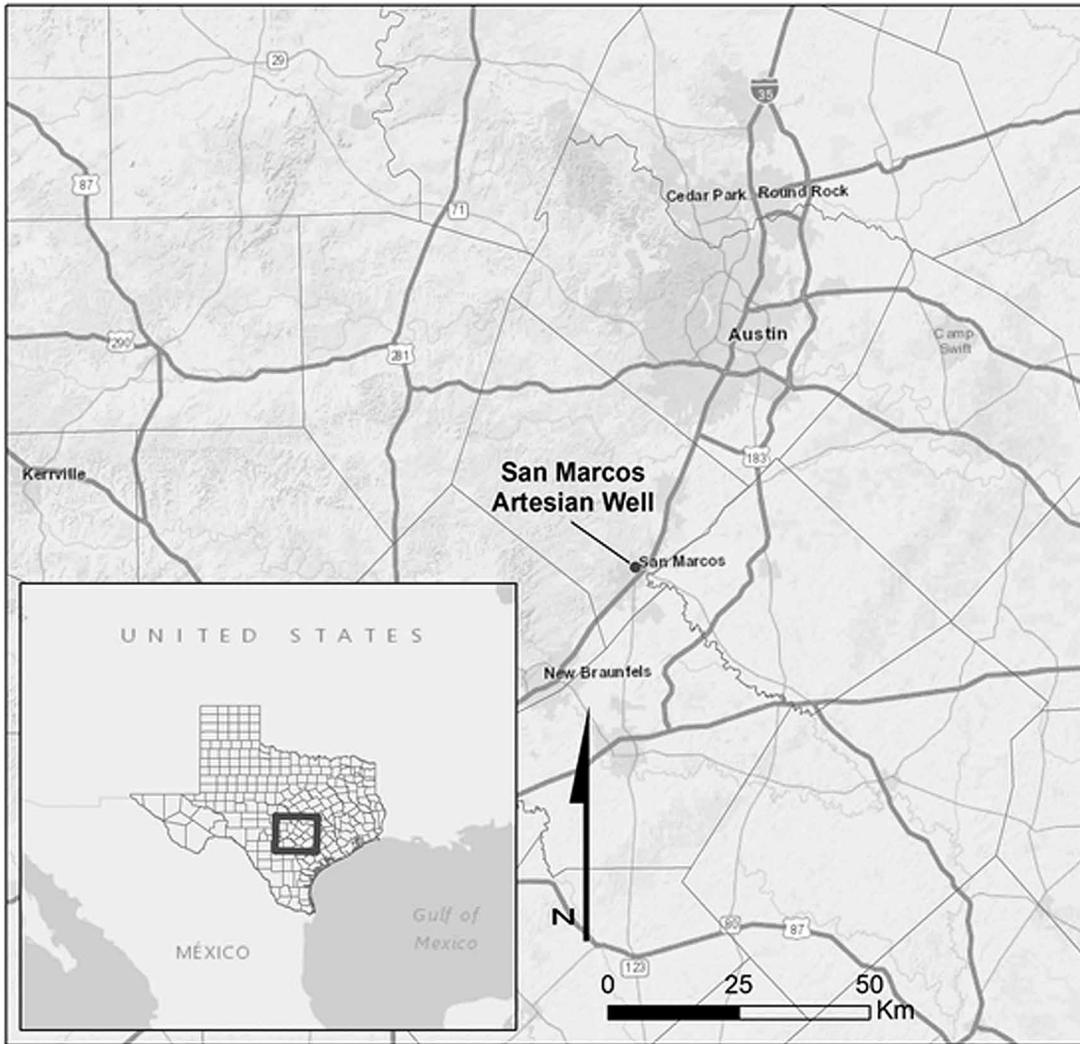


Figure 1. Type locality of *Cabralcandona mixoni* gen. et sp. nov. from Texas, U.S.A.

nal data matrix of Karanovic (2007). However, Mxl appears around the 7th larval (A7) stage (Meisch, 2000; Smith and Martens, 2000; Díaz and Lopretto, 2017) and is therefore an important character used in taxonomic keys. All characters in the data matrix were coded and weighted during computation of consistency (Ci) and retention (Ri) indices. As described in Karanovic (2007), except for the characters 23–30 and 33, which were weighted by 2, all characters were weighted by 1. Phylogenetic analysis was conducted via a heuristic search in WinClada-Nona along with the following default parameters of the Ratchet Island Hopper application whenever possible: 200 replications; 1 tree to hold/

iteration; 3 characters to sample; 10 random constraint levels and amb-poly= (amb: collapsing a branch if the ancestor and descendant have different states under the same resolutions of multi state characters or character states are unknown; poly: treating trees as collapsed). During which, tree bisection and reconnection (TBR+TBR) method of branch-swapping was repeated to search for the trees where the tree is cut about half and reconnected the remaining branches.

Abbreviations

A1, first antenna; A2, second antenna; G1–G3 and GM, Gm, claws on A2; H, height; L, length; LV, left valve; Md, mandibula; Mxl, maxillula; RV, right valve; T1, first thoracopod; T2, second thoracopod; T3, third thoracopod; UR, uropod; W, width.

Results

Systematic Description

- Class:** Ostracoda Latreille, 1802
- Subclass:** Podocopa Sars 1866
- Order:** Podocopida Sars, 1866
- Suborder:** Cypridocopina Baird, 1845
- Superfamily:** Cypridoidea Baird, 1845
- Family:** Candonidae Kaufmann, 1900
- Subfamily:** Candoninae Kaufmann, 1900
- Tribe:** Cabralcandonini tribe n.

Table 1. Total of 36 (0–35) morphological characters used in the cladistic analysis of the 49 genera belonging to nine tribes of the subfamily Candoninae (changed from Karanovic 2007).

Genus	Morphological Characteristic																																									
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
<i>Cypria</i>	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0			
<i>Cyclopyris</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Acandona</i>	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0			
<i>Amphitritecandona</i>	1	0	1	0	0	1	1	1	1	1	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0			
<i>Areaacandona</i>	0	0	1	1	0	1	1	1	1	1	0	0	0	1	1	0	1	1	0	*	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0			
<i>Baicalocandona</i>	1	0	0	0	1	1	0	1	0	0	1	0	1	0	1	0	1	0	?	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	?			
<i>Caaporacandona</i>	0	0	1	1	0	1	1	?	?	0	0	0	0	1	0	?	?	1	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
<i>Candona</i>	0	0	0	0	1	1	1	1	1	0	0	1	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0			
<i>Neglectocandona</i>	0	0	0	0	1	1	1	1	1	0	0	1	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0			
<i>Candonopsis</i>	0	0	0	0	1	1	0	1	0	1	0	0	1	0	0	1	1	0	0	1	*	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0			
<i>Abcandonopsis</i>	0	0	0	0	1	1	0	1	1	0	0	1	0	0	1	1	1	1	1	*	1	*	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0			
<i>Caribecandona</i>	0	0	1	0	1	1	0	1	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	1	0	0	0			
<i>Cryptocandona</i>	0	0	0	0	1	1	1	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?		
<i>Cubacandona</i>	0	0	0	0	1	1	0	1	?	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0			
<i>Danielocandona</i>	0	0	1	1	0	1	1	1	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0			
<i>Deminutiocandona</i>	0	0	1	1	0	1	1	1	*	1	0	0	1	0	1	1	1	1	*	1	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0			
<i>Eucandona</i>	0	0	0	0	1	1	0	1	0	1	0	0	1	0	1	0	1	0	1	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0		
<i>Fabaeformiscandona</i>	0	0	0	0	1	1	1	1	1	0	0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	1	0	0	0	1	1	0	0	0	1	0	0	1	0	0		
<i>Kencandona</i>	0	0	1	1	0	1	1	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0		
<i>Humphreyscandona</i>	1	0	1	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	*	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Indocandona</i>	0	0	0	0	1	1	1	1	0	0	0	0	1	0	1	1	1	?	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	
<i>Leicacandona</i>	0	0	1	1	0	1	1	1	1	1	0	0	1	0	1	1	1	1	*	1	0	*	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0		
<i>Marrococandona</i>	0	0	*	0	1	1	0	1	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	
<i>Meischcandona</i>	0	0	1	1	0	1	1	?	?	1	0	0	0	1	?	?	?	1	1	1	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Meridiescandona</i>	0	0	1	0	0	1	1	1	*	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Narnibcypris</i>	1	1	1	0	0	1	1	?	?	?	1	0	0	1	1	1	1	1	1	1	1	1	1	?	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0		
<i>Nannocandona</i>	0	0	1	1	0	1	1	?	?	1	0	0	0	1	0	?	?	1	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Notacandona</i>	1	0	1	1	0	1	1	1	*	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Origocandona</i>	0	0	1	1	0	1	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Paracandona</i>	0	0	0	0	1	1	?	?	?	?	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phreatocandona</i>	0	0	0	0	1	1	?	?	?	?	0	0	0	1	0	?	?	1	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pierrecandona</i>	1	0	1	1	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

