New distribution records of subterranean crustaceans from cenotes in Yucatan (Mexico)

Dorottya Angyal1,2, Efraín M. Chávez-Solís1,3, Luis A. Liévano-Beltrán1,4, Benjamín Magaña1, Nuno Simoes1,5,6, Maite Mascaró1,5

1 Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma de México, Puerto de abrigo S/N, C.P. 97356, Sisal, Yucatan, Mexico 2 Department of Zoology, Hungarian Natural History Museum, Baross u. 13, 1088 Budapest, Hungary 3 Pogrúzdó Ciencias Biológicas, Universidad Nacional Autónoma de México, Avenida Universidad 3000, Copilco-Universidad, Ciudad de México 04510, México 4 Pogrúzdó Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Avenida Universidad 3000, Copilco-Universidad, Ciudad de México 04510, México 5 Laboratorio Nacional de Resiliencia Costera, Laboratorios Nacionales (LANRESC), CONACYT, Puerto de abrigo S/N, C.P. 97356, Sisal, Yucatan, Mexico 6 International Chair for Ocean and Coastal Studies, Harte Research Institute, Texas A&M at Corpus Christi, Texas, USA

Corresponding author: Maite Mascaró (mmm@ciencias.unam.mx)

Academic editor: Saskia Brix | Received 28 October 2019 | Accepted 3 January 2020 | Published 12 February 2020

Citation: Angyal D, Chávez-Solís EM, Liévano-Beltrán LA, Magaña B, Simoes N, Mascaró M (2020) New distribution records of subterranean crustaceans from cenotes in Yucatan (Mexico). ZooKeys 911: 21–49. https://doi.org/10.3897/zookeys.911.47694

Abstract
New records of 14 stygobiont crustacean species pertaining to six Malacostraca orders from 32 cenotes are presented, with their associated caves of the state of Yucatan, Mexico, together with an individual account for each species. Species composition of most of the investigated cenotes is examined for the first time. A thermosbaenacean and two amphipod species were not formally recorded to the cenote ecosystems of the state of Yucatan prior to our research. Distribution data of a cirolanid isopod previously known only from its type locality is also provided. Barcodes of mitochondrial cytochrome c oxidase subunit I for the reported peracarid species previously lacking this information have been included in present study as tools for species identification and a baseline of further molecular genetic analyses.

Keywords
anchialine ecosystems, barcode sequences, biodiversity, endemic, Eucarida, Peracarida, stygobiont, Yucatan Peninsula
Introduction

'Cenotes' (the local name for water-filled sinkholes) are typical karst features of the Yucatan Peninsula in Mexico. In many cases, far-reaching networks of submerged subterranean cave passages extend from them (Mercado-Salas et al. 2013). Due to the mixing of fresh and saline water, a distinct stratification can be observed inside these anchialine systems (Bishop et al. 2015). Intrusion of saline water is found deeper as the distance from the coastline increases (Bauer-Gottwein et al. 2011). Therefore, most inland cenotes within the state of Yucatan are exclusively freshwater systems, except for a few rather deep ones with haloclines below 50 m in depth, and those located near the northern coastline of the Peninsula (Álvarez et al. 2005; Angyal et al. 2018).

Anchialine ecosystems in Yucatan contain a crustacean-dominated fauna that is adapted to hypogene conditions, such as the lack of sunlight and the low food resource availability (Mejía-Ortíz et al. 2013). Stygobiont species are restricted to aquatic subterranean habitats (Botosaneanu 1986), and often exhibit conspicuous morphological adaptations to hypogene life, known as troglobromorphisms. Such adaptations include structural reductions (e.g., loss of visual organs and pigmentation) or extensions (e.g., lengthening of appendages and complexity of sense organs) (Mejía-Ortíz et al. 2006; González et al. 2018) and physiological modifications (e.g., reduced metabolic rates and starvation resistance) (Hervant et al. 1999, 2001; Bishop and Iliffe 2009). In 2016, prior to our systematic sampling, 47 stygobiotic crustacean species had been reported from anchialine ecosystems of the Mexican federal states of the Yucatan Peninsula, of which 22 were known from cenotes and submerged caves of the state of Yucatan (e.g., Holsinger 1977; Kallmeyer and Carpenter 1996; Álvarez et al. 2005; Suárez-Morales et al. 2006). Fourteen percent of these species belong to the subclass Copepoda (9 spp.), while the remainder belong to the orders Mysida (1 sp.), Stygiomysida (2 spp.), Amphipoda (1 sp.), Isopoda (5 spp.), and Decapoda (4 spp.).

According to the database of the Secretaría de Desarrollo Sustentable (SDS Yucatan), there are more than 3,000 registered cenotes and caves within this state. Current efforts are being directed to complete the descriptions of all registered cenotes, despite that only a small fraction of them have been biologically investigated to date. Ongoing research and explorations are necessary to describe the true biodiversity of these subterranean habitats, their geographical patterns, and changes in time. Thus, our aim was to improve our knowledge on the distribution and ecology of the stygobiotic crustacean fauna of the cenotes and their associated cave passages in the state of Yucatan. We aimed to provide data from cenotes that had never been investigated from a zoological point of view in order to extend the geographical range of crustacean species distribution and contribute to a precise biodiversity mapping of stygofauna in Yucatan. Additionally, we intended to collect samples for molecular and morphological studies so as to gain and make available to the public mitochondrial cytochrome c oxidase subunit I sequences (COI) of species that were lacking barcode information, setting the standard for studies and tools for species identification.
New distribution records of subterranean crustaceans from cenotes in Yucatan

Materials and methods

Sampling sites and sampling

We collected stygobiotic macro-crustaceans from 32 cenotes between May 2016 and January 2018 in cenotes of the state of Yucatan (shorter form: Yucatan) (Figure 1, Table 1). Most of the cenotes studied are several kilometers away from the coast and contain only freshwater. In contrast, some cenotes near the coast have a halocline that divides the cave into freshwater and saline water habitats. Some of the cenotes studied belong to the 'Ring of Cenotes', a fracture zone with high density of sinkholes identified as the outer rim of the crater where the famous asteroid impacted Chicxulub 66 million years ago (González-Herrera et al. 2002; Bauer-Gottwein et al. 2011) (Figure 1). Macro-crustaceans were collected during scientific cave dives using 50 ml sample

Table 1. Location data and identification codes of the studied cenotes.

| Cenote nr. (see Figure 1 map) | Cenote name        | Cenote/Ando cenote code | Municipality | Settlement      | Coordinates latitude | Coordinates longitude |
|-------------------------------|--------------------|-------------------------|--------------|-----------------|-----------------------|------------------------|
| 1                             | Ayun-Nah           | 01980007Y              | Cacalchen    | Cacalchen       | 20°58'49.6"N         | 89°14'39.4"W           |
| 2                             | Bebelchen          | 00028064YC             | Uman         | Sanahcat        | 20°44'11.4"N         | 89°43'55.4"W           |
| 3                             | Cervera            | 00090028YC             | Dzilam de Bravo | Yalshom    | 21°22'29.5"N       | 88°50'01.8"W           |
| 4                             | Chihuho Hol        | 00080001YC             | Abala        | Mucuyche        | 20°38'06.1"N        | 89°36'42.3"W           |
| 5                             | Dzalbay            | 00585085YC             | Temozon      | Dzalbay         | 20°49'53.4"N       | 88°03'23.0"W           |
| 6                             | Dzonbakal          | 00125101YC             | Uman         | San Antonio Mulix | 20°40'11.4"N | 89°46'43.9"W |
| 7                             | Dzonotila          | 00168001YC             | Abala        | Mucuyche        | 20°37'44.0"N       | 89°39'33.0"W           |
| 8                             | Flor de Liz        | -                       | Tixkokob     | Tixkokob        | 21°00'16.0"N       | 89°23'33.0"W           |
| 9                             | Isim Ha            | 00164037YC             | Tixkalak     | Tixkalak        | 20°37'49.0"N       | 89°06'40.0"W           |
| 10                            | Kakuel             | 00142001YC             | Abala        | Mucuyche        | 20°37'40.3"N       | 89°34'26.8"W           |
| 11                            | Kamppinen          | 00042076YC             | Tecoh        | Chiniquila      | 20°42'00.8"N       | 89°22'41.6"W           |
| 12                            | Kantinkinche       | 00002001YC             | Abala        | Mucuyche        | 20°38'13.8"N       | 89°37'58.8"W           |
| 13                            | Tankal             | -                       | Homun        | Homun           | 20°39'38.3"N       | 89°16'42.5"W           |
| 14                            | Kanun              | 01730006Y              | Homun        | Homun           | 20°44'44.2"N       | 89°14'40.7"W           |
| 15                            | Nayah              | 00009076YC             | Tecoh        | Pizyha          | 20°38'13.3"N       | 89°35'26.3"W           |
| 16                            | Noh/Chunck         | 00225011YC             | Chunchumil   | Celestun        | 20°48'48.5"N       | 90°17'47.8"W           |
| 17                            | Nohmozoon          | 00010076YC             | Tecoh        | Pizyha          | 20°62'32.5"N       | 89°38'42.0"W           |
| 18                            | Pixton             | 00064064YC             | Huhi         | Huhi            | 20°34'13.5"N       | 89°15'11.6"W           |
| 19                            | Pol Box            | 00321023YC             | Chochola     | Chochola        | 20°41'24.3"N       | 89°48'54.5"W           |
| 20                            | Sabrun 1           | 00230011YC             | Chunchumil   | Celestun        | 20°51'00.7"N       | 90°14'08.1"W           |
| 21                            | San Elias          | 01171036Y              | Homun        | Homun           | 20°41'21.0"N       | 89°14'19.0"W           |
| 22                            | San Juan           | 00063036YC             | Homun        | Homun           | 20°44'02.6"N       | 89°17'18.6"W           |
| 23                            | Sanitito           | 00108045YC             | Kopoma       | Kopoma          | 20°38'58.1"N       | 89°53'44.3"W           |
| 24                            | El Virgen          | -                       | Sotuta       | Sotuta          | 20°32'01.9"N       | 89°02'19.4"W           |
| 25                            | Tres Oches         | -                       | Homun        | Homun           | 20°43'55.7"N       | 89°16'20.0"W           |
| 26                            | Tza Itza           | 00050076YC             | Tecoh        | Tecoh           | 20°43'49.1"N       | 89°27'59.9"W           |
| 27                            | Xaan               | 00423036YC             | Homun        | Homun           | 20°43'39.3"N       | 89°15'24.6"W           |
| 28                            | X’babero           | 00162023YC             | Chochola     | Chochola        | 20°40'42.5"N       | 89°49'00.7"W           |
| 29                            | X-Batun            | 00005023YC             | Uman         | San Antonio Mulix | 20°40'23.8"N | 89°46'22.8"W |
| 30                            | X’kook             | 00650093YC             | Ekmul        | Ekmul           | 20°56'51.0"N       | 89°20'41.0"W           |
| 31                            | Yalil Ussil        | 00003001YC             | Abala        | Mucuyche        | 20°37'26.0"N       | 89°36'24.0"W           |
| 32                            | Yax-Kis            | 00091001YC             | Abala        | Mucuyche        | 20°37'33.7"N       | 89°35'35.7"W           |
tubes and 10 cm diameter hand nets. Habitat data (e.g., depth, temperature, collected in cavern or cave, position relative to halocline) at the collection site of each individual was recorded along with photographs and video-recordings of the observed crustaceans and their habitats. All crustaceans were individually placed into 70 or 96% ethanol containing tubes immediately after collection. All specimens were collected under the permits of the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT/SPGA/DGVS/05263/14; SEMARNAT/SPGA/DGVS/02068/17). The collected material was deposited in the Yucatán Collección de Crustáceos, Unidad Multidisciplinaria de Docencia e Investigación, Universidad Nacional Autónoma de México in Sisal (UNAM UMDI-Sisal), the Collección Nacional de Crustáceos, Instituto de Biología, UNAM in Mexico City, or in the Collection of Crustaceans of the Hungarian Natural History Museum (HNHM), Budapest.
Morphological analysis

