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Uptaded checklist, historical overview and illustrated guide to the stygobiont Malacostraca (Arthropoda: Crustacea) species of Yucatan (Mexico)

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Abstract

This study provides an updated checklist and an illustrated guide to the 17 currently known stygobiont Malacostraca species of the state of Yucatan (Yucatan Peninsula, Mexico). The compilation is based on the individuals collected during our cave-diving expeditions (2016–2019), and, has the purpose of expanding previous knowledge on the taxonomy of these subterranean crustaceans. The identification guide contains drawings of the main diagnostic characters of the species as well as a brief introduction of the relevant malacostracan orders. The information is further complemented with a historic account and timeline of the stygobiont Malacostraca species of the Yucatan Peninsula. This is the first study that provides a unified tool for the morphological identification of these highly endemic species.

Keywords

amphipods, decapods, groundwater, isopods, mysids, sinkholes, stygiomysids, thermosbaenaceans, Yucatan Peninsula

Introduction

The Yucatan Peninsula (southeastern Mexico) groundwater ecosystems harbour a highly endemic, crustacean-dominated fauna that present a variety of morphological and physiological adaptations to life in subterranean water environments (eg. Álvarez et al. 2008). Currently, 33 stygobiont (subterranean water-restricted) malacostracan species are known from the groundwater ecosystems of the Mexican federal states of the peninsula (eg. Álvarez et al. 2015; Angyal et al. 2020), which belong to six different orders (Decapoda: 14 sp., Amphipoda: 8 sp., Isopoda: 7 sp., Stygiomysida: 2 sp., Mysida: 1 sp., Thermosbaenacea: 1 sp.). All but three of the 33 species are endemic to the Yucatan Peninsula and half of them have bibliographically confirmed distribution records from the state of Yucatan. A timeline and historical data about the description of the groundwater-restricted Malacostraca of the Mexican states of the peninsula can be found in Table 1. The appearance of the species follows a chronological order, starting with the earliest species described and ending with the most recently discovered one.

Discovery of the first stygobiont malacostracan crustaceans in subterranean habitats of the state of Yucatan is dated back to the beginning of the twentieth century, when the Division of Historical Research of Carnegie Institution of Washington invited E. P. Creaser, F. G. Hall and A. S. Pearse to investigate the biology of the aquifers and subterranean ecosystems of Yucatan. In 1932, several ”cenotes” (water-filled sinkholes), ”aguadas” (shallow water-holes) and ”pozos” (karstic wells) were studied (Pearse 1936). Among other findings, this expedition resulted in the description of four subterranean malacostracan species new to science (Creaser, 1936). After a long hiatus, explorations were continued in the 1970’s, when J. R. Reddell and his colleagues (Texas Tech University) studied further cenotes and “grutas” (dry solution caves) of Quintana Roo, Campeche and Yucatan states (Reddell, 1977), resulting in the description of, among others, two stygobiont amphipod and decapod species (Hobbs and Hobbs 1976; Holsinger 1977). Cave diving expeditions in cenotes and the associated submerged cave passages of the peninsula began in the 1980’s. By the early 2000’s, more than ten subterranean malacostracan species had been described from the orders Thermosbaenacea, Stygiomysida, Isopoda and Amphipoda (eg. Bowman and Iliffe 1988; Holsinger 1990; Bowman and Iliffe 1999; Álvarez et al. 2005).

In 2016, the research group “Cenoteando” (www.cenoteando.com), of the Unidad Multidisciplinaria de Docencia e Investigación of the Facultad de Ciencias, Universidad Nacional Autónoma de México in Sisal (UNAM UMDI-Sisal), began their systematic studies of the biodiversity mapping, ecology and taxonomy of the cenote ecosystems in the state of Yucatan. Prior to Cenoteado’s work only less than five percent had been zoologically investigated out of the more than 3,000 officially registered cenotes in Yucatan (SDS Yucatan census). The project’s goal has been to provide data from cenotes that had never been studied, with expedi-

tions leading to the discovery of stygobionts previously unknown in the region and to the description of species new to science (Angyal et al. 2018; Grego et al. 2019). Together with these records and the most recent description of Álvarez et al. (2019) of a new subterranean isopod, the number of stygobiont malacostracan species of the state of Yucatan has elevated to seventeen.

In the absence of a unified taxonomic guide, up to now, the identification of these species was possible only by a thorough knowledge of the original descriptions and other relevant literature on the species' distribution and morphology. In order to facilitate further research of these rare, endemic species, the aim of this paper is to provide an updated checklist accompanied by an illustrated identification guide and a chronological historical account of the stygobiont malacostracan crustaceans of the state of Yucatan.

Materials and methods

Samples of malacostracan species were collected in 32 cenotes and submerged caves in the state of Yucatan between 2016 and 2019, during SCUBA cave-diving expeditions in the following municipalities: Abala, Cacalchen, Chochola, Chunchumil, Dzilam de Bravo, Ekmul, Homun, Huhi, Kopoma, Sotuta, Tecoh, Tixkakal, Tixkokob and Uman. Detailed information about the localities and the collected material can be found in Angyal et al. 2020 (https://zookeys.pensoft.net/article/47694/). The collected material was deposited in the Yucatán Colección de Crustáceos of the UNAM UMDI-Sisal, the Colección Nacional de Crustáceos, Instituto de Biología of the UNAM, Mexico City, and in the Collection of Crustaceans of the Hungarian Natural History Museum (HNHM), Budapest. Individuals were examined with a Nikon SM Z800 stereomicroscope. Thermosbaenaceans, stygiomysids, mysids and amphipods were dissected on slides and were observed with compound light microscope. For this, specimens were cooked in 10% KOH solution, rinsed with HCl and washed in distilled water. Cleared exoskeletons were stained with chlorazol black in glycerol, and then dissected in glycerol gelatin using stereomicroscope (Fišer et al. 2009). Photographs of diagnostic characters were made using an OMAX 14 OMP digital USB microscope camera. Line drawings were made after the collected material, based on (i) slide preparations and intact individuals using drawing tubes mounted in a Leica DM 1000 compound microscope and in a Leica M125 stereomicroscope, respectively, (ii) and on photographs. In the case of three isopod species (*Haptolana bowmani*, *Cirolana yucatana* and *Curassanthura yucatanensis*) which we were not able to collect, we relied solely on the illustrations of the original species descriptions. The drawings were edited graphically via computer, to ensure homogeneity of lines and shades. Species identification and creation of the identification guide were performed with the aid of the literature listed in Table 2.

Table 1. Historical timeline and distribution data of the stygobiont Malacostraca species of the Yucatan Peninsula. Abbreviations: YUC = state of Yucatan; YP = Yucatan Peninsula; ROO = state of Quintana Roo; CAM = state of Campeche; COZ = Cozumel Island (in Quintana Roo); MNHB = Museum der Naturkunde für Humboldt Universität zu Berlin; UMLSA = University of Michigan Museum of Zoology, BMNH = British Museum (National History), London; USNM = National Museum of Natural History, Smithsonian Institution, Washington D.C.; CNCR UNAM = National Collection of Crustaceans, UNAM, Institute of Biology, Mexico City; ZMUA = Zoologisch Museum, University of Amsterdam. Distribution with an asterisk (for example COZ*) = the species is known only from its type locality.

