

A new species of *Laoennea microsnaill* (Stylommatophora, Diapheridae) from a cave in Laos

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Abstract

The genus *Laoennea* (Streptaxoidea, Diapheridae) was erected by Páll-Gergely, 2020. The type species, *Laoennea carychioides* Páll-Gergely, A. Reischütz & Maassen, 2020 is so far only known from the type locality cave in Laos. Herein, we describe a second species, *Laoennea renouardi* sp. nov., from a nearby cave in the same karst region of Vientiane Province.

Résumé

Le genre *Laoennea* (Streptaxoidea, Diapheridae) fût érigé en 2020 par Páll-Gergely in Páll-Gergely, A. Reischütz, Maassen, Grego & Hunyadi. L'espèce type, *Laoennea carychioides* Páll-Gergely, A. Reischütz & Maassen, 2020, est jusqu'à présent uniquement connue de la grotte qui tient lieu de localité type, au Laos. Ici, nous décrivons une seconde espèce, *Laoennea renouardi* sp. nov., trouvée dans une grotte proche de la précédente, dans le même système karstique de la province de Vientiane.

Keywords

Gastropoda, Indochina, karst, Nam Song River, shell, subterranean diversity, Vientiane Province

Mots-clés

Gastropoda, Indochine, relief karstique, rivière Nam Song, coquille, diversité souterraine, Province de Vientiane

Introduction

The taxonomy and systematics of the Asian terrestrial snail family Diapheridae Panha & Naggs in Sutcharit et al. 2010 were recently addressed by Inkhavilay et al. (2019) and Páll-Gergely et al. (2020, 2020b). Based upon morphological evidence, the latter authors identified ten terrestrial genera to this family: *Diaphera* Albers, 1850; *Sinoennea* Kobelt, 1904; *Bruggennea* Dance, 1972; *Platylennea* Páll-Gergely, 2020; *Pupennea* Páll-Gergely, 2020; *Rowsonia* Páll-Gergely, 2020; *Parasinoennea* Z.-Y. Chen & Páll-Gergely, 2020; *Platycochlium* Laidlaw, 1950; *Tonkinia* J. Mabille, 1887 and *Laoennea* Páll-Gergely, 2020. So far, *Laoennea* is only known from its type locality cave, Tham Pou Kham in the Nam Song valley of northern Laos, and comprises one species, *Laoennea carychioides* Páll-Gergely, A. Reischütz & Maassen, 2020 (NHMW 113107) (Fig. 1).

Since the recent designation of *Laoennea*, the shell of another congener from Laos was collected by co-author Marina Ferrand, of the French Club Etude et Exploration des Gouffres et Carrières (EEGC), during the Phouhin Namno speleological expedition in Tham Houey Yè (Tham = cave in Kra-Dai language) in March 2019 (EEGC 2019). Although the new find was documented as “Troglomorpe” in the Phouhin Namno expedition report (EEGC 2019: 114–115), it has remained unidentified. Due to the shell’s distinct morphological differences from that of *Laoennea carychioides*, we describe the new species here and present speleological data regarding its subterranean ecological context. This shell constitutes the second record of *Laoennea* from Laos. The type locality, Tham Houey Yè, lies 2.7 km west of the city of Vang Vieng in Vientiane Province and is located 3.4 km east of the type locality of *L. carychioides* (Fig 2).

Methods

Sampling, imaging and measurements

The *Laoennea* shell was sampled by hand. Different perspectives of the shell were imaged using a Leica MC190 HD digital camera attached to a Leica M205 C stereo microscope (Leica Microsystems GmbH, Wetzlar, Germany). The multifocal images were processed using Leica in-house software LAS X EDOF version 3.6.0.20104 (Leica Microsystems). Original images of the type material, *Laoennea carychioides* Páll-Gergely, A. Reischütz & Maassen, 2020 (NHMW 113107) were kindly provided by Barna Páll-Gergely. These images are treated as comparative material and figured herein (Fig. 1H, I). All measurements are in millimeters (mm). Shell measurements are expressed as SH (shell height), SW (shell width), PH (peristome height) and PW (peristome width). Shell whorl number was counted (to the closest 0.25 whorl) according to Kerney and Cameron (1979: 13).

Taxon naming and depositories

Taxon name. The description of the new species *Laoennea renouardi* sp. nov. is attributed to the first and last authors, Jochum and Wackenheim. The complete citation of this new species is *Laoennea renouardi* Jochum & Wackenheim, 2020 in Jochum et al. 2020. The holotype is deposited at the Naturhistorisches Museum Bern (NMBE), Bern, Switzerland.

Institutional abbreviations

ABIMES	Association des Barbastelles d'Issy-lès-Moulineaux pour l'Exploration Spéléologique (Issy-lès-Moulineaux, France);
EEGC	Étude et Exploration des Gouffres et Carrières;
NHMW	Naturhistorisches Museum Wien (Vienna, Austria);
NMBE	Naturhistorisches Museum Bern (Bern, Switzerland);
SCEP	Spéléo Club de l'EPITA (Meudon-La-Forêt, France).

Taxonomy and systematics

Phylum: Mollusca

Class: Gastropoda

Superfamily: Streptaxoidea

Family: Diapheridae

Genus *Laoennea* Páll-Gergely in Páll-Gergely, A. Reischütz, Maassen, Grego & Hunyadi, 2020

Fig. 1K, L

Type species. *Laoennea carychioides* Páll-Gergely in Páll-Gergely, Reischütz, Maassen, Grego & Hunyadi, 2020 by original designation: 2–3 (NHMW 113107).

***Laoennea renouardi* Jochum & Wackenheim, sp. nov.**

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Fig. 1A–J

Type locality. Laos, Vientiane Province, Tham Houey Yè, 2.7 km W of Vang Vieng, 245 m a.s.l., 18°56'11"N, 102°25'28"E, collected 150 m from cave entrance in a horizontal gallery usually flooded during the rainy season (18°56'15"N, 102°25'25"E) (Fig. 3), 9 March 2019, M. Ferrand leg.

Type material. Holotype: 1 shell, SH: 1.80 mm, SW: 1.00 mm, PH: 0.54 mm, PW: 0.54 mm; Fig. 1A–J (NMBE 565863).

Diagnosis. Shell tiny, compact and less elongate than the type species, *Laoennea carychioides*, conical-ovate with fewer whorls. Penultimate whorl inflated above the

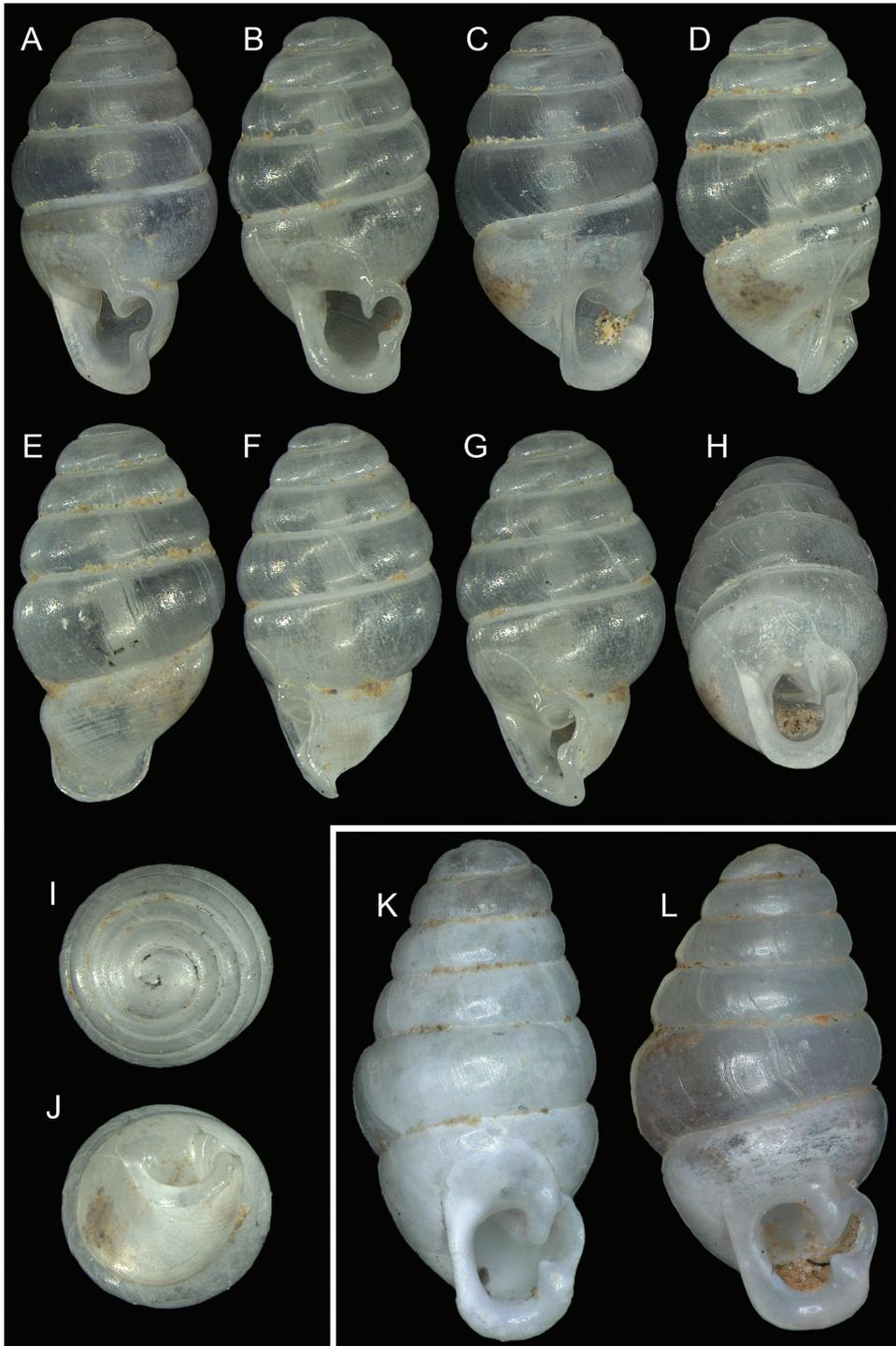


Figure 1. Comparison between species. *Laoenmea renouardi* sp. nov. **A–J** holotype (NMBE 565863) **K, L** holotype and paratype shells of *Laoenmea carychioides* Páll-Gergely, A. Reischütz & Maassen, 2020 (NHMW 113107). Scale bar: 1 mm.

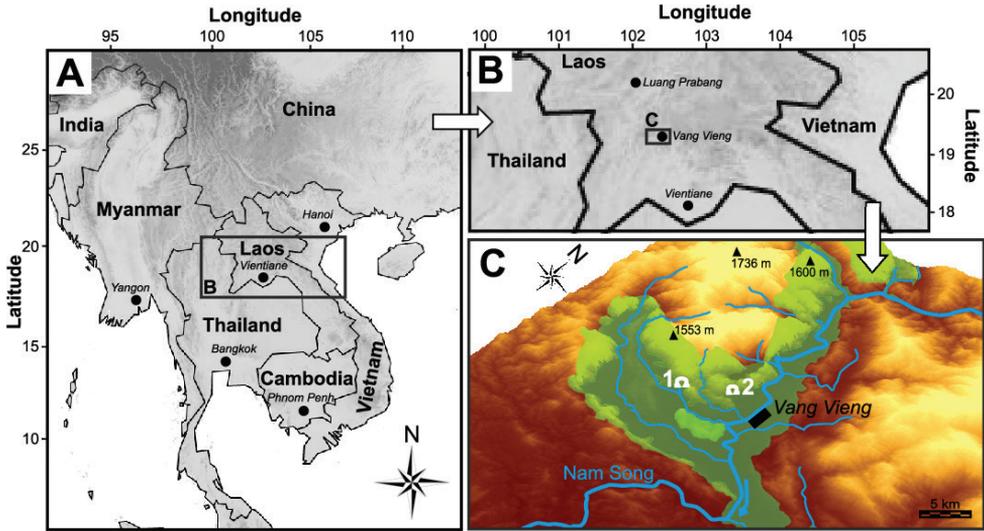


Figure 2. Location and topography of type locality **A, B** maps showing Laos, the geographical origin of the type localities of *Laoennea* species, *L. renouardi* sp. nov. and *L. carychioides*. The greyscale indicates the local mean elevation. This map was downloaded from WORLDCLIM (Hijmans et al. 2005) and political borders were retrieved from Esri Data and Maps (2002) **C** topographical map indicating geological formations and the type locality caves, 1 Tham Pou Kham (*L. carychioides*) and 2 Tham Houey Yè (*L. renouardi* sp. nov.) in two independent karst networks. The map was created using QGIS software 2.18.24. The source of the data for the digital elevation model is SRTM 30 m.

narrower last whorl. Parietal lamella protrudes slightly beyond peristome margin, long, continuing deep into shell. Sinulus in line (on the same plane) with entire peristome and not shifted laterally.

Description. Shell tiny, apical part of the shell dome-shaped, shell white and transparent when fresh, compact with inflated penultimate whorl bulging above the narrower last whorl, shell bears 5 convex whorls separated by a deep suture and a thin white band directly below at the transition of each new whorl; protoconch not clearly discernable. Entire shell glossy, finely pitted, teleoconch streaked by occasional, uneven growth lines. Thin, widely spaced ribs behind peristome extend 1/6 the surface of the last whorl and overlap radial striations of varying thickness embedded within the shell matrix of the last whorl. Aperture heart-shaped, reinforced by thick callus; parietal shield extends to over half the height of the preceding whorl. Apertural dentition three-fold with the parietal lamella and the upper palatal tooth well-formed but not swollen, together forming a round sinulus. Upper columellar side of the aperture shows slight angularity and a low, weak columellar denticle close to peristome. Sinulus opening not shifted laterally but on the same plane as the rest of the aperture. Parietal lamella slender, twisting slightly to the right at the front of the aperture, directed towards the opposing palatal denticle. The parietal lamella forms a smooth ridge which narrows as it continues deep into the shell. Peristome expanded and slightly reflected; umbilicus slit-like, straight columella visible through transparent shell.

Etymology. This species is dedicated to the French speleologist, Louis Renouard, who is a cave and karst specialist of central and northern Laos and who significantly

contributed in the discovery, exploration and mapping of the two caves from which both *Laoennea* species derive.

Distribution. Known only from the type locality, Tham Houey Yè cave.

Ecology. *Laoennea renouardi* sp. nov. was collected 150 m from the cave entrance in a horizontal gallery usually flooded during the rainy season (18°56'15"N, 102°25'25"E). The ambient temperature outside the cave on 9 March 2019 at time of collection was 34 °C. Inside the cave, the temperature measured 26 °C. Tham Houey Yè is located within the Vang Vieng karst region comprising numerous cavities formed in Upper Permian limestone (Dussault 1919; Saurin 1962; Hédouin and Renouard 2000) and harbours 11.2 km of galleries (EEGC et al. 2003; EEGC et al. 2005) (Fig. 3).

Until fresh individuals can be found, it is not yet clear if *Laoennea* is cavernicolous/cave-dwelling or not. The lack of pigment in the transparent fresh shells of *L. renouardi* and the paratype of *L. carychioides* suggests a subterranean ecology. Other taxa encountered March 2019 in Tham Houey Yè during the Phouhin Namno expedition (EEGC 2019) and which are mostly still unidentified include: 1 juvenile cameanid snail, singular members of Rhabdiphoridae, *Zarcosia* sp., Collembola, and different unidentified harvestmen (Arachnida, Opiliones) as well as members of the spider genera, *Sinopoda* and *Heteropoda* (Arachnida, Araneae). The geocological context of Tham Houey Yè is indicated also in its name: “Houey” means stream or river in the Kra-Dai language of the Lao people and “Yè” is the name of the river.

Conservation. Subterranean snails have a low tolerance to pollution and habitat disturbance. Tham Houey Yè is situated very close to a long-time popular tourist cave, Tham Pha Leusi (18°56'06"N, 102°25'27"E, 250 m a.s.l.) (Fig. 3A). The year after its discovery in 2000, Tham Houey Yè was opened for tourism. Direct tourist activity fortunately ceased a few years later due to the inconvenient necessity of having to crawl into the narrow opening of the cave (Fig. 3D). The proximity of these two caves, and the sharing of the wear and tear impact associated with tourism in addition to potentially polluted allogenic runoff draining into their karst cavities, would very probably threaten *Laoennea renouardi* sp. nov. as well as other subterranean fauna. It is paramount that conscientious regulation of tourism and water management schemes guard against this potential threat.

Discussion

The underexplored vast karst landscapes in Laos and Vietnam, are considered global biodiversity hotspots in SE Asia. These karst landscapes are riddled with caves harbouring a rich endemic cave fauna (Steiner 2013). With the caves of both *Laoennea* species geographically so close, consideration of the geological relationship between Tham Houey Yè and Tham Pou Kham is essential to understanding speciation within this newly erected diapherid genus.

Today, in a straight line, Tham Houey Yè and Tham Pou Kham are 3.4 km apart, are separated by the Yè River and appear to belong to two independent karstic networks

Tham Houey Yè Cave

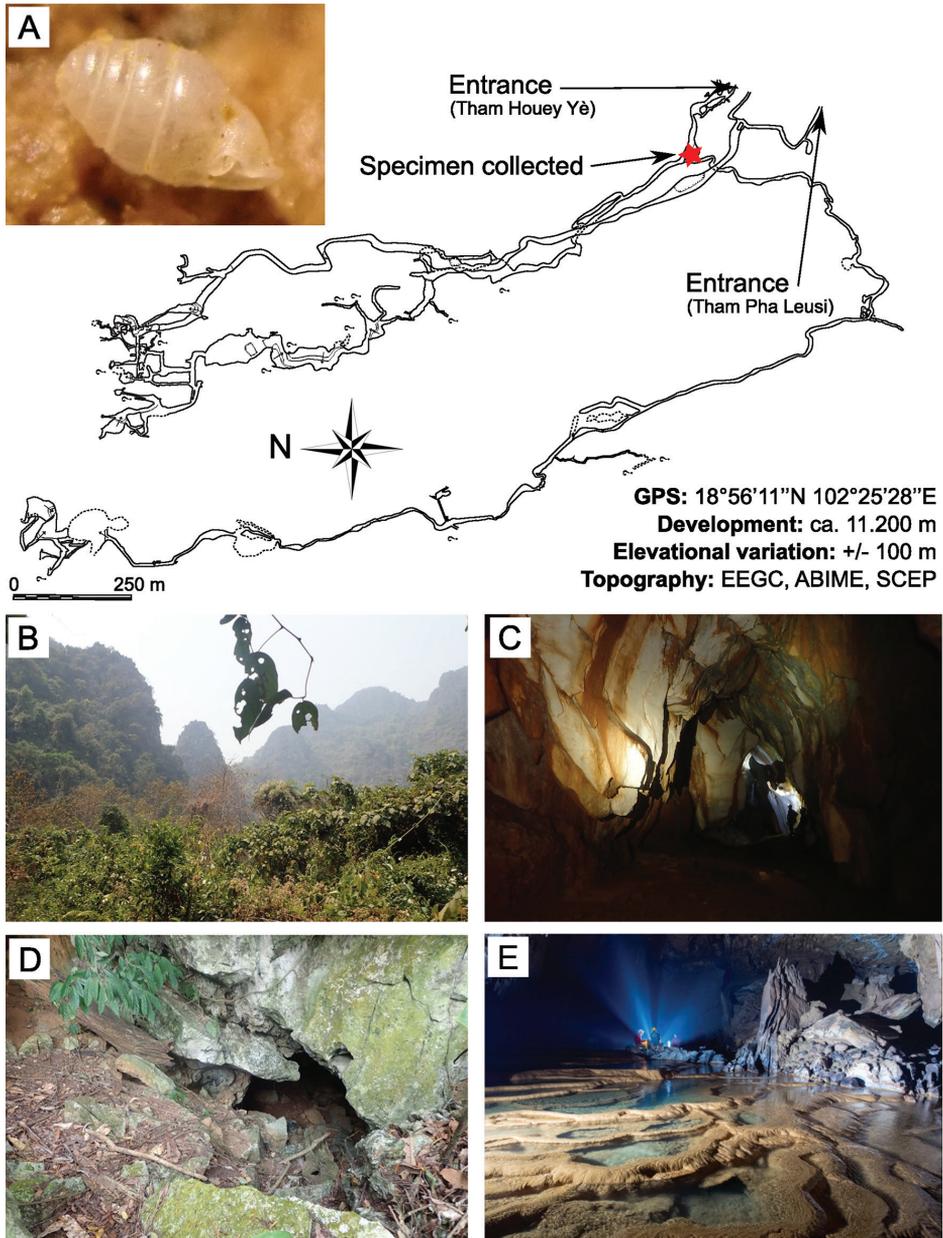


Figure 3. Speleological map and ecology of Tham Houey Yè (18°56'11"N, 102°25'28"E) including 11.2 km of caverns **A** shell of *L. renouardi* sp. nov. on moist substrate (image: M. Ferrand) and map of the cave showing the entrance to the cave, the collection site of *L. renouardi* sp. nov. marked by a red star and the entrance to the nearby touristic cave of Tham Pha Leusi. Tiny question marks on the map indicate uncertainties regarding the continuation of unexplored tiny galleries (EEGC et al. 2003, 2005) **B** landscape view from the entrance of Tham Houey Yè (image: M. Ferrand) **C** west gallery (image: M. Ferrand) **D** natural upper entrance of the cavern system Tham Houey Yè – Tham Pha Leusi (image: M. Ferrand) **E** active section of Yè River during the dry season in Tham Houey Yè (image: J- F. Fabriol).

(Fig. 3C). However, considering surrounding cave altitudes and regional geological history, different phases of karstification (depending on eustatic variations during the Quaternary) can be proposed. One hypothesis supported by the speleologist and specialist of Laotian karst, L. Renouard (pers. comm. 2020), is that Tham Houey Yè and Tham Pou Kham could have been connected during the Quaternary around 100–200 kya. After this time, the river could have additionally formed a vicariant barrier causing formerly contiguous cave systems to become disconnected while allowing populations to become separated and thus, driving the evolution of the two different morphotypes.