Individuals were examined using a stereo-microscope. Specimens of thermosbaenaceans, stygiomysids, mysids, and amphipods were studied as follows: cleared and stained exoskeletons were dissected under a Leica M125 stereo microscope. The dissections were then mounted on slides and examined using a Leica DM 1000 compound light microscope (Fišer et al. 2009; Angyal et al. 2015). For the identification of the collected material the following publications were used: Álvarez et al. 2005; Álvarez and Iliffe 2008; Angyal et al. 2018; Botosaneanu and Iliffe 1999, 2000, 2002, 2006; Bowman 1966, 1977; Bruce 1986; Creaser 1936; Hobbs and Hobbs 1976; Hobbs et al. 1977; Hobbs 1979; Holsinger 1977, 1990; Horwitz et al. 1995; Kallmeyer and Carpenter 1996; Lowry and Myers 2013; Meland et al. 2015; Pérez-Aranda 1983a, 1983b, 1984a, 1984b; Tinnizi and Quddusi 1993; Wagner 1994. Photographs were made using an OMAX 14 OMP digital USB microscope camera, a Nikon D5300, and a Nikon D7000 with 60 mm macro lens.

Molecular studies (COI barcode sequences)

DNA extraction of the peracarids studied was performed using QIAamp DNA Microkit (QIAGEN), following the manufacturer’s instructions. A few pereopods of each animal provided the necessary material to extract DNA. For PCR amplification of mitochondrial COI, we used the primer pair LCO 1490 and HCO 2198 (Folmer et al. 1994). PCR reactions (25 μl) contained 13.85 μl mQ water, 2.5 μl 10× PCR buffer, 2.5 μl dNTP mix (2mM), 1.5 μl of each primers (5μM), 0.15 μl Fermentas Dream Taq (5U/μl), and 3 μl DNA extract. PCR temperature conditions were set as follows: initial denaturation for 3 min at 94 °C, denaturation for 45 sec at 94 °C, hybridization for 45 sec at 48 °C, and polymerization for 1 min at 72 °C. After thirty cycles, a final extension for 3 min at 72 °C was performed. PCR products were purified using Exo SAP-IT Express PCR Product Cleanup (Affymetrix) according to the manufacturer’s instructions. The fragments were sequenced in both directions using PCR amplification primers with an ABI 3130 sequencer. Contigs were assembled and sequences were edited using BioEdit 7.1.11 sequence alignment editor software (Hall 1999): chromatograms of complement reverse and forward strings were compared, gaps were eliminated, while indels and stop codons were checked. 605-651 bp COI barcode sequences have been uploaded to the NCBI GenBank database. Accession numbers and localities are listed in Table 2.

Results

A total of 14 stygobiont crustacean species, belonging to six Malacostraca orders, was collected (Figures 2, 3). New records of each species at each cenote were assessed after an exhaustive literature investigation (Table 3). This evaluation was based only on the
collected material that has been deposited in scientific collections. Additional data based on observations, however, are mentioned in the “Remarks” section in each case. An individual account for each species is subsequently discussed. 605-651 base-pair COI barcode sequences of the analyzed species (Table 2) were obtained and uploaded to NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/).
Subphylum: Crustacea

Class: Malacostraca
Superorder: Peracarida
Order: Thermosbaenacea
Family: Tulumellidae

*Tulumella unident* Bowman & Iliffe, 1988
Figure 2A

**Material examined.** 4 individuals; **Cenote Cervera**, depth 25.6-26.2 m, cave, in hydrogen sulfide layer, around and below halocline, 26 °C, Yalsihom, Yucatan, Mexico; 8 May 2016; colls. D. Angyal & E. Chávez Solís. 4 individuals; **Cenote Sabtun 1**, depth 24.0-25.0 m, cavern, above and around halocline, 25 °C, Chunchumil, Yucatan, Mexico; 10 December 2017; colls. D. Angyal, E. Chávez Solís, S. Drs, Q. Hernández & S. Reyes.

**Previous distribution.** Iliffe 1992; Iliffe 1993; Bowman and Iliffe 1988; Rocha et al. 1998; Pohlman et al. 2000; Pesce and Iliffe 2002; Álvarez et al. 2015; Olesen et al 2015; Benítez et al. 2019.

Type locality is Cenote Naharon (Cristal) in Quintana Roo. This species had only been reported from Quintana Roo from cenotes Calavera (Temple of Doom), Mayan Blue, Actun Ha (Carwash), Muknal, Na’ach Wennen Ha, Bang, Odyssey, Tabano, and Quebrada.

**Remarks.** Our findings extend the distribution area of this thermosbaenacean, previously endemic to Quintana Roo, to the cenotes located in the coastal areas north of Dzilam de Bravo and the east of Celestun. It is most likely that this species has a coastal distribution along the anchialine systems of the Yucatan Peninsula. Previous records were reported from cenotes located 2-10 km from the coastline near Tulum, where they occurred mostly above and at the halocline (Álvarez & Iliffe 2008; Álvarez et al. 2015; Benítez et al. 2019). In Cenote Cervera, 3.6 km inland from the northern coast of the Yucatan Peninsula, we observed individuals both above and below the halocline, as well as in the hydrogen sulfide layer.

Order: Stygiomysida
Family: Stygiomysidae

*Stygiomysis cokei* Kallmeyer & Carpenther, 1996
Figure 2B

**Material examined.** 1 individual; **Cenote Tres Oches**, depth 21.6 m, cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 5 June 2016; colls. D. Angyal & E. Chávez Solís. 2 individuals, **Cenote San Elías**, depth 28.2 m and 32.0 m, cavern, freshwater, 26
Figure 2. A Tulumella unidens (Thermosbaenacea) B Stygiomysis cokei (Stygiomysida) C Stygiomysis cf. holthuisi (Stygiomysida) D Antromysis cenotensis (Mysida) E Mayaweckelia troglomorpha (Amphipoda) F Mayaweckelia cenoticola (Amphipoda) G Tuluweckelia cernua (Amphipoda). Scale bars: 1 mm (A, C, D, F, G); 10 mm (B, E).
New distribution records of subterranean crustaceans from cenotes in Yucatan

°C, Homun, Yucatan, Mexico; 19 November 2017; colls. D. Angyal, E. Chávez Solís, S. Drs & L. Liévano. 2 individuals; Dzonotila, depth 20.8 m and 28.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 20 November 2017; colls. D. Angyal, E. Chávez Solís, S. Drs & B. Magaña. 1 individual; Yax-Kis, depth 12.1 m and 27.0 m, cave, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 27 January 2018; colls. D. Angyal, S. Drs & L. Liévano.

Previous distribution. Kallmeyer and Carpenter 1996; Pesce and Iliffe 2002; Álvarez and Iliffe 2008; Álvarez et al. 2015; Benítez et al. 2019.

Type locality is Cenote Calavera (Temple of Doom) in Quintana Roo. Further known localities in Quintana Roo are cenotes Mayan Blue, Naharon (Cristal), Escandon, Actun Ha (Carwash), Actun Ko, Na’ach Wennen Ha, Muknal and Tabano. From Yucatan the species was known from cenotes Papakal, San Eduardo, Kankirixche, Yaal Utsil and Dzonotila.

Remarks. Our records show that this species is distributed in cenotes of central Yucatan and along the Ring of Cenotes. Among the two Stygiomysis species of the region, S. cokei proved to be rarer than Stygiomysis cf. holthuisi. New occurrences were recorded between 12-32 m deep in freshwater. In cenotes San Elias, Dzonotila and Yax-Kis it co-occurred with S. cf. holthuisi. Previously the species had also been reported in brackish habitats (Álvarez and Iliffe 2008; Álvarez et al. 2015).

Stygiomysis cf. holthuisi (Gordon, 1958)

Figure 2C

Material examined. 2 individuals; Cenote Tres Oches, depth 21.6 m, cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 5 June 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; Cenote Tza Itza, depth 18.9 m, cavern, freshwater, 27 °C, Tecoh, Yucatan, Mexico; 10 May 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; Cenote X-Batun, depth 19.3 m, cavern, freshwater, 27 °C, San Antonio Mulix, Yucatan, Mexico; 14 May 2016; colls. R. Acosta, D. Angyal, J. Baduy & S. Reyes. 3 individuals; Cenote Kanun, depth 10.9-13.0 m, cave, freshwater, 26 °C, Homun, Yucatan, Mexico; 4 June 2016; colls. R. Acosta, D. Angyal, J. Baduy, B. Magaña & S. Reyes. 1 individual; Cenote Kakuel, depth 29.8 m, cave, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 10 June 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; Cenote Kankirixche, depth 3 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 11 June 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; Cenote Santito, depth 5.4 m, cavern, freshwater, 27 °C, Kopoma, Yucatan, Mexico; 10 November 2017; colls. D. Angyal, D. Drs & L. Liévano. 1 individual; Cenote Pol Box, depth 3.0 m, cavern, freshwater, 27 °C, Chochola, Yucatan, Mexico; 12 November 2017; colls. D. Angyal, S. Drs, L. Liévano & E. Sosa. 4 individuals; Cenote Kankal, depth 6.0-27.0 m, cavern, freshwater, 25 °C, Homun, Yucatan, Mexico; 12 November 2017; colls. D. Angyal, S. Drs, L. Liévano & E. Sosa. 2 individuals; Cenote Flor de Liz, depth 3.0 m, cavern, freshwater, 27 °C, Tixkokob, Yucatan, Mexico; 17 December 2017; colls. D. Angyal,
S. Drs, L. Liévano & S. Reyes. 1 individual; **Cenote Bebelchen**, depth 30.0 m, cavern, freshwater, 25 °C, Sanahcat, Yucatan, Mexico; 18 December 2017; colls. D. Angyal, S. Drs, L. Liévano & S. Reyes. 2 individuals; **Cenote Chihuol Hol**, depth 16.0 and 25.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 26 January 2018; colls. D. Angyal, S. Drs, L. Liévano, B. Magaña & N. Simoes. 3 individuals; **Yax Kis**, depth 9.0-25.0 m, cave, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 27 January 2018; colls. D. Angyal, S. Drs & L. Liévano.