Species	Order	Description	Type locality	Holotype	Endemic in the YP	Environment	YP states distribution
Barbouria cubensis (von Martens, 1872)	Decapoda	von Martens 1872	Provincia de La Habana, Cuba	MNHB	No	saline water	ROO
Creaseriella anops (Creaser, 1936)	Isopoda	Creaser 1936	Cenote Sambulá (YUC)	UMLSA	Yes	fresh and saline water	YUC, ROO, CAM
Antromysis cenotensis Creaser, 1936	Mysida	Creaser 1936	Grutas de Balancanché (YUC)	UMLSA	Yes	fresh water	YUC, ROO
Creaseria morleyi (Creaser, 1936)	Decapoda	Creaser 1936	Cueva de San Isidro (YUC)	UMLSA	Yes	fresh water	YUC, ROO, CAM
Typhlatya pearsei Creaser, 1936	Decapoda	Creaser 1936	Grutas de Balancanché (YUC)	UMLSA	Yes	fresh water	YUC, ROO, CAM
Stygiomysis holthuisi (Gordon, 1958)	Stygiomysida	Gordon 1958	Devil's Hole, St. Martin, Lesser Antilles (France)	BMNH	No	fresh water	YUC, ROO
Typhlatya mitchelli H.H.III Hobbs & H.H.Jr. Hobbs, 1976	Decapoda	Hobbs and Hobbs 1976	Cenote Kabahchén (YUC)	USNM	Yes	fresh water	YUC, ROO
Typhlatya campecheae H.H.III Hobbs & H.H.Jr. Hobbs, 1976	Decapoda	Hobbs and Hobbs 1976	Grutas de Xtacumbilxunaán (CAM)	USNM	Yes	fresh water	CAM
Mayaweckelia yucatanensis Holsinger, 1977	Amphipoda	Holsinger 1977	Grutas de Xtacumbilxunaán (CAM)	USNM	Yes	fresh water	CAM*
Mayaweckelia cenoticola Holsinger, 1977	Amphipoda	Holsinger 1977	Cenote Xtacabihá (YUC)	USNM	Yes	fresh water	YUC, ROO, CAM
Parhippolyte sterreri (C.W.J. Hart & Manning, 1981)	Decapoda	Hart and Manning 1981	Tucker's Town Cave, Tucker's Town, Bermuda	USNM	No	saline water	COZ
Metacirolana mayana (Bowman, 1987)	Isopoda	Bowman 1987	Cueva Quebrada (COZ)	USNM	Yes	brakish and saline water	ROO, COZ
Tulumella unidens Bowman & Iliffe, 1988	Thermosbaenacea	Bowman and Iliffe 1988	Cenote Naharon (ROO)	USNM	Yes	brakish and saline water	YUC, ROO
Yagerocaris cozumel Kensley, 1988	Decapoda	Kensley 1988	Cenote Areolito (COZ)	USNM	Yes	saline water	ROO, COZ
Agostocaris bozanici Kensley, 1988	Decapoda	Kensley 1988	Cenote Xcan-Ha (COZ)	USNM	Yes	saline water	COZ*
Tuluweckelia cernua Holsinger, 1990	Amphipoda	Holsinger 1990	Cenote Calavera (ROO)	USNM	Yes	brakish and fresh water	YUC, ROO
Bahadzia bozanici Holsinger, 1992	Amphipoda	Holsinger 1992	Cueva Quebrada (COZ)	USNM	Yes	saline water	ROO, COZ
Bahadzia setodactylus Holsinger, 1992	Amphipoda	Holsinger 1992	Cenote Xcan-Ha (COZ)	USNM	Yes	saline water	COZ
Stygiomysis cokei Kallmeyer & Carpenter, 1996	Stygiomysida	Kallmeyer and Carpenter 1996	Cenote Calavera (ROO)	USNM	Yes	fresh and brakish water	YUC, ROO
Calliasmata nohochi Escobar-Briones, Camacho & Alcocer, 1997	Decapoda	Escobar-Briones et al. 1997	Crack House Cave, (ROO)	CNCR UNAM	Yes	saline water	ROO, COZ
Haptolana bowmani Botosaneanu & Iliffe, 1997	Isopoda	Botosaneanu and Iliffe 1997	Grutas de Tzab-Nah (YUC)	USNM	Yes	fresh water	YUC

Species	Order	Description	Type locality	Holotype	Endemic in the YP	Environment	YP states distribution
Yucatalana robustispina Botosaneanu & Iliffe, 1999	Isopoda	Botosaneanu and Iliffe 1999	Cenote Papakal (YUC)	ZMUA	Yes	fresh water	YUC
Cirolana yunca (Botosaneanu & Iliffe, 2000)	Isopoda	Botosaneanu and Iliffe 2000	Cenote Sabak Ha (YUC)	ZMUA	Yes	fresh water	YUC
Cirolana yucatana Botosaneanu & Iliffe, 2000	Isopoda	Botosaneanu and Iliffe 2000	Cenote Dzonotilá (YUC)	ZMUA	Yes	fresh water	YUC*
Procaris mexicana von Sternberg & Schotte, 2004	Decapoda	Sternberg and Schotte 2004	Cueva Quebrada (COZ)	USNM	Yes	saline water	COZ
Typhlatya dzilamensis Álvarez, Iliffe & Villalobos, 2005	Decapoda	Álvarez et al. 2005	Cenote Buya Uno (YUC)	CNCR UNAM	Yes	saline water	YUC, ROO
Triacanthoneus akumalensis Álvarez, Iliffe, Gonzalez & Villalobos, 2012	Decapoda	Álvarez et al. 2012	Cenote Aak Kimin (ROO)	CNCR UNAM	Yes	saline water	ROO*
Hyalella cenotensis Marrón-Becerra, Hermoso-Salazar, Solís-Weiss, 2014	Amphipoda	Marrón-Becerra el al. 2014	Cenote Aktun Ha (ROO)	CNCR UNAM	Yes	fresh water	ROO*
Cymadusa herrerae Ortiz & Winfield, 2015	Amphipoda	Ortiz and Winifield 2015	Cenote Aerolito (COZ)	CNCR UNAM	Yes	brakish water	COZ*
Agostocaris zabaletai Mejía-Ortíz, Yañez & López-Mejía, 2017	Decapoda	Mejía-Ortíz et al. 2017	Cenote Chempita (COZ)	CNCR UNAM	Yes	saline water	COZ
Anchialocaris paulini Mejía-Ortíz, Yañez & López-Mejía, 2017	Decapoda	Mejía-Ortíz et al. 2017	Cenote Chempita (COZ)	CNCR UNAM	Yes	saline water	COZ*
Mayaweckelia troglomorpha Angyal, 2018	Amphipoda	Angyal et al. 2018	Cenote Dzonbakal (YUC)	CNCR UNAM	Yes	fresh water	YUC
Curassanthura yucatanensis Álvarez, Benitez, Iliffe & Villalobos, 2019	Isopoda	Álvarez et al. 2019	Cenote Nohoch Nah Chich (ROO)	CNCR UNAM	Yes	fresh water	YUC, ROO

Table 2. List of references of the corresponding taxa used for the compilation of the illustrated identification guide.

Reference	Corresponding taxon	Reference	Corresponding taxon
Álvarez et al. 2005	*Typhlatya dzilamensis*	Hobbs and Hobbs 1976	*Typhlatya mitchelli*
Álvarez et al. 2019	*Curassanthura yucatanensis*	Hobbs et al. 1977	genus *Typhlatya*
Angyal et al. 2018	*Mayaweckelia troglomorpha*	Hobbs 1979	genus *Typhlatya*
Botosaneanu and Iliffe 1997	*Haptolana bowmani*	Holsinger 1977	*Mayaweckelia cenoticola*
Botosaneanu and Iliffe 1999	*Yucatalana robustispina*	Holsinger 1990	*Tuluweckelia cernua*
Botosaneanu and Iliffe 2000	*Cirolana yunca*, *Cirolana yucatana*	Holthuis 1950	family Palaemonidae
Botosaneanu and Iliffe 2002	family Cirolanidae	Horwitz et al. 1995	class Malacostraca
Botosaneanu and Iliffe 2006	family Cirolanidae	Kallmayer and Carpenter 1996	*Stygiomysis cokei*
Bowman 1966	family Cirolanidae	Kensley 1981	genus *Curassanthura*
Bowman 1977	genus *Antromysis*	Lowry and Myers 2013	suborder Senticaudata
Bowman and Iliffe 1988	*Tulumella unidens*	Meland et al. 2015	orders Mysida and Stygiomysida
Bowman et al. 1984	genus *Stygiomysis*	Melic 2015	order Thermosbaenacea
Bruce 1986	family Cirolanidae	Pérez-Aranda 1983a	*Typhlatya pearsei*
Bruce 2008	family Cirolanidae	Pérez-Aranda 1983b	*Creaseria morleyi*
Bruce and Humphreys 1993	family Cirolanidae	Pérez-Aranda 1984a	*Typhlatya mitchelli*
Bruce et al. 2017	family Cirolanidae	Pérez-Aranda 1984b	*Creaseriella anops*
Brusca et al. 1995	family Cirolanidae	Poore 2001	family Cirolanidae
Caroli 1937	family Cirolanidae	Rioja 1953	family Cirolanidae
Creaser 1936	*Antromysis cenotensis*, *Creaseriella anops*, *Creaseria morleyi*, *Typhlatya pearsei*	Tinnizi and Quddusi 1993	class Malacostraca
De la Fuente 1994	class Malacostraca	Wagner 1994	order Thermosbaenacea
Gordon 1960	*Stygiomysis holthuisi*		

Results

Updated checklist of the stygobiont Malacostraca of the state of Yucatan

Table 3 contains an updated checklist of the seventeen stygobiont malacostracan crustacean species that have been described to date from the state of Yucatan (12 species), or else, have bibliographically confirmed distribution records from the state up to september 2020 and were described elsewhere (5 species).