Acknowledgements

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A new species of *Neocarus* (Opilioacaridae) from a Brazilian ferruginous geosystem and notes on natural history

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Abstract

A new species of *Neocarus* is described from adult female and male specimens collected from an epigeal and hypogean ferruginous geosystem located in southeast Brazil. The new species, *Neocarus simmonsii* **sp. nov.**, possesses 15–17 *ch*-type palp setae, nude female pregenital region, cylindrical ovipositor without setae, and a peculiar variation of setae in the genital and pregenital region of the male, with smooth and tapering setae and/or barbed and tapering setae and/or stout and ribbed setae. Female genital setae are barbed, tapering and with a thin tip. Aspects of the ecology and life history of these mites are also presented.

Keywords

Acari, Biodiversity, Cave, Opilioacarida, Parasitiformes, South America

Introduction

The order Opilioacarida constitutes a cosmopolitan group whose distribution encompasses 26 countries (United States, Mexico, Belize, Cuba, Puerto Rico, Nicaragua, Costa Rica, Panama, Venezuela, Brazil, Argentina, Uruguay, Italy, Greece, Algeria, Angola, Gabon, Madagascar, Ivory Coast, Tanzania, South Africa, Yemen, Kazakhstan, India, Thailand and Australia) and all continents except Antarctica (e.g. Coineau and van der Hammen 1974; Juvara-Bals and Baltac 1977; Walter and Proctor 1998; Thaler and Knoflach 2002; Das and Bastawade 2006; Vázquez and Klompen 2009; Vázquez and Klompen 2010; Bernardi et al. 2012; Vázquez et al. 2014; Vázquez and Klompen 2015; Vázquez and Klompen 2018). The Americas stand out as a region of great diversity with 26 described species and four genera. Brazil presents the greatest diversity known to date, with 11 species and four genera, of which *Brasilacarus* and *Amazonacarus* are endemic to the country, while *Neocarus* and *Caribeacarus* also occur in other regions (van der Hammen 1969; Vázquez and Klompen 2009; Bernardi et al. 2013b, c; Vázquez et al. 2015; Araújo et al. 2018a; Bernardi and Borges-Filho 2018; Vázquez et al. 2020). Nonetheless, the number of known species is likely to represent only a small fraction of the group's diversity, as new records of undescribed Opilioacarida have been reported (Bernardi and Borges-Filho 2018; Monte and Bichuette 2020).

Opilioacarida are edaphic mites found in a wide breadth of habitats, such as soils of forests or dry areas, in the midst of litter, under rocks or tree trunks, and in caves. Several of the species in Brazil have been collected in caves, in spite of not presenting morphological specializations for subterranean environments. However, it is still unclear whether these species have a preference for this type of environment or whether these records are due to the increased sampling effort directed to cave fauna in recent years (Bernardi et al. 2012, 2013b, 2013c, 2014; Araújo et al. 2018a; Bernardi and Borges-Filho 2018). Collections of Opilioacarida in inventories of cave communities have generally been sporadic, with little information being recorded about the biology of these organisms. Such collections in general, result from two types of researches; ecological or faunistic studies focused on describing cave invertebrate communities (e.g. Simões et al. 2015; Monte and Bichuette 2020), and legal obligations in compliance with the environmental licensing of infrastructure projects (e.g. mining, hydroelectric plants, road construction), with the main objective of estimating species richness in the environment of interest (MMA 2009). These observations of specimens of Opilioacarida in Brazilian caves have raised questions about the importance of this type of environment in the life cycle of such organisms, especially considering that some species are abundant in cave environments throughout the year (Bernardi et al. 2013b, 2013c, 2014; Araújo et al. 2018a). The present study describes a new species of *Neocarus* observed in caves and epigeal environments in a ferruginous geosystem in Southeast Brazil. In addition, we elucidate some aspects of the biology of this new species of Opilioacarida, such as feeding habits (stomach contents) and seasonality in the subterranean environment.

Material and methods

Morphological study and gut content analysis

Specimens were collected during inventories of cave fauna, which involved thoroughly investigating caves for invertebrates under blocks, in accumulations of organic matter, and in fissures in the soil or cave walls (Wynne et al. 2019). Additionally, a few occasional collections of specimens in epigeal environment were performed. Specimens were collected with brushes and stored in containers with 100% alcohol.

Most of the material was studied as slide-mounted specimens. For this purpose, specimens were dissected, cleared in lactic acid and mounted on slides using Hoyer's medium (Walter and Krantz 2009). Stomach contents were extracted from some specimens ($n = 10$) using micro-needles through a cut in abdomen. Fecal pellets were removed and mounted on microscope slides using Hoyer. Some specimens ($n = 12$) did not require the removal of the stomach contents since clearing of the specimens was sufficient for analysis of the food items present in the fecal pellets.

For the terminology for the palp tarsal sensilla we followed Grandjean (1936) as modified by Vázquez and Klompen (2002), for the sternitogenital region we followed Klompen et al. (2015), and for the leg sensory structures Grandjean (1936), van der Hammen (1966), and Araújo et al. (2018b). Morphological characters were processed in the data matrix development mode of vSysLab (Johnson 2010) and were exported as proto-species descriptions.

Drawings were prepared using a Leica MDLS phase contrast microscope (Leica Microsystems, Wetzlar, Germany), connected to a drawing tube. Measurements were taken from adults using an ocular micrometer and are presented in micrometers (μm), average length is presented first, followed by length range in parentheses. Photos were taken with a 3.2 mega-pixel digital camera attached directly to a microscope.

Collection sites of the specimens examined were georeferenced using coordinates in degrees, minutes and seconds with the World Geodesic System (Datum WGS84).

All specimens are deposited in the following collections:

- MZLQ** Coleção de Referência Acarológica, Universidade de São Paulo, Escola Superior de Agricultura 'Luiz de Queiroz', Departamento de Entomologia e Acarologia, Piracicaba, São Paulo, Brazil;
- ISLA** Coleção de Invertebrados Subterrâneos de Lavras, Universidade Federal de Lavras, Departamento de Biologia, Setor de Zoologia, Lavras, Minas Gerais, Brazil;
- UFMG AC** Acarological Collection at Centro de Coleções Taxonômicas, Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas, Belo Horizonte, Minas Gerais, Brazil.

Abbreviations: **F** = female, **M** = male.

Biological remarks

Observations on seasonality were obtained from data produced by inventories of cave fauna in the municipalities of São Gonçalo do Rio Abaixo and Barão de Cocais, state of Minas Gerais, which used the method of active search as described above. The study was carried out in 109 cavities, with rainy season collections being made in January 2015 and dry season collections in October 2016.

Generalized linear models (GLMs), with contrast analysis were used to determine if there was a significant difference in the size of the *Neocarus* populations in the two seasonal campaigns. The models were built using abundance in each of the caves where *Neocarus* was observed as the response variable and each campaign as the explanatory variable. A negative binomial distribution with a log link functions was used since data presented significant overdispersion for Poisson error distribution (3.860). The GLM regression analysis was performed with R software (R Development Core Team 2019).

Taxonomic section

All specimens examined in this study are assigned to the genus *Neocarus* Chamberlin and Mulaik. Generic assignment is based on the following characteristics:

1. adults with 3 ribbed and stout setae on the penultimate body segment;
2. 4–6 foliate setae on the palp tarsus with no more than 5 lobes each;
3. pectinate (*d2*) setae on palp absent;
4. eupathidium ($\zeta 1$) in the main sensillar group of tarsus I and not crown like;
5. shiny fleshy setae with a whip-like tip absent from the palps;
6. dorsal segments VII to XVI and ventral segments X to XVI of the body without setae (according to Klompen et al. 2015).

Arachnida Lamarck, 1802

Parasitiformes Reuter, 1909

Opilioacaridae With, 1902

***Neocarus* Chamberlin & Mulaik, 1942**

***Neocarus simmonsii* sp. nov.**

<http://zoobank.org/6DFAE428-71BE-46DF-B6C2-F9F124A27428>

Diagnosis. Palp genu without *p*-type setae, tarsus with 15–17 *ch*-type sensilla and typical 6 pairs of foliate setae each with 1 small and thin lobe, plus 3 larger lobes with rounded, not filiform, tips. Sexual dimorphism in setation of prodorsal shield absent. Sternal setae *St2* and *St3* with attenuate tips. Pregenital area in female nude, and genital area with 6–12 barbed, tapering setae with thin tip. Pregenital areas in male with

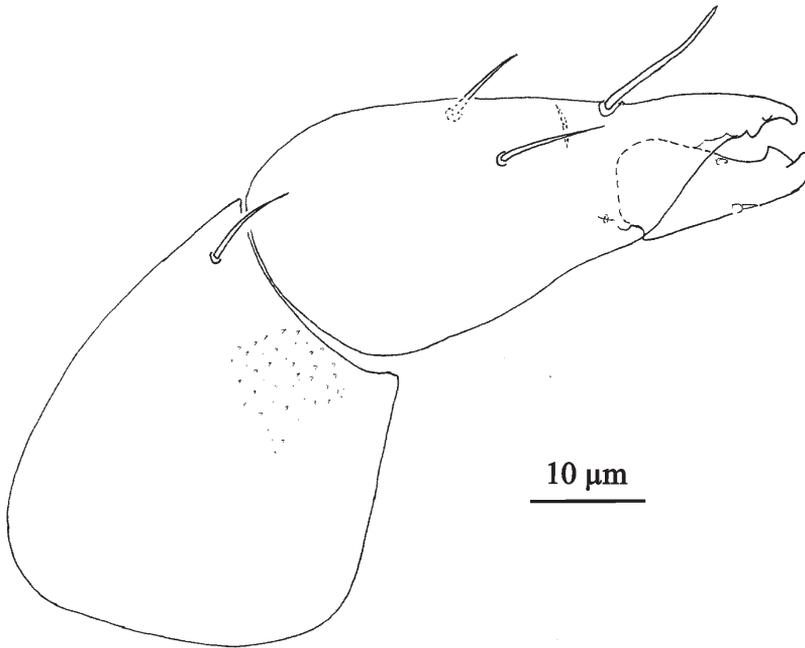


Figure 1. *Neocarus simmonsii* sp. nov., chelicera.

1–6 stout, ribbed, and relatively blunt-tipped setae and 3–7 smooth/light barbed and tapering setae; genital area with 0–6 stout, ribbed, relatively blunt-tipped setae and 4–7 smooth/light barbed and tapering setae. Ovipositor nude, simple tube-like structure, without terminal setiform sensilla or lobes.

Description. Based on 13 females and 6 males.

Gnathosoma. *Chelicera* (Fig. 1). Basal segment in adults with 1 seta, fixed digit with 3, one of which (*ch1''*) distinctly larger. Seta *cht* on basal segment of male chelicera shorter than seta *ch1''* on fixed digit. Setae *ch2'*, *ch2''* and *cht* simple, with an attenuated tip. Movable digit with one ventral denticle in a basal portion. Axial scale-like processes on movable digit in both adults absent. Basal segment 166 (136–190 μm), fixed digit 231 (217–259 μm) and movable digit 79 (74–83 μm).

Subcapitulum (Figs 2, 3). All four pairs of paralabial setae present: *pl1* relatively large, conical, With's organ (*pl2*) membranous and discoid with a biramous core; rutellum (*pl3*) with one row of 5 teeth, inserted dorso-lateral; *pl4* small, inserted dorsal. With 4 circumbuccal (*cb*) and 8–13 median and subcapitular setae (*vm*, *lvm*, *ldm*, *vp*, *lvp*). Seta *vm1* on the male subcapitulum present. Lateral lips with distinct canals (*ogl1* and *ogl2*). Sexual dimorphism evident; in female some circumbuccal setae with a rounded tip (*vm1* and/or *lm1* or/and *vp1*).

Palp (Figs 4, 5, 7D). Trochanter with 0–1 papilliform (= *p*-type) and 3–4 ribbed, tapering setae (= *r*-type); femur with 9–11 papilliform (= *p*-type) and 6–8 *r*-type setae; genu with 2–7 *p*-type and 20–28 *r*-type setae; tibia with 21 long, lightly serrate and pointed setae, 38 *r*-type setae, and 2 long, thin, and smooth sensilla. Tibia and genu ventrally with

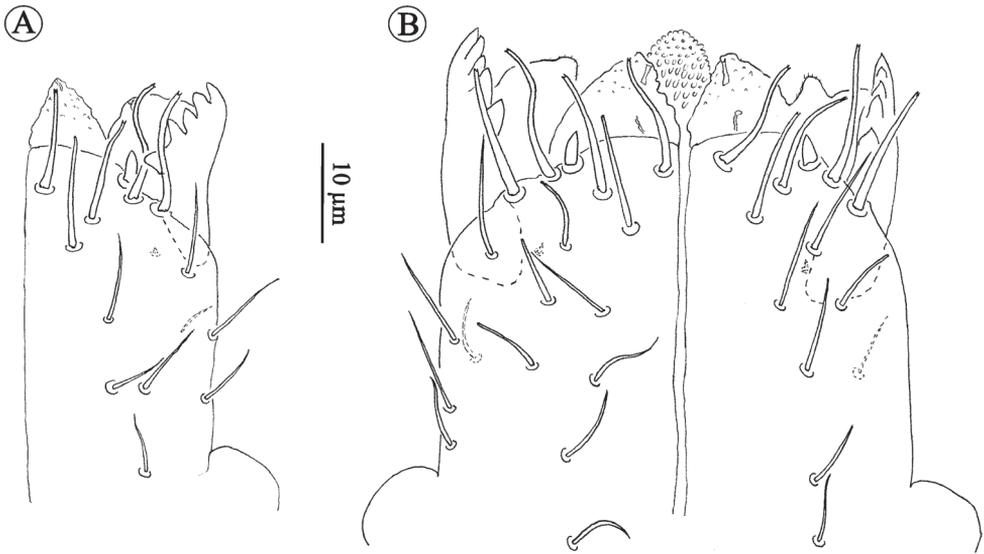


Figure 2. *Neocarum simmonsii* sp. nov., details of subcapitulum **A** male **B** female.

a small indistinct gland. Tibia and tarsus partially fused. Tarsus with 5–6 foliate (*d*-type), 10 *v*, 20 *ch*, and 10–12 *sm* sensilla, plus 3 solenidia (= *s*-type sensilla). Foliate setae each with 1 small, thin plus 3 larger lobes with rounded, not filiform, tips. Modified *sm3*-type sensilla on male palp tarsus absent. Lyrifissures *ip* and *ia* distinct. Pretarsus in shape of a pair of well-developed sessile claws. Total length of palp 638 (606–733 µm).

Idiosoma. *Color:* Violet-blue with the usual banding pattern. Color observed for live and alcohol preserved specimens (Fig. 6). Total length of idiosoma 1827–1926 µm.

Dorsum. Prodorsal shield with two pairs of lateral eyes. One pair of prodorsal lyrifissures present. Chaetotaxy in females and males consisting of, respectively, 186–204 and 218–242 setae. Sexual dimorphism in anterior portion of prodorsal shield absent. Dorsal idiosoma between the prodorsal shield and the preanal segment without setae, but with numerous lyrifissures arranged in transverse rows. Setation preanal segment limited to 1 dorsal, and 2 ventro-lateral setae. Anal valves with 7–12 stout, ribbed setae (9–12 in females; 7–9 in males).

Sternitogenital region (Figs 7–9). Sternal verrucae in adults each with 3 large pointed, and 1 composite (*St1*) setae. Setae *St1* subequal in size to *St5*. Setae *St2* and *St3* in females and males barbed, tapering to a fine tip. Remaining sternal region with 4–6 pairs of stout, ribbed setae with blunt tips. Pregenital capsules each with 1 long, tapering seta (*St5*) and 6–8 (female) or 5–6 (male) stout, ribbed setae. Pregenital and genital areas in female with 0–1 ribbed, stout setae (1 seta condition rare, observed in only 2 individuals), and genital area with 6–12 barbed, tapering setae with thin tip. Pregenital areas in male with 1–6 stout, ribbed, and relatively blunt-tipped setae and 3–7 smooth/light barbed and tapering setae; genital area with 0–6 stout, ribbed, and relatively blunt-tipped setae and 4–7 smooth/light barbed and tapering setae. Ovipositor simple tube-like structure, without terminal setiform sensilla. Male genital valves rectangular or curved, not triangular.

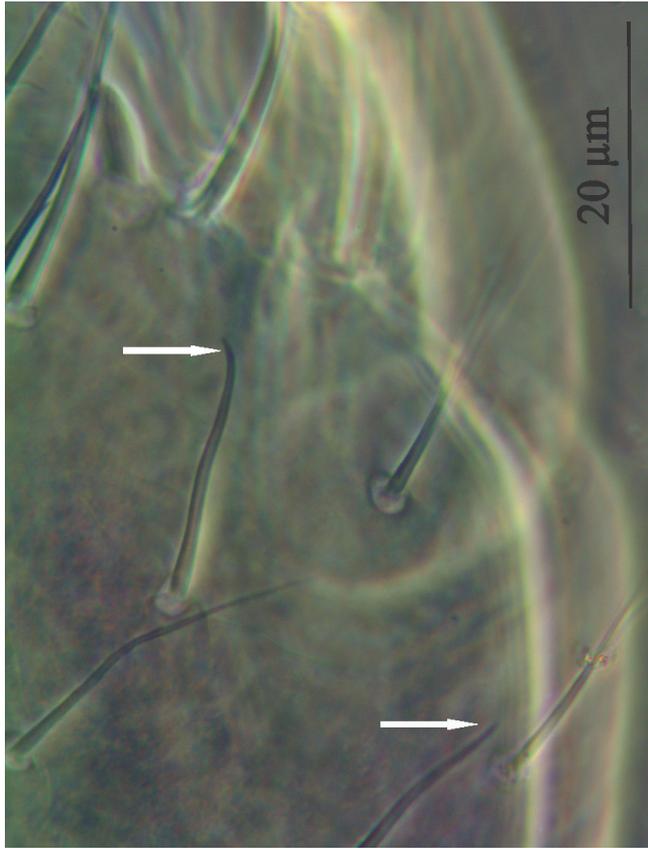


Figure 3. *Neocarus simmonsii* sp. nov., detail of setae with a rounded tip on female (arrowed).

Legs. Length of legs I–IV in females and males very similar, combined as “adults”, 3884 (3619–3941), 1973 (1812–2411), 1906 (1652–2047) and 3065 (2741–3520). Eupathidium *z1* on tarsus I inserted in dorsal sensory field; simple, without enlarged tip. Solenidion *wa* on legs II positioned on acrotarsus; *wa* on tarsi III–IV absent. Solenidion *wd* on basitarsi II–IV inserted apically, not sunk into the segment. Ambulacra II–IV in adults with 2 smooth and attenuate setae (*d* and *l*). Ventral portion of acrotarsi II–IV with 3 pairs of setae; lateral portion with 2 pairs distinctly lateral, plus 1 pair of ventro-lateral and one pair of dorso-lateral setae. Setae *lv* of acrotarsi II–IV with one small barb. Papilliform setae on dorsal portion of the basitarsi II–III present. On leg I in both sex, thin and smooth setae restrict to telotarsus and distal portion of basitarsus. Coronidia present on basitarsi II–IV of all adults (basitarsus II 8–14; III 10–16, IV 13–19), absent on tibiae and genua II–IV.

Material examined. Type depository: **Holotype** female, UFMG AC: BRAZIL, Minas Gerais State, São Gonçalo do Rio Abaixo city, Simmons' cave, 19°53'55"S, 43°28'22"W Datum WGS84, 10 Oct 2016, Oliveira MP & Bernardi LFO.

Paratypes: 2 female and 1 male specimens deposited at MZLQ, Cave PDI_0034, 19°53'48.99"S, 43°28'15.29"W Datum WGS84, col Oliveira MP, 06

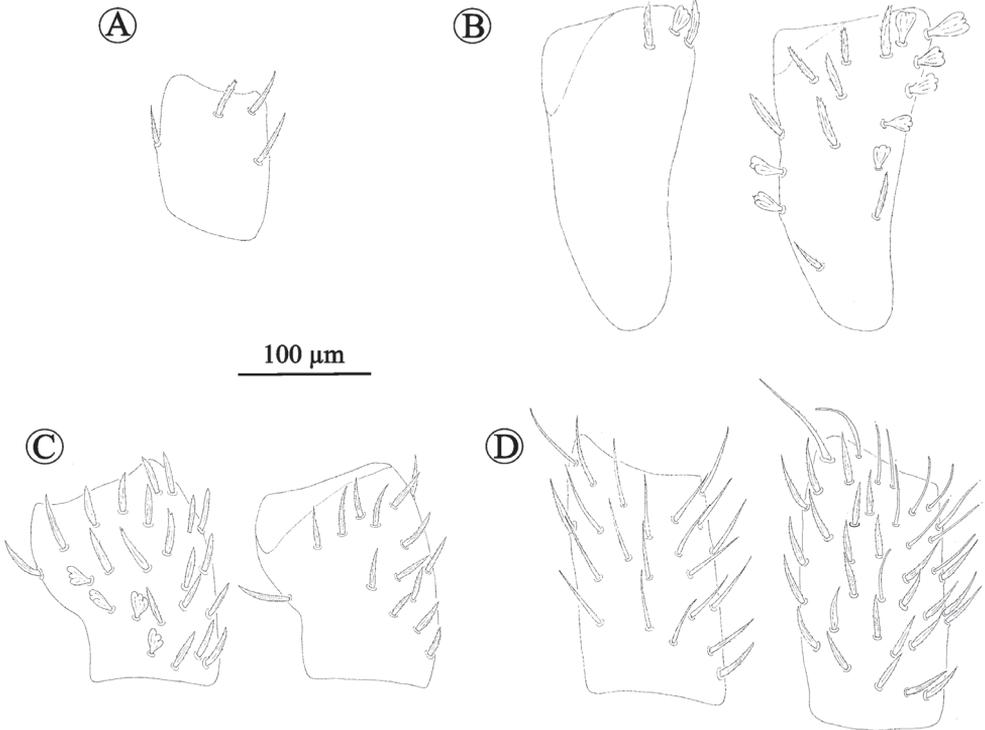


Figure 4. *Neocarum simmonsii* sp. nov., detail of setae on male palp **A** trochanter **B** femur **C** genu **D** tibia.