**Previous distribution.** Gordon 1958; Botosaneanu 1980; Bowman et al. 1984; Pesce and Iliffe 2002; Álvarez and Iliffe 2008, Álvarez et al. 2015, Benítez et al. 2019.

Type locality is Devil’s Hole, St. Martin, Lesser Antilles (France). The species is known from the Bahamas, Anguilla, Puerto Rico, and the Yucatan Peninsula. In Quintana Roo *S. cf. holthuisi* was recorded from cenotes Mayan Blue, Casa Cenote, Na’ach Wennen Ha, Bang, Odyssey, Muknal, and Tabano. From Yucatan the species was previously known only from a single locality, Cenote Mucuyche.

**Remarks.** We have also recorded the species from cenotes Yaal Utsil, San Elias, and Dzonotilta in freshwater bodies in both cavern and cave sections, between 3 and 30 m deep. Álvarez and Iliffe (2008) and Álvarez et al. (2015) reported observations in both freshwater and around the halocline from cenotes in Quintana Roo.

**Order:** Mysida  
**Family:** Mysidae

**Antromysis cenotensis** Creaser, 1936

Figure 2D

**Material examined.** 21 individuals; **Cenote Tza Itza**, depth 12.7-13.5 m, cavern, freshwater, 27 °C, Tecoh, Yucatan, Mexico; 10 May 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; **Cenote Dzonbakal**, depth 25.3 m, cavern, freshwater, 27 °C, San Antonio Mulix, Yucatan, Mexico; 14 May 2016; colls. R. Acosta, D. Angyal, J. Baduy & S. Reyes. 1 individual; **Cenote Nayah**, depth 27.9 m, entrance of cave part, freshwater, 26 °C, Pixyah, Yucatan, Mexico; 17 May 2016; colls. D. Angyal & B. Magaña. 3 individuals; **Cenote Kampepen**, depth 9.3-12.5 m, cavern, freshwater, 27 °C, Chinquila, Yucatan, Mexico; 17 May 2016; colls. D. Angyal & B. Magaña. 4 individuals; **Cenote Kanun**, depth 0.5 m, cenote entrance, freshwater, 26 °C, Homun, Yucatan, Mexico; 4 June 2016; colls. R. Acosta, D. Angyal, J. Baduy, B. Magaña & S. Reyes. 4 individuals; **Cenote Xaan**, depth 22.2-24.2 m, cavern and cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 9 June 2016; colls. D. Angyal & E. Chávez Solís. 15 individuals; **Cenote Kakuel**, depth 7.2-10.8 m, cavern, freshwater, 27 °C, Homun, Yucatan, Mexico; 10 June 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; **Cenote Kankirixche**, depth 9.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 11 June 2016;
New distribution records of subterranean crustaceans from cenotes in Yucatan

colls. D. Angyal & E. Chávez Solís. 4 individuals; Cenote Kankirixche, depth 10.0-25.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 25 January 2018; colls. D. Angyal, S. Drs, B. Magaña & L. Liévano. 18 individuals; Cenote Santito, depth 0.2-1.0 m, cavern, freshwater, 27 °C, Kopoma, Yucatan, Mexico; 10 November 2017; colls. D. Angyal, S. Drs & L. Liévano. 17 individuals; Cenote Pol Box, depth 5.2-9.3 m, cavern, freshwater, 27 °C, Chochola, Yucatan, Mexico; 12 November 2017; colls. D. Angyal, S. Drs & L. Liévano. 1 individual; Cenote Kankal, depth 24.6 m, cavern, freshwater, 25 °C, Homun, Yucatan, Mexico; 18 November 2017; colls. D. Angyal, E. Chávez Solís, S. Drs & L. Liévano. 21 individuals; Dzonotila, depth 3.0-27.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 20 November 2017; colls. D. Angyal, E. Chávez Solís, S. Drs & B. Magaña. 5 individuals; Cenote Ixim Ha, depth 10.0 m, cavern, freshwater, 25 °C, Tixkakal, Yucatan, Mexico; 25 November 2017; colls. D. Angyal, E. Chávez Solís, S. Drs, L. Liévano & E. Sosa. 1 individual; Cenote Noh’Chunck, depth 12.0 m, cavern, freshwater, 25 °C, Chunchumil, Yucatan, Mexico; 25 November 2017; colls. D. Angyal, E. Chávez Solís, S. Drs, Q. Hernández & S. Reyes. 11 individuals; Cenote X’kobob, depth 1.0-4.0 m, cavern, freshwater, 25 °C, Ekmul, Yucatan, Mexico; 17 December 2017; colls. D. Angyal, S. Drs, L. Liévano & S. Reyes. 14 individuals; Cenote Flor de Liz, depth 0.3-3.0 m, cavern, freshwater, 27 °C, Tixkokob, Yucatan, Mexico; 17 December 2017; colls. D. Angyal, S. Drs, L. Liévano & S. Reyes. 19 individuals; Cenote Pixton, depth 3.0 m, cavern, freshwater, 27 °C, Huhi, Yucatan, Mexico; 18 December 2017; colls. D. Angyal & L. Liévano. 11 individuals; Cenote Bebelchen, depth 27.0 m, cavern, freshwater, 25 °C, Sanahcat, Yucatan, Mexico; 18 December 2017; colls. D. Angyal, L. Liévano & S. Reyes. 6 individuals; Cenote El Virgen, depth 25.0 m, cavern, freshwater, 26 °C, Sotuta, Yucatan, Mexico; 20 December 2017; colls. L. Liévano & N. Simoes. 3 individuals; Cenote Chihuo Hol, depth 11.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 20 December 2017; colls. D. Angyal, S. Drs, B. Magaña, L. Liévano & N. Simoes.

Previous distribution. Creaser 1936, 1938; Nicholas 1962; Bowman 1977; Reddell 1977, 1981; Holsinger 1990; Iliffe 1992, 1993; Fiers et al. 1996; Rocha et al. 1998, 2000; Suárez-Morales and Rivera Arriaga 1998; Pohlman et al. 2000; Pesce and Iliffe 2002; Schmitter-Soto et al. 2002; Álvarez and Iliffe 2008; Álvarez et al. 2015; Benítez et al. 2019.

Type locality is Grutas de Balankanche (Yucatan). Widely distributed in the central and northern parts of the Yucatan Peninsula, known from several wells, cenotes and caves of Quintana Roo and Yucatan.

Remarks. Antromysis cenotensis was present in all the cenotes studied, except for Cenote Cervera. Álvarez et al. (2015) mentions that A. cenotensis occurs mostly above or occasionally below the halocline up to a depth of 16 m. In the present study, the species was only observed in freshwater habitats, in some cases as deep as the scope of the survey. Our findings prove this species as a common representative of the stygofauna of Yucatan, as it was found in more than 95% of the visited sites. Antromysis cenotensis is listed as “threatened” in the Mexican Red List of Threatened Species (NOM-059 SEMARNAT 2010).
Order: Amphipoda  
Family: Hadziidae

*Mayaweckelia troglomorpha* Angyal, 2018

**Figure 2E**

**Material examined.** 2 individuals; **Dzonbakal**, depth 26.3 and 26.5 m, cave, freshwater, 27 °C, San Antonio Mulix, Yucatan, Mexico; 14 May 2016; colls. R. Acosta, D. Angyal, J. Baduy & S. Reyes. 1 individual; **Cenote Kanun**, depth 24.3 m, cave, freshwater, 26 °C, Homun, Yucatan, Mexico; 4 June 2016; colls. R. Acosta, D. Angyal, J. Baduy, B. Magaña & S. Reyes. 1 individual; **Cenote Xaan**, depth 25.4 m, cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 9 June 2016; colls. D. Angyal & E. Chávez Solís. 2 individuals; **Cenote Kankirixche**, depth 20.4 and 33.3 m, cavern and cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 11 June 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; **Cenote Ayun-Nah**, depth 14.0 m, cave, freshwater, 27 °C, Cacalchen, Yucatan, Mexico; 22 May 2016; colls. D. Angyal, B. Magaña & E. Sosa Rodríguez. 1 individual; **Dzonotila**, depth 18.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 20 November 2017; colls. D. Angyal, E. Chávez Solís, S. Drs & B. Magaña. 2 individuals; **Cenote X’kokob**, depth 4.0-10.0 m, cavern, freshwater, 26 °C, Ekmul, Yucatan, Mexico; 17 December 2017; colls. D. Angyal, E. Chávez Solís, S. Drs & B. Magaña. 2 individuals; **Cenote Chihuo Hol**, depth 8.0-27.2 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 26 January 2018; colls. D. Angyal, S. Drs, L. Liévano, B. Magaña & N. Simoes. 1 individual; **Cenote Yax-Kis**, depth 8.0 m, cave, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 27 January 2018; colls. D. Angyal, S. Drs & L. Liévano.

**Previous distribution.** Angyal et al. 2018. Type locality is Dzonbakal (Yucatan). Allotype female is from Cenote Kankirixche, paratypes are from Dzonbakal and cenotes Kanun, Xaan and Kankirixche (all in Yucatan).

**Remarks.** At present, collected material is available from eight localities and a small *M. troglomorpha* population was also observed in Cenote San Elias. All the individuals were found in freshwater habitats, both in cave and cavern sections, where water temperature was between 26 and 27 °C. In cenote Kankirixche, some individuals were observed below 45 meters in depth. As a species recently described by our research group, one of the outcomes of present expeditions. As *M. troglomorpha* was found in approximately 30% of the visited sites, it does not appear to be a rare freshwater stygobiotic element in the Yucatan cenotes.