Table 1. (Continued).

Genus	Morphological Characteristic																																							
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35				
<i>Pilbarcandona</i>	1	0	1	1	0	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0			
<i>Pioneeracandonopsis</i>	0	0	1	1	0	1	1	0	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0			
<i>Schellencandona</i>	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0		
<i>Terrestricandona</i>	0	0	1	0	1	1	1	?	?	1	0	0	0	1	0	?	?	0	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
<i>Terrestricypris</i>	0	0	1	1	1	1	?	?	?	1	0	0	0	1	0	?	?	0	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
<i>Trajanacandona</i>	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0			
<i>Trapezicandona</i>	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	1	0	*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	*	0	0	
<i>Typhlocypris</i>	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Pseudocandona</i>	0	0	0	0	1	1	1	1	*	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Latinopsis</i>	0	0	0	0	1	1	1	0	1	1	?	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	0	0	1	0	0	
<i>Rugosuscandona</i>	1	0	1	0	0	1	1	*	*	0	0	0	0	*	0	1	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	
<i>Ufocandona</i>	0	0	*	1	1	1	1	0	1	0	0	1	0	*	0	1	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0
<i>Cabraicandona gen. n.</i>	1	0	0	0	1	1	1	0	1	0	1	0	*	0	1	0	1	1	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lacrimacandona</i>	0	0	0	0	1	1	1	0	0	0	1	0	*	0	1	1	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Schornikovdona</i>	0	0	1	0	1	1	1	1	*	0	0	0	0	*	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bicornucandona</i>	1	0	0	0	1	1	1	0	0	0	0	0	0	*	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Comalcandona</i>	1	0	0	0	1	1	1	0	1	1	0	1	*	1	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hancockcandonopsis</i>	0	0	0	0	1	1	1	0	1	1	*	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Candobrasillopsis</i>	0	0	0	0	1	1	1	0	1	1	0	0	1	1	0	1	1	0	0	0	1	0	0	?	1	1	0	0	?	0	0	0	0	0	0	0	0	0	0	

Note that the two out group genera (*Cyprina* and *Cyclocypris*) placed in the first two rows in the matrix. Character states: O: Surface of carapace: smooth / rarely ornamented (0), usually ornamented with hard ridges and/or holes (1); 1: Marginal pore canals: straight and equally long (0), branched and unequally long (1); 2: Number of AI segments: seven/eight (0), less (1); 3: Number of AI segments: 7/6 (0), 5 (1); 4: Exopod on A1: present (0), absent (1); 5: Rome's organ: present (0), absent (1); 6: Swimming setae on A2: present (0), absent (1); 7: Seta z1 on male A2: seta-like (0), claw-like (1); 8: Seta z2 on male A2: seta-like (0), claw-like (1); 9: G2 claw on female A2: shorter than G1 and G3 (0), equally long as G1 and G3 (1); 10: Number of rays on vibratory plate of Mid: numerous (0), maximum of two (1); 11: Number of setae in bunch on Mid palp: three (0), more (1); 12: Terminal segment on Mid palp: square-shaped (0), several times longer than wide (1); 13: Setae in bunch on Mid palp: wide and armed with only one row of setules (0), thin, and armed with many small setules all along and around (1); 14: Number of setae on protopod T1: numerous (0), only four (1); 15: Prehensile palps: segmented (0), unsegmented (1); 16: Prehensile palps: with additional subterminal bumps (0), without such bumps (1); 17: Basal seta on T2: present (0), absent (1); 18: Seta d2 on T3: present (0), absent (1); 19: T1 seta on T3: present (0), absent (1); 20: Posterior seta on CR: always present / very rarely absent (0), never present (1); 21: Posterior claw on CR: normal (0), reduced (1); 22: Appendage on genital field: never / extremely rarely present (0), always / most usually present (1); 23: Lobe g on hemipenis: very strongly sclerotized (0), not strongly sclerotized (1); 24: Lobe b on hemipenis: without chitinized dorsal part (0), with chitinized dorsal part (1); 25: Lobe a: normal (0), tiny and thin (1); 26: Lobe a: present (0), absent (1); 27: Lobe a: different (0), centrally positioned with lower and usually flat b and h lobes, or b lobe with a ventral projection (1); 28: Terminal segment of T3: with two short and one long setae (0), different (1); 29: Terminal segment of T3: different (0), with two long and one short setae (1); 30: Terminal segment of T3: different (0), Th2 seta transformed into long claw (1); 31: Exopod on A2: present (0), absent/reduced (1); 32: t setae on A2: present (0), absent (1); 33: Male sexual bristles on A2: absent (0), present (1); 34: Setae in bunch on Mid palp: with row of setules (0), without setules (1); 35: Terminal segment of MXI palp: normal (0), minute (1). Note that multiple and missing character states correspond to *, ?, respectively (adapted from Karanovic 2007, 2018) and characters (31–35) are newly used in this study.

Type genus: *Cabralcandona* gen. n.

Other genera: *Bicornucandona* Külköylüoğlu et al., 2011, *Rugosuscandona* Külköylüoğlu et al., 2017, *Ufocandona* Külköylüoğlu et al., 2017, *Lacrimacandona* Külköylüoğlu et al., 2017, *Schornikovdona* Külköylüoğlu et al., 2017, *Comalcandona* Külköylüoğlu and Gibson 2017.

Etymology. The name is a combination of the last name of Dr. Maria Cristina Cabral with the genus *Candona* of the subfamily Candoninae. Gender feminine.

Diagnosis: A small candonine (< 0.5 mm in average). Carapace subrectangular (or at most one valve oval). Carapace partially or fully ornamented with hexagonal and/or pentagonal cells. Pore canals short to long with sensory setae. Four to five central muscle scars (also see discussion). Dorsally, carapace wide or narrow. Inner lamella broader on at least one marginal side than the other. Inner lamella with or without node-like structure (tubercles). A1 six- to eight-segmented. A2 four-segmented without exopod. t1-4-setae absent or not transformed to bristles in male. Aesthetasc Y very long with at least two segments. Md palp with a squarish terminal segment fused with medial claw. Third endite of Mx1 with one or two smooth bristles. Prehensile palps of T1 not segmented and symmetric to slightly asymmetric. T2 five-segmented with one basal (d1) seta. T3 four segmented without dp seta and e seta. Terminal segment of T3 with two long and one short setae. UR with one anterior claw and rami or flagellum (whip) type (cf. Cypridopsinae type), without setae. Hemipenis moderate in size and with rounded *h* lobe. Zenker's Organ small, with six or seven whorls of spines. Female genital field without processes.