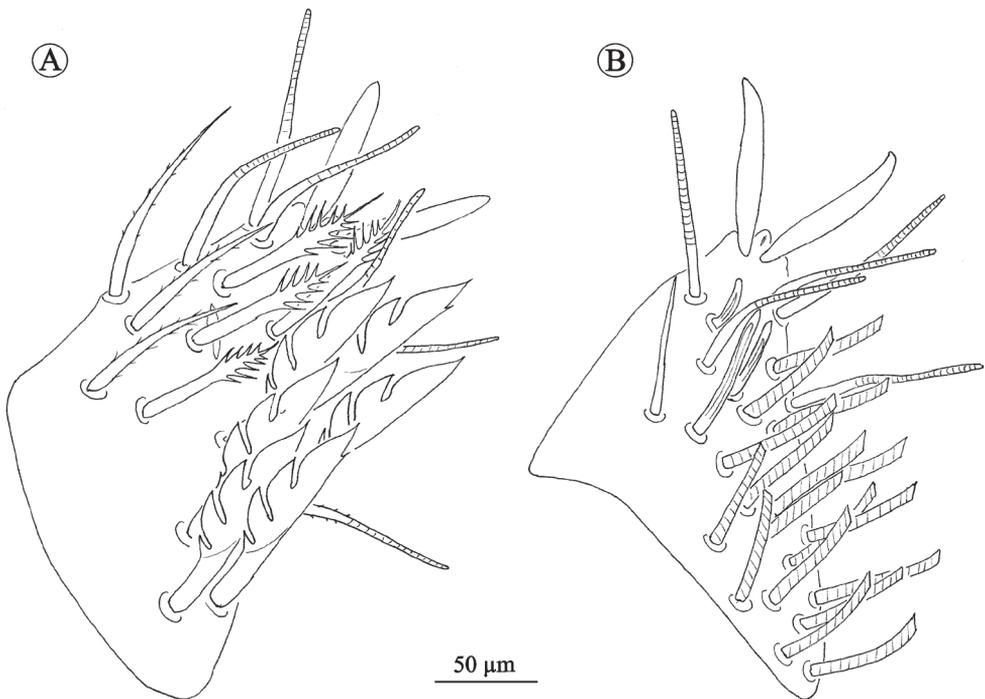


Figure 5. *Neocarum simmonsii* sp. nov., detail of setae on male palp tarsus, dorsal (**A**) and ventral (**B**).

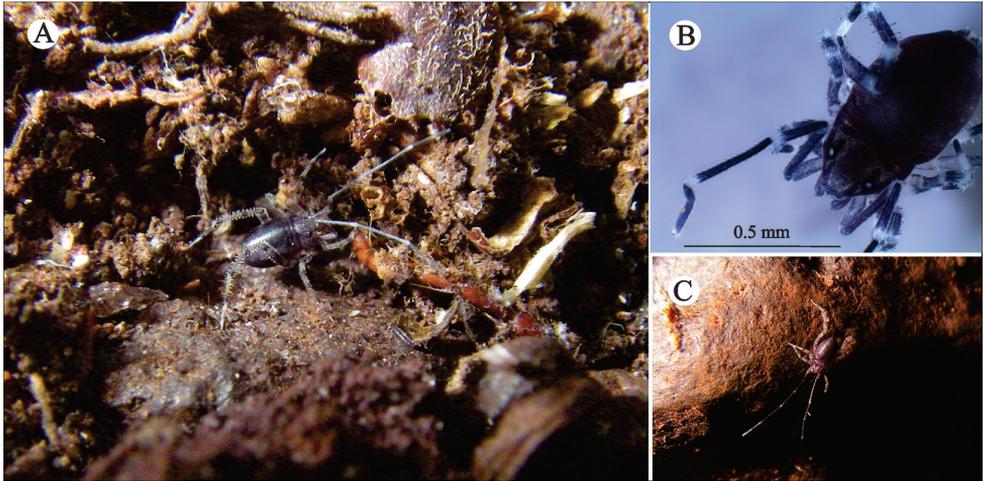


Figure 6. *Neocarus simmonsii* sp. nov., specimens alive observed on cave soil (**A**, **C**), view of male prodorsal region (**B**).

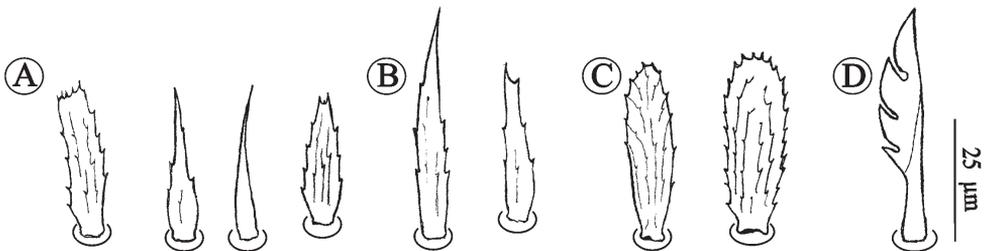


Figure 7. *Neocarus simmonsii* sp. nov., details of setae. **A** Variation on shape of pregenital and genital setae on male **B** variation on shape of genital setae on female **C** detail of setae on prodorsal region **D** detail of *d*-type (foliate seta) on palp tarsus.

Oct 2016; 1 female specimen deposited at MZLQ, cave PDI_0029, 19°53'29.61"S, 43°28'19.74"W Datum WGS84, col Oliveira MP, 26 Nov 2015; 1 female specimen deposited at MZLQ, cave PDI_0059, 19°54'0.75"S, 43°28'9.91"W Datum WGS84, col Oliveira MP, 09 Jan 2016; 1 male specimen deposited at ISLA, cave PDI_0039, 19°53'51.37"S, 43°28'12.51"W Datum WGS84, col Oliveira MP, 05 Oct 2016; 2 females and 1 male specimens deposited at ISLA, cave PDI_0024, 19°53'38.98"S, 43°28'39.14"W Datum WGS84, col Oliveira MP, 26 Nov 2015; 1 female specimen deposited at ISLA, cave PDI_0031, 19°53'49.62"S, 44°28'13.36"W Datum WGS84, col Oliveira MP, 06 Oct 2016; 1 male specimen deposited at UFMG AC, cave PDI_0052, 19°53'59.82"S, 43°28'7.34"W Datum WGS84, col Oliveira MP, 17 Oct 2016; 3 female and 1 male specimens deposited at UFMG AC, cave PDI_0065, 19°53'58.12"S, 43°28'14.68"W Datum WGS84, col Oliveira MP, 12 Oct 2016; 1 female specimen deposited at UFMG AC, cave PDI_0059, 19°54'0.75"S, 43°28'9.91"W Datum WGS84, col Oliveira MP, 19 Oct 2016; 1 male specimen deposited at UFMG AC, cave PDI_0084, 19°53'52.83"S, 43°28'11.95"W Datum WGS84, col Oliveira

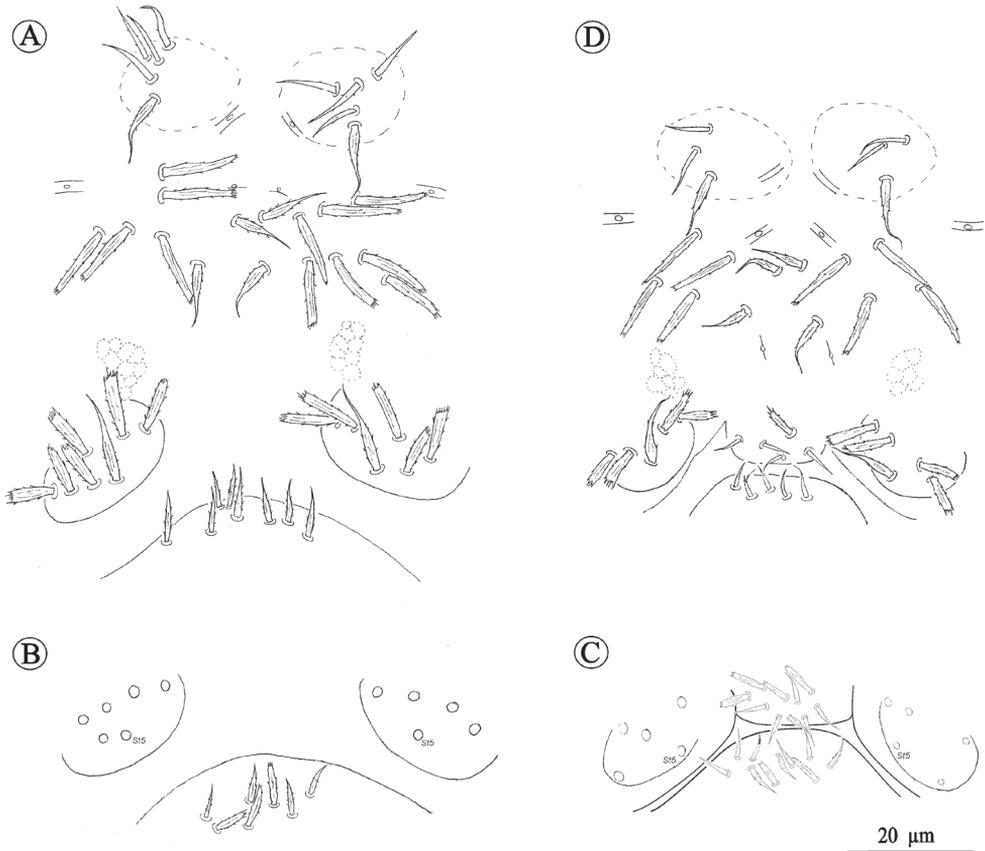


Figure 8. *Neocarus simmonsii* sp. nov., view of sternitogenital region; View of female sternitogenital region (A) and view of variation on genital region (B); View of male sternitogenital region (C) and view of variation on pregenital and genital region (D).

MP, 24 Nov 2015, 1 female specimen deposited at UFMG AC, cave MDIR_0015/16, 19°53'28.88"S, 43°27'40.17"W Datum WGS84, col Oliveira MP, 10 Oct 2016.

Etymology. The specific name is in honor of George C. Simmons due his contributions to studies on caves genesis and mineralogy. Simmons produced seminal papers in iron ore caves and karst in Brazil and one of his important research projects was conducted in cave MDIR_0020 (Simmons cave), near the type locality of the new *Neocarus* species.

Comparative notes. *Neocarus simmonsii* differs from *N. potiguar* Bernardi, Zacarias & Ferreira, 2012, *N. proteus* Bernardi, Klompen, Zacarias & Ferreira, 2013, and *N. platensis* (Silvestri, 1905) from Brazil by the absence of pregenital setae in the female. It differs from *N. coronatus* Araújo & Feres, 2018 by the presence of 6 (vs. 4) foliate setae on the palp tarsus; from *N. potiguar*, *N. caipora* Bernardi, Klompen & Ferreira, 2014, *N. platensis* (from Argentina and Uruguay) and *N. misiones* Vázquez, Bernardi & Klompen, 2020 by the absence (vs. presence) of *p*-type setae on the palp genu (*N. pro-*

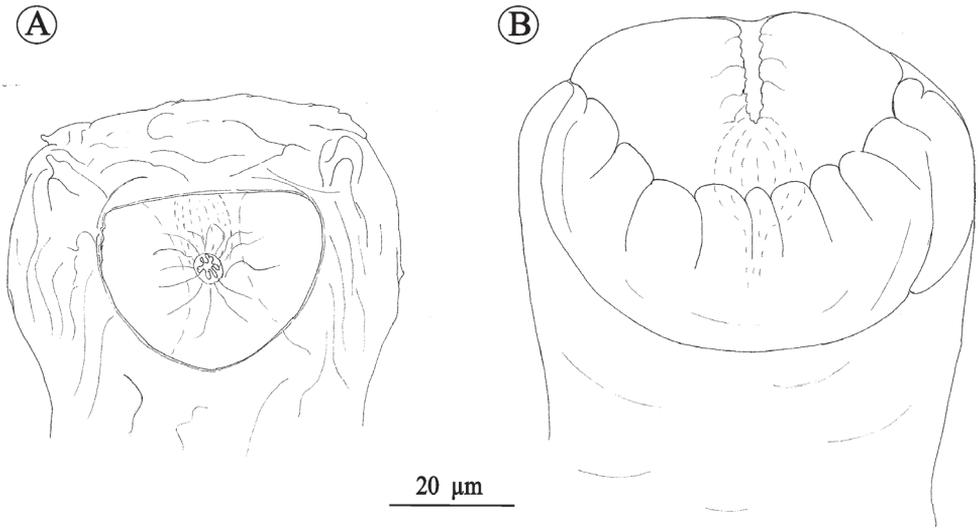


Figure 9. *Neocarus simmonsii* sp. nov., view of invaginated ovipositor (A) and evaginadted (B).

teus and *N. spelaion* Bernardi, 2018 are somewhat intermediate as they carry small numbers (1–7) of *p*-type setae on the palp genu), and from *N. spelaion* by the uniformity (vs. variability) in shape of the pregenital and genital setae in the male. *N. simmonsii* differs from *N. entrerios* Vázquez, Bernardi & Klompen, 2020 and *N. coronatus* by the absence (vs presence) of sexual differentiation in the setae on the prodorsal shield.

The ovipositor is a unique structure and its characteristic is useful to differentiate Opilioacarida species. *Neocarus simmonsii* presents an ovipositor cylindrical with a rounded tip similar only to *N. potiguar*, but differentiates from the species with terminal lobes, such as *N. misiones* (three small and very distinct roundish terminal lobe), *N. entrerios* (with a distinct pair of papillate hooks), *N. spelaion* (with a rounded and distinct lobes) and *N. proteus* (two rounded structures plus three membranes at tip. *Neocarus coronatus* and *N. caipora* differs from all South American species due the presence of setae on ovipositor. *Neocarus platensis* and *N. ojasitii* have a poorly described ovipositor structure.

Life history remarks

Development and morphological abnormalities

The ability to regenerate appendages can be a great advantage for species of Opilioacarida since these organisms easily lose their appendages during different stages of development or even in adulthood (Coineau and Legendre 1975; Klompen 2000; Bernardi et al. 2013a). As described in previous works (Coineau and Legendre 1975; Klompen 2000; Bernardi et al. 2013a), regeneration has been observed in young specimens of

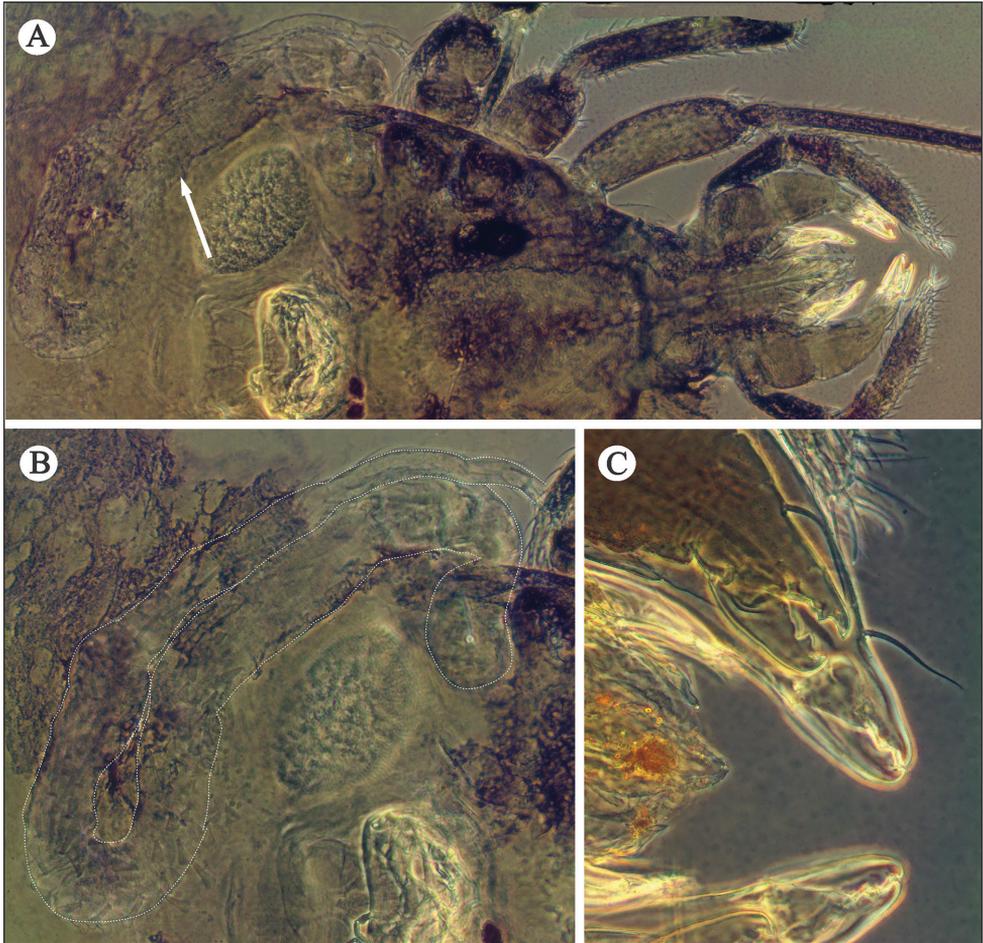


Figure 10. *Neocarus simmonsii* sp. nov., view of regeneration process on leg (arrowed) in adult female (**A, B**); details of the molting process on chelicera.

N. simmonsii, namely deutonymphs and tritonymphs. Here, we observed for the first time this replacement of appendages in adults. The specimen, a female, was collected while changing its integument, which made it possible to observe the old integument and the new integument formed below, with leg IV in regeneration (Fig. 10). Integumentary molting and continuous growth in Opilioacarida, even in adulthood, can be a physiological advantage for species of this group because they have a fragile integument, a possible autotomy behaviour and these mites can easily lose appendages.

It is not possible to say how many molts an adult can experience even after reaching sexual maturity, but the size of a male and female collected during field study suggests that growth may continue, and thus there can be more than one molt in adulthood. This is based on the observation that collected adult specimens exhibited the molting process, with two specimens (1 male and 1 female) having an old integument (exuvia), which was covering the new one. The new integument presented some

Table 1. Comparative setal patterns and shape for the pregenital and genital region, ovipositor and palp of *Neocarus* adults.

OCCURENCE	SPECIES/ SUBSPECIES	FEMALE		MALE		Palp	
		Pregenital region	Genital / Eugenital region	Pregenital region	Genital region	ch-type	d-type
		No. and type of setae	No. and type of setae	No. and type of setae	No. and type of setae		
North America							
USA	<i>Neocarus texanus</i>	2 st/r	nude	4–6 st/r	8–9 sh	10–14(21)	5
Mexico	<i>Neocarus nobbecanus</i>	nude	nude	4–5 st/r	5–7 ^a /r	17–19	4
Mexico	<i>Neocarus siankaanensis</i>	nude	nude	2 st/r	4 st/r	14–15	5
Mexico	<i>Neocarus bajacalifornicus bajacalifornicus</i>	2 st/r	nude	5–8(13 ^a) st/r	7–8(11 ^a) st/r	14–18 (21 ^a)	5
Mexico	<i>Neocarus bajacalifornicus chamelaensis</i>	2–3 st/r	nude	4–5 st/r	4–6 st/r	16	5
Mexico	<i>Neocarus calakmulensis</i>	2–3 st/r	nude	2–6 st/r	3–8 st/r	17	5
Mexico	<i>Neocarus venacruzensis</i>	2 st/r	nude	6–8 st/r, 0–1 s	6–8 st/r	13	5
Mexico	<i>Neocarus comalensis</i>	5–7 st/r	3 st/r			14–18	5
Mexico	<i>Neocarus chactemalensis</i>	nude	nude	4–6 st/r	4–6 st/r	11–13	4
Central America							
Nicaragua	<i>Neocarus nicaraguensis</i>	2–5 st/r	nude	2–7 st/r	3–6 st/r	18–22	5 or 6
Cuba	<i>Neocarus orchidani</i>	nude	nude	4–5 st/r	5–7 st/r	20–24	4
Belize	<i>Neocarus belizensis</i>	nude	nude	2–3 st/r	4–5 st/r	17–21	5 or 6
South America							
Venezuela	<i>Neocarus ojustii</i> **	nude	nude	6–9?	13 st/r	–	–
Brazil	<i>Neocarus proteus</i>	2–5 st/r	4–6 wb	2–5 st/r	3–5 sh	12 or 13	5 or 6
Brazil	<i>Neocarus potiguar</i>	1 tp/r	4–8 sh	5 st/r	7–10 st/r	25–27	5 or 6
Brazil	<i>Neocarus coronatus</i>	nude	6 tp/b	1–7 st/r	5–15 tp/r	18–25	4
Brazil	<i>Neocarus caipora</i>	nude	8–12 sh	4–8 st/r	5–8 tp/r	15–16	6
Brazil	<i>Neocarus spelaion</i>	nude	10–12 sh	9–12 sh or tp/r	7–11 sh and/ or tp/r	14–18	5 or 6
Brazil	<i>Neocarus simmonsii</i>	nude	6–12 st/b or tp/b	4–10 sh or tp/r or st/r	4–10 sh or tp/r or st/r	15–17	6
Brazil/Argentina/Uruguay	<i>Neocarus platensis</i>	0–2 st/r	6–9 sh	6–10 st/r	5–10 sh	14	5 or 6
Argentina	<i>Neocarus misiones</i>	nude	12–13 tp/b	7–9 st/r and/ or tp/b	12–13 tp/b	15	6
Argentina	<i>Neocarus enterrios</i>	nude	6–12 sh	6–10 st/r	8–10 tp/r	20	6

* number of setae in super adults. **The description of *Neocarus ojustii* does not provide sufficient detail for an adequate comparison. Setae type: sh: smooth setae; st/r – stout and ribbed setae; tp – tapering; tp/b: tapering and barbed setae; wb: weakly barbed setae.

characters already 9 to 18% larger than in any of the other adults collected. Based on the measurements of body setae, Bernardi et al. (2013a) suggested that there is a continuous increase in adult body size after molts. Vazquez and Klompen (2002) observed a greater number of setae in super-adults, but this morphological change was not observed in the specimens studied here.