*Mayaweckelia cenoticola* Holsinger, 1977

**Figure 2F**

**Material examined.** 1 individual; **Cenote Ayun-Nah**, depth 14.0 m, cave, freshwater, 27 °C, Cacalchen, Yucatan, Mexico; 22 May 2016; colls. D. Angyal, B. Magaña & E. Sosa Rodríguez. 1 individual; **Dzonotila**, depth 18.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 20 November 2017; colls. D. Angyal, E. Chávez Solís, S.
New distribution records of subterranean crustaceans from cenotes in Yucatan

Drs & B. Magaña. 1 individual; **Cenote Ixim Ha**, depth 4.7 m, cavern, freshwater, 25 °C, Tixkakal, Yucatan, Mexico; 25 November 2017; colls. D. Angyal, E. Chávez Solís, S. Drs, L. Liévano & E. Sosa. 3 individuals; **Cenote Bebelchen**, depth 0.5-7.3 m, cavern, freshwater, in water column and in roots at cavern entrance, 25 °C, Sanahcat, Yucatan, Mexico; 18 December 2017; colls. D. Angyal, S. Drs, L. Liévano & S. Reyes.

**Previous distribution.** Holsinger 1977, 1990; Reddell 1981; Álvarez and Iliffe 2008, Álvarez et al. 2015, Angyal et al. 2018, Benítez et al. 2019.

Type locality is Cenote Xtacabiha (Yucatan). From Yucatan the species was also known from Cueva de Orizaba, Cenote Nohchen, Grutas de Tzab-Nah and Grutas de Santa Maria. From Quintana Roo there were records from Cenote Actun Ha (Carwash), Cenote de las Ruinas, Cenote de San Martin, Cenote de Santo Domingo, Cueva de Tancah, Odyssey, Bang and Tabano. From the state of Campeche, the species was known from the Volcán de los Murciélagos cave.

**Remarks.** *Mayaweckelia cenoticola* proved to be rarer than *M. troglomorpha*, since it was recorded from only four cenotes. In Cenote Bebelchen we found some individuals in the roots of trees near the surface at the entrance region. Holsinger (1990) found that the species is associated mainly with freshwater habitats, with few populations occurring in weak brackish water. Individuals found in the Ox Bel Ha System (Quintana Roo) by Álvarez et al. (2015) and Benítez et al. (2019) also occurred in freshwater.

**Tuluweckelia cernua** Holsinger, 1990

Figure 2G

**Material examined.** 3 individuals; **Cenote San Juan**, depth 27.0-27.1 m, cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 7 May 2016; colls. D. Angyal & E. Chávez Solís. 2 individuals; **Cenote Dzonbakal**, depth 29.0 m, cave, freshwater, 27 °C, San Antonio Mulix, Yucatan, Mexico; 22 May 2016; colls. D. Angyal, J. Baduy & B. Magaña. 10 individuals; **Cenote Tres Oches**, depth 15.8-22.9 m, cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 5 June 2016; colls. D. Angyal & E. Chávez Solís. 3 individuals; **Cenote Xaan**, depth 22.7-26.6 m, cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 9 June 2016; colls. D. Angyal & E. Chávez Solís. 3 individuals; **Cenote Kakuel**, depth 32.2-38 m, cave, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 10 June 2016; colls. D. Angyal & E. Chávez Solís. 3 individuals; **Cenote Kankirixche**, depth 20.4-49.6 m, cavern and cave, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 11 June 2016; colls. D. Angyal & E. Chávez Solís. 2 individuals; **Cenote Santito**, depth 5.3-6.0 m, cavern, freshwater, 27 °C, Kopoma, Yucatan, Mexico; 10 November 2017; colls. D. Angyal, S. Drs & L. Liévano. 1 individual; **Cenote X’baba**, depth 26.0 m, cavern, freshwater, 27 °C, Chochola, Yucatan, Mexico; 26 November 2017; colls. S. Drs, L. Liévano & E. Sosa. 1 individual; **Cenote Sabtun 1**, depth 25.0 m, cavern, above the halocline, 25 °C, Chuncheumil, Yucatan, Mexico; 10 December 2017; colls. D. Angyal, S. Drs, E. Chávez Solís, Q. Hernández & S. Reyes. 1 individual; **Cenote Pixton**, depth 7.0 m, cavern, freshwater, 26 °C, Huhi, Yucatan, Mexico; 18 December
2017; colls. D. Angyal & L. Liévano. 3 individuals; **Cenote Yax-Kis**, depth 23.4-32.0 m, cave, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 27 January 2018; colls. D. Angyal, S. Drs & L. Liévano.

**Previous distribution.** Holsinger 1990; Álvarez and Iliffe 2008; Álvarez et al. 2015; Angyal et al. 2018; Benítez et al. 2019.

Type locality is Cenote Calavera (Temple of Doom) in Quintana Roo. This species was known only from coastal caves of Quintana Roo: Mayan Blue, Actun Ha (Carwash), Mojara, Naharon (Cristal), Na’ach Wennen Ha, Bang, Muknal, Odyssey, and Tabano.

**Remarks.** *Tuluweckelia cernua* was both the most frequent and abundant stygobiotic amphipod in the present study. Additional observations were from cenotes Yaal Utsil, El Virgen, and Dzalbay. In contrast with previous reports (e.g. Holsinger 1990), *T. cernua* always occurred in freshwater habitats. Individuals were collected between depths of 5-50 m. The species co-occurred with *M. troglomorpha* in five cenotes. These are the first distributional records of *T. cernua* for the state of Yucatan. Known localities of this species have almost tripled, increasing its distribution range into the Yucatan inland area.

**Order: Isopoda**
**Family: Cirolanidae**

*Creaseriella anops* (Creaser, 1936)

Figure 3A

**Material examined.** 3 individuals; **Cenote San Juan**, depth 20.0-28.0 m, cavern and cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 7 May 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; **Cenote Cervera**, depth 24.0 m, cave, below halocline, 26 °C, Yalsihom, Yucatan, Mexico; 8 May 2016; colls. D. Angyal & E. Chávez Solís. 2 individuals; **Cenote Tza Itza**, depth 12.5-13.5 m, cavern, freshwater, 27 °C, Tecoh, Yucatan, Mexico; 10 May 2016; colls. D. Angyal & E. Chávez Solís. 2 individuals; **Cenote Tres Oches**, depth 18.2-21.7 m, cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 5 June 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; **Cenote Kankirixche**, depth 3.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 11 June 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; **Cenote Chihuo Hol**, depth 15.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 26 January 2018; colls. D. Angyal, S. Drs, L. Liévano, B. Magaña & N. Simoes.

**Previous distribution.** Creaser 1936, 1938; Nicholas 1962; Reddell 1977, 1981; Holsinger 1990; Iliffe 1992, 1993; Fiers et al. 1996; Rocha et al. 1998; Botosaneanu and Iliffe 1999, 2002; Álvarez et al. 2005; Iliffe and Botosaneanu 2006; Álvarez and Iliffe 2008; Sánchez-Rodríguez 2008; Ruiz-Cancino et al. 2013; Álvarez et al. 2015; Ortiz and Chazaro-Olvera 2015; Benítez et al. 2019.
New distribution records of subterranean crustaceans from cenotes in Yucatan

Type locality is Cenote Sambula (Motul, Yucatan). Known from numerous caves and cenotes in Quintana Roo and Yucatan, and a well in Campeche.

**Remarks.** The species was also observed in cenotes Yaal Utsil, Pol Box, X'kokob, Bebelchen, Kankan, San Elias, Dzonotila, Yax-Kis, Xaan and X'baba. *Creaseriella anops* was found both in cavern and cave sections, between 3 and 40 m deep. Our observations generally agree with the records of Iliffe and Botosaneanu (2006) and Álvarez et al. (2015) as a freshwater species. However, as Benítez et al. (2019) reported, we also observed individuals around or below the halocline. *Creaseriella anops* is listed as “threatened” in the Mexican Red List of Threatened Species (NOM-059-SEMARNAT 2010).

*Yucatalana robustispina* Botosaneanu & Iliffe, 1999

**Figure 3B**

**Material examined.** 1 individual; **Cenote Xaan**, depth 27.6 m, cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 9 June 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; **Cenote Kakuel**, depth 19.9 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 10 June 2016; colls. D. Angyal & E. Chávez Solís. 5 individuals; **Cenote Kankirixche**, depth 20-49.3 m, cavern and cave, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 11 June 2016; colls. D. Angyal & E. Chávez Solís. 3 individuals; **Cenote Kankirixche**, depth 10.0-27.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 26 January 2018; colls. D. Angyal, S. Drs, L. Liévano & B. Magaña. 1 individual; **Cenote Yaal Utsil**, depth 35.5 m, cave, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 3 November 2017; colls. D. Angyal, S. Drs & E. Chávez Solís. 1 individual; **Cenote Tza Itza**, depth 15.0 m, cavern, freshwater, 27 °C, Tecoh, Yucatan, Mexico; 3 November 2017; colls. D. Angyal, S. Drs & L. Liévano. 1 individual; **Cenote Pol Box**, depth 3.0 m, cavern, freshwater, 27 °C, Chochola, Yucatan, Mexico; 12 November 2017; colls. D. Angyal, S. Drs, L. Liévano & E. Sosa. 2 individuals; **Dzonotila**, depth 14.0 and 16.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 12 November 2017; colls. D. Angyal, S. Drs, E. Chávez Solís & B. Magaña. 1 individual; **Cenote X'baba**, depth 12.0 m, cave, freshwater, 25 °C, Chochola, Yucatan, Mexico; 12 November 2017; colls. S. Drs, L. Liévano & E. Sosa. 1 individual; **Cenote El Virgen**, depth 12.6 m, cavern, freshwater, 26 °C, Sotuta, Yucatan, Mexico; 20 December 2017; colls. L. Liévano & N. Simoes. 1 individual; **Cenote Chihuo Hol**, depth 20.6 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 26 January 2018; colls. D. Angyal, S. Drs, L. Liévano, B Magaña N. Simoes. 3 individuals; **Cenote Yax Kis**, depth 12.0-33.0 m, cave, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 27 January 2018; colls. D. Angyal, S. Drs & L. Liévano.