Illustrated guide to the stygobiont Malacostraca species of Yucatan with the introduction of the orders

Order: THERMOSBAENACEA Monod, 1927
Figure 1

Antenna 1 biramous, antenna 2 uniramous. Mandibular palp present. Carapace short, forming dorsal brood pouch in females. Thoracic legs reduced, mostly two-branched. Gills lacking. Pleopods reduced or lacking.

Family: Tulumellidae Wagner, 1994
***Tulumella unidens* Bowman & Iliffe, 1988**

Body length up to 3.5 mm of both gender. Antennula with scale (exopod) (Fig. 2A). Carapace covering pereonites 1–6, dorsally enlarged in ovigerous females (Fig. 2A). Pereopod I biramous, endopod five-segmented. Pereopods II-VII biramous, with two-segmented exopod and six-segmented endopod (Fig. 2B).

Order: STYGIOMYSIDA Caroli, 1937
Figure 3

Body elongated, vermiform. Second thoracopods are enlarged, dactylus and nail bend down to form a subchelate gnathopod. Both male and female pleopods are reduced to comprise a sympod/protopod, a one-segmented endopod and three-segmented exopod.

Family: Stygiomysidae Caroli, 1937
***Stygiomysis holthuisi* (Gordon, 1958)**

Body length up to 9 mm of both gender. Body rather vermiform, carapace reduced. Pereopods 1–3 prehensile. Telson only slightly longer than wide at base; posterior margin with 15 spines in 5 groups, 1st, middle and 5th groups consist of strong, long spines

Table 3. Checklist of the stygobiont malacostracan species of the state of Yucatan, with data on their distribution. Abbreviations: YUC = state of Yucatan, YP = Yucatan Peninsula, ROO = state of Quintana Roo, CAM = state of Campeche. Species with an asterisk (*) = the species was discovered and described from cenotes of YUC.

Superorder	Order	Family	Genus	Species valid name	Original name	Published distribution
	Thermosbaenacea	Tulumellidae	*Tulumella*	***Tulumella unidens*** Bowman & Iliffe, 1988	*Tulumella unidens*	Less than 20 cenotes and caves in YUC and ROO.
	Stygiomysida	Stygiomysidae	*Stygiomysis*	***Stygiomysis holthuisi*** (Gordon, 1958)	*Rhopalonurus holthuisi*	Anguilla, Bahamas, Lesser Antilles (France), Puerto Rico. From the YP: less than 30 cenotes and caves in YUC and ROO.
				Stygiomysis cokei Kallmeyer & Carpenter, 1996	*Stygiomysis cokei*	Less than 20 cenotes and caves in YUC and ROO.
	Mysida	Mysidae	*Antromysis*	***Antromysis cenotensis*** Creaser, 1936*	*Antromysis cenotensis*	Widely distributed in the central and northern parts of the YP, known from several wells, cenotes and caves in YUC and ROO.
		Leptanthuridae	*Curasshantura*	***Curassanthura yucatanensis*** Álvarez, Benítez, Iliffe & Villalobos, 2019	*Curassanthura yucatanensis*	Cenote Nohoch Nah Chich (ROO), Cenote Chen Ha (YUC), Cenote Dzonotilá (YUC)
Peracarida	Isopoda	Cirolanidae	*Cirolana*	***Cirolana yunca*** (Botosaneanu & Iliffe, 2000)*	*Haptolana yunca*	Cenotes Sabak Ha, Tres Oches, X'baba, Chihuo Hol (all in YUC)
				Cirolana yucatana Botosaneanu & Iliffe, 2000*	*Cirolana (Anopsilana) yucatana*	Cenote Dzonotilá (YUC)
			Creaseriella	***Creaseriella anops*** (Creaser, 1936)*	*Cirolana anops*	Known from numerous caves and cenotes in YUC and ROO, and a well in CAM.
			Haptolana	***Haptolana bowmani*** Botosaneanu & Iliffe, 1997*	*Haptolana bowmani*	Grutas de Tzab-Nah, Cenotes Kambul, Mucuyché and Yuncú (all in YUC)
			Yucatalana	***Yucatalana robustispina*** Botosaneanu & Iliffe, 1999*	*Yucatalana robustispina*	Less than 20 cenotes and caves in YUC.
	Amphipoda	Hadziidae	*Mayaweckelia*	***Mayaweckelia cenoticola*** Holsinger, 1977*	*Mayaweckelia cenoticola*	Less than 20 cenotes and caves in YUC, ROO and CAM.
				Mayaweckelia troglomorpha Angyal, 2018*	*Mayaweckelia troglomorpha*	Less than 20 cenotes and caves in YUC.
			Tuluweckelia	***Tuluweckelia cernua*** Holsinger, 1990	*Tuluweckelia cernua*	Some cenotes and caves in Yucatan and Quintana Roo.
Eucarida	Decapoda	Atydae	*Typhlatya*	***Typhlatya pearsei*** Creaser, 1936*	*Typhlatya pearsei*	Widely distributed in cenotes and caves in YUC, ROO and CAM.
				Typhlatya mitchelli H.H.III Hobbs & H.H.Jr. Hobbs, 1976*	*Typhlatya mitchelli*	Widely distributed in cenotes and caves in YUC and ROO.
				Typhlatya dzilamensis Álvarez, Iliffe & Villalobos, 2005*	*Typhlatya dzilamensis*	Less than 20 cenotes and caves in YUC and ROO.
		Palaemonidae	*Creaseria*	***Creaseria morleyi*** (Creaser, 1936)*	*Palaemon morleyi*	Widely distributed in cenotes and caves in YUC, ROO and CAM.

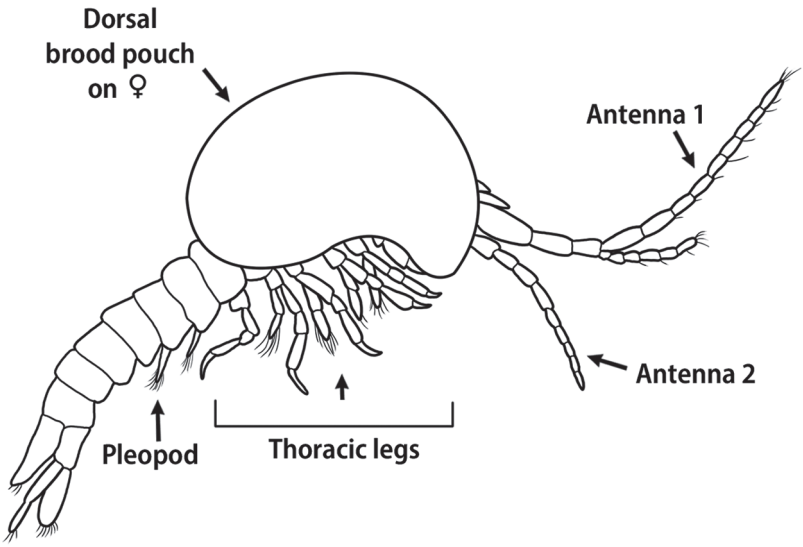

Figure 1. Thermosbaenacea, schematic drawing.

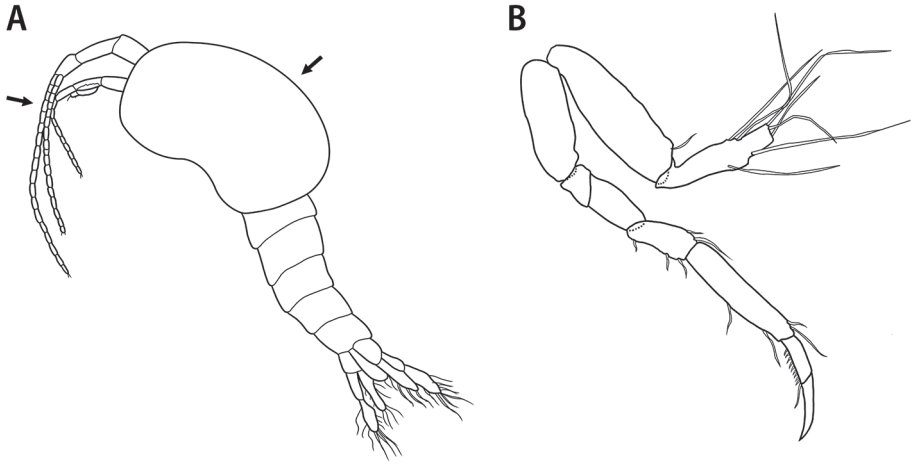

Figure 2. A *Tulumella unidens* habitus simplified drawing **B** *T. unidens* pereopod VI.