Another interesting observation made on an adult male of *N. simmonsii* was the presence of morphological abnormalities of the palp, with the reduction and reorganization of setae as well as changes in the shape of the structure itself (Fig. 11). Small abnormalities in body setae (Araújo et al. 2018a) or the duplication of pores (Bernardi and Borges-Filho 2018) has been observed in other species. Here, for the first time, abnormalities are seen in complete structures, such as the palp. The potential behavioral consequences for individuals remain unclear.

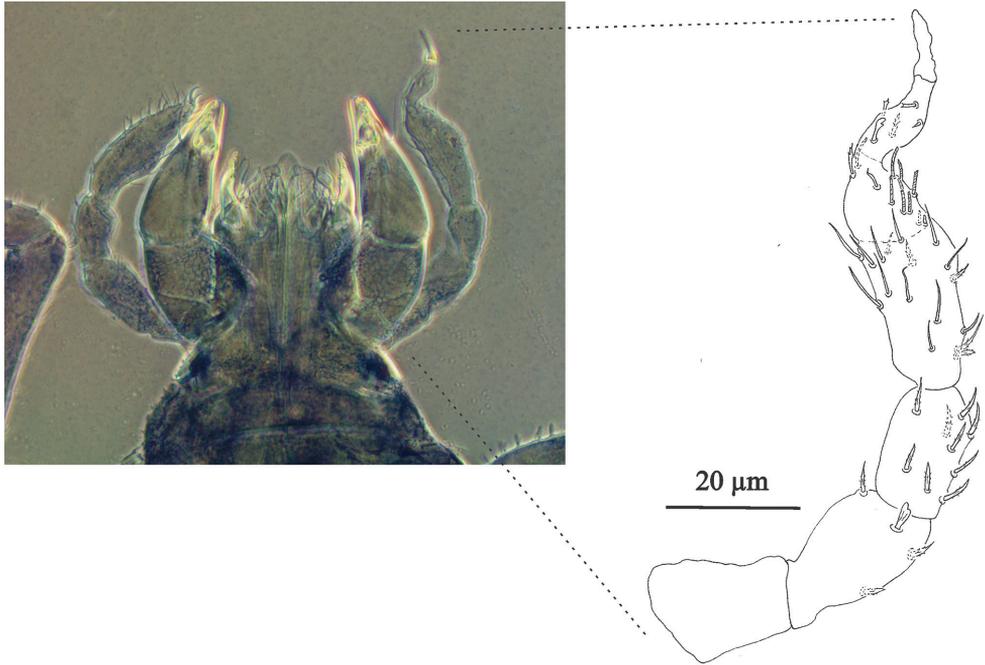


Figure 11. *Neocarus simmonsii* sp. nov., detail view of the morphological abnormality on palp of male.

Gut contents

The gut contents of specimens of *N. simmonsii* includes unidentified plant fragments, arthropod remains, pollen, and fungal hyphae (Fig. 12). The observation of plant fragments and pollen in the stomach contents of specimens collected in the deepest areas of caves (more than 40 m from the entrance to aphotic zones in some caves) suggests that these organisms feed on decomposing matter from the epigeal environment that is transported by water action. Three specimens of *N. simmonsii* had also specimens of mites, possibly of the family Tarsonemidae and Oribatida. This feed plasticity can assist in the colonization of a great diversity of habitats, including caves, where resources generally tend to be scarce.

In addition to these materials, the stomach contents of three specimens evaluated under microscopy possessed remains of integuments (exuvia) of Opilioacarida (Fig. 12). When reviewing the stomach contents of other specimens of other species present in the collect of Universidade Federal de Lavras (ISLA), we also observed materials of this nature in *Caribeacarus brasiliensis* (4 individuals), *N. caipora* (3 individuals), *N. proteus* (4 individuals) and other undescribed species of Opilioacarida (8 individuals).

During the observation of *N. proteus* kept laboratory condition in 2012, for about 4 months, also allowed documenting specimens feeding on their own exuvia after molting (2 observations) and even exuvia of other dead individuals (2 observations). Such

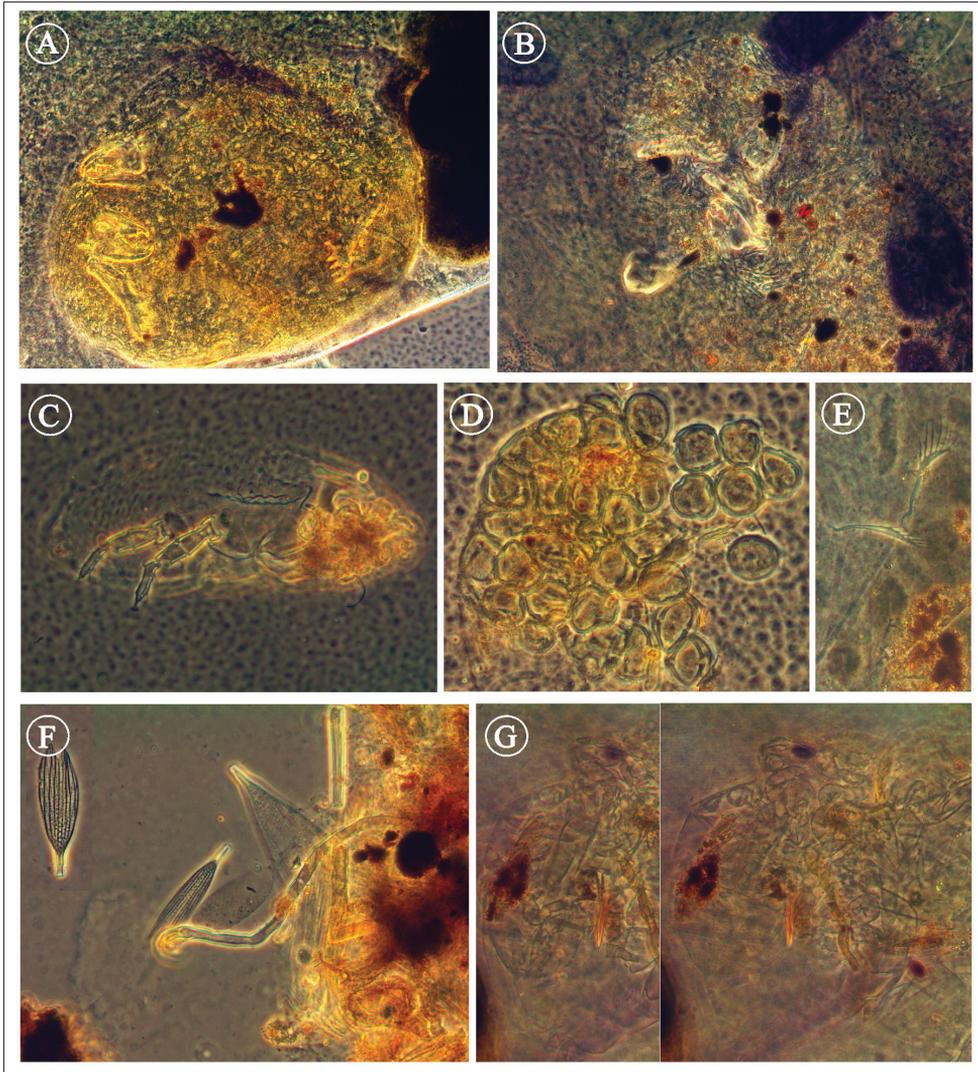


Figure 12. Example images of the gut content of individuals *Neocarus simmonsii* sp. nov., **A, B** exuvia of Opilioacarida, **C** mite (Astigmatina), **D** pollen, **E** probably a bothridial seta (oribatida), **F** plants, fungi and arthropods parts, **G** mite exuvia, probably an Endeostigmata.

laboratory data, associated with the observations of stomach contents of specimens of *N. simmonsii* in the present study and the absence of records of cannibalism among Opilioacarida bred and maintained in the laboratory (Vázquez and Palacios-Vargas 1989; Klompen 2000; personal observations), allows us to infer that these species feed on their own exuvia. This behavior is not unique among arachnids, but is apparently rare. Some observations made by Dondale (1965) suggest that spiders feed on exuvia because they contain a set of proteins that can be an important source of nutrients for

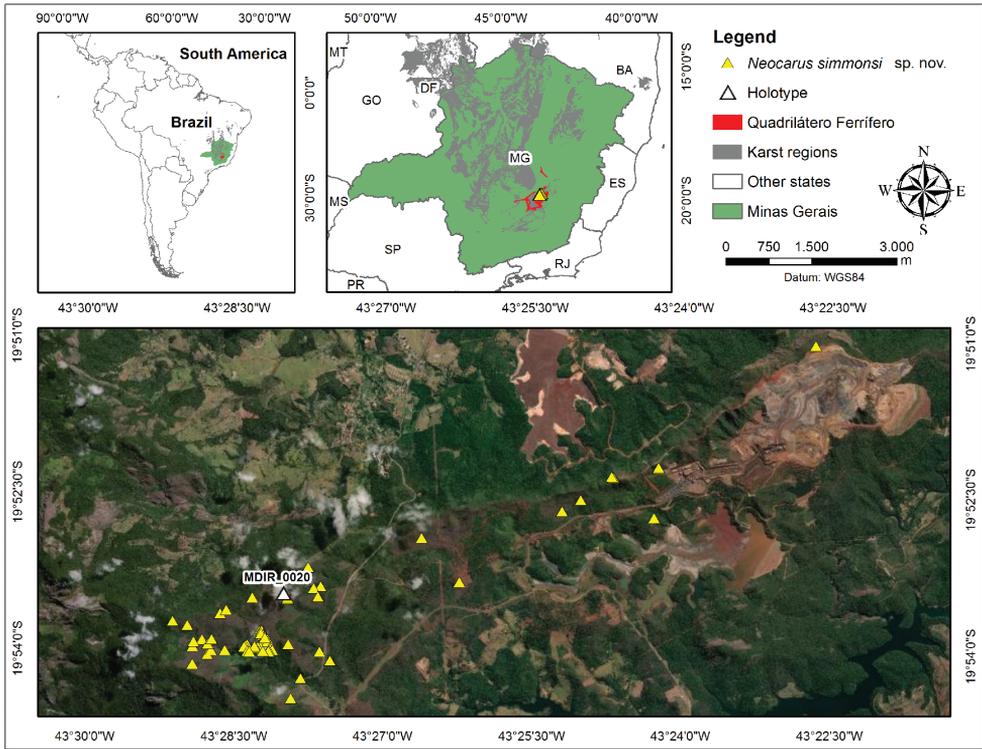


Figure 13. Distribution of *Neocarur simmonsii* sp. nov..

individuals after going through the stress of molting, and the period without energy intake. This is an interesting behavior, because it allows Opilioacarida to reabsorb energy present in the tissue or liquid, discarded in the process of ecdysis. This behavior can be an important strategy in an environment with scarce resources, such as some caves.

Distribution, habitat, and seasonality

Neocarur simmonsii does not have morphological characteristics arising from isolation in subterranean environments and was found both in caves and the epigeal environment. The only species whose morphology has been modified to the point of being considered troglobitic are *Siamacarur dalgeri* and *S. withi*, described by Leclerc (1989) from caves in Thailand. As adaptations to the subterranean realm, these species lack eyes, possess elongated appendages, have a pale coloration, and even modified sensory setae. Similar traits have not been found in cave species in Brazil thus far.

The distribution of *N. simmonsii* extends across the entire Serra do Tamanduá and Dois Irmãos (municipalities of São Gonçalo do Rio Abaixo and Barão de Cocais) in a strip of at least 12 km. However, the effective distribution of the species is expected to be much greater, considering that it is a common species in the sampled area and that it is not restricted to subterranean environments (caves) (Figs 13, 14).



Figure 14. General aspects of Simmons' cave (MDR_0020), (**A**, **B**) and epigeal environmental (**C**), habitat of *Neocarus simmonsii* sp. nov.

The study area is located northeast of the Quadrilátero Ferrífero (Iron Quadrangle), in an area of Atlantic Forest near the transition zone with the Cerrado biome (Brazilian savanna). The vegetation cover consists of forest formations and “campos rupestres” (rupestrian fields) at higher altitudes and shallow soils rich in metals (e.g. iron). Since it is a geomorphologically diversified area and located close to the transition between two biomes, there is a great diversity of flora and fauna. The region, therefore, is considered a priority area for conservation in the state of Minas Gerais with “extreme biological importance” due to the high floristic and faunal richness and the presence of several endemic and endangered species (Drummond et al. 2005). There are a few hundred registered caves in the study area including the largest caves in the Quadrilátero Ferrífero.

The type locality, Simmons' cave, was mapped in 1960 and is one of the few examples of caves formed by dissolution in the region. The cave is located at approximately 1140 meters above sea level and has only one entrance, aphotic zones, different compartments (halls), perennial lakes, and 146 meters of horizontal projection. With regard to organic resources, litter deposits were observed in the entrance area, along with guano of carnivorous and hematophagous bats. Lichens and fungi were observed on the walls and floor near the entrance to the cavity.

Neocarus simmonsii is an abundant species in caves in the region, having been found in 73 of the 109 studied caves. The abundance of specimens was significantly higher in

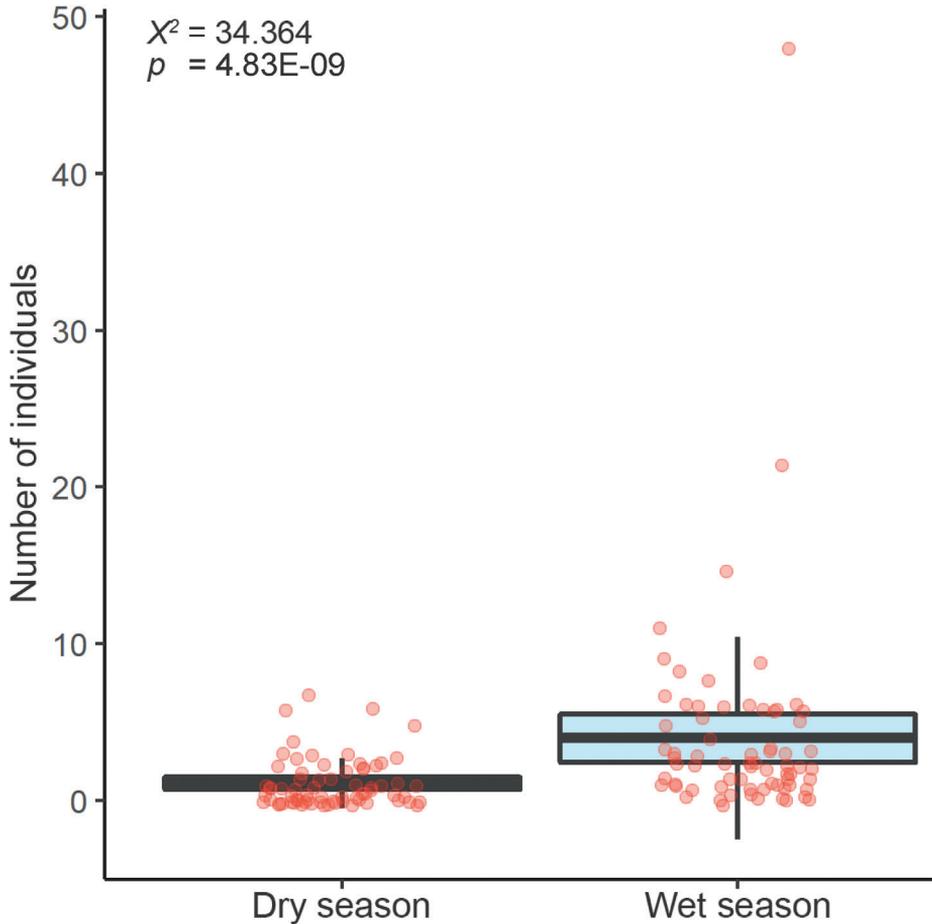


Figure 15. Average sampled individuals of *Neocarus simmonsii* sp. nov. per cave according to seasonality. The abundance values are significantly different between the two seasons according to the Generalized linear model analysis ($z = 5.853$; $p\text{-value} = 4.83e^{-9}$). In the boxplots, the turquoise areas refer to the interquartile range around the observed median (central black line) and vertical bars represent the maximum-minimum range (excluding outliers).

the wet season (estimated $\beta \pm \text{S.E.} = 1.29328 \pm 0.22096$; $z = 5.853$; $p\text{-value} = 4.83e^{-9}$), ranging from few to dozens of individuals as the case of BRU_0012 cave ($n = 48$ during the wet season and $n = 0$ during the dry season), BRU_0023 cave ($n = 21$ during the wet season and $n = 1$ during the dry season), and BRU_0002 cave ($n = 15$ in the wet season and $n = 1$ during the dry season). This great oscillation may be explained by the fact that the number of individuals observed increases during the rainy season, or else it may be due to the migratory behavior of the species (Fig. 15). Even in caves, where the environment is generally stabler than at the surface, seasonality can still influence the general climate (Bento et al. 2016; Mammola and Isaia 2018), and decrease the availability of water and food (Simon et al. 2007; Silva et al. 2011; Souza-Silva et al. 2012). Nevertheless, further investigations are needed to verify the generality of this pattern.

In some caves individuals of *N. simmonsii* were found aggregated in groups of up to eight and ranging from protonymph stages to adult males and females. The species' behavior is similar to that observed for *N. caipora* and *Caribeacarus brasiliensis* (Bernardi et al. 2014). As suggested by Vázquez et al. (2018), this gregarious behavior can increase the survival rate, especially for young individuals. *Neocarus simmonsii* was significantly more abundant during the wet season (Fig. 15), when there is greater rainfall in the region (above 1000 mm). Besides climate, another factor that may determine variations in the abundance of this species is the availability of organic resources. Organic matter is imported into caves by biological agents (e.g. bats), wind or rain (Simon et al. 2007; Silva et al. 2011; Souza-Silva et al. 2012), with this transport being generally greater during the wet season.

Final remarks

The number of described species of Opilioacarida from collections in karst areas and caves in Brazil is increasing (Bernardi et al. 2013b, c, 2014; Araújo et al. 2018a; Bernardi and Borges-Filho 2018). This is due to the intensification of sampling efforts in this habitat as the result of environmental licensing processes. Environmental licensing requires speleological studies to be carried out in karst areas or other sites that potentially bear caves in Brazil among them the inventory of cave fauna (BRASIL, 6.640, IN MMA 2017). This legal requirement has led to the discovery and description of several new species in the country, in addition to the acquisition of information on the range and biology of various species.

Brazil stands out for its diversity of described species of Opilioacarida (11 spp.) and its great potential for new records in view of its territorial extension and the large concentration of caves in different lithologies and biomes (Lewinsohn and Prado 2005; Oliveira et al. 2016; CECAV 2019). Thus, an increase in the number of new species is expected with intensification of sampling effort in different ecosystems and greater investment in taxonomic research and training of new specialists.

Mites and other soil invertebrates generally exhibit seasonal fluctuations, with their richness and abundance being determined by environmental factors such as precipitation and temperature (Badejo 1990). Although caves are confined systems and have greater environmental stability than the surrounding epigeal environment (Culver 1982; Freitas and Littlejohn 1987), the cave microclimate can also influence the structure and composition of fauna, with fluctuations in populations and communities throughout the year. Such variation is often a response to variation in the external climate (Ferreira et al. 2015; Bento et al. 2016), as indirectly observed for *N. simmonsii*.

Opilioacarida is a group of species with interesting feeding habits. The material ingested by them is composed of large fragments of solid material of vegetable, animal and/or microbiological origin (van der Hammen 1966; Walter and Proctor 1998; Klompen 2000; Araújo et al. 2018a; Bernardi and Borges-Filho 2018). Although small invertebrates (especially mites) have been observed in the stomach contents of *N. simmonsii*, it is still not possible to say whether species in this group are predators or scavengers. For example, our observations of the stomach contents of *N. simmonsii*

would suggest that these organisms are one of the few known “scavengers” of Parasitiformes, but this remains an anecdotal observation.

Finally, the order Opilioacarida always occupies a prominent position when referring to the study of development among mites. The development of these taxa comprises an embryonic phase (prelarva), subsequent larva, protonymphs, deutonymphs, tritonymphs and adults, but its growth can continue beyond the adult phase. The regeneration of appendages in adult individuals, however, is a peculiarity known only in this group among Parasitiformes and is rarely observed among a few Acariformes and arachnids in general (Michener 1946; Imamura 1952; Furumizo and George 1976; Bernardi et al. 2013a). Growth in adulthood can result in individuals with larger bodies and morphological structures and a greater number of setae in some areas of the body (Vázquez and Klompen 2002; Bernardi et al. 2013a). In the present study, we observed that growth and regenerative ability occur in all life stages of Opilioacaridae, which may eventually increase their survival rate.