**Previous distribution.** Botosaneanu and Iliffe 1999, 2002, 2006; Álvarez and Iliffe 2008.

Type locality is Cenote Pabakal (Papakal), Yucatan. It was also found in cenotes Kankirixche, Kakuel, Chuhi-Hol Dos, Xacha, and San Geronimo (all in Yucatan).
Figure 3. A Creaseriella anops (Isopoda) B Yucatalana robustispina (Isopoda); C Cirolana yunca (Isopoda) D Typhlatya dzilamensis (Decapoda) E Typhlatya mitchelli (Decapoda) F Typhlatya pearsei (Decapoda) G Creaseria morleyi (Decapoda). Scale bars: 1 mm (B, C, F); 10 mm (A, D, E, G).
Remarks. Individuals of *Y. robustispina* were collected in a third of all localities visited, where it occurred in freshwater between 3 and 49 m in depth. In eight cenotes *Y. robustispina* co-occurred with the isopod *C. anops*. Agreeing with our observations, previous records referred specimens caught in freshwater between 5-50 m in depth (Botosaneanu and Iliffe 1999, 2002, 2006). Known localities of this species have been doubled.

*Cirolana yunca* (Botosaneanu & Iliffe, 2000)
Figure 3C

**Material examined.** 1 individual; *Cenote Tres Oches*, depth 22.4 m, cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 5 June 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; *Cenote X’baba*, depth 25.0 m, cave, freshwater, 25 °C, Chochola, Yucatan, Mexico; 26 November 2016; colls. S. Drs, L. Liévano & E. Sosa. 1 individual; *Cenote Chihuo Hol*, depth 19.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 26 January 2018; colls. D. Angyal, S. Drs, L. Liévano, B Magaña & N. Simoes. 1 individual.

**Previous distribution.** Botosaneanu and Iliffe 2000, 2006; Álvarez and Iliffe 2008; Rocha-Ramírez et al. 2009.

Type locality is Cenote Sabak Ha (Yucatan). This species had only been collected from its type locality until our expeditions.

Remarks. We here provide the first records after the original description, which was based on a single specimen collected at 60 m in depth near the halocline at a salinity of 1.4 g/l (Botosaneanu and Iliffe 2000, 2006). The three newly collected individuals were found in freshwater habitats, both in cavern and cave zones below 19 m in depth. The species was found in approximately 10% of the studied cenotes always as solitary individuals. Therefore, *C. yunca* seems to be a rare element of the Yucatan freshwater cenote ecosystems.

Superorder: Eucarida
Order: Decapoda
Family: Atydae

*Typhlatya dzilamensis* Álvarez, Iliffe & Villalobos, 2005
Figure 3D

**Material examined.** 1 individual; *Cenote Cervera*, depth 27.4 m, cave, below halocline, 27 °C, Yalsihom, Yucatan, Mexico; 8 May 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; *Cenote Sabtun 1*, depth 28 m, cavern, below halocline, 26 °C, Chunchumil, Yucatan, Mexico; 10 Dec 2017; colls. D. Angyal & E. Chávez.

**Previous distribution.** Álvarez et al. 2005, 2015; Álvarez and Iliffe 2008; Benítez et al. 2019; Espinasa et al. 2019.
Type locality is Buya Uno, allotype was collected from Cenote Cervera and paratypes from Dzilamway, all cenotes in Dzilam de Bravo region (Yucatan north coast). This species was recently recorded at the Ox Bel Ha system south of Tulum (Benítez et al. 2019) and the Ponderosa system north of Tulum (Espinasa et al. 2019).

Remarks. In accordance with previous records by Álvarez et al. (2005, 2015), our specimens were also collected in fully marine water. Recent observations of this species increase the expected distribution, suggesting an underground coastal and saline habitat that could extend from the south of Quintana Roo (Ox Bel Ha) to the west coast of Yucatan (Sabtun 1).

*Typhlatya mitchelli* Hobbs & Hobbs, 1976

Figure 3E

Material examined. 3 individuals; **Cenote San Juan**, depth 4.3-9.1 m, cave and cavern, freshwater, 27 °C, Homun, Yucatan, Mexico; 7 May 2016; colls. D. Angyal & E. Chávez Solís. 11 individuals; **Cenote Tza Itza**, depth 4.3-16.5 m, cave, freshwater, 27 °C, Tecoh, Yucatan, Mexico; 10 May 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; **Cenote Dzonbakal**, depth 9.3 m, cavern, freshwater, 27 °C, San Antonio Mulix, Yucatan, Mexico; 14 May 2016; colls. R. Acosta, D. Angyal, J. Baduy & S. Reyes. 1 individual; 1 individual; **Cenote Dzonbakal**, depth 14 m, cavern, freshwater, 27 °C, San Antonio Mulix, Yucatan, Mexico; 29 May 2016; colls. D. Angyal, J. Baduy & B. Magaña. 5 individuals; **Cenote Kampepen**, depth 10.1 m, cavern, freshwater, 27 °C, Chinquila, Yucatan, Mexico; 17 May 2016; colls. D. Angyal & B. Magaña. 2 individuals; **Cenote Ayun-Nah**, depth 9 m, cave, freshwater, 27 °C, Cacalchen, Yucatan, Mexico; 22 May 2016; colls. D. Angyal, B. Magaña & E. Sosa Rodríguez. **Cenote Tres Oches**, depth 8.1-22 m, cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 5 June 2016; colls. D. Angyal & E. Chávez Solís. 7 individuals; **Cenote Kakuel**, depth 5-25.8 m, cave and cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 10 June 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; **Cenote Kankirixche**, depth 30.2 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 10 December 2016; colls. D. Angyal & E. Chávez Solís. 2 individuals; **Cenote Sabtun 1**, depth 24.0 and 25.0 m, cavern, above the halocline, 25 °C, Chun-chumil, Yucatan, Mexico; 10 December 2017; colls. D. Angyal, E. Chávez Solís, S. Drs, Q. Hernández & S. Reyes. 1 individual; **Cenote Bebelchen**, depth 34.0 m, cavern, freshwater, 25 °C, Sanahcat, Yucatan, Mexico; 18 December 2017; colls. D. Angyal, S. Drs, L. Liévano & S. Reyes. 1 individual; **Cenote El Virgen**, depth 19.9 m, cavern, freshwater, 26 °C, Sotuta, Yucatan, Mexico; 20 December 2017; colls. L. Liévano & N. Simoes. 1 individual; **Cenote Chihu Hol**, depth 26.0 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 26 January 2018; colls. D. Angyal, S. Drs, B. Magaña, L. Liévano & N. Simoes.
**Previous distribution.** Hobbs and Hobbs 1976; Hobbs et al. 1977; Hobbs 1979; Reddell 1977, 1981; Iliffe 1992; Rocha et al. 1998; Webb 2003; Botello and Álvarez 2013; Benítez 2014; Álvarez et al. 2015; Chávez Solís 2015; Benítez et al. 2019.

Type locality is Cenote Kabahchen (Yucatan). The species occurs in numerous caves and cenotes throughout the peninsula in Quintana Roo and Yucatan.

**Remarks.** Our findings corroborate that *T. mitchelli* is a widespread common crustacean in the freshwater cenotes of Yucatan. This species was caught from the shallow zones to 34 m in depth, indicating a wide vertical range as well as a wide geographical range. The species was also observed (but not collected) in cenotes Yaal Utsil, Santito, Pol Box, Kankal, San Elias, Dzonotila, X’baba, X’kokob, Pixon, Dzalbay, and Yax-Kis. *Typhlatya mitchelli* is listed as “least concern” in the IUCN Red List (De Grave et al. 2013a) and as “threatened” in the Mexican Red List of Threatened Species (NOM-059-SEMARNAT 2010).

**Typhlatya pearsei** Creaser, 1936

Figure 3F

**Material examined.** 1 individual; **Cenote Tres Oches**, depth 21.6 m, cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 6 June 2016; colls. D. Angyal & E. Chávez Solís. 2 individuals; **Cenote Xaan**, depth 25.8 and 26.1 m, cave, freshwater, 27 °C, Homun, Yucatan, Mexico; 9 June 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; **Cenote Kankirixche**, depth 3 m, cavern, freshwater, 27 °C, Mucuyche, Yucatan, Mexico; 11 June 2016; colls. D. Angyal & E. Chávez Solís. **Cenote Nohmozon**, depth 12.2 m, cavern, freshwater, 25 °C, Pixyah, Tecoh, Yucatan, Mexico; 11 March 2016; colls. E. Chávez Solís.

**Previous distribution.** Creaser 1936; Nicholas 1962; Hobbs et al. 1977; Holthuis 1977; Hobbs 1979; Reddell 1977, 1981; Pérez-Aranda 1983a; Holsinger 1990; Iliffe 1992; Webb 2003; Hunter et al. 2007; Yager and Madden 2010; Botello and Álvarez 2013; Mejía-Ortíz et al. 2013; Benítez 2014; Pakes et al. 2014; Álvarez et al. 2015; Chávez Solís 2015; Benítez et al. 2019.

Type locality is ‘Balam Canche Cave’ (Grutas de Balankanche, Yucatan). The species is widely distributed within the northern part of the Yucatan Peninsula; it occurs in Quintana Roo, Yucatan, and Campeche.

**Remarks.** Despite previous studies stating that *T. pearsei* has the largest of *Typhlatya*’s distribution range in the Yucatan Peninsula (Álvarez et al. 2015), we only collected individuals in a few localities, where it occurred in freshwater, both near the surface in open cenote pools and in deeper cave passages up to 26 m in depth. This species is listed as “least concern” in the IUCN Red List (De Grave et al. 2013b) and as “threatened” in the Mexican Red List of Threatened Species (NOM-059-SEMARNAT 2010).
Family: Palaemonidae

Creaseria morleyi (Creaser, 1936)

Figure 3G

Material examined. 2 individuals; Cenote Tza Itza, depth 15.4 m, cavern, freshwater, 27 °C, Tecoh, Yucatan, Mexico; 10 May 2016; colls. D. Angyal & E. Chávez Solís. 2 individuals; Cenote Kampepen, depth 6-9.5 m, cavern, freshwater, 27 °C, Chiquinoa, Yucatan, Mexico; 17 May 2016; colls. D. Angyal & B. Magaña. 2 individuals; Cenote Kakuel, depth 3 and 13.9 m, cavern, freshwater, 27 °C, Mucuyeche, Yucatan, Mexico; 10 June 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; Cenote Kankirixche, depth 3.6 m, cavern, freshwater, 27 °C, Mucuyeche, Yucatan, Mexico; 11 June 2016; colls. D. Angyal & E. Chávez Solís. 1 individual; Cenote Santito, depth 4.0 m, cavern, freshwater, 27 °C, Kopoma, Yucatan, Mexico; 18 November 2017; colls. D. Angyal, S. Drs & L. Liévano. 1 individual; Cenote Kankal, depth 0.3 m, cavern, freshwater, 25 °C, Homun, Yucatan, Mexico; 18 November 2017; colls. D. Angyal, S. Drs, E. Chávez Solís & L. Liévano. 1 individual; Cenote Bebelchen, depth 30.0 m, cavern, freshwater, 25 °C, Sanahcat, Yucatan, Mexico; 18 December 2017; colls. D. Angyal, L. Liévano & S. Reyes. 1 individual; Cenote El Virgen, depth 25.0 m, cavern, freshwater, 26 °C, Sotuta, Yucatan, Mexico; 20 December 2017; colls. L. Liévano & N. Simoes. 1 individual; Cenote Dzalbay, depth 4.3 m, cavern, freshwater, 23 °C, Sotuta, Yucatan, Mexico; 20 December 2017; colls. D. Angyal & L. Liévano.