(Fig. 4A). Uropod protopodal process with five long spines on apical margin and with several spines along the distal half of medial margin (Fig. 4B).

Stygiomysis cokei Kallmeyer & Carpenter, 1996

Body length up to 15 mm of males and 22 mm of females. Body rather vermiform, carapace housing mouthparts and anterior three pairs of pereopods (Fig. 5A). Telson 1.7–2.0× longer than wide at base; posterior margin with 15–16 spines in five groups (Fig. 5B). Uropod slightly shorter than telson; protopodal process with seven or eight spines along medial and apical margins (Fig. 5C).

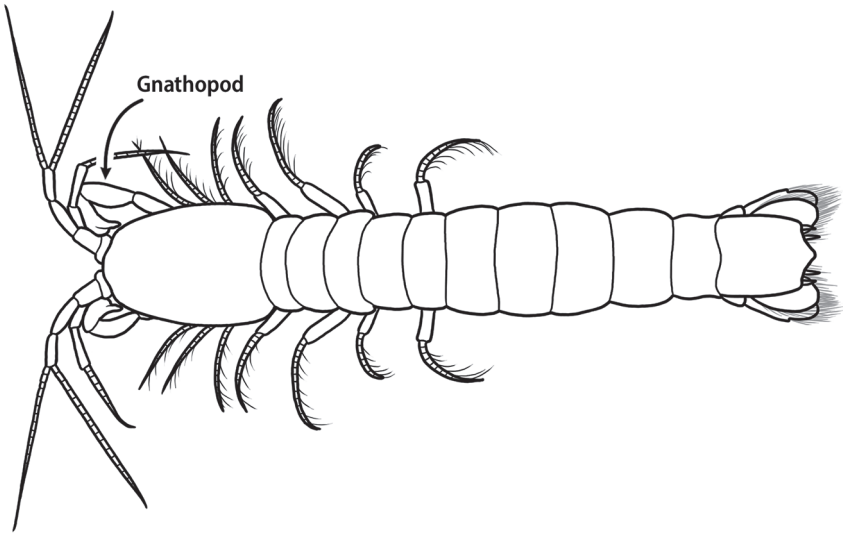

Figure 3. Stygiomysida, schematic drawing.

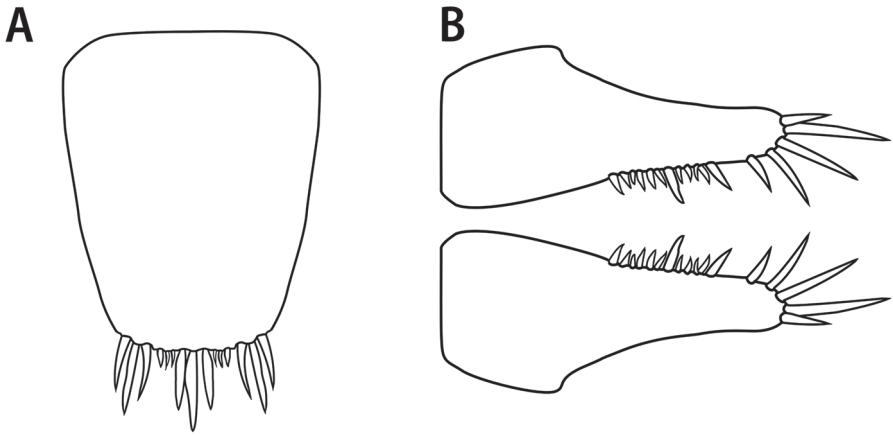

Figure 4. A *Stygiomysis holthuisi* telson **B** *S. holthuisi* uropod protopodal process.

Order: MYSIDA Boas, 1883
Figure 6

The eight thoracic segments are covered by the carapace which is attached only to the first three. First two thoracic segments bear maxilliped, other six pairs of thoracic appendages are biramous perepoods. Ventral brood pouch enclosed by large, flexible oostegites present on females. Fourth pleopod longer than others in males and has a specialized reproductory function. Statocysts on uropods present.

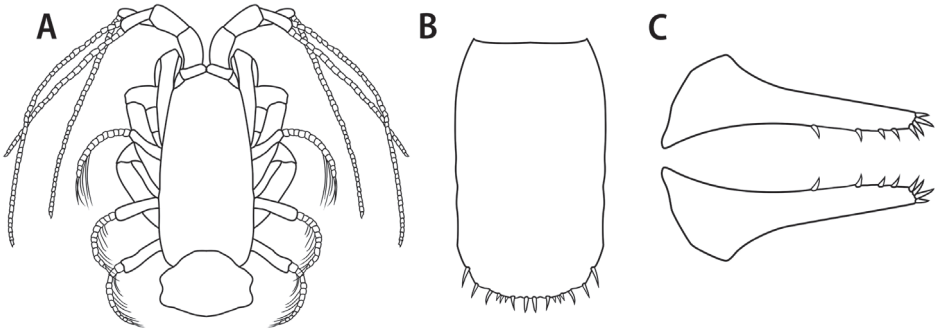

Figure 5. A *Stygiomysis cokei* carapace with appendages **B** *S. cokei* telson **C** *S. cokei* uropod protopodal process.

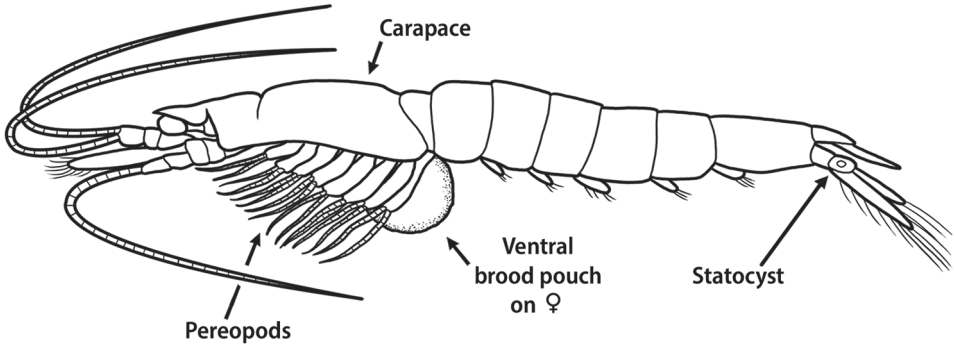

Figure 6. Mysida, schematic drawing.

Family: Mysidae Haworth, 1825
***Antromysis cenotensis* Creaser, 1936**

Body length up to 4.5 mm of both gender. Antenna 2 scale is about 4–4.5 times as long as wide, two-segmented (Fig. 7A). Telson nearly as long as wide at base, gradually narrowing posteriorly, armed with robust spine at each corner and one or two short spine in center (Fig. 7B). Inner ramus of uropod with static organ on basal half (Fig. 7C).

Order: ISOPODA Latreille, 1817
Figure 8

Body cylindrical or depressed dorsoventrally. Thorax of seven somites (peraeon), each somite bearing a pair of uniramous appendages, coxa bearing side-plates. First pair of thoracic appendages often subchelate, remaining thoracic appendages similar in structure. Abdomen of six somites (pleon), pleotelson present. Pleon bears five pairs of pleopods and one pair of uropod. Gills are on pleopods.

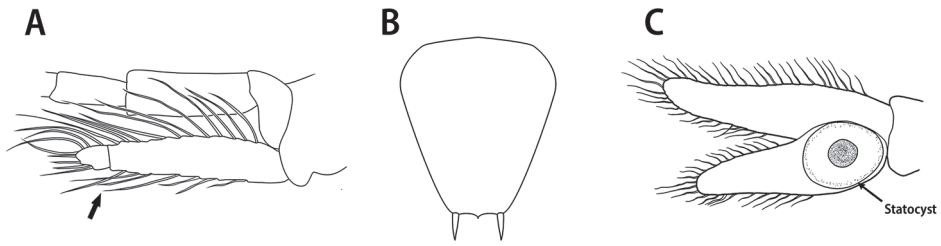

Figure 7. A *Antromysis cenotensis* scale of antenna 2 **B** *A. cenotensis* telson **C** *A. cenotensis* uropod with statocyst.