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Groundwater annelids from Gran Canaria and Fuerteventura (Canary Islands), with the description of two new species of *Namanereis* (Namanereidinae, Nereididae, Polychaeta)

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Abstract

The Canary Islands are the richest volcanic region in the world in subterranean adapted fauna, followed by the Hawaiian Islands and the Undara Cave in Australia. Most of the subterranean adapted aquatic fauna from the Canary Islands is restricted to the anchialine environments in La Corona lava tube in Lanzarote, while the oligohaline stygobiont fauna, usually found in groundwater or interstitial freshwaters, is scarcer and represented by a few species of amphipods, copepods, and a single polychaete annelid recorded from Fuerteventura and doubtfully identified as *Namanereis hummelincki* (*non* Augener, 1933) (Hartmann-Schröder, 1988). Two new species of polychaete annelids belonging to the subfamily Namanereidinae are described from Gran Canaria and Fuerteventura. Both species live in groundwater, are depigmented and eyeless, and have bifid jaws. Although they are seemingly more related to each other than to other members of the bifid-jaw group, *Namanereis canariarum* **sp. nov.** can be diagnosed by its relatively longer tentacular cirri and parapodial dorsal cirri, as well as the presence of pseudospiniger chaetae. In contrast, *Namanereis llanetensis* **sp. nov.** has shorter cirri and usually lacks pseudospiniger chaetae. *Namanereis canariarum* **sp. nov.** and *Namanereis llanetensis* **sp. nov.** increase to 20 the total number of currently described species within this enigmatic genus. More than half of those species are adapted to live in groundwaters.

Keywords

Oligohaline, Stygobiont, volcanic region, water mine, wells

Introduction

The Canary Islands hypogean fauna is highly interesting by its remarkable richness in adapted species, and the endemic character of most of them (Culver and Pipan 2009). In addition, a large part of the Canarian troglobionts are biogeographic relicts or belong to taxonomic groups absent in most continental faunas (Naranjo et al. 2020). The knowledge on the Canary Islands hypogean fauna has much evolved in recent times, especially since the 1980s, when local biologists began to systematically survey terrestrial volcanic caves (Oromí and Martín 1990) and other subterranean environments, such as the mesovoid shallow substratum (MSS) (Medina and Oromí 1990), pyroclastic deposits (Oromí et al. 2018), and artificial mines (Naranjo et al. 2020). Currently, the Canary Islands are the richest volcanic region in the world in subterranean fauna, with up to 294 troglobionts and stygobionts (Oromí et al. in press; Naranjo et al. 2020). In fact, Cueva de Felipe Reventón (37 species) and Cueva del Viento-Sobrado (36 species), both in Tenerife, are the second and third caves with the greatest number of troglobiont species in the world ranking (Culver and Pipan 2009), while La Corona lava tube, in Lanzarote, is the fourth richest in anchialine species (Culver and Pipan 2009; Martínez et al. 2016). The first stygobiont annelid recorded in the Canary Islands was the polynoid *Gesiella jameensis* (Hartmann-Schröder 1974), described for Jameos del Agua anchialine cave; followed by the scalibregmatid *Speleobregma lanzaroteum* from Túnel de la Atlántida (Berthelsen 1986). The first stygobiont interstitial cave species described from the Canary Islands were the fauveliopsid *Fauveliopsis jameoquensis* and the nerillid *Leptonerilla diatomeophaga* from Jameos del Agua (Núñez et al. 1997). In the first two decades of the 21st century, studies of polychaetes in cave-dwelling environments intensified, both in Los Jameos del Agua and in submarine lava tubes of Tenerife (Cueva de los Cerebros), describing new nerilids, silids, scalibregmatids and protodrilids (Núñez et al. 2009; Worsaae et al. 2009, 2018, 2019; Martínez et al. 2013, 2016a, b). In contrast, in inland groundwater there are fewer species, mainly corresponding to amphipods of the genus *Pseudoniphargus* (Stock 1988; Sánchez 1989; Stokkan et al. 2018), three species of harpacticoid copepods from anchialine environments of Tenerife (Schminke 1971; Huys 1988) and a single annelid doubtfully identified as *Namanereis hummelincki* (*non* Augener, 1933), from inland brackish underground waters on Fuerteventura (Hartmann-Schröder 1988).

Polychaetes are mostly marine worms, characterized by their segmented body provided with chaetae (Read and Fauchald 2020). They cover some 9,000 species worldwide (Glasby 2008). The subfamily Namanereidinae, with the genera *Namanereis* and *Namalycastis*, is a monophyletic group with over 40 described species of nereidids adapted to live in low salinity habitats (Glasby et al. 2016), with some species that have even

colonized semi-terrestrial and subterranean environments (Solís-Weiss and Espinasa 1991; Glasby, 1999; Shoobs et al. 2016). The genus *Namanereis* currently contains about 20 valid species distributed from the tropics to high latitudes (Read and Bellan 2014; Conde-Vela 2017), almost exclusively occurring in intertidal and uplifted coastal areas, often far from the sea. Fourteen of the species of *Namanereis* are found in groundwater and hyporheic environments (Glasby et al. 2014; Conde-Vela 2017; Alves et al. 2018).

Recent surveys of freshwater aquifers through wells and water mines at the islands of Gran Canaria and Fuerteventura have yielded several individuals of *Namanereis* that could not be assigned to any known species (Fig. 1, see distribution). They likely belong to two species and show troglomorphic characters, such as depigmented epidermis and lack of eyes. Both species are described based on their morphological characters, since a previous molecular study with specimens from the Canary Islands have not been conclusive (Glasby et al. 2013; Shoobs et al. 2016).

Material and methods

A total of 20 individuals of *Namanereis* were collected from three localities: Los Llanetes water mine (27°59'12.63"N, 15°28'52.03"W, Valsequillo, Gran Canaria) (Fig. 1d), Fataga water mine (27°47'59.18"N, 15°35'12.57"W, Barranco de Fataga, Gran Canaria), and a well in Las Playitas (28°13'56.29"N, 13°59'10.41"W, Tuineje, Fuerteventura). Los Llanetes water mine is an artificial cavity excavated between slope debris and ravine alluvia, holding abundant troglobionts and stygobionts species (Naranjo et al. 2020). This mine is about 420 m above sea level on the east of Gran Canaria. The vegetation is composed of secondary shrub replacing the original thermophilic forests of *Pistacia atlantica* and *Olea cerasiformis*. The Fataga water mine is in the south of Gran Canaria, about 120 m a.s.l. The mine is excavated in ravine alluvia and has flooded sections with presence of the endemic stygobiont amphipod *Pseudoniphargus fontinalis* (Naranjo & Martín 2016). The specimens studied from the small coastal town of Las Playitas, at the east of Fuerteventura, near to Gran Tarajal, comes from an artificial brackish water well, excavated in a rural area at 14–18 m a.s.l.

The specimens were collected by hand and using meat baited traps, and preserved in 95% ethanol, except for one individual of *N. canariarum* sp. nov., which was fixed in 10% formaldehyde-seawater and preserved in 70% ethanol solution after manually protruding the pharynx. Parapodia from the anterior, mid, and posterior sections of the trunk were removed from individuals of the two species and mounted in semi-permanent microscopic slides using glycerine jelly. The morphological examinations were made with a compound Leica DMLB light microscope (LM) equipped with differential interference contrast (Nomarski). An Olympus DP70 camera was used to take digital images, whereas drawings were done using a camera-lucida drawing tube. The material was deposited in the collections of the Department of Animal Biology of the University of La Laguna (DBAULL), Museum of Natural Sciences of Tenerife (TFMC), and Museum & Art Gallery Northern Territory (NTM).

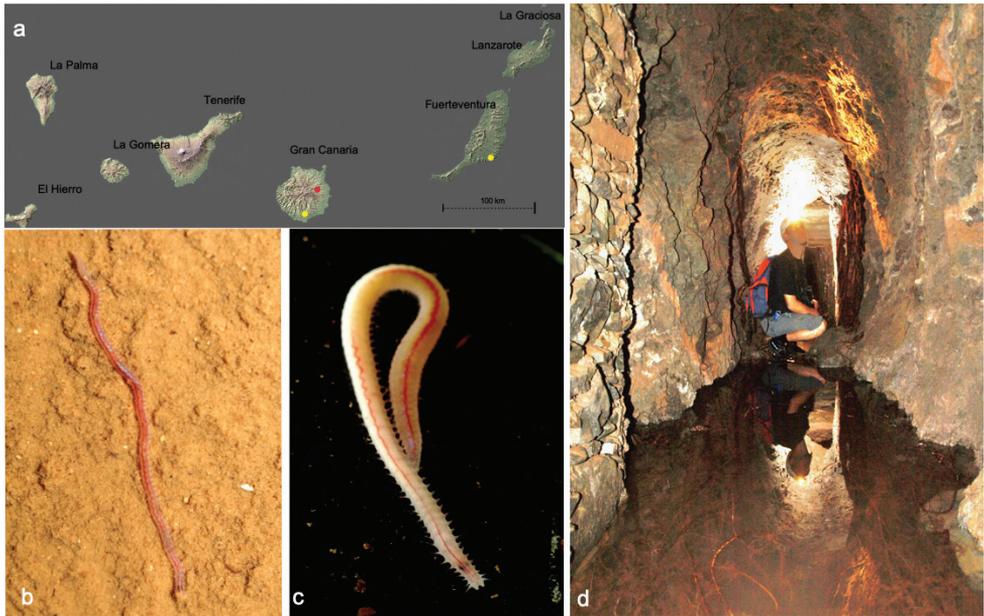


Figure 1. **a** Distribution in Canary Islands of *Namanereis canariarum* sp. nov. (yellow dot) and *Namanereis llanetensis* sp. nov. (red dot) **b** *Namanereis canariarum* sp. nov. live specimen, dorsal view **c** *Namanereis llanetensis* sp. nov. live specimen, dorsal view **d** Los Llanetes water mine (Valsequillo, Gran Canaria) type locality of *N. llanetensis* sp. nov.

Results

Family Nereididae Blainville 1818

Subfamily Namanereidinae Hartman, 1959

Type genus. *Namanereis* Chamberlin, 1919

Genus *Namanereis* Chamberlin, 1919

Namanereis Chamberlin, 1919. Mem. Mus. Comp. Zool. Harv. Coll., 48: 194

Type species. *Lycastis quadratriceps* Blanchard, 1849

Namanereis canariarum sp. nov.

<http://zoobank.org/B7836D85-CC52-4284-A34E-F1BA66BB8BC0>

Figs 1a, b; 2; 4a–d

Namanereis hummelincki.– Hartmann-Schröder, 1988: 181–182. *Non* Augener, 1933.

Namanereis sp. nov. 1 Glasby, Fiege & Van Damme, 2014: 28 (Table 1).

Type locality. Canary Islands, Fuerteventura, Las Playitas (28°13'55.42"N, 13°59'4.92"W) 14 m above sea level, brackish water well.

Type material. Holotype. TFMCBM-AN/240, coll. J. Núñez, 8-2-2002; 2 **Paratypes:** TFMCBM-AN/241, 2 spec., Fuerteventura, Las Playitas, Canary Islands, 28°13'56.73"N, 13°59'10.26"W, 18 m above sea level, coll. L. Santos & J.R. Docoito, 28-9-2011.

Additional material. Fataga water mine (Barranco de Fataga, Gran Canaria, (27°47'59.18"N, 15°35'12.57"W, 160 m above sea level), 12 spec. (6 spec. TFM-CBM-AN/242; 6 spec. DBAULL/2020), coll. P. Oromí & M. Naranjo, 6-12-2013.

Comparative material examined. Material identified by G. Hartmann-Schröder (1988) as *Namanereis hummelincki* from Canary Islands, Fuerteventura, well S. of Betancuria, 400 m a.s.l., coll. J.H. Stock, 4-5-1987, 8 ex ZMA VPol 2953 (now in Naturalis, Leiden).

Description. Holotype with 133 chaetigers, 46 mm long and 0.7 mm wide excluding parapodia and chaetae. Two paratypes, fragmented, one with 77 and the other with 88 chaetigers; one paratype female with gametes in the coelom.

Living individuals with depigmented epidermis, highlighting the red dorsal blood vessel over the fleshy pink coloured body. Body slender, with uniform width in the anterior and middle regions, abruptly tapering only near the posterior end; trunk convex dorsally and flattened ventrally (Fig. 1b).

Prostomium semi-circular in shape, slightly wider than long; cleft absent, shallow dorsal hollow present; two short conical frontal antennae, smooth, extending beyond tip of palpophore; palps broad and globose, biarticulated, with globular palpostyles; eyes absent (Fig. 2a). Tentacular segment as wide as first chaetiger, but half its length, bearing three pairs of short tentacular cirri, cirrophores inconspicuous, cirrostyles smooth and tapering. The longest pair of cirrostyles extends to reach the third chaetiger (Fig. 2a). Pharynx divided into a maxillary and an oral region, lacking paragnaths or papillae, but possessing a pair of delta-shaped jaws, dark, with only bifid terminal teeth (Figs 2a, b, 4a).

Parapodia with notopodial branch reduced to the inner acicula; neuropodium well-developed, acicular neuropodial ligule subconical (Fig. 2c, d) with prominent acicular lobes (Fig. 4b). Dorsal cirri acuminate, similar in length throughout the body and clearly surpassing the parapodial lobe; ventral cirri short and thin, being about a third of the length of the dorsal cirri (Fig. 2c, d). Notochaetae absent, neurochaetae arrangement as in Type A (Glasby 1999), although with slight modifications. Overall, less than 7 chaetae on each parapodium; supraneuroacicular chaetae normally includes 1 sesquigomph spiniger chaeta in the postacicular fascicle (Fig. 2h, i) and 1 heterogomph falciger chaeta in the preacicular fascicle throughout the whole body (Fig. 2e, k). Subneuroacicular chaetae normally includes 1 heterogomph pseudospiniger chaeta (Figs 2g, j; 4c) and 2–3 falciger chaetae in the preacicular fascicles (Figs 2f, l, 4d); less frequently 2 pseudospiniger chaetae, and exceptionally up to 3 falciger and no pseudospiniger chaetae might be found. In the posterior region, starting from chaetiger 60, pseudospiniger chaetae are generally longer, resembling spiniger chaetae. Supraneuroacicular falciger chaetae in chaetiger 10 with blades 4.90× longer than width of shaft head (4.7–5.0), finely serrated, about 30 teeth, length of the teeth decreasing towards

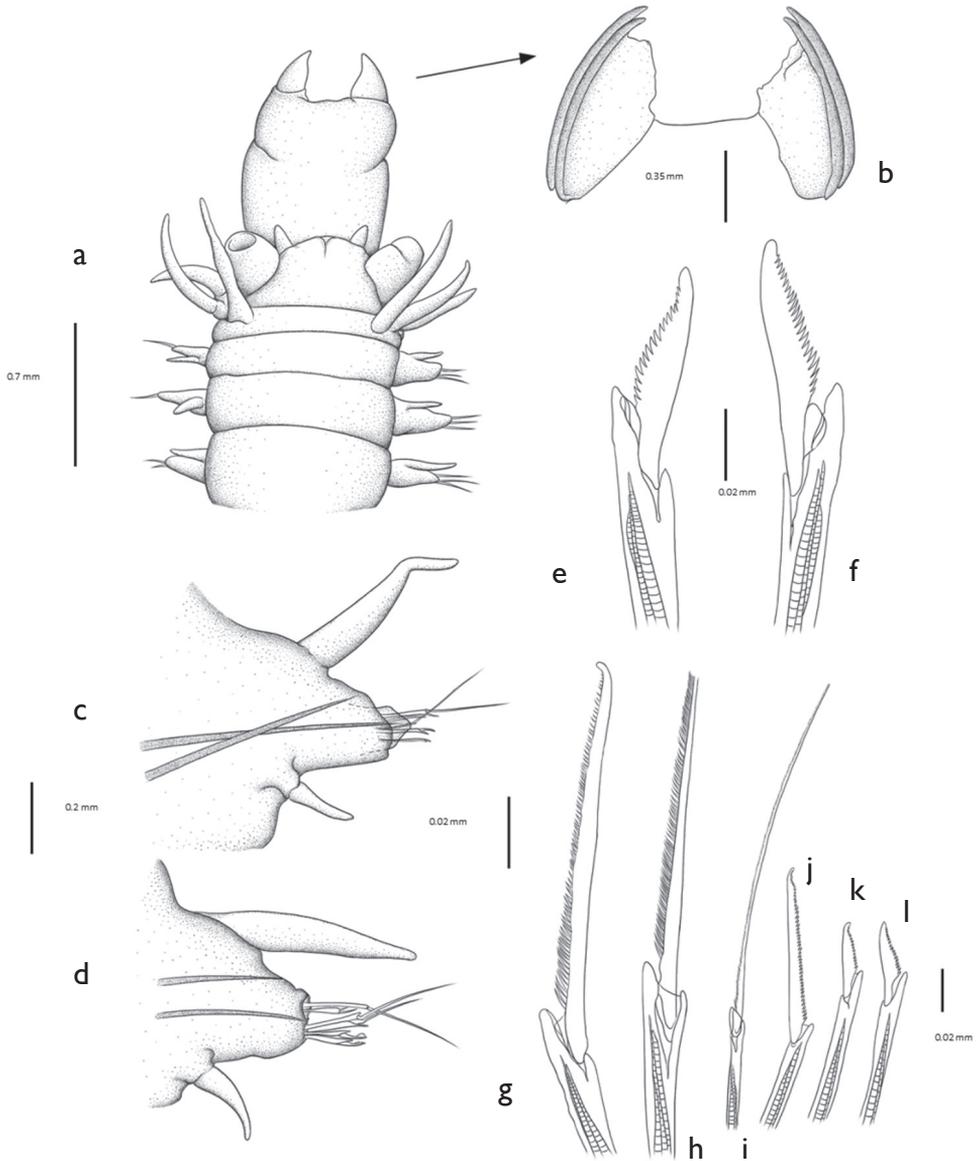


Figure 2. *Namanereis canariarum* sp. nov. **a** anterior end, everted pharynx, dorsal view **b** jaw pieces of the pharynx, frontal view **c** parapodium from chaetiger 10 **d** parapodium from chaetiger 60 **e** supraneuroacicular falciger, chaetiger 30 **f** subneuroacicular falciger, chaetiger 10 **g** subneuroacicular pseudospiniger, chaetiger 30 **h** supraneuroacicular spiniger, blade not fully shown, chaetiger 10 **i** supraneuroacicular spiniger, blade fully shown, chaetiger 10 **j** subneuroacicular pseudospiniger, chaetiger 10 **k** supraneuroacicular falciger, chaetiger 30 **l** subneuroacicular falciger, chaetiger 30.

the apex. Subneuroacicular falciger chaetae in chaetiger 10 with blades 5.5× longer than width of shaft head (5.2–5.7), finely serrated (similar to supraneuroacicular falcigers), length of the teeth decreasing towards the apex. Supraneuroacicular sesquiomph spiniger chaetae in chaetiger 10 with boss (vertical length of blade joint opposite collar) of the joint about 1.6× length of collar. Aciculae dark honey coloured. Pygidium with terminal anus, and two short ventrolateral anal cirri, slender and smooth.

Remarks. Morphologically, *Namanereis canariarum* sp. nov. belongs to the bifid-jaw group of *Namanereis*: this includes *N. araps* Glasby, 1997 (Arabian Peninsula), *N. cavernicola* (Solís-Weiss & Espinasa 1991) (Mexico, Caribbean side), *N. christopheri* Conde-Vela 2017 (Saint Vincent, Caribbean), *N. hummelincki* (Augener 1933) (Caribbean), *N. minuta* Glasby, 1999 (Caribbean), *N. llanetensis* sp. nov. (Canary Islands), *N. serratis* Glasby, 1999 (Caribbean), *N. socotrensis* Glasby, Fiege & Van Damme, 2014 (Socotra Archipelago) and *N. stocki* Glasby, 1999 (Caribbean). The new species can be distinguished from *N. cavernicola*, *N. minuta* and *N. stocki* by the number and size of teeth on the blades of the supraneuroacicular falciger chaetae. *Namanereis canariarum* has 20–30 moderate-sized teeth, compared to 35–80 very fine teeth in *N. cavernicola*, 50–60 fine teeth in *N. minuta*, and 9–14 moderate-sized teeth in *N. stocki*. Furthermore, *N. canariarum* has much shorter antennae and tentacular cirri than the three aforementioned species. On the other hand, *N. minuta* and *N. stocki* differ from *N. canariarum* in having four pairs of tentacular cirri. *Namanereis canariarum* has shorter tentacular cirri and smooth antennae, unlike *N. araps* that has faintly jointed and longer tentacular cirri, with the posterodorsal one extending back to chaetiger 5; antennae in *N. araps* slightly exceed the length of the prostomium. *Namanereis canariarum* is most similar to *N. hummelincki*, *N. christopheri*, and *N. llanetensis* sp. nov. However, *N. canariarum* differs from (1) *N. llanetensis* sp. nov. in the longer tentacular and parapodial dorsal cirri, as well as the absence of pseudospiniger chaetae; (2) from *N. christopheri* in the absence of long pseudospiniger chaetae, as well as the presence of shorter and most uniform spinulation in the falciger chaetae, with a longer blade with a greater number of denticles than in *N. canariarum*; (3) and from *N. hummelincki* by the shape of the jaws, in *N. canariarum* they are delta-shaped in the toothless area, and *N. hummelincki* is oblong in shape; as well as the greater number of pseudospiniger chaetae per parapodium in *N. hummelincki*. Finally, *N. canariarum* differs from *N. serratis* and *N. socotrensis* because these two species only have heterogomph falcigers setae in subneuroacicular fascicle.

Habitat. The type material was collected from a brackish water well at 14 metres above sea level and about 400 metres from the coastline, located on the south of Fuerteventura. Additional material comes from the southern sector of Gran Canaria, collected in a water mine about 140 m a.s.l.. The mine had waterlogged sections rich in plant roots and slime. The stygobiont amphipod *Pseudoniphargus fontinalis* and the diving beetle *Bidessus minutissimus* (Naranjo & Martín 2016) were also found in this locality.

Distribution. Type locality: Canary Islands, Fuerteventura, Las Playitas. Other specimens from Fataga water mine, Barranco de Fataga, Gran Canaria.

Etymology. The species name derives from the Canary archipelago, in plural for being found in two islands.

***Namanereis llanetensis* sp. nov.**

<http://zoobank.org/99E2991B-A2E2-4587-BF83-3CAFDA747571>

Figs 1a, c, 3, 4e, f

Namanereis sp. nov. 2 Glasby, Fiege & Van Damme, 2014: 28 (Table 1).