Previous distribution. Creaser 1938; Hobbs and Hobbs 1976; Holthuis 1977; Hobbs et al. 1977; Reddell 1977, 1981; Hobbs 1979; Pérez-Aranda 1983b; Iliffe 1992; Botello and Álvarez 2006; Botello and Álvarez 2010; Benítez 2014; Álvarez et al. 2015; Chávez Solís 2015; Chávez Solís et al. 2017; Benítez et al. 2019.

Type locality is San Isidro Cave (Yucatan). Widely distributed in cenotes and caves of Yucatan, Campeche, and Quintana Roo.

Remarks. Reddell (1981) mentions the species as an “ever-present element of fauna of pools and lakes in caves in the Yucatan Peninsula”. In addition to the above listed localities, we also observed the species in cenotes Yaal Utsil, Pol Box, San Elias, Dzontotila, Flor de Liz, X’baba, Chihuo Hol, and Yax-Kis. Specimens were recorded in both cave and cavern sections, up to 38 m in depth. Benítez et al. (2019) also found individuals around and below the halocline in cenotes belonging to the Ox Bel Ha system. Creaseria morleyi is listed as “threatened” in the Mexican Red List of Threatened Species (NOM-059-SEMARNAT 2010) and as “least concern” in the IUCN Red List (De Grave et al. 2013c).

Discussion

While there are more than 3,000 registered cenotes in the state of Yucatan (SDS Yucatan census), less than five percent have been zoologically investigated. Results herein confirm that the region deserves more attention and that the geographical, bathymet-
ric, and fresh/salt water distribution of stygobiotic species is far from being fully understood. In order to contribute to the management of the vulnerable cenote ecosystems and their highly specialized endemic stygofauna, collecting as much information as possible about the biology of Yucatan aquifers would be paramount. This data should include reports on the species’ distribution, density and rarity, taxonomy, ecology, as well as characteristics of their habitats related to their biology, such as the amount of epigean originated organic sources or the degree of anthropogenic pollution in cenotes.

Prior to this study, the amphipod *T. cernua* was only known from Quintana Roo, mostly associated with saltwater habitats in anchialine cenotes near the northeastern coastline of the Peninsula (Holsinger 1990; Rocha et al. 1998; Álvarez and Iliffe 2008; Álvarez et al. 2015). Contrary to previous findings, all individuals were found in freshwater habitats during our study (Angyal et al. 2018). Rocha et al. (1998) and Pesce and Iliffe (2002) mentioned observation records of ‘thermosbaenaceans’ from cenotes Yun-cu, Mucuyche, Pabakal (Papakal), and Grutas de Tzab-Nah (all in Yucatan). However, these individuals had never been identified at the species level and it seems no voucher information of the potentially collected specimens is available. The present study confirms first records for *T. cernua* and *T. unidens* in the state of Yucatan. Together with the amphipod *M. troglomorpha*, which was discovered and described within the frame of herein presented expeditions (Angyal et al. 2018) and the new cave isopod *Curasanthura yucatanensis* Álvarez, Benítez, Iliffe & Villalobos, 2019 (Álvarez et al. 2019), the list of stygobiotic crustaceans recorded for the state of Yucatan raised from 22 (in 2016) to 26. In addition, the cirolanid isopod *C. yunca* was only known from its type locality, but we now provide distribution data for this species in three other localities. Our results show that the stygiomysid *S. cf. holthuisi* has historically been unrecognized, unsampled or ignored. This specific contribution proves that inland cenotes have been understudied and distribution patterns of stygofauna are still unknown. Due to the previously lacking zoological information for the vast majority of the cenotes investigated in our study, most of the distribution records presented here are new.

A closer morphological and molecular analysis of the *Typhlatya* species in Yucatan is recommended in order to distinguish cryptic species that may be causing confounding biodiversity and ecological patterns in the Yucatan Peninsula.

Among the 14 crustacean species listed, prior to this study, cytochrome c oxidase subunit I sequences were publicly available only for the decapods *T. mitchelli*, *T. pearsei*, *T. dzilamensis*, and *C. morleyi*. The currently published COI barcode gene fragments can aid future molecular research on the peracarid fauna of Yucatan’s cenote ecosystems by facilitating their identification, as well as in the recognition of cryptic species.

The mysid *A. cenotensis*, the atyid shrimps *T. mitchelli* and *T. pearsei* and the palazonid shrimp *C. morleyi* are listed in the Mexican and IUCN red lists of threatened species (SEMARNAT 2010; De Grave et al. 2013a, b, c). These species are present in most cenotes throughout the Yucatan Peninsula and can be considered a selected group of species whose protection will act as an umbrella in protecting other less common ones. On the other hand, there are rare species with an extremely narrow distribution range, which are not yet under legal protection. This makes these species even more vulnerable to urbanization and environment deterioration. Therefore, we suggest the
inclusion of narrow endemic species into the national and international protection lists, such as the isopod *C. yunca* or the atyid shrimp *T. dzilamensis*.

The number of new records provided in this work shows a historic lack of biodiversity surveys in underwater caves of inland cenotes of the state of Yucatan. Most of the biodiversity and its distribution patterns are currently biased towards large populations, easily accessible sites, and touristic attractions. Our efforts yield a greater understanding of the distribution patterns of stygofauna in Yucatan cenotes.

**Acknowledgements**

We are grateful to Sophia Drs (Van Hall Larenstein University of Applied Sciences) for her support during the field trips and for her contribution in compiling cenote biodiversity databases. Silvia Reyes, Quetzali Hernández, Juan Baduy Infante, Rafael Acosta, Cristian Selún, Nori Velázquez Juárez, Jonathan Mondragón, Ricardo Riestra, Lorenzo Ortiz, Erick Sosa Rodríguez, and the Ecologistas sub-acuáticos de Yucatán (Subaquatic Ecologists of Yucatan) are greatly acknowledged for their assistance during the field trips and cave dives. Isaac Chacón and Ricardo Riestra (UNAM) are acknowledged for the information collected in the cenote databases. We thank Sergio Rodríguez Morales (UNAM) for providing facilities of the Chemistry Laboratory during the pretreatment of the dissected individuals. Virág Krízsik (HNHM, Laboratory of Molecular Taxonomy) is acknowledged for her professional help provided in molecular studies. We are grateful to Alberto Guerra (Nature Art) for making the photo tables. We thank László Dányi (HNHM, Department of Zoology) for the photograph of *C. yunca*. We would like to express our deep gratitude to the reviewers Thomas Iliffe (Texas A&M University of Galveston) and Alejandro Martínez (Italian National Research Council) for their useful suggestions, which helped us to improve the manuscript. DA is thankful for the scholarship received from “DGAPA-UNAM Programa de Becas Posdoctorales en la UNAM, 2019”. ECS is grateful for the scholarship received from CONACyT 545277/294499 through “Posgrado en Ciencias Biológicas” of the UNAM. LLB gratefully acknowledges the scholarship provided by CONACyT 864025/628560 through “Posgrado en Ciencias del Mar y Limnología” of the UNAM. Financial support was provided by project PAPIIT IN222716 “Biodiversidad y Ecología de la fauna de cenotes de Yucatán” and “Hacia un mapa de biodiversidad acuática de cenotes de la Península de Yucatán”, DGAPA-PAPIIT 2019 – IN228319 to NS.

**References**

Álvarez F, Iliffe TM, Villalobos JL (2005) New species of the genus *Typhlatya* (Decapoda: Atyidae) from anchialine caves in Mexico, the Bahamas and Honduras. Journal of Crustacean Biology 25(1): 81–94. https://doi.org/10.1651/C-2516
Álvarez F, Iliffe TM (2008) Fauna anquihalina de Yucatan. In: Álvarez F, Rodríguez-Almaraz R (Eds) Crustáceos de Mexico: Estado Actual de su Conocimiento. Universidad Autónoma de Nuevo León-PROMEP, 379–418.

Álvarez F, Iliffe TM, Benítez S, Brankovits D, Villalobos JL (2015) New records of anchialine fauna from the Yucatan Peninsula, Mexico. Check List 11(1): 1505. https://doi.org/10.15560/11.1.1505

Álvarez F, Benítez S, Iliffe TM, Villalobos JL (2019) A new species of isopod of the genus Curassanthura (Cymothoida, Anthuroide, Leptanthuridae) from anchialine caves of the Yucatan Peninsula, Mexico. Crustaceana 92(5): 545–553. https://doi.org/10.1163/1685403-00003892

Angyal D, Balázs G, Zakšek V, Krízsik V, Fišer C (2015) Redescription of two subterranean amphipods Niphargus molnari Méhely, 1927 and Niphargus gebhardti Schellenberg, 1934 (Amphipoda, Niphargidae) and their phylogenetic position. ZooKeys 509: 53–85. https://doi.org/10.3897/zookeys.509.9820

Angyal D, Chávez Solís EM, Magaña B, Balázs G, Simoes N (2018) Mayaweckelia troglo-morpha, a new subterranean amphipod species from Yucatan State, Mexico (Amphipoda, Hadziidae). ZooKeys 735: 1–25. https://doi.org/10.3897/zookeys.735.21164

Bauer-Gottwein P, Gondwe BRN, Chauvert G, Marín LE, Rebollo-Vieyra M, Merediz-Alonso G (2011) The Yucatan Peninsula karst aquifer, Mexico. Hydrogeology Journal 19(3): 507–524. https://doi.org/10.1007/s10040-010-0699-5

Benítez SA (2014) Variación en la estructura y composición de la fauna anquihalina del sistema Ox Bel Ha (península de Yucatan) a través de un gradiente de distancia desde la zona litórica. MSc Thesis, Universidad Nacional Autónoma de Mexico, Mexico DF.