Genus *Cabralcandona* gen. n.

Type species: *Cabralcandona mixoni* sp. n.

Other species: The genus is presently monospecific.

Etymology. The generic name is dedicated to the genus *Candona* after Dr. Maria Cristina Cabral for her continuous contribution to the knowledge and work on Ostracoda. Gender feminine.

Diagnosis.

In lateral view, carapace subrectangular, LV overlaps RV. LV with two horns; one dorso-anteriorly and one dorso-posteriorly. In dorsal view, carapace is very narrow with greatest width near mid-line. Hinge adont. Valve surface ornamented with hexagonal cells with normal pores bearing sensory setae. Internal view, LV with 8–10 well-developed tubercles ventrally on the posterior end. Four to five muscle scars visible in about the center of the valves. RV without such tubercles. A1 seven-segmented. A2 four-segmented with a well-developed claw-like seta on protopodite in both sexes. Exopodial plate and setae absent. t setae absent. Aesthetasc Y very long. G1-3 claws dimorphic in sexes, G2 claw in females long, about the same length as all segments. Md palp with a wide terminal segment and with three claws, claw in the middle fused with terminal segment. Gamma seta absent. Mx1-palp with a very short terminal segment. Third endite with one short, smooth bristle. Prehensile palps slightly asymmetric in the males. No vibratory plate and no *a* seta present in T1. T2 five-segmented with one long basal seta (d1). T3 four-segmented with one basal seta (d1), “*e-f-g*” setae absent. Terminal segment of T3 with two long and one slightly shorter claw-like setae. UR with flagellum type (rod-like) anterior claw, without setae and posterior claw. Hemipenis with rounded *h* lobe. Zenker's organ with seven (5+2) whorls of spines. Female genital field small, without appendages.

Type species: *Cabralcandona mixoni* sp. n. (Figs 2–5)

Etymology. The species is named after Bill Mixon for his contributions to the Texas Speleological Survey, Texas Cave Management Association, and Association for Mexican Cave Studies.

Type locality. San Marcos Artesian Well (SMAW), Hays County, Texas, U.S.A.:

29°53'22.5" N, -97°56'11.3" W, ~177 m ASL.

Material Examined.

Holotype: One male dissected, with soft body parts in lactophenol solution and sealed with translucent nail polish on one slide (no: OK-TX-AW036:01). Valves kept in micropaleontological slides (no: OK-TX-AW036:02). Collected on April 15, 2013 by Benjamin F. Schwartz and Benjamin T. Hutchins from the type locality.

Allotype: One female dissected, with soft body parts in lactophenol solution and sealed with translucent nail polish on one slide (no: OK-TX-AW36:03-04). Collected on April 15, 2013 by Benjamin F. Schwartz and Benjamin T. Hutchins from the type locality.

Dissected paratypes: One male (no: OK-TX-AW052:05-06) and one female (no: OK-TX-AW052:07-08) from the type locality. Collected November 29, 2013 by Benjamin F. Schwartz and Benjamin T. Hutchins from type locality.

Non-dissected paratypes: three males and four females, and six juveniles kept in 70 % ethanol. Collected on May 21, 22, and 23, 2013; November 6, 16, and 29, 2013; December 5, 9, 13, and 16, 2013; June 23 and 26, 2015; July 30, 2015; December 7, 2015 and November 2, 2016 by Benjamin F. Schwartz and Benjamin T. Hutchins from the type locality.

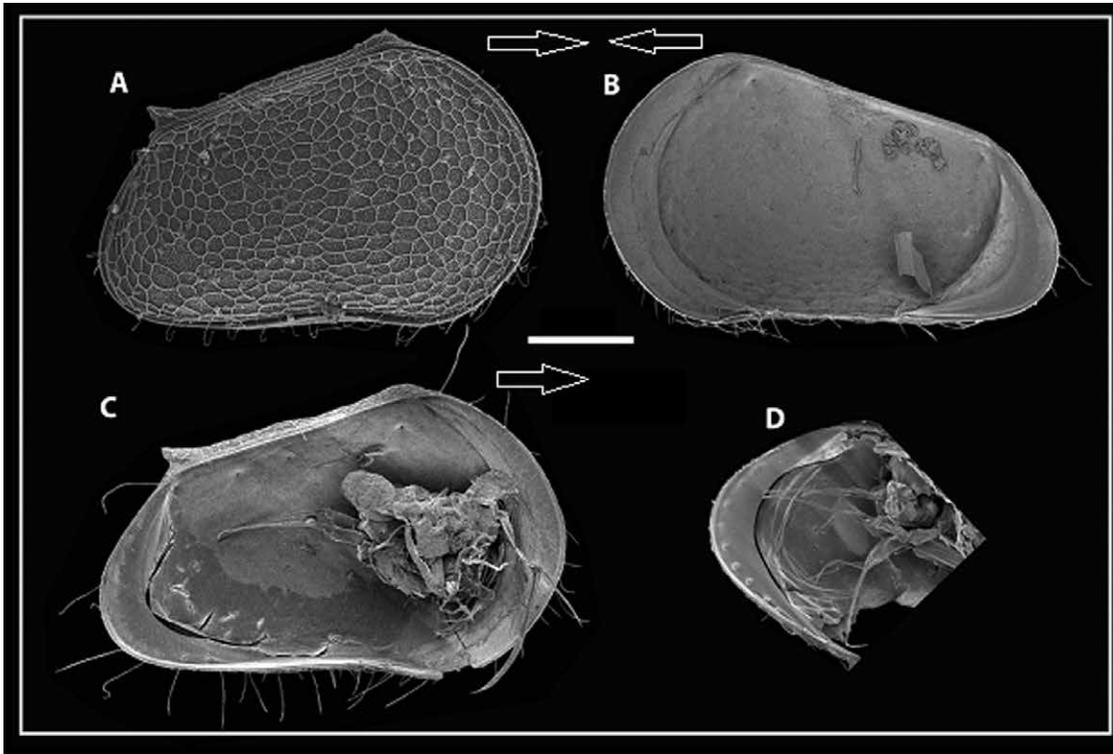


Figure 2. *Cabralcandona mixoni* gen. et sp. nov. male (A-C), female (D). A) Right side external view of whole carapace; B) RV internal view; C) LV internal view; D) LV internal view with node-like tubercles on posterior end. Arrows point anteriorly. Scale bar: 100 μ m.

Description

Diagnosis: The diagnosis of the new species is similar to that of the genus.