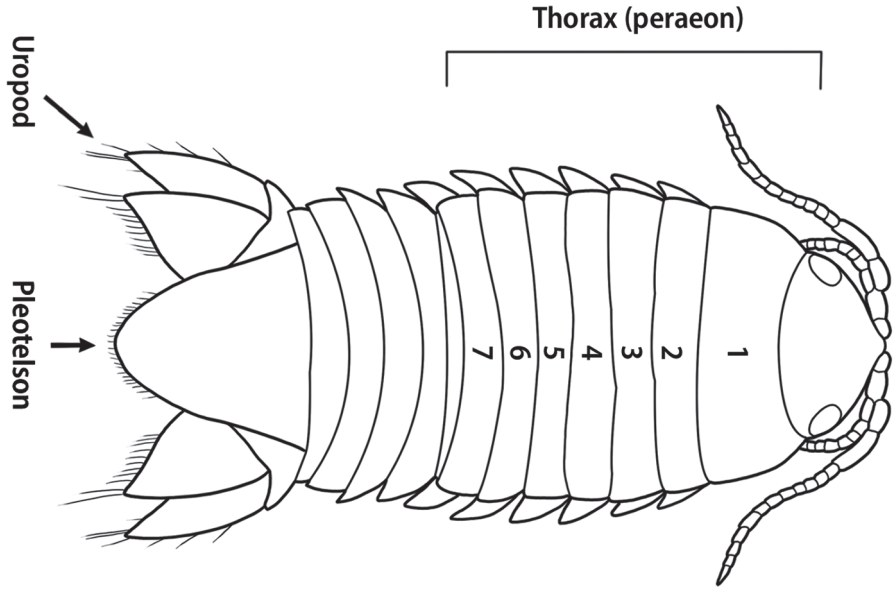

Figure 8. Isopoda, schematic drawing.

Family: Leptanthuridae Poore, 2001
***Curassanthura yucatanensis* Álvarez, Benítez, Iliffe & Villalobos, 2019**

Body length up to 9 mm of females. Body slender, elongated (Fig. 9A). Head wider than long (Fig. 9A). Propodus palmar margins of pereopod I with 30 spines (Fig. 9B). Pereopods II-VI similar, much narrower than long (Fig. 9A). Pereopod VII lacking (Fig. 9A). Posterior margin of pleonite 6 rounded (Fig. 9C).

Family: Cirolanidae Dana, 1852
***Cirolana yunca* (Botosaneanu & Iliffe, 2000)**

Body length up to 10 mm of females. Body margins only slightly convex. Cephalon more than twice longer than maximal length, posterior margine deeply depressed

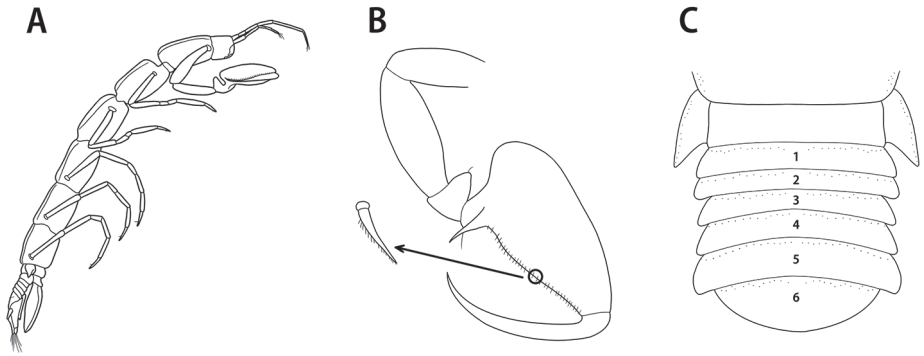

Figure 9. A *Curassanthura yucatanensis* habitus **B** *C. yucatanensis* propodus of pereopod I **C** *C. yucatanensis* pleonites. Drawings were adatpted from Álvarez et al. 2019.

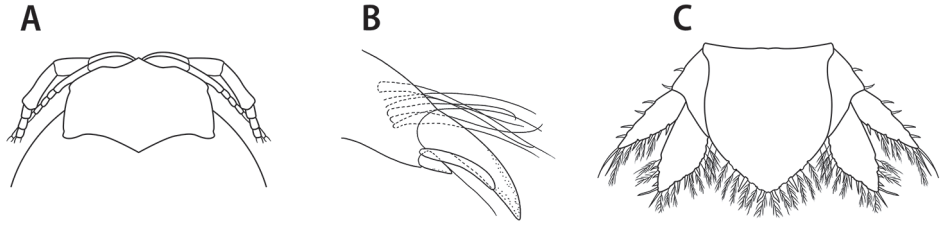

Figure 10. A *Cirolana yunca* cephalon with rostrum **B** *C. yunca* nails of pereopod III dactylus (adapted from Botosaneanu & Iliffe 2000) **C** *C. yunca* pleotelson and uropods.

(Fig. 10A). Rostrum small and blunt ending in dorsal view (Fig. 10A). Additional nails present on propodi of pereopods: one long, slightly curved blunt ending, and one short, conical (Fig. 10B). Uropodal exopodite slightly shorter than endopodite (Fig. 10C). Pleotelson with length equaling its width at the base (Fig. 10C).

Cirolana yucatana (Botosaneanu & Iliffe, 2000)

Body length up to 6 mm of females. Body rather strongly widened in the middle. Cephalon large, strongly vaulted anteriorly, posterior margin slightly depressed (Fig. 11A). Rostrum small, triangular (Fig. 11A). Pereopods only with few spines (Fig. 11B). Uropods exopodite shorter and slender than endopodite, but rather thick-set (Fig. 11C). Pleotelson maximum width only slightly exceeding maximum length (Fig. 11C).

Creaseriella anops (Creaser, 1936)

Body length up to 23 mm of both gender. Able to roll into a ball (Fig. 12A). Cephalon oblong, twice as wide as long; posterior margin slightly concave (Fig. 12B). Pleotelson

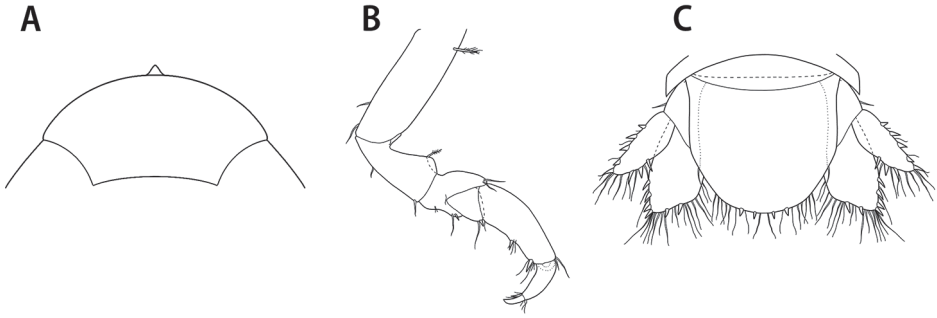

Figure 11. A *Cirolana yucatana* cephalon **B** *C. yucatana* pereopod II **C** *C. yucatana* pleotelson and uropods. Drawings were adapted from Botosaneanu & Iliffe 2000.

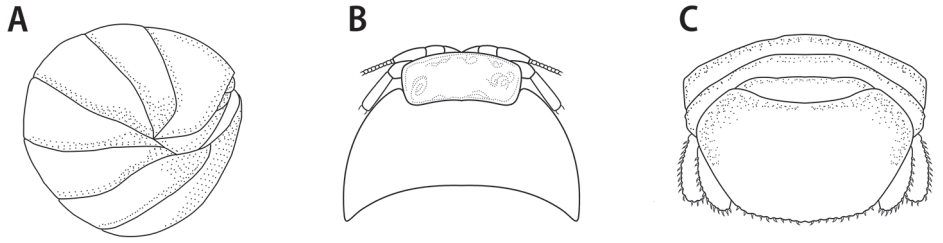

Figure 12. A *Creaseriella anops* rolled position **B** *C. anops* cephalon **C** *C. anops* pleotelson and uropods.

wider than long, along the distal margin several very short setae (Fig. 12C). Uropodal exopodite slightly shorter than endopodite; endo- and exopodite with row of very short setae on external margin and apex (Fig. 12C).