Type locality. Canary Islands, Gran Canaria, Los Llanetes water mine (Valsequillo) (27°59'12.63"N, 15°28'52.03"W) 415 m above sea level.

Type material. *Holotype*: TFMCBM-AN/243, coll. M. Naranjo, 8-6-2010. *Paratypes*: TFMCBM-AN/244, 1 spec., coll. M. Naranjo, 28-7-2010; TFMCBM-AN/245, 1 spec., coll. M. Naranjo, 12-8-2010; Los Llanetes water mine (Valsequillo, Gran Canaria), 1 spec., coll. M. Naranjo, 28-7-2010; 1 spec., coll. C. González, 12-8-2010.

Description. Holotype with 86 chaetigers, 34 mm long and 1.3 mm wide excluding parapodia and chaetae. Paratypes with 83–88 chaetigers, 28–35 mm long and 0.8–1.0 mm wide; one paratype female with gametes in coelom (Fig. 1c).

Living individuals with depigmented epidermis, highlighting the red dorsal blood vessel over the fleshy pink coloured body. Body uniform in width in anterior and middle region, tapering abruptly only in far posterior region; trunk convex dorsally and flattened ventrally (Fig. 1c).

Prostomium hexagonal, two times wider than long, without a cleft but with a shallow dorsal hollow; two conical frontal antennae, smooth, extending beyond the tip of palpostyle; palps broad and globose, biarticulated, with globular palpostyles; eyes absent (Fig. 3a). Tentacular segment as wide as first chaetiger, but slightly shorter in length. Three pairs of short tentacular cirri with indistinct cirrophores, and smooth tapering cirrostyles, the longest posterodorsal pair extending posteriorly to chaetiger 1–2 (Fig. 3a). Pharynx without paragnaths or papillae, but with a pair of brown, delta-shaped jaws, bearing bifid terminal teeth (Fig. 3b, c).

Parapodia with notopodial branch reduced to the inner acicula; neuropodium well-developed, acicular neuropodial ligule subconical (Fig. 3e, f). Dorsal cirri similar in length throughout the trunk, not surpassing the parapodial lobe; ventral cirri short, only about half as dorsal cirri in length (Fig. 3e, f). Notochaetae absent, neurochaetae as in Type A (Glasby 1999), with slight arrangement modifications; 7 chaetae in each parapodium. Supraneuroacicular chaetae normally include 2 sesquigomph spiniger chaetae in postacicular fascicles (Fig. 3k, n) and 1 heterogomph falciger chaeta in preacicular fascicles (Fig. 3g, i), less frequently 1 sesquigomph spiniger chaeta and exceptionally up to 3 and no heterogomph falciger chaetae; subneuroacicular chaetae normally include 2 heterogomph spiniger chaetae in postacicular fascicles (Fig. 3l, m) with long basal spinulation (Fig. 4e), and 2–3 heterogomph falciger chaetae in preacicular fascicles (Figs 3h, j, 4f), less frequently 1 heterogomph spiniger chaeta or none; exceptionally in anterior parapodia 4 heterogomph falciger and no spiniger chaetae; 1 heterogomph pseudospiniger chaeta and 3 heterogomph falciger chaetae were observed on a single anterior parapodium. No blade length gradation was observed in heterogomph falciger chaetae. Supraneuroacicular falciger chaetae in

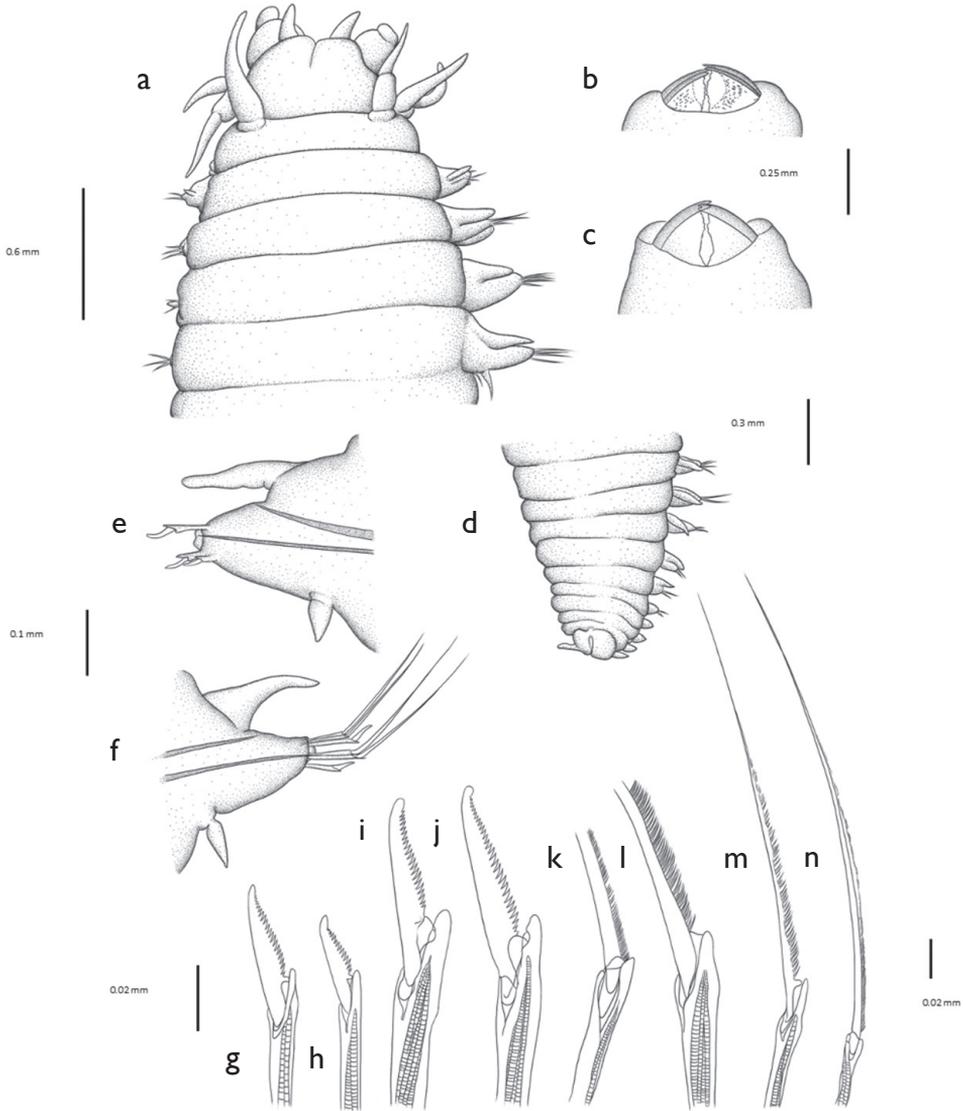


Figure 3. *Namanereis llanetensis* sp. nov. **a** anterior end, dorsal view **b** everted pharynx with jaws, dorsal view **c** jaws ventral view **d** posterior end, dorsal view **e** parapodium from chaetiger 3 **f** parapodium from chaetiger 60 **g** supraneuroacicular falciger, chaetiger 60 **h** subneuroacicular falciger, chaetiger 3 **i** supraneuroacicular falciger, chaetiger 3 **j** subneuroacicular falciger, chaetiger 3 **k** supraneuroacicular spiniger, blade not fully shown, chaetiger 3 **l** subneuropodial spiniger, blade not fully shown, chaetiger 3 **m** subneuroacicular spiniger, blade fully shown, chaetiger 10 **n** supraneuroacicular spiniger, blade fully shown, chaetiger 60.

chaetiger 10 with blades 3.8× longer than width of shaft head (3.6–4.0), with 18 finely serrated teeth (15–22), length of the teeth decreasing towards the apex. Subneuroacicular falciger chaetae in chaetiger 10 with blades 4.3× longer than width of

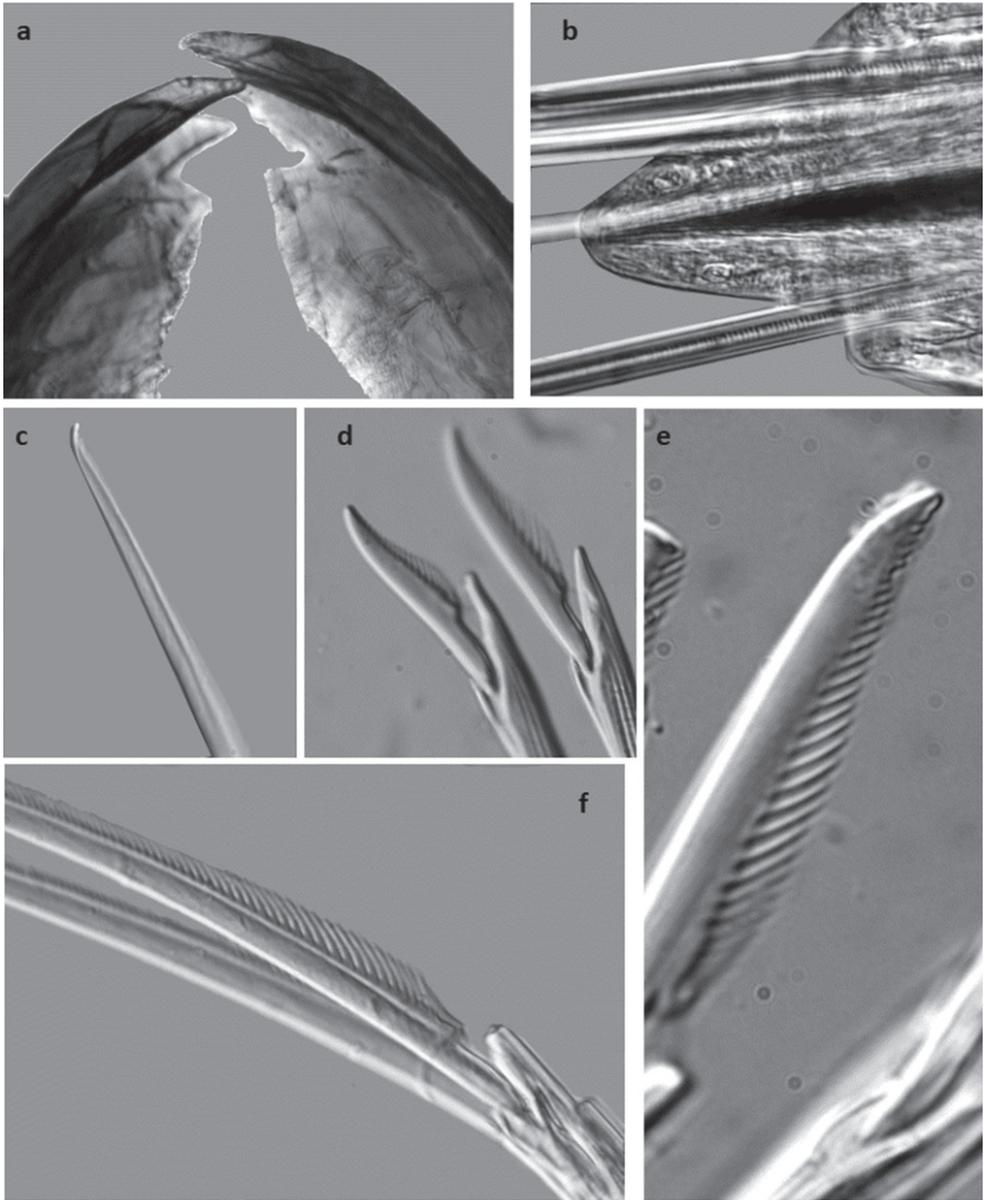


Figure 4. *Namanereis canariarum* sp. nov. **a** jaw pieces of the pharynx, ventral view **b** parapodium, detail of the acicular lobes **c** pseudospiniger blade tip **d** subneuroacicular heterogomph falciger, chaetiger 60. *Namanereis llanetensis* sp. nov. **e** Holotype, detail of the basal spinulation, hererogomph spiniger, chaetiger 10 **f** Holotype, detail of spinulation, subneuroacicular heterogomph falciger, chaetiger 10.

shaft head (4.1–4.5), and 16 (15–20), length of the teeth decreasing towards the apex. Supraneuroacicular sesquigomph spiniger chaetae in chaetiger 10 with boss (vertical length of blade joint opposite collar) about 3.0 times length of collar. Aciculae dark

honey coloured. Pygidium with terminal anus and two short ventrolateral anal cirri, slender and smooth (Fig. 3d).

Remarks. *Namanereis llanetensis* sp. nov. also belongs to the so-called bifid-jaw group of groundwater *Namanereis*, bearing only a single pair of terminal teeth in the jaws (Glasby et al. 2014). *Namanereis llanetensis* can be distinguished from all the above described species except *N. serratis* by the absence of long-bladed falcigers (= pseudospiniger chaetae) in the subacicular neuropodia; although, as reported above it can exceptionally occur in some anterior parapodia. The new species can be distinguished from *N. serratis* due to the greater number of teeth (and finer teeth) on the blades of the supraneuroacicular falcigers (only 6–11 coarse teeth in *N. serratis*).

Habitat. - Type material from a freshwater mine extending into an aquifer at 415 metres above sea level, located on the eastern sector of the island of Gran Canaria. Individuals were collected in the flooded sections of the mine, with abundant plant roots, were the stygobiont amphipod *Pseudoniphargus pedunculatus* was also found (Naranjo et al. 2014).

Distribution. Type locality: Canary Islands, Gran Canaria, Valsequillo, Los Llanetes water mine.

Etymology. The species is named after the type locality “Llanetes water mine”.

Discussion

The genus *Namanereis* has a wide distribution ranging from America to Oceania, may be resulting from vicariance after the fragmentation of Gondwana in Late Jurassic (Glasby et al. 2014). The marine ancestor of *Namanereis* group reached epigeal environments in the late Jurassic, whereas the widely distributed, marine ancestor of bifid-jawed *Namanereis* group colonized semiterrestrial and groundwater environments in the Cretaceous (Glasby et al. 2014). During posterior uplifting events, these ancestors were trapped and obligated to colonize the subterranean realm (Glasby et al. 2014). This hypothesis is consistent with the *Namanereis* colonization of the Canary Islands, where uplifting events and regression sea has been described (Meco et al. 2007). The Canary archipelago emerged in the Miocene and is located 100 km off the coast of Africa. Therefore, the Canary Islands had to be colonized by marine *Namanereis* ancestors from the African continent, ancient islands of Palaeo-Canaries (Carracedo 2011), or the Mediterranean basin.

Shoobs et al. (2016) found that the two new Canarian species together were sister to specimens identified as *N. hummelincki* from Montserrat, Caribbean. This is not surprising considering the general morphological similarity between the Caribbean *N. hummelincki* and *N. canariarum*. However, as we have shown here, material from Fuerteventura identified as *N. hummelincki* by Hartmann-Schröder (1988) does agree in detail with the specimens of *N. canariarum* collected both in Fuerteventura and Gran Canaria. Thus, the widely distributed Caribbean species *N. hummelincki* does not occur in the Canary Islands. As described above, the differences between *N. canariarum* and *N. llanetensis* are

in the relative length of tentacular and dorsal cirri (longer in *N. canariarum* sp. nov.), the number of teeth on the supraneuroacicular falciger (15–22 in *N. canariarum* and about 30 in *N. llanetensis*), and the presence of heterogomph pseudospingerous in *N. canariarum* which are essentially absent in *N. llanetensis*. In addition, although part of these differences might be explained by post-mortem contraction in the fixed material, the specimens of *N. llanetensis* are more robust and have fewer chaetigers than the those of *N. canariarum*, which are more elongated, filiform in appearance and have greater number of segments. Although both COI and histone H3 data for the two new species have been archived on Genbank, they are, at least partially contaminated, limiting the amount of comparative data available for a molecular analysis of the genus (Glasby et al. 2013).

In an ecological classification, obligate residents of subterranean habitats in aquatic systems are called stygobionts. Hence, *Namanereis canariarum* and *N. llanetensis* must be considered as stygobionts since they inhabit only freshwater aquifers of Fuerteventura and Gran Canaria. Furthermore, they also show troglomorphic characters, such as depigmented epidermis and eyelessness, in contrast with epigeal species of the same genus that have developed eyes and are well pigmented (Glasby et al. 2014). In addition, *N. canariarum* and *N. llanetensis* have bifid jaws that can be an adaptive character to subterranean habitats (Conde-Vela 2017). Glasby et al. (2013) suggest that broadly dished jaws reflect a possible shift toward a primarily deposit-feeding. In the water mines where *N. canariarum* and *N. llanetensis* occur, they can be observed wandering between submerged roots or moving in the mud, where it is supposed they feed on organic detritus and small invertebrates. *Namanereis* occurs in the eastern islands of the Archipelago, with the exception of Lanzarote and La Graciosa, where their scarce wells and water mines have not been explored. *Namanereis* species have never been found in the western islands of the Canary archipelago, which could be due to the low exploration of the aquifer, but these islands are also much younger than Gran Canaria and Fuerteventura, and the colonization of the *Namanereis* ancestor could take place in the early or medium Miocene (Glasby et al. 2014).

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First record of the genus *Graeconiscus* Strouhal, 1940 (Isopoda, Oniscidea, Trichoniscidae) in the Iberian Peninsula with the description of a new troglobitic species

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Abstract

Graeconiscus gevi **sp. nov.**, a new troglobitic terrestrial isopod (family Trichoniscidae, subfamily Haplophthalminae), is described. The specimens of the new species are found in the Cueva del Yeso III, in the province of Málaga (SE Spain). *Graeconiscus gevi* **sp. nov.** is closely related to *Graeconiscus thermophilus* (Çaglar, 1948), an oculate species from Turkey and some Eastern Mediterranean islands. The morphological differences between both species are discussed and illustrated by SEM images of specimens from Málaga and Cyprus. The studied material represents the first record of the genus *Graeconiscus* in the Iberian Peninsula.

Keywords

Iberian Peninsula, cave biodiversity, terrestrial isopods, Haplophthalminae, new species

Introduction

Within the family Trichoniscidae, the subfamily Haplophthalminae is characterized by presenting, among other characters, a complex tergal ornamentation that contrasts with a remarkable homogeneity in its sexual characters. For this reason its classification

has been based generally on body ornamentation (see Vandel 1960; Schmölzer 1965; Andreev 2004; Taiti and Bedek 2009).

So far, 14 species of Haplophthalminae belonging to the genera *Balearonethes*, *Haplophthalmus*, *Iberoniscus* and *Moserius* have been recorded in the Iberian Peninsula and the Balearic Islands (Legrand and Vandel 1950; Vandel 1952; Dalens 1977; Cruz and Dalens 1989; Reboleira et al. 2015). More recently, the genus *Baeticoniscus* (Garcia et al. 2020) has been described, with only one species.

In the framework of biospeleological studies which have been carried out in the south and southeast of the Iberian Peninsula, several specimens have been collected. Based on their morphological characters, we include them in the genus *Graeconiscus* Strouhal, 1940, known so far from the eastern Mediterranean islands, continental Greece, North Macedonia and western Turkey (Schmalfuss 2003; Alexiou and Sfenthourakis 2013) as well as from North Africa (Morocco) (Taiti and Rossano 2015) but not from the Iberian Peninsula.

The specimens collected from a cave in the province of Málaga, due to their specific combination of morphological features, have been included in a new species, *Graeconiscus gevi* sp. nov., which is described and fully illustrated in this article. It is also proposed to include the specimens recorded in Morocco by Taiti and Rossano (2015), tentatively identified as *G. thermophilus* (Çaglar, 1948), as part of the new species, since their small morphological differences in comparison to those of Spain do not seem sufficient to be considered as belonging to a different species.

Material and methods

Several specimens have been dissected under a stereomicroscope (Euromex NZ). For its morphological study, appendages, mouthparts and tergites have been mounted in micropreparations using glycerin or Faure liquor as appropriate, after treatment in some cases with Amann's lactophenol. The drawings have been made using a camera lucida attached to an optical microscope (Olympus CH30). The tergal structure of one specimen has been analyzed under a scanning electron microscope (Hitachi S-3400N). The final illustrations were prepared according to the method described by Montesanto (2015) and with the additional help of a drawing tablet (Wacom Intuos). The specimens of the new species have been directly compared to others of *G. thermophilus*, collected in Cyprus, which have also been examined under a scanning electron microscope.

Type locality and habitat

The Cueva del Yeso III (Fig. 1A, B) is a cave located in the municipality of Antequera (Málaga, Spain). The cave is 700 meters long and 61 meters deep and it is set in Triassic formations composed of large gypsum banks (Wallace and Berrocal 2002). The specimens were collected on bat guano.



Figure 1. Cueva del Yeso III of Antequera, Málaga, Spain **A** exterior of the cave **B** view of the interior (Photos provided by Baltasar Felguera, G.E.A., Campillos).

Depositories

MNCN: National Museum of Natural Sciences-Museo Nacional de Ciencias Naturales, Madrid, Spain. MBCN: Balearic Museum of Natural Sciences-Museu Balear de Ciències Naturals, Sóller, Mallorca, Spain. CLLG: Lluc Garcia personal collection, Sóller, Mallorca, Spain.

Results

Family Trichoniscidae Sars 1989

Subfamily Haplophthalminae Verhoeff, 1908

Genus *Graeconiscus* Strouhal, 1940

Graeconiscus gevi sp. nov.

<http://zoobank.org/60367B28-51C4-4B61-98D3-00CD706DB836>

Figs 2–4

Graeconiscus thermophilus. – Taiti and Rossano 2015: 2073, figs 3–5.

Etymology. Derived from G.E.V., the acronym in Spanish of the Villacarrillo Speleological Group, for its great contribution to the knowledge of the subterranean biodiversity of the Andalusian region.