Male: Measurements: L= 0.44–0.52 mm (average 0.48 mm) (n = 3), H = 0.27–0.30 mm (average 0.28 mm) (n = 3), W = 0.13–0.14 mm (average 0.14 mm) (n = 2). LV overlapping RV from all sides (Fig. 2A). Carapace sub-rectangular in lateral view. Anterior margin rounded and broader than posterior margin, dorsal margin tapering posteriorly. Greatest height located in front of mid-length closer

to anterior margin (Fig. 2A–C). Carapace surface ornamented with wrinkled hexagonal cells, with small angular crenulated ridges inside these cells (Figs. 3D–F). Dorsal margin straight (not rounded). LV with two well-developed horn-like structures dorsally, anterior one slightly bent over RV (Fig. 2C). Normal pore canals with long sensory setae (Fig. 3F). Marginal pore canals reduced or short and not branched. Hinge adont. Carapace thick and opaque white in color. Four to five central muscle scars located near center (Fig. 3E). In dorsal view, carapace is fusiform-shaped, anterior margin more pointed and compressed than posterior end. Calcified inner lamella in RV smooth, slightly broader on posterior margin than on anterior margin (Fig. 2B). LV with 8–10 node-like tubercles posteriorly (Fig. 2C). Fused zone wide in both ends. Selvage thin in LV, not seen in RV.

A1 (Fig. 4A): seven-segmented. First segment articulated, with two anterior setae, one long claw-like stiff seta reaching about to the end of the third segment, and another medium-sized seta extending to midpoint of second segment. Rome and Wouters organs not seen. Second to fifth segments without setae. Penultimate segment with three equally long distal setae. Terminal segment with two equally long setae and one slightly short aesthetasc ya. All setae of A1 smooth. Length ratio of seven segments measured on centerline: 1.00 : 1.20 : 0.50 : 0.33 : 0.33 : 0.33 : 0.25.

A2 (Fig. 4B): four-segmented. First segment (protopodite) with a long claw-like postero-distal seta. Exopod absent on the second segment. Aesthetasc Y three segmented, very long and whip-like. Antero-distal setae is long and about the size of the GM claw. Setae t1-4 absent. Natatory (swimming) setae and aesthetascs y1-3 not seen (cf. female). z1 and z3 setae short and about the size of terminal segment, z2 seta is claw-like and about the same size as the G2 claw. G1 claw absent, G3 seta-like about one half of the GM claw. Gm claw less than half the length of G3. Claws and setae almost smooth.

Md (Fig. 4C): Md-coxa small compared to the palp, with six to seven smooth teeth and a small seta about one half the length of the longest tooth. Dorsal seta is almost the same size as the teeth. Md-palp four-segmented. First segment with two almost equally long smooth setae (S1, S2) posteriorly, and one shorter alpha (α) seta about one third the length of the S2-seta. Vibratory plate not seen. Second segment with four (3+1) sub-equally long claw-like setae. Beta seta absent. Third segment with one well-developed claw-like slightly plumose seta posteriorly and one small seta. Gamma seta absent. Terminal segment wide, with three claws, the middle one fused with the terminal segment. The middle and posterior claws plumose, anterior claw smooth and longer than the former two claws. No setae seen on anterior edge of the segments. Length ratios of four segments measured along centerline: 1.10 : 1.00 : 1.00 : 0.50.

Mxl (Fig. 4D): with three endites and a palp. Vibratory plate with seven to eight long plumose setae. Base of the first endite bearing one long seta slightly plumose about the length of the palp. First and second endites bearing four

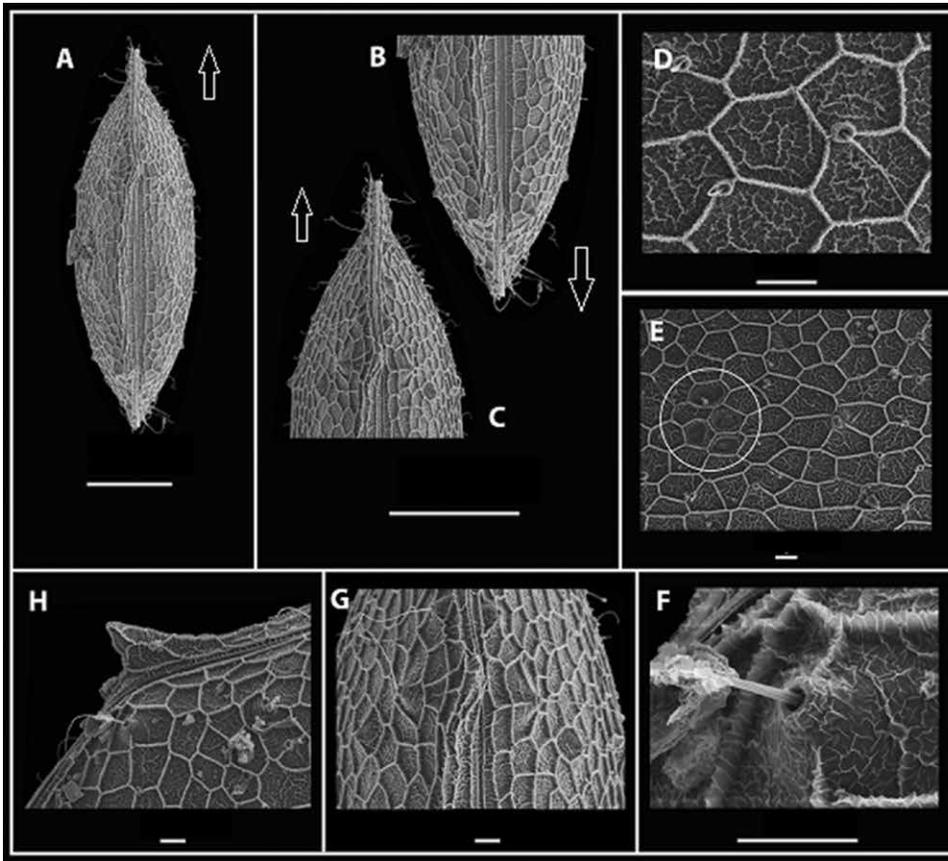


Figure 3. *Cabralcandona mixoni* gen. et sp. nov. female (A–C, H–G), male (D–F). A) Dorsal view of carapace; B) Dorsal view of posterior horn C) Dorsal view of anterior horn ; D) Close view of hexagonal ornamentations; E) Muscle scars; F) Close view of pore opening with sensory seta (note wrinkled cells on surface); G) Close dorsal view of anterior horn; H) Lateral view of posterior horn. Scale: 10 μ m for D–E. Arrows point anteriorly.

about the same size as the second segment. Setae *dp* and *d2* absent. *e*, *f*, and *g* setae ($e > f > g$) present on second, third and penultimate segments, respectively. Terminal segment with one well-developed long and smooth claw (*h2*), reaching about half the length of the second segment. Setae *h1* and *h3* not seen.

T3 (Fig. 5A) four-segmented. First segment with a medium sized smooth *d1* seta. *d2* and *dp* setae absent; *e*, *f*, and *g* setae absent. Terminal segment quadrate to trapezoidal, with three smooth claw-like setae (length: $h3 = h1 > h2$). Setae *h1* and *h3* long about the length of last two segments. Hemipenis (Fig. 5C) with a rounded lobe *h*. Lobe *b* sub-triangular. Lobe *a* with a pointing end dorsally. M process not visible. UR flagellum like with elongated ramus. Anterior and posterior setae absent. UR attachment simple. Zenker's organ (Fig. 5D) with seven (5+2) whorls of spines, ending with a wide sperm canal.

Female: L = 0.37–0.44 mm (average 0.41 mm) ($n = 2$), H = 0.23–0.24 mm (average 0.23 mm) ($n = 2$), W = 0.14–0.14 mm (average 0.14 mm) ($n = 2$). Carapace similar to that of male in shape (Figs. 2D, 3A–C, G–H), except for slight differences in size. All G-claws on A2 smooth (Fig. 5E). A short subapical seta present on the anterior end of the penultimate segment. Aesthetascs *y1* and *y2* absent, aesthetasc *y3* small and about the size of terminal segment. Lengths: $G3 > G1 > GM > G2 > Gm$. *G2* claw about half length of *G1* and *G3* claws. *Gm* seta-like and about 4x the length of the terminal segment. Genital field small without appendages (Fig. 5G). All other soft parts are similar to those of the male. T1 normally developed with three subequally long *h1*, *h2*, and *h3* setae on distal end of endopod (Fig. 5F). Masticatory process with 5 plumose and 1 smooth setae. One medium-sized smooth “*d*” seta present.