Haptolana bowmani Botosaneanu & Iliffe, 1997

Body length up to 7.5 mm of males and 9.5 mm of females. Body slender, cephalon having the shape of a helmet, wider than long, rostrum narrowly triangular (Fig. 13A). All pereopods clearly prehensile, with robust propodus, pereopods II-VII very spinose (Fig. 13B). Pereopods VI and VII distinctly longer than I-V. Uropods exopodite distinctly shorter than endopodite (Fig. 13C). Pleotelson longer than wide (Fig. 13C).

Yucatalana robustispina Botosaneanu & Iliffe, 1999

Body length up to 4.5 mm of both gender. Cephalon with round lateral bulges and well developed triangular rostrum (Fig. 14A). Pereopod I with very long spines with particular structure on propod (2 spines), carpus (1 spine) and merus (1 spine) (Fig. 14B). Pleotelson subtrapezoidal (Fig. 14C). Uropodal exopodite with spines along external margin (Fig. 14C).

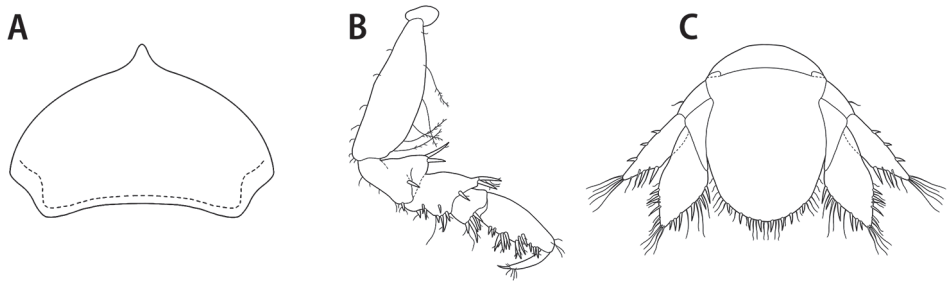

Figure 13. A *Haptolana bowmani* cephalon with rostrum **B** *H. bowmani* pereopod III **C** *H. bowmani* pleotelson and uropods. Drawings were adapted from Botosaneanu & Iliffe 1997.

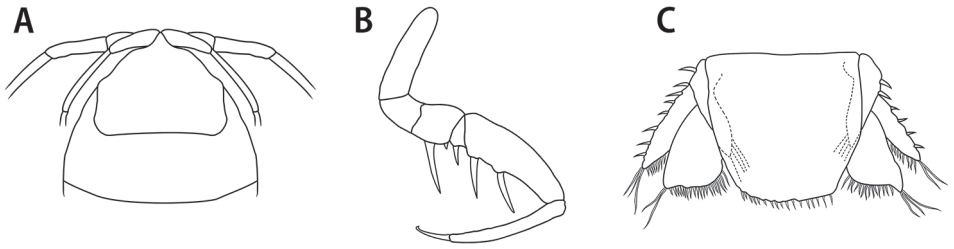

Figure 14. A *Yucatalana robustispina* cephalon with rostrum **B** *Y. robustispina* pereopod I **C** *Y. robustispina* pleotelson and uropods.

Order: AMPHIPODA Latreille, 1816
Figure 15

Body laterally compressed, slightly arched. Thorax of seven somites (peraeon), each segment bearing uniramous appendages, coxae bearing side-plates. Appendages of the first two thoracic somites modified as gnathopods. Abdomen six-segmented, abdominal somites 1–3 with large pleopods. Last three somites bear uropods, pleotelson absent. Gills at the inner base of pereopods.

Family: Hadziidae Karman, 1943
***Mayaweckelia cenoticola* Holsinger, 1977**

Body length up to 4 mm of males and 5.5 mm of females. Antenna 1 as long as, or a little longer than body, primary flagellum with 37–41 segments. Propodus of gnathopod 1 narrow, palm without distally notched spine teeth (Fig. 16A). Carpus of gnathopod 1 slightly longer than propodus (Fig. 16A). Pereopod VI and VII 60% of body length. Epimeral plates ventro-posterior corner not acuminate (Fig. 16B).

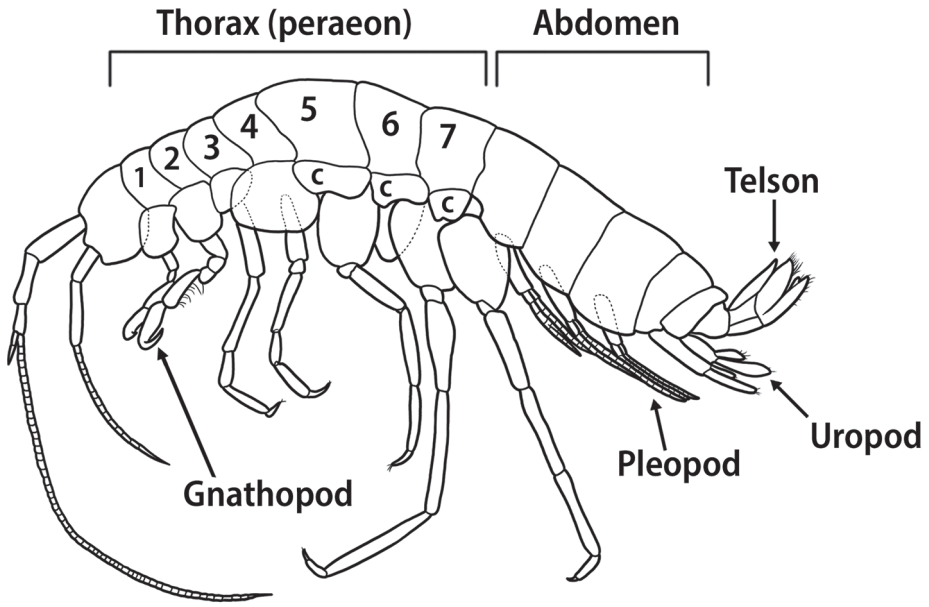

Figure 15. Amphipoda, schematic drawing.

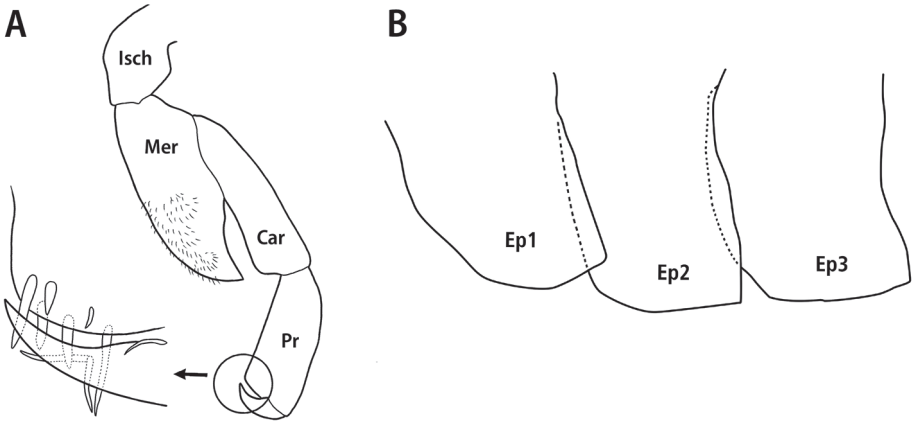

Figure 16. A *Mayaweckelia cenoticola* propodus of gnathopod 1 (Ish = ischium, Mer = merus, Car = carpus, Pr = propodus) **B** *M. cenoticola* epimeral plates 1-3 (Ep = epimeral plates).