Examined material. *Holotype*. SPAIN • 1 male; Málaga, Antequera, Cueva del Yeso III; ETRS89 UTM 30S 345702 4094826, 441 m a.s.l.; 27 Apr. 2008; Toni Pérez-Fernández leg.; MNCN 20.04/12093. *Paratypes*. Spain • 3 males, same data as holotype; MNCN 20.04/12094, MNCN 20.04/12095, MNCN 20.04/12096. 4 females, same data as holotype; MNCN 20.04/12097, MNCN 20.04/12098, MNCN 20.04/12099, MNCN 20.04/12100. 1 male, 3 females, same data as holotype; CLLG 153. 1 male, 2 females, same locality as holotype, 26 Sep. 2009; Toni Pérez-Fernández leg.; CLLG 185. 1 male, 3 females, same locality as holotype; 28 Sep. 2008; Toni Pérez-Fernández leg.; CLLG 183. 1 male, 2 females, same locality as holotype; 29 Mar. 2008, Toni Pérez-Fernández leg.; CLLG 144.

Non type material. Spain • 7 damaged specimens; same locality as holotype; 24 Oct 2009; Toni Pérez-Fernández leg.; MBCN 23370.

Comparison material. *Graeconiscus thermophilus*. Cyprus • 5 males, 3 females; Loutra Afroditis; 4 Feb. 2020; Spyros Sfenthourakis leg.; CLLG 582.

Diagnosis. A blind and unpigmented species of *Graeconiscus*. Head with central anterior tubercle bilobed; posterior row of tubercles with the central ones almost fused. Pereon-tergites 1–6 with four individualized rounded, swollen, tubercles (2+2) not reaching the pereonites hind margin. Seventh pereonite with two large paramedian rounded, swollen, tubercles not reaching the hind margin. Pleonite 3 with a single, large and swollen, transversal tubercle.

Description. Maximum size observed: 3.2 mm (female), 3 mm (male). Body unpigmented. Eyes absent. Contour regularly ovoid, without interruption between pereon and pleon (Figs 2A, 4A–D). Pereon tergites very convex, with epimera expanded towards outside. Pleon epimera directed backwards. Cephalon (Fig. 4B) with triangular frontal lobe, apically rounded, and almost quadrangular lateral lobes with rounded anterior margin; head with 1 large central bilobed tubercle and 2 accessories; maxillipedal segment with 4 tubercles, central ones almost fused. Pereon-tergites with 4 rounded tubercles (2+2), slightly longer than wide in tergites 1–4, larger and swollen in 5–6, without exceeding its hind margin; pereonite 7 with 2 large paramedian rounded tubercles and small rugosities in its anterolateral part. Pleonite 3 with single, large and rounded, transverse tubercle, wider than long (Fig. 4C, D). Telson basally trapezoidal, with straight hind margin. Uropods: exopod longer than endopod. First antenna (Fig. 2C) tri-segmented; last antennular article longest, with 3 aesthetascs. Second antenna (Fig. 2B): flagellum with 3 poorly distinct articles; basal article with 2 thin aesthetascs; second article with 3–4, thicker. Mandibles with strong molar teeth. Right mandible (Fig. 2G) with 1 free penicil near the *lacinia mobilis*; left mandible (Fig. 2H) with 2 free penicils. Maxillule (Figure 2E): external branch with 5+4 undivided teeth; internal branch with 3 penicils, external penicil twice larger than internal ones. Maxilla (Fig. 2F) with bilobed distal part; internal lobe with 14–15 sensillae; external lobe with 3–4 sensilla and fine and long hairs; internal lobe approximately twice as wide as external one. Maxilliped (Fig. 2D): endite with subconical distal penicillium provided with fine hairs and subapical seta; palp with 2 setae in their basal article; distal part triangular with numerous sensillae. Pereopods (see male sexual characteristics). Uropods: sympodite reaching posterior edge of pleotelson.

Male: Pereopod 1 (Fig. 3A, B) not modified. Pereopod 7 (Fig. 3C) without modifications. Pleopod 1 (Fig. 3D) exopod subtriangular with concave external margin from their apical third; endopod with thick distal part, conical, striated, with fine setae in the middle part. Pleopod 2 (Fig. 3E): exopod with basal part rectangular, posterior lobe narrow with rounded apex; endopod sharply narrowed from middle and very small apical seta.

Remarks. This new species is included in the genus *Graeconiscus* Strouhal, 1940 due to its tergal ornamentation, which is characterized by two transversal rows of tubercles on the cephalon, 2+2 tubercles on the pereon-tergites 1–6, two paramedian tubercles on the seventh pereonite and a single central tubercle on the third pleonite (Schmalfuss et al. 2004). Currently, a total of 12 species are included in this genus, most of them initially assigned to other genera (see Schmalfuss et al. 2004; Alexiou and Sfenthourakis 2013). Almost all of them were originally described from islands, or continental sites, in Greece. *G. caecus* (Vandel, 1958), *G. guanophilus* Schmalfuss, Paragamian & Sfenthourakis, 2004, *G. kournasenseis* Schmalfuss, Paragamian & Sfenthourakis, 2004 and *G. strouhali* (Vandel, 1958) were found on the island of Crete (Aegean Sea). *G. dryoperorum* (Vandel, 1964) was initially described from the island of Evia, in the Aegean; *G. liebegotti* Schmalfuss, 1981, from the island of Gioura, in the northern Sporades; *G. multicostatus* (Karaman, 1961), from

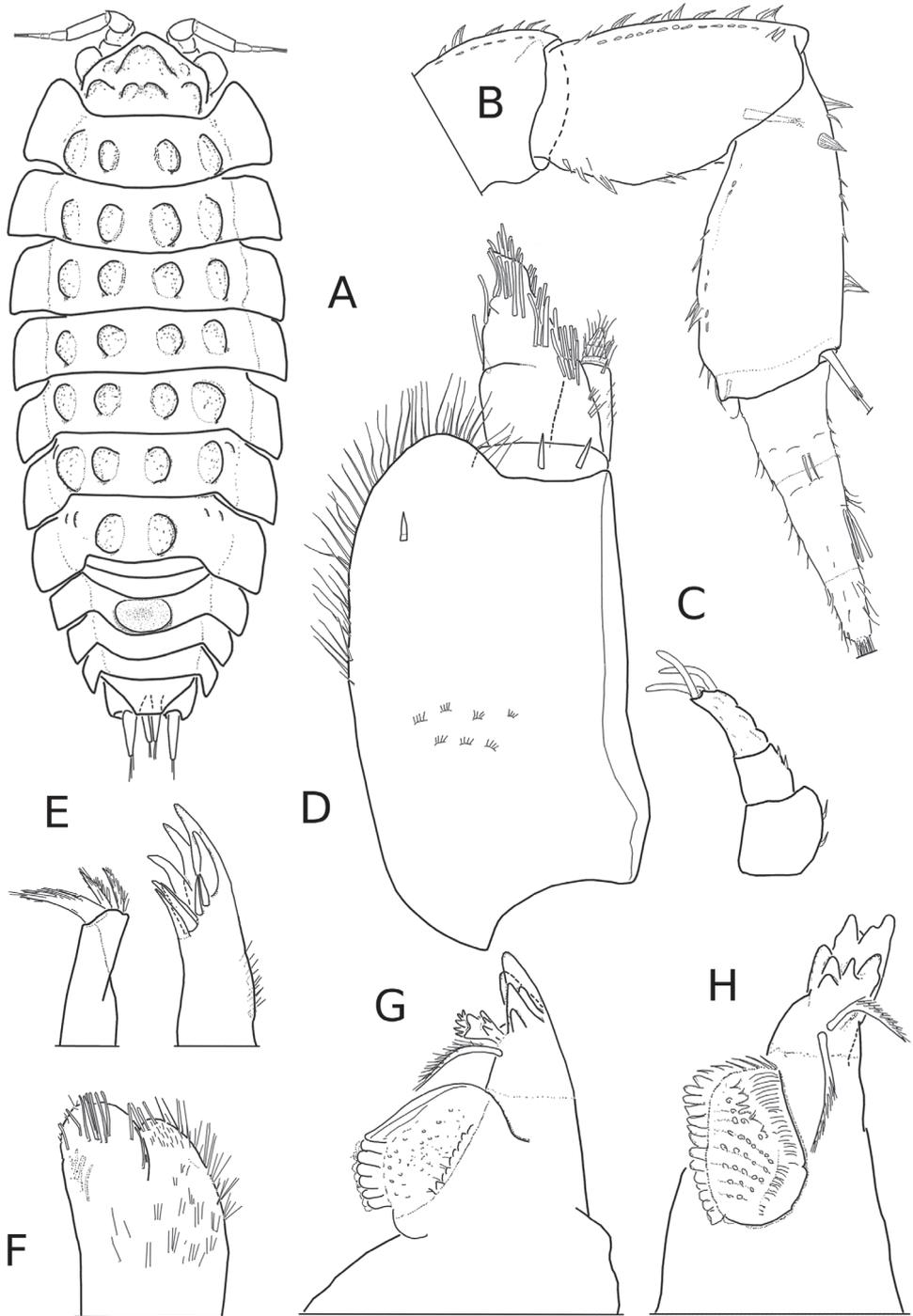


Figure 2. *Graeconiscus gevi* sp. nov. Male paratype **A** habitus, dorsal view **B** second antenna (apical cone omitted) **C** first antenna **D** maxilliped **E** first maxilla, distal portion of inner and outer endites **F** second maxilla, distal part **G** right mandible **H** left mandible.

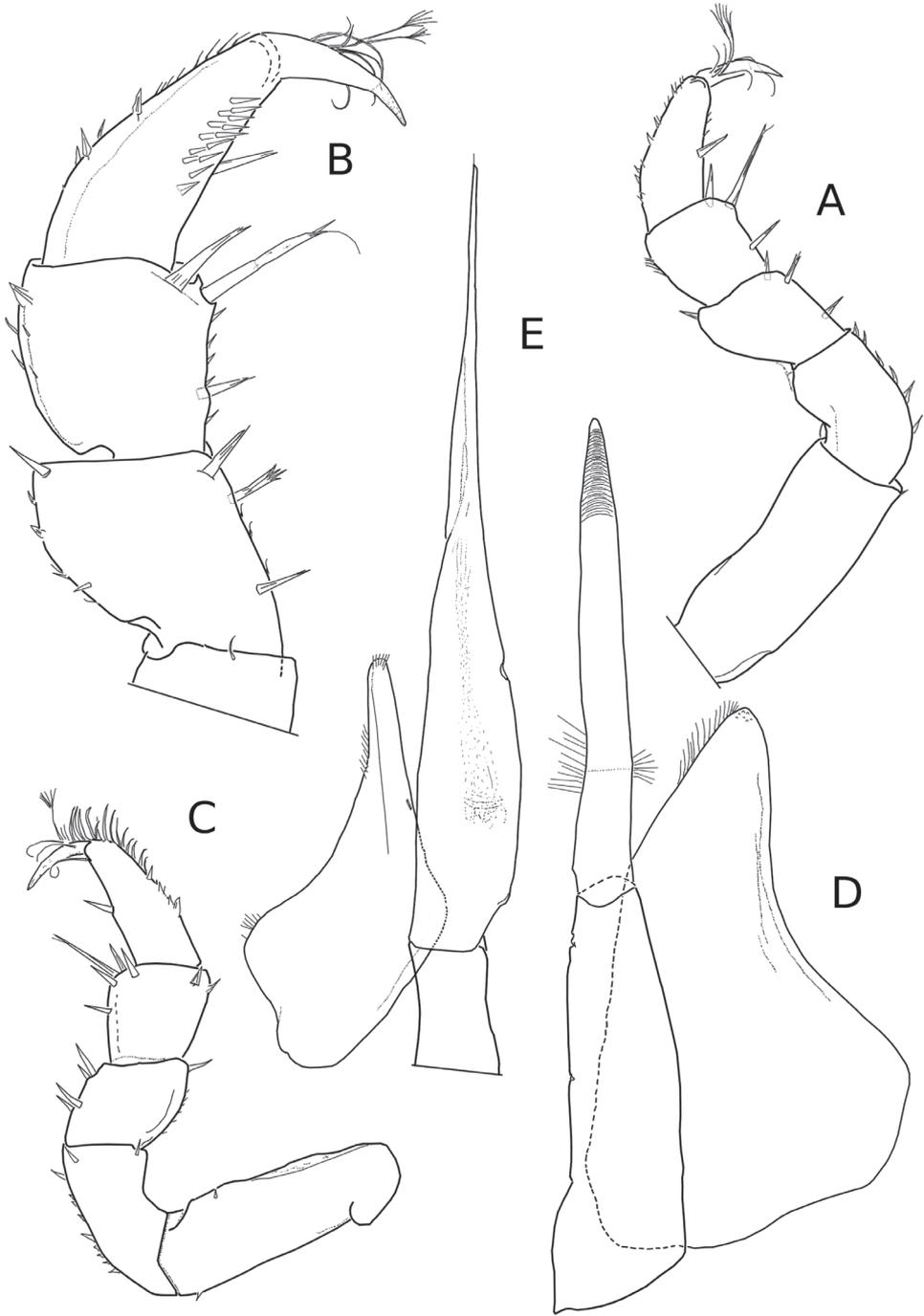


Figure 3. *Graeconiscus gevi* sp. nov. Male paratype **A** first pereopod **B** detail of meros, carpus, propodus and dactylus of the first pereopod **C** seventh pereopod **D** first male pleopod **E** second male pleopod.

the Titov Veles region, in North Macedonia; *G. paxi* Strouhal, 1961 and *G. tricornis* (Strouhal, 1936), from the island of Corfu; *G. strinatii* (Vandel, 1955) from the outskirts of Athens; *G. xerovunensis* (Strouhal, 1954) from NW Greece and, finally, *G. thermophilus* (Çaglar, 1948) was originally described from western Turkey and has been recorded in the southern Aegean islands, including Crete (Schmalfuss 2003; Alexiou and Sfenthourakis 2013).

Discussion

Graeconiscus gevi sp. nov. is morphologically closely related to *G. thermophilus*, which was initially included in the genus *Haplophthalmus* (Çaglar, 1948), and re-described by Strouhal (1963). The new species differs in that it presents a different pattern in the shape and dimensions of the tubercles of the pereon-tergites 1–7 and the single tubercle of the third pleonite (see Strouhal 1963 and Fig. 4E–H). In the central part of the cephalothorax *G. thermophilus* has two individualized tubercles whereas in *G. gevi* there is a single, large central tubercle, slightly divided at the apex. *G. thermophilus* presents four clearly individualized tubercles in the posterior part of the cephalon, while in *G. gevi* sp. nov. the two medians are almost fused into a single tubercle. The ornamentation of the pereon-tergites 1–7 is similar in both species, but in *G. thermophilus* the protuberances are narrower, elongated, laterally compressed, reaching the hind margin of the pereonites and, in the seventh one, surpassing it, while in *G. gevi* they are located in the middle part of the tergites. The tubercle of pleonite-3 is small and transversal in *G. thermophilus* and highly developed in *G. gevi*. Finally, *G. thermophilus* is an oculated and slightly pigmented species and with more setose integument, characters that are not present in the new species. The male pleopods, appendages and mouthparts are very similar in both species. According to the redescription of Strouhal (1963), *G. thermophilus* does not show a thick honeycomb tegumentary structure. However in the specimens studied, the integument presents a honeycomb basal structure similar to that of *G. gevi* sp. nov. and of other Haplophthalminae (Fig. 4H).

The examined specimens of *G. gevi* sp. nov. are almost identical to those described, and fully illustrated, by Taiti and Rossano (2015) from a cave in northern Morocco, which were tentatively identified as *G. thermophilus*. These specimens from North Africa only differ from those of southern Spain by smaller and well-rounded tubercles of the posterior border of the head and the pereonites, instead of the more swollen and larger ones of the new species. The tubercle of pleonite III also presents the same differences. These small morphological differences may be due to geographic variability and do not seem to be sufficient to assign the Moroccan specimens to a different species from that of southern Spain.

The genus *Graeconiscus* was so far unknown in the Iberian Peninsula. Its presence in localities of the western Mediterranean (north Morocco and southeast Spain), contrasts with its apparent cantonment in southeastern Europe, some eastern Mediterranean islands and the Marmara region of Turkey.

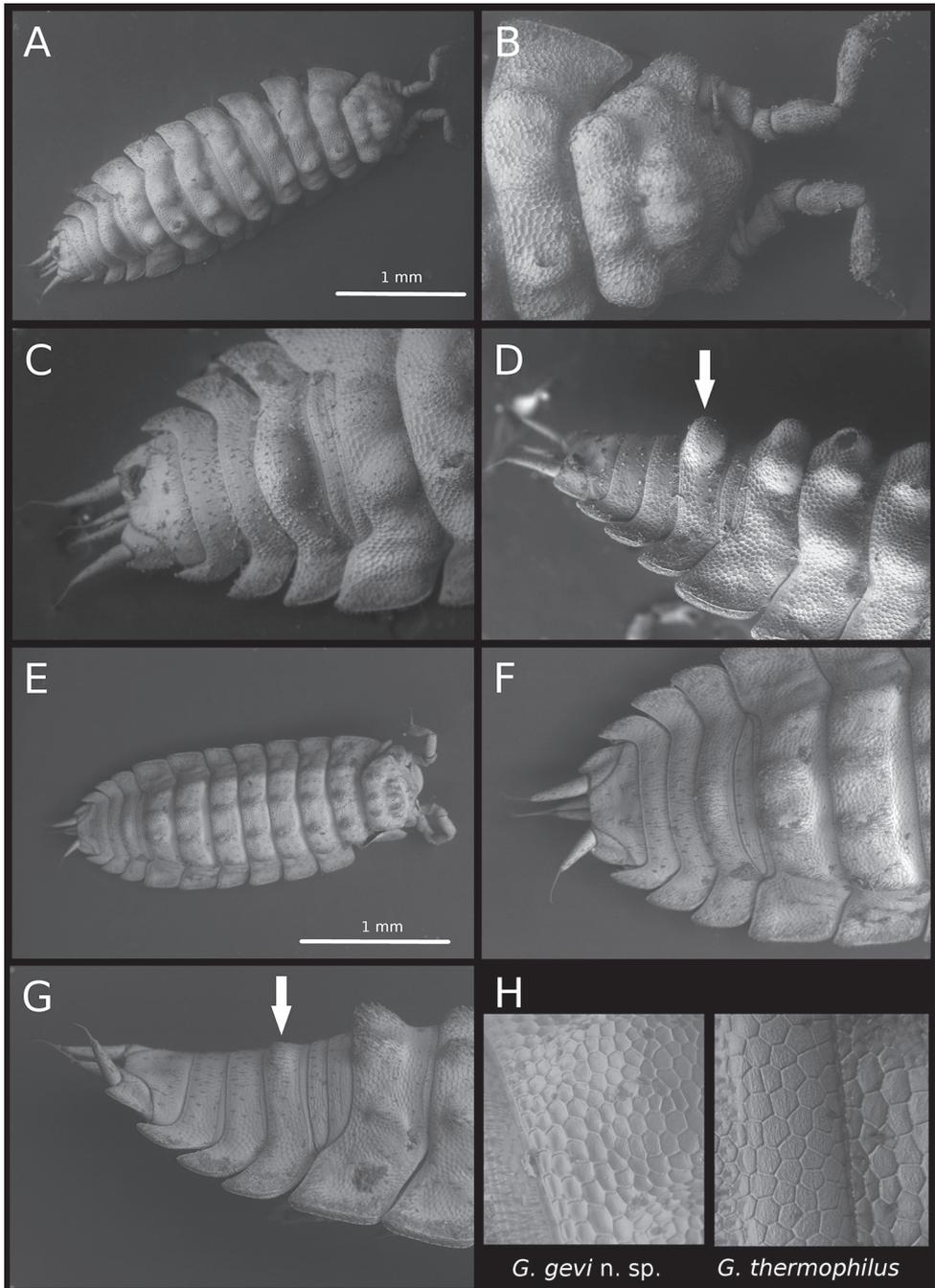


Figure 4. *Graeconiscus gevi* sp. nov., male paratype **A** dorsal view **B** cephalon, dorsal **C** last pereonite, pleon and pleotelson, dorsal **D** last pereonites, pleon and pleotelson, lateral view (arrow points the tubercle of third pleon-tergite) **E–G** *Graeconiscus thermophilus*, male specimen from Cyprus **E** dorsal view **F** last pereonites, pleon and pleotelson **G** last pereonite, pleon and pleotelson, lateral view (arrow points the tubercle of third pleon-tergite) **H** tegumentary basal structure (left *G. gevi* sp. nov.; right, *G. thermophilus*).

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Let research on subterranean habitats resonate!

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Abstract

Whereas scientists interested in subterranean life typically insist that their research is exciting, adventurous, and important to answer general questions, this enthusiasm and potential often fade when the results are translated into scientific publications. This is because cave research is often written by cave scientists for cave scientists; thus, it rarely “leaves the cave”. However, the *status quo* is changing rapidly. We analysed 21,486 articles focused on subterranean ecosystems published over the last three decades and observed a recent, near-exponential increase in their annual citations and impact factor. Cave research is now more often published in non-specialized journals, thanks to a number of authors who are exploiting subterranean habitats as model systems for addressing important scientific questions. Encouraged by this positive trend, we here propose a few personal ideas for improving the generality of subterranean literature, including tips for framing broadly scoped research and making it accessible to a general audience, even when published in cave-specialized journals. Hopefully, this small contribution will succeed in condensing and broadcasting even further the collective effort taken by the subterranean biology community to bring their research “outside the cave”.

Keywords

Bibliometric, Cave science, Citation analysis, Impact Factor, Jargon, Model organism, Natural laboratory, Scientific progress, Scientific writing, Temporal trend in citations

The model systems' roulette

Whether it is about birds or bugs, ants or antelopes, and no matter their ecology, systematics, or sexual behaviour, natural scientists tend to fall in love with the systems they study. This is nothing surprising considering how subtle and complex some eco-evolutionary patterns are, demanding the personal involvement of those seeking to unravel them. As this engagement increases, the distinction between work and passion often fades, promoting the idea of the stereotypical Stakhanovist scientist working tirelessly in the lab without realizing that the hours pass by. This hardworking attitude has blinded many scientists to the point of prioritizing their career over personal development and time with friends and family (Woolston 2017; Maestre 2018). Natural scientists might even take this engagement one step further, as the curiosity of a child, the passion for nature and collection, or simply the willingness of being outdoors is behind many successful careers. Have you ever taken advantage of a walk around your house or your family holidays to collect a few samples? Well, evidence suggests that you are not alone (Fontaneto et al. 2012).