Sympatric Ostracods

In addition to *Cabralcandona mixoni* sp. n. et gen. n., five other hypogean ostracod species (*Ufocandona hannaleeae*, *Rugosuscandona scharfi*, *Lacrimacandona wisei*, *Cypria lacrima*, *Namiotkocypria haysensis*, (Külköylüoğlu et al., 2017a–d, Külköylüoğlu 2018) have also been documented at the San Marcos Artesian Well.

Phylogeny

Cluster analysis produced a majority consensus tree with 117 steps (Ci = 27, Ri = 72) for the 49 genera, using the 36 morphological characters in more than 100 equally parsimonious trees (Fig. 6). *Cabralcandona* gen. n. is clearly

and six short apical setae, respectively. Third endite with one smooth bristle-like seta about one half the length of the longest seta, and two long and one short slightly plumose setae. MxI palp with elongated penultimate segment and two smooth setae, terminal segment about one quarter length of first segment, quadrate, and with three setae about the same length of two segments. Rake-like organ (Fig. 4E): comb-like with small teeth. Hypostome (Fig. 4F) simple rounded.

T1 (Fig. 4G–H): with well-developed and slightly asymmetric prehensile palps. Palps not divided, distal end hook-shaped. End of apical margin of the palps with three spine-like structures and one smooth seta above these spines. Left palp slightly longer and thinner than right palp. Vibratory plate not visible. *a* seta absent. Setae *b*, *c*, and *d* smooth and almost equally long. Masticatory process with 5 medium-sized apical setae.

T2 (Fig. 5B): five segmented with a long (*d1*) slightly serrated basal seta on the first segment,

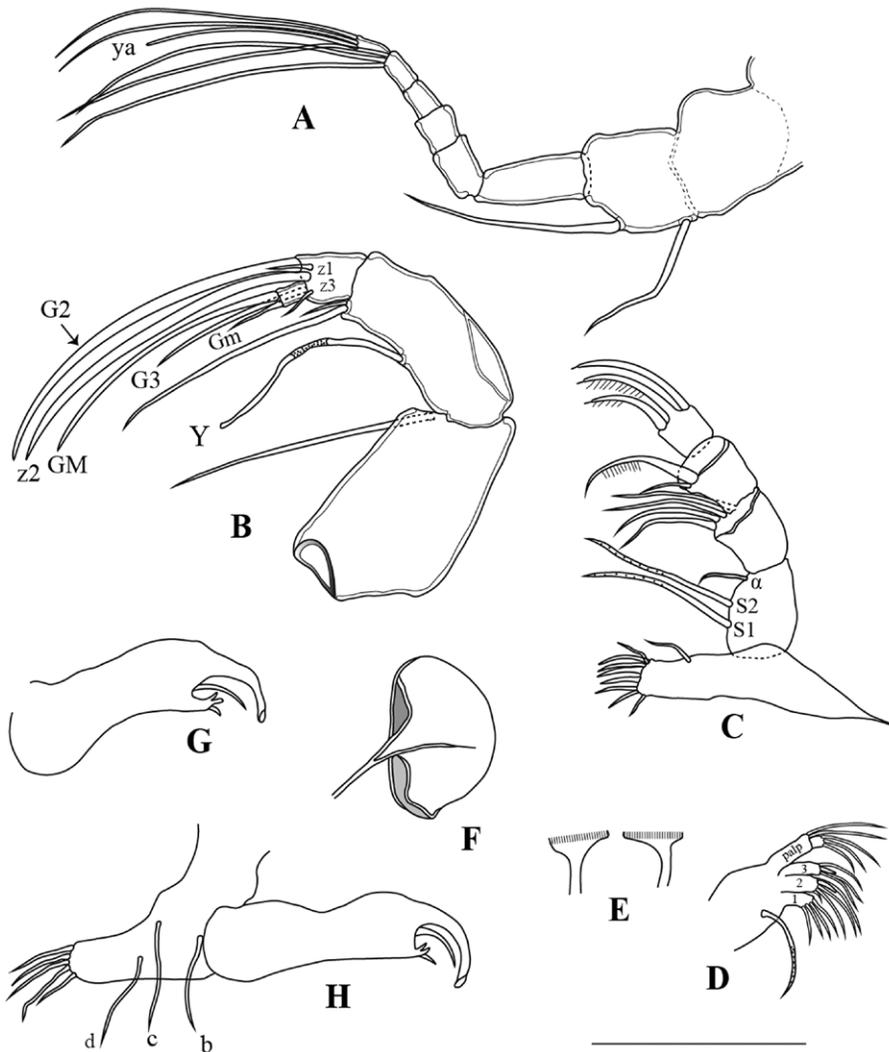


Figure 4. *Cabralcandona mixoni* gen. et sp. nov. Male: A) Antennule (A1); B) Antenna (A2); C) Mandible (Md); D) Maxillule (Mx1); E) Rake-like organ; F) Hypostome; G) Right clasp organ; H) Left clasp organ. Scale: 50 μ m for A–C, E; 40 μ m for D; 60 μ m for F; 25 μ m for G–H.

brasilopsis in Higuti and Martens (2012) and *Abcandonopsis* in Karanovic (2004).

Several characteristics distinguish *Cabralcandona* from other genera, notably the two horn-like structures positioned dorsally on the LV, on nearly opposite ends of the hinge. *Bicornucandona* bears two horns on the LV but they are located in about the center of dorsal margin. We consider these structures diagnostic for the new genus, since they are also present in juveniles. Three of the genera placed closely to each other in the new tribe (*Cabralcandona* gen. n., *Rugosuscandona* and *Ufocandona*) seem to exhibit more similarities with one another than with other genera. For example, all three bear hexagonal and/or pentagonal cell-type ornamentations on the carapace surface although these structures are scarce and mostly restricted to marginal zones in *Ufocandona*.

Külköylüoğlu et al. (2017 a-c) stressed the importance of carapace ornamentation for species identification and as indication of microhabitat characteristics. The authors point out that carapace ornamentation may be more prominent in fossil (i.e., Paleogene-Neogene) forms (Krstić, 1972; Krstić and Guan, 2000) relative to recent forms. The ornamentations unique to Cabralcandonini may imply that the tribe shares a close relationship to ancestral forms. However, without fossil representatives of the Cabralcandonini genera, this hypothesis remains unsupported. Below, we discuss some body parts, and compare each with other taxonomic groups.

Several body parts are informative about the relationship between Cabralcandonini and other taxonomic groups:

1. Muscle scars: The subfamily Candoninae and tribe Candonopsini are characterized by six (one elongated + 3 anterior + 2 posterior) central muscle scars (Karanovic, 2004), previously characteristic for the Candonidae family (Meisch, 2000). In Cabralcandonini, there are only five internal scars, one of which is faint or invisible in external view. Muscle scars are invisible (or not very obvious) in external view in three genera (*Ufocandona*,

separated from other genera but clustered together with six other genera (*Rugosuscandona*, *Ufocandona*, *Bicornucandona*, *Lacrimacandona*, *Schornikovdona*, *Comalcandona*) in the new tribe. However, cluster tree results suggest uncertainty in the taxonomic placement of several other genera. Indeed, relatively high Ci and Ri values suggest the prevalence of homoplastic change and/or convergence among the genera of the subfamily. However, following the current taxonomic keys (see discussion), the scenario may be seen differently where placement of some genera among the tribes differs.