Benítez S, Iliffe TM, Quiroz-Martínez B, Álvarez F (2019) How is the anchialine fauna distributed within a cave? A study of the Ox Bel Ha System, Yucatan Peninsula, Mexico. Subterranean Biology 31: 15–28. https://doi.org/10.3897/subtbiol.31.34347

Bishop RE, Iliffe T (2009) Metabolic rates of stygobiontic invertebrates from the Tunel de la Atlantida, Lanzarote. Marine Biodiversity 39(3): 189–194. https://doi.org/10.1007/s12526-009-0018-3

Bishop RE, Humphreys WF, Cukrov N, Zič V et al. (2015) ‘Anchialine’ redefined as a subterranean estuary in a crevicular or cavernous geological setting. Journal of Crustacean Biology 35(4): 511–514. https://doi.org/10.1163/1937240x-00002335

Botello A, Álvarez F (2006) Allometric growth in Creaseria morleyi (Creaser, 1936) (Decapoda: Palaemonidae), from the Yucatan Peninsula, Mexico. Caribbean Journal of Science 42: 171–179.

Botello A, Álvarez F (2010) Genetic variation in the stygobitic shrimp Creaseria morleyi (Decapoda: Palaemonidae), evidence of bottlenecks and re-invasions in the Yucatan Peninsula. Biological Journal of the Linnean Society 99(2): 315–325. https://doi.org/10.1111/j.1095-8312.2009.01355.x

Botello A, Álvarez F (2013) Phylogenetic relationships among the freshwater genera of palaemonid shrimps (Crustacea: Decapoda) from Mexico, evidence of multiple invasions. Latin American Journal of Aquatic Research 41(4): 773–780. https://doi.org/10.3856/vol41-issue4-fulltext-14
Botosaneanu L (1980) *Stygiomysis holthuisi* found on Anguilla (Crustacea: Mysidacea). Studies on the Fauna of Curacao and other Caribbean Islands 61(190): 128–132.

Botosaneanu L (1986) Stygofauna mundi: A Faunistic, Distributional, and Ecological Synthesis of the World Fauna inhabiting Subterranean Waters. Journal of Crustacean Biology 7(1): 203. https://doi.org/10.2307/1548640

Botosaneanu L, Iliffe TM (1999) On four new stygobitic cirolanids (Isopoda: Cirolanidae) and several already described species from Mexico and the Bahamas. Bulletin de l’Institute Royal des Sciences Naturelles de Belgique, Biologie 69: 93–123.

Botosaneanu L, Iliffe TM (2000) Two new stygobitic species of Cirolanidae (Isopoda) from deep cenotes in Yucatan. Bulletin de l’Institute Royal des Sciences Naturelles de Belgique, Biologie 70: 149–161. https://www.biotaxa.org/Zootaxa/article/view/zootaxa.1823.1.4

Botosaneanu L, Iliffe TM (2002) Stygobitic isopod crustaceans, already described or new, from Bermuda, the Bahamas, and Mexico. Bulletin de l’Institut Royal des Sciences Naturelles de Belgique, Biologie 72: 101–111. https://www.tamug.edu/cavebiology/reprints/Reprint-139.pdf

Botosaneanu L, Iliffe TM (2006) The remarkable diversity of subterranean Cirolanidae (Crustacea: Isopoda) in the peri-Caribbean and Mexican Realm. Bulletin de l’Institute Royal des Sciences Naturelles de Belgique, Biologie 76: 5–26. http://biblio.naturalsciences.be/rbins-publications/bulletin-of-the-royal-belgian-institute-of-natural-sciences-biologie/76-2006/biologie-2006-76_5-26.pdf

Bowman TE (1966) *Cirolana trichostoma*, a new genus and species of troglobitic cirolanid isopod from Cuba. International Journal of Speleology 2: 105–108. https://doi.org/10.5038/1827-806X.2.1.8

Bowman TE (1977) A review of the genus *Antromysis* (Crustacea: Mysidacea), including new species from Jamaica and Oaxaca, Mexico, and a redesription and new records for *A. cenotensis*. In: Reddell J (Ed) Studies on the caves and cave fauna of the Yucatan Peninsula. Association for Mexican Cave Studies Bulletin 6: 27–38.

Bowman TE, Iliffe TM, Yager J (1984) New records of the troglobitic mysid genus *Stygiomysis*: *S. clarkei*, new species, from the Caicos Islands, and *S. holthuisi* (Gordon) from Grand Bahama Island (Crustacea: Mysidacea). Proceedings of the Biological Society of Washington 97: 637–644. https://biodiversitylibrary.org/page/34642466

Bowman TE, Iliffe TM (1988) *Tulumella unidens*, a new genus and species of thermosbaenacean crustacean from the Yucatan Peninsula, Mexico. Proceedings of the Biological Society of Washington 101: 221–226. http://biodiversitylibrary.org/page/34645902

Bruce NL (1986) Cirolanidae (Crustacea: Isopoda) of Australia. Records of the Australian Museum, Supplement 6. The Australian Museum, Sydney, 239 pp. https://journals.australianmuseum.net.au/bruce-1986-rec-aust-mus-suppl-6-1239/

Chávez Solís EM (2015) Aspectos ecológicos y etológicos de decápodos estigobios (Creaseria morleyi y Typhlatya spp.) en cenotes de Yucatan: utilización espaciotemporal, cambios anuales y relaciones interespecíficas. MSc Thesis, Mexico D. F., Mexico: Universidad Nacional Autónoma de Mexico.

Chávez Solís EM, Mejía-Ortíz L, Simoes N (2017) Predatory behavior of the cave shrimp *Creaseria morleyi*(Creaser, 1936) (Caridea: Palaemonidae), the blind hunter of the Yucatan cenotes, Mexico. Journal of Crustacean Biology. 38. https://doi.org/10.1093/jcbiol/rux098
New distribution records of subterranean crustaceans from cenotes in Yucatan

Creaser EP (1936) Crustaceans from Yucatan, In: Pearse AS, Creaser EP, Hall FG (Eds): The Cenotes of Yucatan. Carnegie Institute of, Washington Publications 457: 117–132.

Creaser EP (1938) Larger cave crustacea of the Yucatan Peninsula. Carnegie Institute of Washington Publications 491: 159–164.

De Grave S, Álvarez F, Villalobos J (2013a) *Typhlatya mitchelli.* The IUCN Red List of Threatened Species 2013: e.T197618A2493242. https://doi.org/10.2305/IUCN.UK.2013-1.RLTS.T197618A2493242.e [Downloaded on 23 December 2019]

De Grave S, Villalobos J, Álvarez F (2013b) *Typhlatya pearsei.* The IUCN Red List of Threatened Species 2013: e.T197616A2493158. https://doi.org/10.2305/IUCN.UK.2013-1.RLTS.T197616A2493158.e [Downloaded on 23 December 2019]

De Grave S, Álvarez F, Villalobos J (2013c) *Creaseria morleyi.* The IUCN Red List of Threatened Species 2013: e.T198148A2513584. https://doi.org/10.2305/IUCN.UK.2013-1.RLTS.T198148A2513584.e [Downloaded on 23 December 2019]

Espinasa L, Chávez Solís EM, Mascaró M, Rosas C, Violette G (2019) A new locality and phylogeny of the stygobitic *Typhlatya* shrimps for the Yucatan Peninsula. Speleobiology Notes 10: 19–27. https://doi.org/10.5563/spbn.v10i0.91

Fiers F, Reid JW, Iliffe TM, Suárez-Morales E (1996) New hypogean cyclopoid copepods (Crustacea) from the Yucatan Peninsula, Mexico. Contributions to Zoology 66(2): 65–102. https://doi.org/10.1163/26660644-06602001

Fišer C, Trontelj P, Luštrik R, Sket B (2009) Towards a unified taxonomy of *Niphargus* (Crustacea: Amphipoda): a review of morphological variability. Zootaxa 2061: 1–22.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.

González-Herrera R, Sanchez-Pinto I, Gamboa-Vargas J (2002) Groundwater-flow modeling in the Yucatan karstic aquifer, Mexico. Hydrogeology Journal 10(5): 539–552. https://doi.org/10.1007/s10040-002-0216-6

González BC, Worsaae K, Fontaneto D (2018) Anophthalmia and elongation of body appendages in cave scale worms (Annelida: Aphroditiformia). Zoologica Scripta 47(1):106–121. https://doi.org/10.1111/zsc.12258

Gordon I (1958) A new subterranean crustacean from the West Indies. Nature 181: 1552–1553. https://doi.org/10.1038/1811552a0

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98. https://doi.org/10.4236/sgr2.2015.64887

Hervant F, Mathieu J, Barré H (1999) Comparative study on the metabolic responses of subterranean and surface-dwelling amphipods to long-term starvation and subsequent refeeding. Journal of Experimental Biology 202: 3587–3595. https://jeb.biologists.org/content/202/24/3587

Hervant F, Mathieu J, Durand J (2001) Behavioural, physiological and metabolic responses to long-term starvation and refeeding in a blind cave-dwelling (*Proteus anguinus*) and a surface-dwelling (*Euproctus asper*) salamander. Journal of Experimental Biology 204: 269–281. https://jeb.biologists.org/content/204/2/269
Hobbs HH III, Hobbs HH Jr (1976) On the troglobitic shrimps of the Yucatan Peninsula, Mexico (Decapoda: Atyidae and Palaemonidae). Smithsonian Contributions to Zoology 240: 1–23. https://doi.org/10.5479/si.00810282.240

Hobbs HH III, Hobbs HH Jr, Daniel MA (1977) A review of the troglobic decapod crustaceans of the Americas. Smithsonian Contributions to Zoology Number 244, Washington, 196 pp. https://doi.org/10.5479/si.00810282.244

Hobbs HH III (1979) Additional notes on cave shrimps (Crustacea: Atyidae and Palaemonidae) from the Yucatan Peninsula, Mexico. Proceedings of the Biological Society of Washington 92(3): 618–633.

Holsinger JR (1977) A new genus and two new species of subterranean amphipod crustaceans (Gammaridae s. lat.) from the Yucatan Peninsula in Mexico. Association for Mexican Cave Studies, Bulletin 6: 15–25.

Holsinger JR (1990) *Tuluweckelia cernua*, a new genus and species of stygobiont amphipod crustacean (Hadziidae) from anchialine caves on the Yucatan Peninsula in Mexico. Beaufortia 41: 97–107.

Holthuis LB (1977) Cave shrimps (Crustacea: Decapoda, Natantia) from Mexico. Accademia Nazionale dei Lincei Quodernio 171: 173–195.

Horwitz P, Knott B, Williams WD (1995) A preliminary key to the malacostracan families (Crustacea) found in Australian inland waters. Research Centre for Freshwater Ecology Identification Guide No. 4.Albury, 38 pp.