Mayaweckelia troglomorpha Angyal, 2018

Body length up to 10 mm of both gender. Antenna 1 almost twice as long as body, primary flagellum with more than 60 articles. Propodus of gnathopod 1 less narrow, distally notched spine teeth present on palm (Fig. 17A). Carpus of gnathopod 1 1.5–1.7

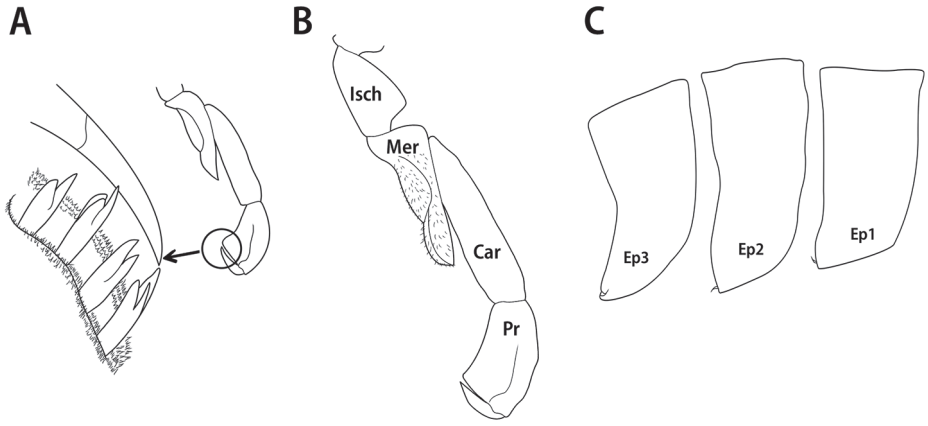

Figure 17. A *Mayaweckelia troglomorpha* notched spine teeth of gnathopod 1 propodus **B** *M. troglomorpha* gnathopod 1 schematic drawing (Ish = ischium, Mer = merus, Car = carpus, Pr = propodus) **C** *M. troglomorpha* epimeral plates 1-3 (Ep = epimeral plates).

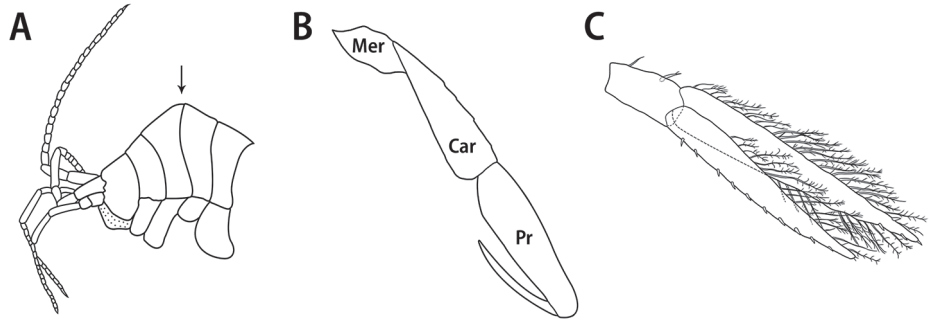

Figure 18. A *Tuluweckelia cernua* anterior body part **B** *T. cernua* gnathopod 2, schematic drawing (Mer = merus, Car = carpus, Pr = propodus, C = coxa) **C** *T. cernua* uropod III.

times longer than propodus (Fig. 17B). Pereopod VI and VII 130% of body length. Epimeral plates ventro-posterior corner more distinct (Fig. 17C).

Tuluweckelia cernua Holsinger, 1990

Anterior body region bend markedly downward (Fig. 18A). Body length up to 7 mm of males and 10 mm of females. Antenna 1 reaches at least 75% of body length. Gnathopod 2 propod long and relatively narrow (Fig. 18B). Uropod III proportionally long to body size, rami narrow, outer ramus of outer margin with small spines but lacking setae (Fig. 18C).

Order: DECAPODA Latreille,1802
Figure 19

First 3 pairs of thoracopods transformed on maxillipeds. First pair of pereopods usually bears chelae. Gills are usually enclosed by carapace' folds. One pair of uropods is expanded and together with telson form caudal fin.

Family: Atydae De Haan, 1849
***Typhlatya pearsei* Creaser, 1936**

Body length up to 19 mm of both gender. Rostrum extending anteriorly to at least midlength of second podomere of antennular peduncle (Fig. 20A). Exopod of pereopod V reduced, shorter than total length of basipodite (Fig. 20B).

***Typhlatya mitchelli* Hobbs & Hobbs, 1976**

Body length up to 22 mm of both gender. Rostrum not extending anteriorly beyond eyes (Fig. 21A). Exosceleton sometimes with pigmentation pattern (Fig. 21A). Ratio of carpus/propodus of pereopod II is more than 2.5 (Fig. 21B). Exopod of pereopod V reaching at least distal extremity of basis and often as far as proximal 5th of merus (Fig. 21C).

***Typhlatya dzilamensis* Álvarez, Iliffe & Villalobos, 2005**

Body length up to 24 mm of both gender. Rostrum unarmed, anteriorly oriented, reaching distal margin of eyes, triangular in dorsal view (Fig. 22A). Ishium and merus

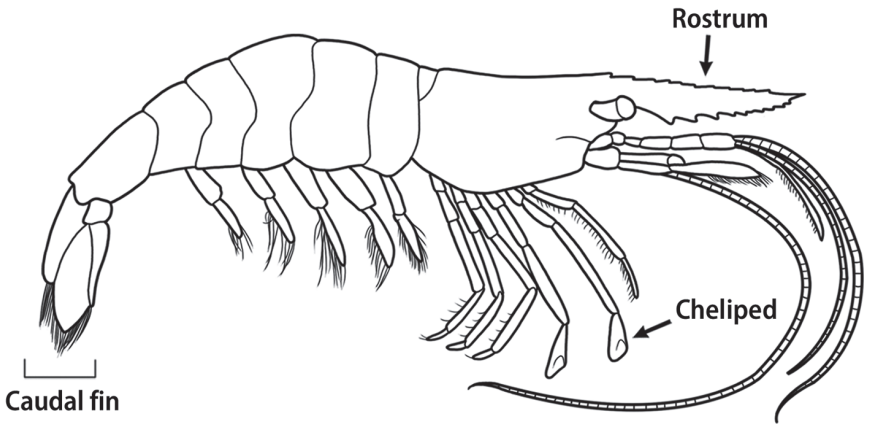

Figure 19. Decapoda, schematic drawing.

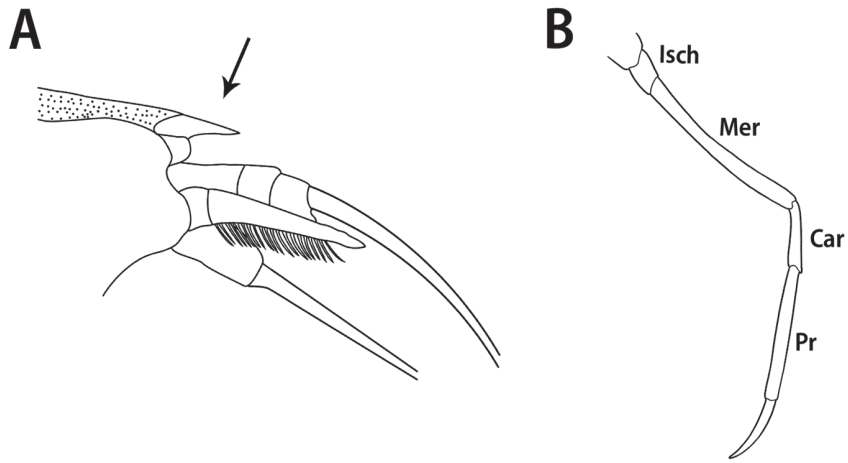

Figure 20. A *Typhlatya pearsei* rostrum and eyestalk **B** *T. pearsei* pereopod V schematic drawing.

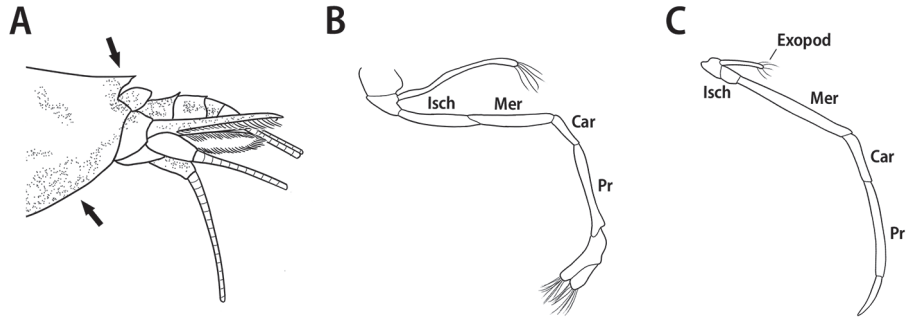

Figure 21. A *Typhlatya mitchelli* rostrum and eyestalks **B** *T. mitchelli* pereopod II schematic drawing **C** *T. mitchelli* pereopod V schematic drawing.

of pereopod III-V fused (Fig. 22B). Pleura of second abdominal somite with ventral margin not bilobed (Fig. 22C).