Discussion

Cabralcandona gen. n. is assigned as the type genus of the new tribe Cabralcandonini tribe n., which shares some common characteristics with genera of the tribe Candonopsini, including a trapezoidal carapace, short marginal pore canals, A1 six or seven segmented, absence of bristles on A2 in males, terminal claw of Md palp fused with the apical segment, presence of two long and one short setae on the terminal segment of T3, female genital field without appendages, numbers of rows of spines on Zenker's organ, and absence of posterior seta on UR. Also see discussion about the taxonomic placements of *Cando-*

Rugosuscandona, *Lacrimacandona*) although they can be seen more clearly in *Cabralcandona mixoni* sp. n. et gen. n., and others (*Schornikovdona*, *Comalcandona*, *Bicornucandona*).

2. A1: The numbers of segments and chaetotaxy of A1 differ among genera (Karanovic, 2005a, b, c). Five genera (*Ufocandona*, *Lacrimacandona*, *Comalcandona*, *Bicornucandona*, *Cabralcandona* gen. n.) possess about seven segments while *Schornikovdona* bears five segments in A1. However, *Pioneercandonopsis*, and both *Rugosuscandona* and *Caribecandona* possess four and six A1 segments, respectively. As suggested previously (Karanovic and Marmonier (2003), Higuti and Martens (2014), Smith and Kamiya (2015), and Külköylüoğlu et al. (2017a-c, e)), a reduction in the numbers of segments of any organ or appendage (i.e., A1) likely represents a derived character state, possibly arising via paedomorphosis (Danielopol, 1978, 1980).

3. A2: Both females and males of the new genus have four segments in A2 without an exopodial plate. Although four or five A2 segments are found in different candonid genera (Karanovic, 2001, 2003a,b, 2012), absence of the exopod (or exopodial plate) is only known from *Rugosuscandona* and *Ufocandona* (but see exception in the males of *Ufocandona*) (Külköylüoğlu et al., 2017a,b). There are no sensory bristles on the A2 of males of the new genus, which is similar to five other genera (*Rugosuscandona*, *Ufocandona*, *Comalcandona*, *Cubacandona* and *Marococandona*). The new genus exhibits a sexually dimorphic character in the length of G-claws (G1–G3, GM, Gm), similar to those seen in several other genera in the tribe Candonopsini (Karanovic, 2006; Külköylüoğlu et al., 2017c). For example, G1–G3 claws on A2 are unequally long in three genera (*Lacrimacandona*, *Pioneercandonopsis* and *Meridiescandona*), but several North American species (e.g., *Candona peircei* Turner, 1895; *C. sigmoides* Sharpe, 1897; *C. suburbana* Hoff, 1942; *C. acuta* Hoff, 1942; *C. crogmaniana* Turner, 1894; *C. inopinata* Furtos, 1933; *C. intermedia* Furtos, 1933; *Eucandona rectangulata* (Alm, 1914); *Typhlocypris elliptica* (Furtos, 1933)) bear subequally sized claws (Karanovic, 2006; Külköylüoğlu et al., 2017a-d).

4. Md-palp: This is also one of the important diagnostic characteristic that separates the new tribe Cabralcandonini from other tribes of the subfamily (Table 1). While setae in bunch on the Md palp have no setules in the new tribe, these setae bear setules in other tribes. Besides, there are important differences in the numbers and shape of setal structures of the palp between *Cabralcandona* gen. n. and other members of the subfamily. For example, only the alpha (α) seta is present (beta and gamma setae absent on the other segments) on the first segment of the palp in the new genus. While alpha seta absent in *Rugosuscandona*, none of these setae (alpha, beta, and gamma) are present in the genus *Ufocandona*. Furthermore, *Cabralcandona* gen. n. has a group of 4 claw-like setae on the second segment (diagnostic character) while some other genera have 3 (e.g., *Rugosuscandona*) (Külköylüoğlu et al., 2017b), four (e.g., *Candonopsis*, *Ufocandona*, *Comalcandona*) or five (3+2) setae (e.g., *Maroco-*

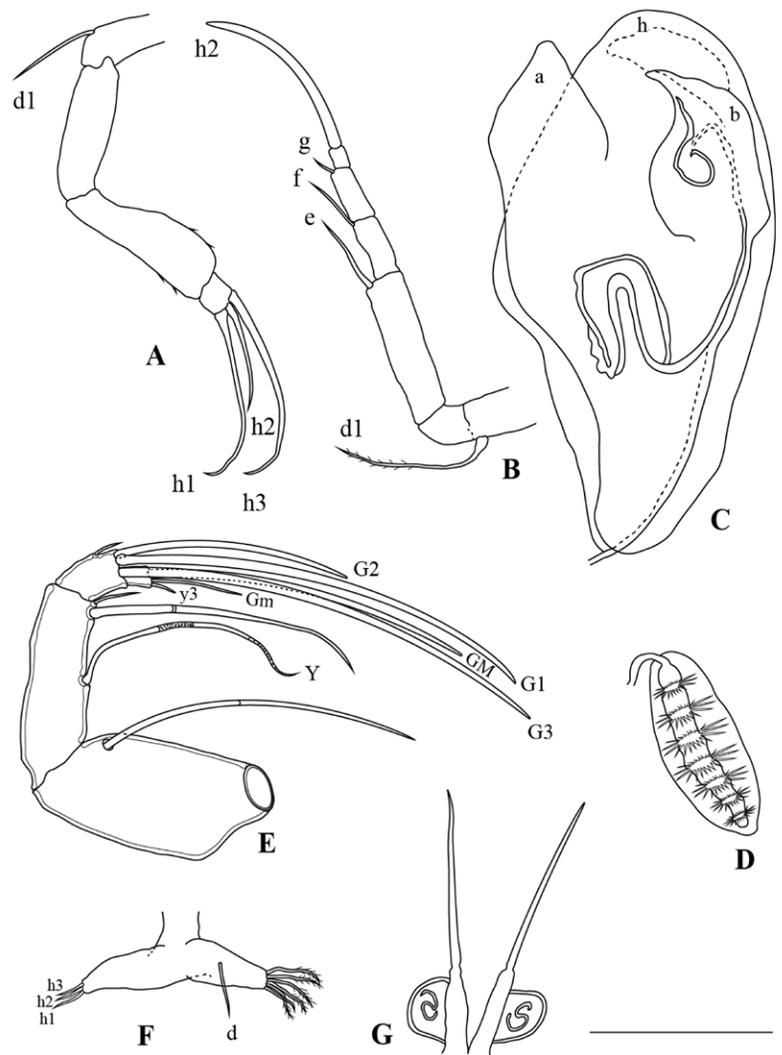


Figure 5. *Cabralcandona mixoni* gen. et sp. nov. A) T3; B) T2; C) Hemipenis; D) Zenker's organ; E) Female Antenna (A2); F) T1; G) Uropod of female with genital organ. Scale: 50 μ m for A–C, E; 60 μ m for D; 55 μ m for F–G.