Hunter RL, Webb MS, Iliffe TM, Bremer JRA (2007): Phylogeny and historical biogeography of the cave-adapted shrimp genus *Typhlatya* (Atydae) in the Caribbean Sea and western Atlantic. Journal of Biogeography. https://doi.org/10.1111/j.1365-2699.2007.01767.x

Iliffe TM (1992) An annotated list of the troglobitic, anchialine and freshwater cave fauna of Quintana Roo. In: Navarro D, Suárez-Morales E (Eds) Diversidad Biológica en la Reserva de la Biosfera de Sian Ka’an, Quintana Roo, Mexico, Vol. II. CIQRO, Chetumal, Mexico, 197–215. https://www.academia.edu/5416051/An_annotated_list_of_the_troglobitic_anchialine_and_freshwater_fauna_of_Quintana_Roo

Iliffe TM (1993) Fauna troglobia acuatica de la Peninsula de Yucatan. pp. 673–686 in: Biodiversidad marina y costera de Mexico. S.I. Salazar-Vallejo & N.E. González (eds.) Comision National para el Conocimiento y Uso de la Biodiversidad y CIQRO, México, 865 pp.

Iliffe TM, Botosaneanu L (2006) The remarkable diversity of subterranean Cirolanidae (Crustacea: Isopoda) in the peri-Caribbean and Mexican realm. Bulletin de l’Institut Royal des Sciences Naturelles de Belgique. Biologie 76: 5–26. https://dare.uva.nl/search?identifier=51551d10-097d-4609-832f-74bde6066add

Kallmeyer DE, Carpenter JH (1996) *Stygionysis cokei*, new species, a troglobitic mysid from Quintana Roo, Mexico (Mysidacea: Stygiomysidae). Journal of Crustacean Biology 16: 418–427. https://doi.org/10.2307/1548897

Lowry JK, Myers AA (2013) A phylogeny and classification of the Senticaudata subord. nov. (Crustacea: Amphipoda). Zootaxa 3610(1): 1–80. https://doi.org/10.11646/zootaxa.3610.1.1
Mejía-Ortíz LM, Hartnoll RG, López-Mejía M (2006) Progressive troglomorphism of ambulatory and sensory appendages in three Mexican cave decapods. Journal of Natural History 40(5-6): 255–264. https://doi.org/10.1080/00222930600628382

Mejía-Ortíz LM, López-Mejía M, Pakes J, Hartnoll G, Zarza-González E (2013) Morphological adaptations to anchialine environments in species of five shrimp families (Barbouria yanezi, Agostocris bozanici, Procaris mexicana, Calliasmata nobochi and Typhlatya pearsei). Crustaceana 86(5): 578–593. https://doi.org/10.1163/15685403-00003197

Mercado-Salas NF, Morales-Vela B, Suárez-Morales E, Iliffe T (2013) Conservation status of the inland aquatic crustaceans in the Yucatan Peninsula, Mexico: shortcomings of a protection strategy. Aquatic conservation: Marine and freshwater ecosystems. Wiley Online Library. https://doi.org/10.1002/aqc.2350

Meland K, Mees J, Porter M, Wittmann KJ (2015) Taxonomic Review of the orders Mysida and Stygiomysida (Crustacea, Peracarida). PLoS ONE 10(4): e0124656. https://doi.org/10.1371/journal.pone.0124656

Nicholas G (1962) Checklist of troglobitic organisms of Middle America. American Midland Naturalist 68(1): 165–188. https://doi.org/10.2307/2422643

Olesen J, Boesgaard T, Iliffe TM (2015) The unique dorsal Brood pouch of Thermosbaenacea (Crustacea, Malacostraca) and description of an advanced developmental stage of Tulunmella unidens from the Yucatan Peninsula (Mexico), with a discussion of mouth part homologies to other Malacostraca. PLoS ONE 10(4): e0122463. https://doi.org/10.1371/journal.pone.0122463

Ortiz M, Cházar-Olvera S (2015) A new species of cirolanoid isopod (Peracarida, Isopoda) collected from cenote Aerolito, Cozumel Island, Northwestern Caribbean. Crustaceana 88(2): 152–163. https://doi.org/10.1163/15685403-00003402

Pakes MJ, Weis AK, Mejía-Ortiz L (2014) Arthropods host intracellular chemosynthetic symbionts, too: cave study reveals an unusual form of symbiosis. Journal of Crustacean Biology 34(3): 334–341. https://doi.org/10.1163/1937240X-00002238

Pérez-Aranda L (1983a) Atyidae: Typhlatya pearsei. Fauna de los cenotes de Yucatán 3. Universidad de Yucatán, Mérida, 11 pp.

Pérez-Aranda L (1983b) Palaemonidae: Creaseria morleyi. Fauna de los cenotes de Yucatán 1. Universidad de Yucatán, Mérida, 11 pp.

Pérez-Aranda L (1984a) Atyidae: Typhlatya mitchelli. Fauna de los cenotes de Yucatán 5. Universidad de Yucatán, Mérida, 14 pp.

Pérez-Aranda L (1984b) Cirolanidae: Cirolana anops. Fauna de los cenotes de Yucatán 7. Universidad de Yucatán, Mérida, 13 pp.

Pesce GL, Iliffe TM (2002) New records of cave-dwelling mysids from the Bahamas and Mexico with description of Palaumysis bahamensis n. sp. (Crustacea: Mysidacea). Journal of Natural History 36(3): 265–278. https://doi.org/10.1080/0022293010005033

Pohlman JW, Cifuentes LA, Iliffe TM (2000) Food web dynamics and biogeochemistry of anchialine caves: a stable isotope approach. In: Wilkens H, Culver DC, Humphreys WF (Eds) Ecosystems of the World. 30. Subterranean Ecosystems.: Elsevier Science, Amsterdam, 345–357.
ReddTell JR (1977) A preliminary survey of the caves of the Yucatan Peninsula. In: ReddTell JR (Ed.) Survey of the caves and cave fauna of the Yucatan Peninsula. Association for Mexican Cave Studies, Bulletin 6: 215–296.

ReddTell JR (1981) A review of the cavernicolc fauna of Mexico, Guatemala, and Belize. Texas Memorial Museum, The University of Texas at Austin, Bulletin 27, 327 pp. https://www.mexicanacaves.org/other/TMM_B27.pdf

Rocha CEF, Iliffe TM, Reid JW, Suárez-Morales E (1998) A new species of Halicyclops (Copepoda, Cyclopoida, Cyclopidae) from cenotes of the Yucatan Peninsula, Mexico, with an identification key for the species of the genus from the Caribbean region and adjacent areas. Sarsia 83: 387–399. https://doi.org/10.1080/00364827.1998.10413698

Rocha CEF, Iliffe TM, Reid JW, Suárez-Morales E (2000) Prehendocyclops, a new genus of the subfamily Halicyclopinae (Copepoda, Cyclopoida, Cyclopidae) from cenotes of the Yucatan Peninsula, Mexico. Sarsia 85: 119–140. https://doi.org/10.1080/00364827.2000.10414562

Rocha-Ramírez A, Álvarez F, Alcocer J, Chávez-López R, Escobar-Briones E (2009) Annotated list of the aquatic epicontinental isopods of Mexico (Crustacea: Isopoda). Revista Mexicana de Biodiversidad 80: 615–631. https://doi.org/10.22201/ib.20078706c.2009.003.159

Ruíz-Cancino G, Mejía-Ortíz LM, Lozano-Álvarez E (2013) Dinámica poblacional de Creaseriella anops (Crustacea: Isopoda) en cenotes dulceacuícolas de Quintana Roo. In: López-Mejía M, Mejía-Ortíz LM (Eds) La carcinología en México: El legado del Dr. Alejandro Villalobos 30 años después. Universidad de Quintana Roo, México DF, 180 pp.

Sánchez-Rodríguez G (2008) Distribución de la abundancia del isópodo Creaseriella anops (Creaser, 1936) en sistemas anquihaílicos de Quintana Roo, México. BSc Tesis, Universidad Nacional Autónoma de México, Facultad de Ciencia, 68 pp.

Schmitter-Soto JJ, Comin FA, Escobar-Briones E, Herrera-Silveira J, Alcocer J, Suárez-Morales E, Elías-Gutiérrez M, Díaz-Arce V, Marín LE, Steinich (2002) Hydrogeochemical and biological characteristics of cenotes in the Yucatan Peninsula (SE Mexico). Hydrobiologia 467: 215–228. https://doi.org/10.1007/978-94-010-0415-2_19

SEMARNAT (2010) Norma Oficial Mexicana Nom-059-Semarnat-2010, Protección ambiental- Especies nativas de México de flora y fauna silvestres- Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio- Lista de especies en riesgo. Diario Oficial, 30 de diciembre de 2010. https://www.dof.gob.mx/normasOficiales/4254/semarnat/semarnat.htm

Suárez-Morales E, Rivera Arriaga E (1998) Hidrología y fauna acuática de los cenotes de la Península de Yucatán. Revista de la Sociedad Mexicana de Historia Natural 48: 37–47. http://bibliotecasibe.ecosur.mx/sibe/book/000054250

Suárez-Morales E, Ferrari FD, Iliffe TM (2006) A new epacteriscid copepod (Calanoida: Epacteriscidae) from the Yucatan Peninsula, Mexico, with comments on the biogeography of the family. Proceedings of the Biological Society of Washington 119(2): 222–238. https://doi.org/10.2988/0006-324X(2006)119[222:ANECE][2.0.CO;2

Tinnizi NM, Quddusi BK (1993) An illustrated key to Malacostraca (Crustacea) of the Northern Arabian Sea. Pakistan Journal of Marine Sciences 2(1): 49–66. https://aquaticcommons.org/16058/1/PJMS2.1_049.pdf
New distribution records of subterranean crustaceans from cenotes in Yucatan

Wagner HP (1994) A monographic review of the Thermosbaenacea (Crustacea: Peracarida). A study on their morphology, taxonomy, phylogeny and biogeography. Zoologische Verhandelingen 291(3): 1–338. https://www.jstor.org/stable/20088754

Webb MS (2003) Intraspecific relationships among the stygobitic shrimp *Typhlatya mitchelli*, by analyzing sequence data from mitochondrial DNA. MSc Thesis, Texas, United States of America: Texas A&M University. http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.174.684&rep=rep1&type=pdf

Yager J, Madden ME (2010) Preliminary analysis of the ecology of a cenote in Quintana Roo, Mexico, characterized by its extraordinary quantities of remipeds. Karst Frontiers, Karst Water Institute Special Publication 7: 138–140.