Family: Paleomonidae Rafinesque, 1815
***Creaseria morleyi* (Creaser, 1936)**

Body length up to 42 mm of both gender. Rostrum with dorsal and ventral teeth (Fig. 23A). Telson with two-two short spines on distal half, apex with strong spines on both side and some long, fine setae in center (Fig. 23B).

Discussion

One third of the stygobiont Malacostraca fauna of the Yucatan Peninsula has been discovered in the last 20 years, showing an increasing interest of biodiversity surveys

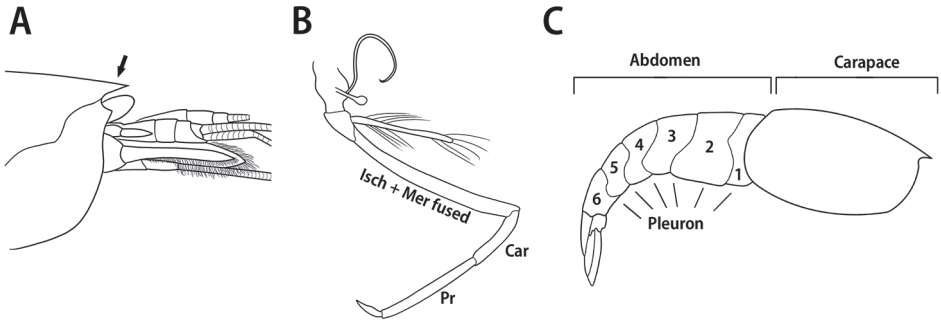

Figure 22. A *Typhlatya dzilamensis* rostrum and eyestalks **B** *T. dzilamensis* pereopod III schematic drawing **C** *T. dzilamensis* carapace and abdomen schematic drawing.

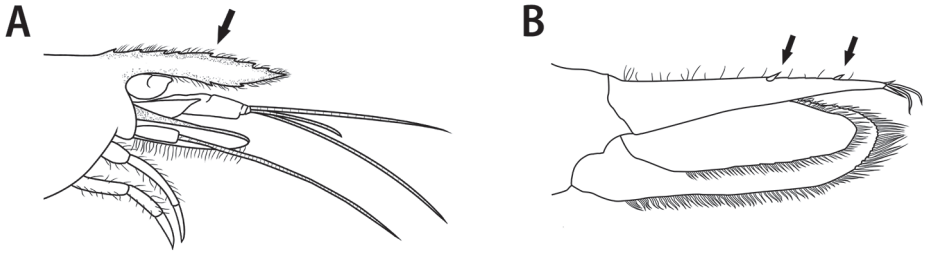

Figure 23. A *Creaseria morleyi* rostrum and eyestalks **B** *C. morleyi* telson and uropods.

in underwater ecosystems in this region. Half of the currently known species were described from the state of Quintana Roo, partly due to the intensive diving explorations of the Nohoch Nah Chich and Sac Actun submerged cave systems conducted since the late eighties (Álvarez et al. 2015). The diversity of the stygofauna of the anchialine caves of Cozumel Island (Quintana Roo) is remarkable: nine malacostracan species have been discovered in the island in the last three decades (e.g. Bowman 1987; Mejía-Ortíz et al. 2017; Ortiz and Winfield, 2015). Only twelve of the stygobiont malacostracan species of the peninsula have been described from the state of Yucatan, but five additional species have distribution data from this state (Angyal et al. 2020). New discoveries of recent years indicate the need of further subterranean biological explorations to gain deeper knowledge on the species richness and distribution of these cryptic habitats of Yucatan (e.g. Angyal et al. 2018; Álvarez et al. 2019).

The taxonomic status of five species of the presented checklist has been changed since the original descriptions. *Creaseriella anops* was originally described as *Cirolana anops* Creaser, 1936. In a thorough taxonomic revision of cirolanid isopods from Mexico, Rioja (1953) considered necessary to establish a new monotypic genus: *Creaseriella* Rioja, 1953, of which *Creaseriella anops* (Creaser, 1936) was the type species.

Fourteen years after the discovery of the new paleomonid shrimp *Paleomon morleyi* Creaser, 1936, a new genus, *Creaseria* Holthuis, 1950 was established, of which *Creaseria morleyi* (Creaser, 1936) is the type species by monotypy (Holthuis 1950).

Two years after its discovery, the stygiomysid *Rhopalonurus holthuisi* Gordon, 1958 had been reallocated to the genus *Stygiomysis* by Gordon (1960), as *Stygiomysis holthuisi* (Gordon, 1958).

The cirolanid isopod *Cirolana yunca* was originally described as *Haptolana yunca* Botosaneanu & Iliffe, 2000. More recently, however, the species has been reallocated to the widely distributed genus *Cirolana* by Bruce (2008).

Eight years after the discovery of the isopod *Cirolana* (*Anopsilana*) *yucatana* Botosaneanu & Iliffe, 2000, Boyko et al. (2008) considered the subgenus *Anopsilana* Paulin & Delamare Deboutteville, 1956 to be the junior synonym of the genus *Cirolana* Leach, 1818, therefore the current valid combination of the species is *Cirolana yucatana* (Botosaneanu & Iliffe, 2000).

There are four monotypic, highly endemic genera (*Tuluweckelia* Holsinger, 1990; *Creaseriella* Rioja, 1953; *Yucatalana* Botosaeanu & Iliffe, 1999; *Creaseria* Holthuis, 1950) known from subterranean waters of Yucatan. The other eight genera presented in the updated checklist have more than one species and have a wider distribution range, as follows.

Apart from *Tulumella unidens*, there are two other species of the genus *Tulumella* Bowman & Iliffe, 1988, described from anchialine caves of the Bahamas (Yager 1988).

Currently, the genus *Stygiomysis* Caroli, 1937 contains five species from the Dominican Republic, the Caicos Island, Cuba, Jamaica and Italy (Bowman et al. 1984). There are two described species of the genus within the Yucatan Peninsula.

Further species of the genus *Antromysis* Creaser, 1936 are known from Suriname, The Bahamas, Jamaica, Costa Rica and Cuba. The second species discovered of the genus *Antromysis* in Mexico was *Antromysis reddelli* Bowman 1977 from Cueva de las Maravillas in Oaxaca (Bowman 1977).

The genus *Curassanthura* Kensley, 1981 consists five species. The four previously known species are from Caribbean and North Atlantic islands. *C. yucatanensis* is the first *Curassanthura* species to be described from a continental environment (Poore 2009; Álvarez et al. 2019).

The isopod *Cirolana* Leach, 1818 is a widely distributed genus with more than 200 species worldwide.

Currently, there are five more valid species of the genus *Haptolana* Bowman, 1966, known from subterranean waters of Belize, Cuba, Somalia, and Western Australia. *H. bowmani* is the only species reported from Mexico.

The genus *Mayaweckelia* Holsinger, 1977 consists of three species. Validity of the third species, *M. yucatanensis* Holsinger, 1977, known from a single locality in Campeche is questionable, as the author points out that „the original description was based on what appear to be submature specimens, therefore raising the strong possibility that the differences noted between *M. yucatanensis* and *M. cenoticola* are due primarly to age" (Holsinger 1990).

The currently known seventeen valid species of the genus *Typhlatya* are characterized by a disjunct distribution around the Caribbean (Yucatan Peninsula, Cuba, Honduras, Bermuda, The Bahamas and the United States of America), in Europe

(France and Spain) and the Galapagos and Ascension Islands, which makes this genus an interesting group to test biogeographical hypotheses (Álvarez et al. 2005; Espinasa et al. 2019; Chávez-Solís et al. 2020). Currently, there are four described species of this genus within the Yucatan Peninsula.

Conclusions

Subterranean habitats of Yucatan are characterized by a remarkable diversity of highly adapted, narrowly distributed crustacean species. Seventeen out of the 33 groundwater-restricted malacostracan species of the peninsula are currently known from waterfilled sinkoles (cenotes) and the associated submerged cave passages of the state of Yucatan. The scope of this paper was to present an updated checklist and the first unified identifiaction guide for the morphological determination of these stygobiont crustaceans. We hope this study will motivate future researches to focus on the taxonomy of the highly endemic stygofauna of the groundwater ecosystems of the Yucatan Peninsula.

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