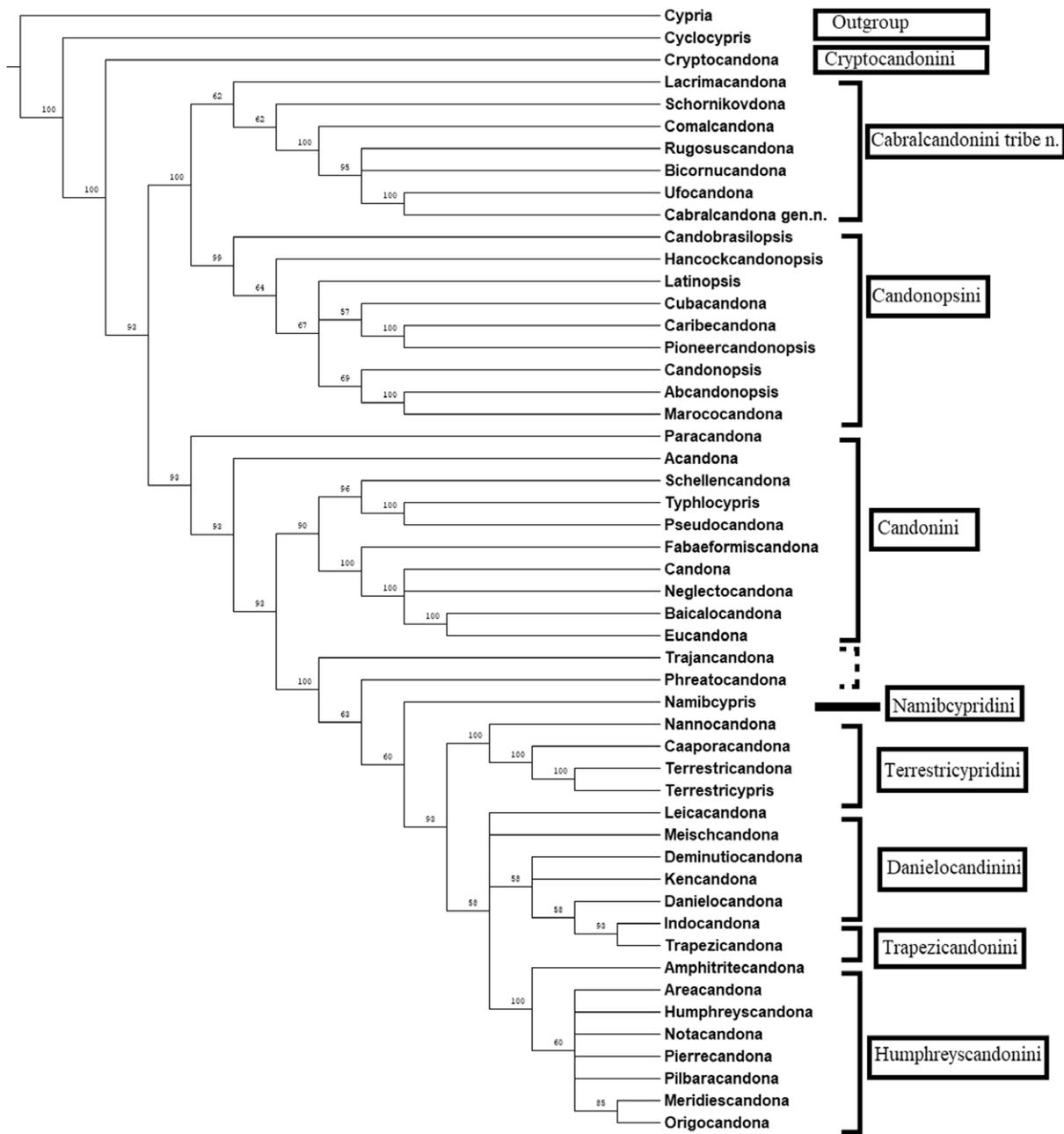


Figure 6. Clustering relationships of nine tribes of the subfamily Candoninae with Cabralcandonini tribe n. and its new genera *Cabralcandona* gen. n.

candona) (Marmonnier et al., 2005). The size of the terminal segment is variable among genera of both tribes Candonopsini and Cabralcandonini tribe n. According to the taxonomic key of Karanovic (2012), one of the main differences between the Md-palp of *Candonopsis* and *Latinopsis* is the size of the Md palp. While the former has a long palp (length of terminal segment more than 3× longer than width), the latter genus has a nearly

square terminal segment (Karanovic and Datry, 2009). *Cabralcandona* gen. n. has a relatively large terminal segment fused with the center claw. The segment is relatively large with an almost square shape. Such differences are common not only in the new tribe but also among other tribes within Candonidae (e.g., see Broodbakker, 1983; Karanovic, 2001, 2008, 2012; Karanovic and Datry, 2009; Higuti and Martens, 2012, 2014; Külköylüoğlu et al., 2017a-d).

5. Mxl: *Cabralcandona* gen. n. is the only genus within the tribe that bears a short and smooth seta on the third endite of Mxl. The number of setae on the palp varies from 5 to 10 among the genera of the tribe Candonopsini but in *Cabralcandona* gen. n., there are two and three smooth setae on the penultimate and terminal segments of the palp, respectively. *Ufocandona* is the only genus with 5 setae, whereas the other genera have 8, 9, or 10 setae and claws (e.g., *Candonopsis linnaei* Karanovic, 2008). Herein, we only consider the differences in the number of setae. However, there are additional differences in the type of seta (e.g., plumose, setose or smooth: Smith and Kamiya, 2015; Karanovic, 2011; Külköylüoğlu and Gibson, 2018).

6. T1: *Cabralcandona* gen. n. has nearly symmetrical male prehensile palps, like three other genera of the subfamily **Candoninae** (cf. *Latinopsis*, *Pioneercandona*, *Rugosuscandona*). The absence of a vibratory plate in T1 in *Cabralcandona* gen. n. is also unusual, first reported for *Rugosuscandona*, and not common in members of the tribe Candonopsini. Additionally, *Rugosuscandona* and *Cabralcandona* gen. n. are the only genera in the new tribe that do not have a seta. This warrants further investigation since description of this seta along with others (*b*, *c*, *d* setae) can be difficult due to their small size.
7. T2–T3: The numbers of setae (*e*, *f*, *g* and basal (d1) setae) on T2 in the new genus is similar to related genera (but compare the type and size of setae in Külköylüoğlu et al., 2017a–d; Külköylüoğlu and Gibson, 2018) except for *Cubacandona*, *Candonopsis* and *Lacrimacandona*. In contrast, T3 of *Cabralcandona* gen. n. has only one basal (d1) seta and no *e*, *f*, *g* setae, similar to *Rugosuscandona*. Considering that all other genera of the new tribe bear at least two basal and one of the three other setae, the reduced setation on thoracic legs may be an additional adaptation to underground environments.
8. UR: *Cabralcandona* gen. n. has a flagellum type UR (diagnostic character of the genus) that is very similar to members of the subfamily Cypridopsinae. This character is also present in *Ufocandona* and *Rugosuscandona*. Two claws and two setae on UR is a common character state in cypridoid ostracods (Meisch, 2000) although the appendage is variable among members of Candoninae. *Caribecandona* (Broodbakker, 1983), *Indocandona* (Gupta, 1984), *Candonopsis* (e.g., see *Candonopsis (Abcandonopsis) aula*) (Karanovic, 2004), and *Bicornucandona* (Külköylüoğlu et al., 2011) have a single claw on the UR while *Lacrimacandona* has two small claws. A flagellum (or whip-like) type UR is very rare among the species of Candoninae (but see e.g., *Danielocandona lieshoutae* (Broodbakker, 1983)). Once again, the new genus exhibits a reduction in soft body parts. Indeed, McKenzie (1982) and Higuti and Martens (2012) pointed out that such reduction in size and chaetotaxy in the uropodal ramus of cypridoid species has occurred many times in different lineages, as an example of parallel evolution (homeomorphy) in non-marine ostracods. Knowledge about increased appendage length or reduction may provide additional understanding about habitat type. For example, in amphipods and isopods, increased setation and increased appendage length is often associated with open water type subterranean habitats (i.e. phreatic zones, vadose zones) while reduced setation and reduced appendage length is often associated with closed water type habitats (i.e. hyporheic zones) (Marmonier et al., 2005; Culver and Pipan, 2009).
9. Zenker's Organ: The new genus has 5+2 whorls of spines on the Zenker's organ. A similar pattern can be found in the members of the tribe Candonopsini (see discussion in Külköylüoğlu et al., 2017b, c).
10. Hemipenis: *Cabralcandona* gen. n. has a relatively small hemipenis (and Zenker's Organ) compared to other genera (e.g., cf. *Lacrimacandona*, *Rugosuscandona*). We were not able to observe an M-process in the hemipenis, but other parts (lobes) are unique to the genus. For example, lobe *a* with a sharp pointing end is clearly visible.

Cabralcandona gen. n. and two other congeners (*Rugosuscandona* and *Ufocandona*) are closely separated from others and clustered in the new tribe (Fig. 6). Although these three genera show clear morphological differences at the genetic level, they also share the following characters (Table 1) in common: 1) carapace ornamented with hexagonal or pentagonal cells, 2) numbers of segments in A2, 3) absence of t seta on A2, 4) absence of gamma seta on Md, 5) absence of seta *a* on T1, 6) presence of basal seta on T2 and T3, 7) absence of seta *e* on T3, 8) two long and one short setae on T3, 9) presence of rod-like (flagellum) claw on UR, 10) square or medial lobe in hemipenis. The tribe Candonopsini (Candoninae, Candonidae) previously included 13 subgenera (*Abcandonopsis*, *Candobrasilopsis*, *Candonopsis*, *Caribecandona*, *Comalcandona*, *Cubacandona*, *Hancockcandonopsis*, *Lacrimacandona*, *Latinopsis*, *Marococandona*, *Pioneercandonopsis*, *Rugosuscandona*, *Ufocandona*) but four genera (*Comalcandona*, *Lacrimacandona*, *Rugosuscandona*, *Ufocandona*) are now transferred to the new tribe Cabralcandonini tribe n.

Relationships among genera depicted in Figure 6 differ from the consensus tree of Karanovic (2007), because of potential factors including 1) the use of additional characters (e.g., absence of exopod in A2, flagellum-like UR), and 2) the number of genera included (49 versus 39 (sub)genera). Presence of polytomies among some genera also suggests that the number of characters may not be enough to discriminate clustering groups. Based on the cluster tree (Fig. 6), four other genera (*Bicornucandona*, *Comalcandona*, *Lacrimacandona*, *Schornikovdona*) can be tentatively placed with three closely related genera (*Cabralcandona* gen. n., *Rugosuscandona*, *Ufocandona*) of the new tribe. Considering that all these seven genera are found from the same geographic location and similar habitats (artesian well and/or spring waters), placement of these genera into the new tribe may be supported by the cluster tree. However, this placement does not correspond to the most current taxonomic keys (e.g., see Karanovic, 2007, 2012, 2018), in which some of these genera have already been described in other tribes. For example, presence or absence of posterior seta on the uropod is one of the main taxonomic character states separating the two close tribes Candonini (seta present) and Candonopsini (seta absent) (Karanovic, 2012). Following the key, for example, two genera (*Bicornucandona* and

Schornikovdona) belong to the tribe Candonini while two others (*Comalcandona*, *Lacrimacandona*) are placed in the tribe Candonopsini. Similarly, *Trajancandona* and *Phreatocandona* are supposed to be found in the tribe Candonini but the tree (Fig. 6) apparently separates these two from others. Although Karanovic (2007) reached a similar result, she included these two genera into the tribe Candonini following the taxonomic key. Relatively high Ci and Ri values suggest considerable uncertainty in the placement of genera within tribes because of a high degree of homoplasy. Karanovic (2007, 2018) emphasized that the phylogeny and evolution of Candonopsini needs to be investigated with molecular data (also see Hiruta et al., 2016). Although we agree that molecular data is valuable for phylogenetic analysis, obtaining adequate sample size across all or most taxa can present a challenge for construction of comprehensive molecular-based phylogenies.

Adaptations and Ecology

According to Marmonier et al. (2005, and references therein), and Külköylüoğlu et al. (2017b,c), hypogean (ground-water) ostracods may exhibit at least seven different morphological and reproductive specializations to groundwater conditions: 1) smaller body size, 2) anophthalmy or reduction in eye pigmentation, 3) reduction or loss of appendage length and setation, 4) changes in carapace shape, 5) elongation in appendages (e.g. legs and/or claws) or sensory setae (e.g., Y aesthetasc), 6) reduction of some extremities in males, 8) increase in egg size. Almost all genera in Cabralcandonini tribe n. exhibit these adaptations, although we currently do not have information on reproductive characteristics, including clutch and egg size. Overall, these adaptations clearly suggest that members of *Cabralcandona* gen. n. are restricted to hypogean habitats. Additionally, we can make some hypotheses about microhabitats in which these species may occur. For example, *Ufocandona hannaleeae* possesses asymmetric valves (oval LV and more subrectangular RV) while *Rugosuscandona wisei* and *Cabralcandona mixoni* sp. n. are rectangular and subrectangular in shape, respectively. According to Pipík and Bodergat (2005, 2007), some Candonine species with triangular and rectangular carapaces and a pointed posteroventral margin inhabit relatively stable habitats with minimal environmental fluctuations and species with a subcircular outline (e.g., *Cypria*) inhabit unstable environments.

Conclusions

Based on the characteristics discussed above, we propose Cabralcandonini tribe n. as a new tribe of the subfamily Candoninae. Hence, there are now nine tribes (Candonini Kaufmann, 1900; Candonopsini Karanovic, 2004; Cryptocandonini Karanovic, 2007; Danielocandonini Karanovic, 2007; Humphreyscandonini Karanovic, 2005, Namibcypriidini Martens, 1992; Terrestrialcypriidini Pinto et al., 2005; Trapezicandonini Karanovic, 2007, Cabralcandonini tribe n. Külköylüoğlu et al., in here) in the subfamily. However, ongoing studies strongly suggest that ostracod species diversity in at least some underground waters is unique and higher than currently acknowledged.

Key to the Tribes of Subfamily Candoninae: (Modified from Karanovic 2012).

1. Setae in bunch on Md palp without row of setules.....Cabralcandonini tribe n.
 – Setae in bunch on Md palp with row of setules.....2
2. Terminal segment of T3 with one long claw.....Terrestrialcypriidini
 – Terminal segment of T3 without long claw.....3
3. Terminal segment of T3 with two long and one short setae.....4
 – Terminal segment of T3 with two short and one long setae.....6
4. T3 without basal seta.....Namibcypriidini
 –T3 with seta.....5
5. Posterior seta on the UR present..... Candonini
 – Posterior seta on the UR absent..... Candonopsini
6. Chitinized projection on the inner lobe of hemipenis present.....Humphreyscandonini
 – Chitinized projection on the inner lobe of hemipenis absent.....7
7. A1 5-segmented.....Danielocandonini
 – A1 7-segmented.....8
8. Basal seta on T2 present, outer lobe on hemipenis robust.....Cryptocandonini
 – Basal seta on T2 absent, outer lobe on the hemipenis thin.....Trapezicandonini

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