Since most natural scientists share this very same passion for the natural world, how to explain the uneven impact of their research as individuals (Sinatra et al. 2016)? Well, different scientists concentrate their research efforts on different model systems (Ankeny and Leonelli 2011). And model systems are like a box of chocolate: *you never know what you're gonna get*. However, knowing the literature and playing well your cards may help to pick exactly that cherry-flavoured chocolate that you're dying for.

Selecting a natural organism or system might be seen as a trade-off between subjective features making it appealing to study (aesthetic characteristics, peculiar adaptations, etc.) and objective features making it a good model (ease to raise in the lab, generation time, genome size, etc.). And since many of these features are not obvious when selecting a new model organism (Hedges 2002; Maher 2009; Alfred and Baldwin 2015), we cannot deny a certain role of luck in this choice when, for example, a favourite organism turns out to be ideal to tackle an important question or to develop a new method. For example, the status of *Arabidopsis thaliana* as an anonymous flowering plant or of *Caenorhabditis elegans* as just-another-round-worm radically changed when pioneering researchers turned them into cutting-edge model systems in evolutionary biology (Mitchell-Olds 2001; Kaletta and Hengartner 2006). And while the love for a cavefish from Mexico probably came first, is the discovery that it can help curing type 2 diabetes that featured it on the front cover of *Nature* (Riddle et al. 2018).

Cave biologist as prisoners in the cave

Have subterranean biologists picked a tasty chocolate too? There are plenty of arguments suggesting that caves are amongst the appealing model systems (Itescu 2019). Humans' fascination for caves traces so deep in time that it is intertwined with the evolutionary history of *Homo sapiens*. Since the dusk of humanity, communities of hunter-

gatherers have found shelter in the darkness of caves (Granger et al. 2015). Caves were the places where we buried our dead (Sealy 2006), accomplished rituals (Moyes 2012), and expressed our very first artistic manifestations (Valladas et al. 2001). Plato's Myth of the Cavern, Jules Verne's *Journey to the Center of Earth*, and even the overrepresentation of caves in modern cinema (Figueiredo 2013) are just a few examples illustrating how the underground world became a colliding point of several archetypical ideas forming the collective identity of our species (Campbell 1949).

At some point, human curiosity took this ancestral fascination one step further. This is how geologists turned anthropomorphic rocks into speleothems, taxonomists re-named puppet-dragons as *Proteus anguinus* (Aljančič 2019), and hydrologists explained Biblical miracles (*Exodus* 17: 1–7) as artesian wells (Owen and Fensham 2016). As reason prevailed upon mythology, caves became the arena for debating scientific ideas and ultimately good model systems for understanding the outside world (Poulson and White 1969). Yet, while we typically insist that our research is exciting, adventurous, and important to answer cutting-edge questions (Juan et al. 2010; Sánchez-Fernández et al. 2018; Mammola 2019; Mammola et al. 2019, 2020), this potential is often lost when the results are translated into scientific publications. Too often, the generality of our results remains unexpressed insofar as cave research is written by cave scientists for cave scientists. In other words, it rarely leaves the cave.

Escaping from the cave

However, this *status quo* is changing. Over the last decade or so, we have witnessed how more and more cave-based research resonates outside our specialized community. To show this, we here analysed the citations and impact factor of articles focusing on subterranean ecosystems, using a database of 21,486 research articles published between 1991 and 2019 (full details on data collection are in Martínez and Mammola 2020). We observed how, recently, there has been a steady increase in the annual average citations that cave-based papers receive (Figure 1a) and in the average impact factor of the journals in which they are published (Figure 1b). This pattern is seemingly due to a greater number of scientists publishing in general journals, given that the average citation over time is not increasing, but rather fluctuating, when considering papers published in cave-specific journals only (Figure 2).

A quick scrutiny of these highly cited papers shows that most of them used caves as systems to address general questions. The peculiarities of caves as simplified model systems in ecology and evolution have been summarized elsewhere (Mammola 2019), including their discrete nature, the partially stable conditions, as well as the presence of few, highly specialized organisms. Interestingly, some of these properties make caves useful in a broad range of scientific areas. The stable microclimatic conditions, for example, favour the preservation of fossils (Berger et al. 2015; Harvati et al. 2019) and makes caves natural laboratories for paleoclimatic reconstructions and global change biology studies (Yuan et al. 2004; van Hengstum et al. 2018; Mammola et al. 2019;

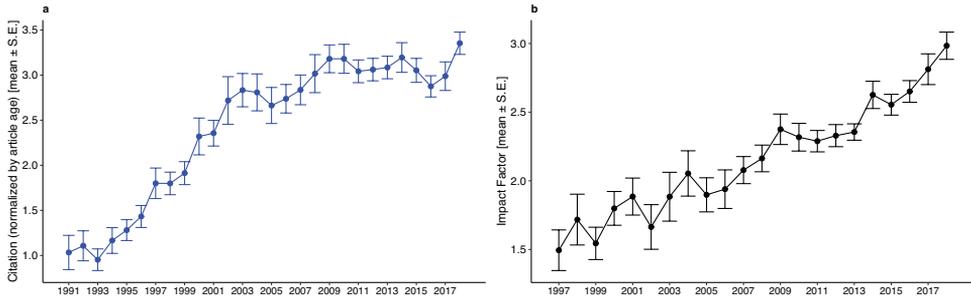


Figure 1. Variations in citations and impact factor of papers focused on subterranean systems over time. **a** Average \pm standard error number of Web of Science citations to articles. Citation counts are normalized by the year of publication **b** Average \pm standard error Impact Factor of the journals in which the papers are published. Graphs are based on a database of 21,486 research articles focused on caves and other subterranean habitats published between 1991 and 2018 (Martínez and Mammola 2020). The yearly Impact factor of journals is based on the periodical reports by the Journal Citation Reports of Clarivate. For this graph, the year 1997 was chosen as a starting point because around this date the use of Impact Factor started to become widespread (Archambault and Larivière 2009). Note also that the overall Impact Factor of scientific journals increased over the last 21 years, a feature that may have partly inflated this trend.

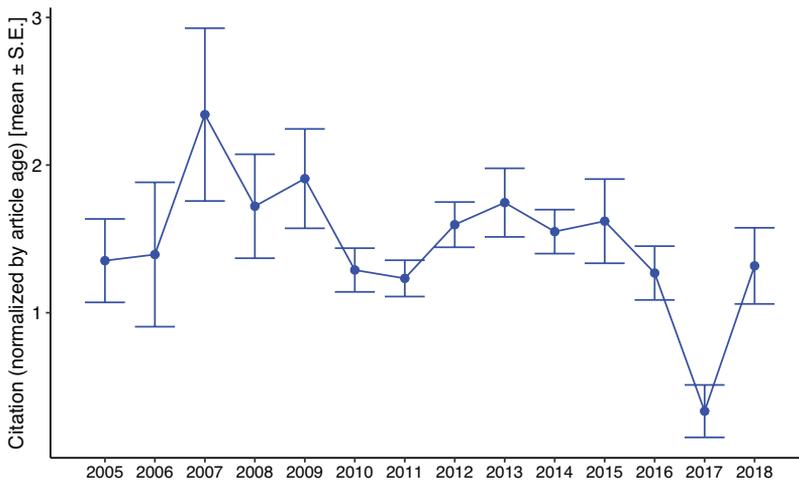


Figure 2. Variations in citations over time in papers focused on subterranean systems published in specialized journals. The average \pm standard error number of Web of Science citations is based on a subset of articles published in *Acta Carsologica*, *International Journal of Speleology*, *Journal of Cave and Karst Studies*, and *Subterranean biology* ($n=969$). Note that prior to 2005, no data was available for these journals in Web of Science.

Pipan et al. 2019). The stability of the underground is so even to cosmic radiation, making old mines as unique windows into quantum mechanics (Wolfendale 1968; Curceanu et al. 2017). For the very same reason, lava tubes are projected to host our

first Martian and Lunar colonies (Sauro et al. 2020), whereas, in the domain of exobiology, cave microbiological studies are expected to bring important clues on the origin of extraterrestrial life (Northup et al. 2011; Popa et al. 2011). Not to mention, coming back on Earth, the role that cave organisms can play in the realm of medicine (Riddle et al. 2018; Yoshizawa et al. 2018) and pharmaceuticals (Cheeptham et al. 2013; Ghosh et al. 2017; Genilloud 2018).

A return to the cave

Notably, darkness, isolation, and weirdness—the properties that constitute caves as excellent models to address timely questions in modern science—were also those that amazed our ancestors, symbolically rooting caves deeply in our human nature as a representation of our myths, tales, and pop-culture memes (Campbell 1956; Bassie-Sweet 1996; Ustinova 2009). Therefore, and even at the risk of over-romanticising these model systems, we argue that caves not only hold some of the clues of our past; but also, if used wisely, may help to unlock some of our hidden future scientific enigmas. However, to speak nature's most intimate secrets, caves need to be asked the right questions.

Encouraged by the inherent peculiarities of caves, we might have forgotten the importance of trying to address broad questions with our research, favouring the isolation of our research community and increasing our intellectual inbreeding. We believe that being aware of this potential is a fundamental step to frame broad-in-scope subterranean research (Mammola et al. 2020), regardless of the journal in which it will end-up published. Inspired by the writer and philosopher Umberto Eco (1997), we propose a few bullet-point ideas for improving the generality of the literature on subterranean habitats, including both tips for framing broad-scoped research and for writing texts accessible to a general audience (Box 1). These are just personal ideas, sometimes based on literature published on caves, sometimes borrowed from other disciplines, collected here

Box 1. Ideas for making research on subterranean habitats to resonate.

1. Try to identify general questions that are scalable to other systems (Mammola et al. 2020). Greeks brought philosophy into caves: we can also introduce our field into them.
2. Read and cite as many non-cave papers as possible. We say, baby, take a walk on the *bright side*.
3. It is advantageous to collaborate with non-cave scientists. They might even come up with good ideas...
4. Make your text understandable to a general audience (Plavén-Sigraý et al. 2017; Barnett and Doubleday 2020). Facultative troglaphiles, troglroxenes, and even accidental cave scientists should be able to grasp your wisdom (Martinez and Mammola 2020).
5. Don't overemphasize your findings with superlatives and exaggerations (Mammola 2020). By doing so, your research will turn out unique, remarkable, and ground-breaking!!!
6. When discussing the importance of your findings, don't appeal to authority. We say so.
7. Don't be jealous: data-sharing only brings you benefits (Piwowar et al. 2007; Piwowar and Vision 2013; Colavizza et al. 2020). Even the data supporting this study will be available *tomorrow* from the corresponding author upon a reasonable request.
8. And, well, don't forget to come back to good old cave literature from time to time. There is still a lot of wisdom in the Rock Art of our ancestors.

without any imperative intention. We do not want to tell anyone how to proceed, but rather encourage a debate around these topics with the ultimate hope of supporting the ongoing transition of our research from the darkness of caves out to the lighted world.

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Data and R code to generate the plot are available in Figshare (<https://doi.org/10.6084/m9.figshare.13129604>). Raw data can be obtained from the Web of Science using the search query and data cleaning procedure detailed in Martínez and Mammola (2020).

A.M. did the search on the Web of Science. S.M. plotted the graphs. Then, the idea came along, and both authors wrote and approved the text together.

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The Wynberg Cave System, the most important site for cave fauna in South Africa at risk

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Abstract

The Wynberg Cave System, located on the Cape Peninsula, represents one of the most significant sites of cave fauna in southern Africa. However, the continuous increase in cave visitation is severely impacting the system as evidenced by graffiti, the trampling and destruction of cave habitats and even a reduction in the sizes of bat colonies. In October 2019, the Wynberg Cave System was visited by a group of scientist, who discovered unregistered troglomorphic species. This, subsequently increased the number of troglóbites occurring in the system to 19, which likely means that this system has the potential to become the first hotspot of subterranean biodiversity in Africa. Protecting the Wynberg Cave System is therefore of great importance. Here, we propose short and long-term strategies that include educating local communities on the importance of conserving caves and installing gated entrances.

Keywords

Cave protection, Invertebrates conservation, Subterranean biodiversity

The caves from the Cape Peninsula in South Africa are associated with quartzite rocks, occurring at altitudes ranging from 450 m to 750 m asl. The region is characterized by a temperate climate with hot and dry summers and cold and humid winters (Marker and Swart 1995). Inside the caves, the average temperature is approximately 10 °C (Sharratt 1998). Caves within Table Mountain National Park are at higher altitudes and vary in morphology, but are predominantly vertical with passages of different sizes. These passages were formed by the removal of debris from cracks and joints by the action of water (Marker and Swart 1995). The caves such as Bats, Climbers, Giants, Hangman, Metro, Smugglers and Wynberg, along with other smaller caves, form the largest cave system in the region (more than 1.2 km in length), which is referred to as the Wynberg Cave System (WCS; CPSS 2017).

The Cape Peninsula is a biodiversity hotspot, in the heart of the Cape Floristic Region, with the highest concentration of plant species in the world (Forest et al. 2007), presenting a remarkable set of endemic taxa of epigeal fauna and flora (Picker and Samways 1996; Trinder-Smith et al. 1996). Similarly, the caves harbour several endemic invertebrates, substantially contributing to the biological importance and conservation priority of this area (Sharratt et al. 2000). Studies on the cave's ecology and conservation were carried out mainly by Picker and Samways (1996), Sharratt (1998) and Sharratt et al. (2000), which generated a comprehensive list of references regarding the cave fauna (e.g. Attems 1928; Lawrence 1931, 1932, 1935, 1964, 1984; Dybas 1960; Grindley 1963; Cook 1991; Griswold 1987, 1990) and added important information on the ecology and distribution of many subterranean taxa. A more recent study focused on the ecology of cave invertebrates (Giribet et al. 2013).

The WCS hosts remarkable cave fauna, especially when considering the endemism and rarity of some species. Sharratt et al. (2000) listed 13 cave-restricted species occurring in the Table Mountains quartzite caves, plus another 72 non-troglobitic invertebrate species. All troglobitic species mentioned by these authors from the WCS are Cape Peninsula endemics. Some of these species are considered as highly specialized Gondwanan relicts and many can be considered rare. Such cave adapted species account for 12% of the total endemic invertebrate fauna of the Cape Peninsula (Picker and Samways 1996).

The cave-restricted species occurring in the WCS include *Peripatopsis alba* Lawrence, 1931 (Onychophora: Peripatopsidae) (Fig. 1A); *Spelaeogriphus lepidops* Gordon, 1957 (Spelaeogriphacea: Spelaeogriphidae) (Fig. 1B); *Paramelita capensis* (Barnard, 1916) (Amphipoda: Paramelitidae) (Fig. 1C); *Trichoniscus tabulae* (Barnard, 1932) (Isopoda: Trichoniscidae) (Fig. 1D); *Harpethrix caeca* Lawrence 1962 (Diplopoda: Dalodesmidae) (Fig. 1E); *Habnia* sp. (Araneae: Hahniidae) (Fig. 1F); *Crozetulus scutatus* (Lawrence, 1964) (Araneae: Anapidae); *Leptyphantus rimicola* Lawrence, 1964 (Araneae, Linyphiidae); *Purcellia argasiformis* (Lawrence, 1931) (Opiliones: Pettalidae) (referred in Sharratt et al. 2000, as *Speleosiro argasiformis*) (Fig. 1G); *Speleomontia cavernicola* Lawrence, 1931 (Opiliones: Triaenonychidae) (Fig. 1H); *Selachochthonius cavernicola* (Lawrence, 1935) (Pseudoscorpiones: Pseudotyranochthoniidae) ((referred in Sharratt et al. (2000), as *Cthoniella* [sic.] *cavernicola*); Japygidae sp.n. (Diplura – probably erroneously referred to as Dermaptera in Sharratt et al. 2000) (Fig. 1J); *Anisocampa leleupi*

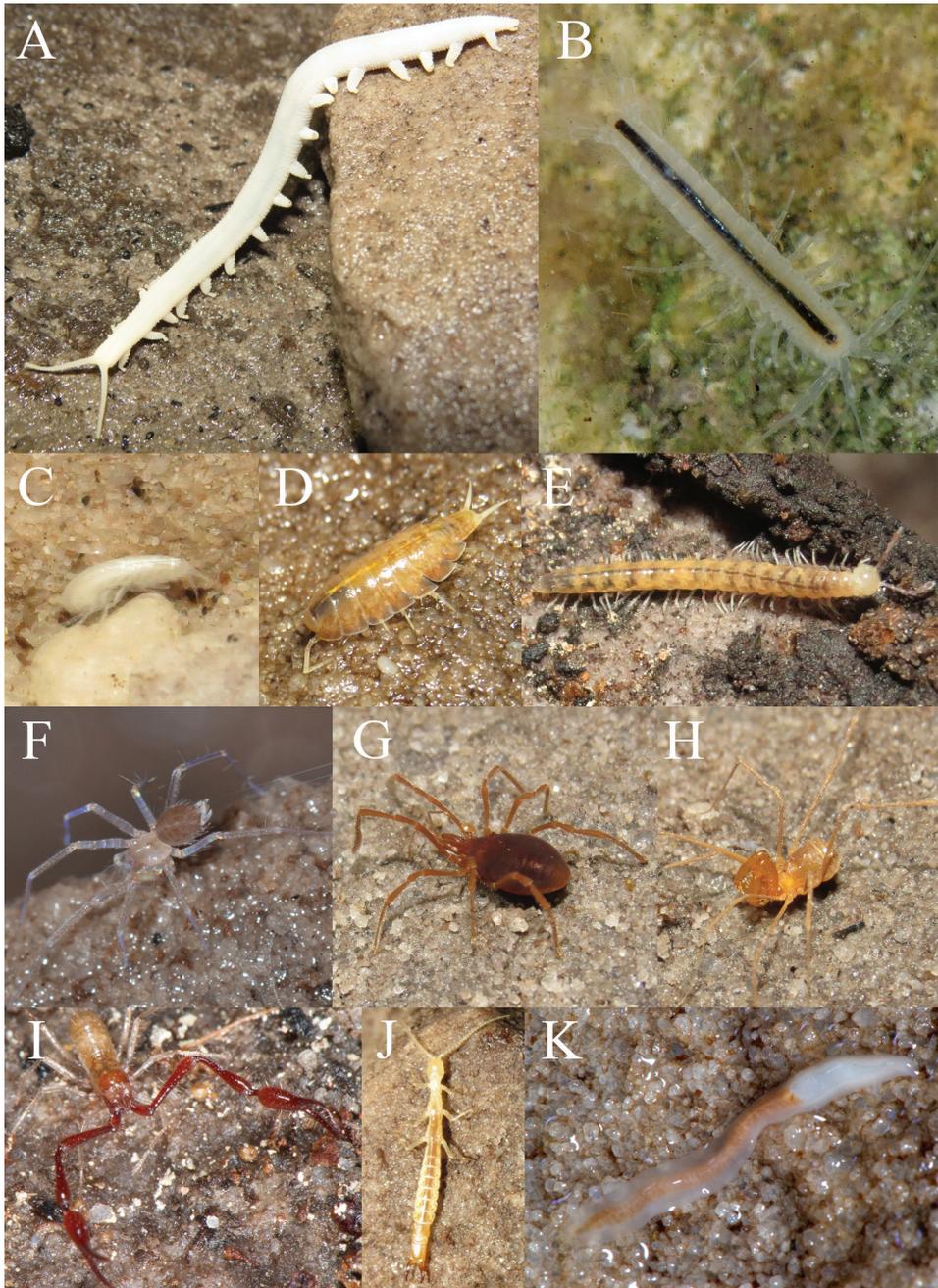


Figure 1. Wynberg Cave System and some troglomorphic taxa: **A** *Peripatopsis alba* (Onychophora: Peripatopsidae) **B** *Spelaeogriphus lepidops* (Spelaeogriphacea: Spelaeogriphidae) **C** *Paramelita capensis* (Amphipoda: Paramelitidae) **D** *Trichoniscus tabulae* (Isopoda: Trichoniscidae) **E** *Harpethrix caeca* (Diplopoda: Dalodesmidae) **F** *Hahnia* sp. (Araneae: Hahniidae) **G** *Purcellia argasiformis* (Opiliones: Pettalidae) **H** *Speleomontia cavernicola* (Opiliones: Triaenonychidae) **I** *Gymnobisium inukshuk* (Pseudoscorpiones: Gymnobiidae) **J** Japygidae sp.n (Diplura) **K** *Prorhynchus* cf. *brincki* (Platyhelminthes: Prorhynchida). Photographs **A, C–E, G, H, J** from Rodrigo Ferreira; photographs **B, I, K** from Gonzalo Giribet; photograph **F** from Peter Swart.

Condé, 1964 (Diplura Campodeidae) and *Prorhynchus* cf. *brincki* (Platyhelminthes: Prorhynchida – probably erroneously referred to as *Dendrocoelum* sp. in Sharratt et al. 2000) (Fig. 1K). Further on, Harvey et al. (2016) described the first troglobitic Gymnobiidae pseudoscorpion from the region (*Gymnobiium inukshuk* Harvey & Giribet, 2016) (Fig. 1I), increasing the number of cave-restricted species of the WCS to 14.

Furthermore, during a visit to WCS in October 2019, by some of the authors of this study, troglomorphic species not previously recorded were found. This included two spiders (eyeless Pholcidae and Symphytognatidae), one Sminthuridoidea spring-tail (Collembola), one eyeless Ptiliidae beetle (Coleoptera) and one Rhagidiidae mite (Trombidiformes). The discovery of these species raised the number of cave-restricted species of the WCS to 19. Culver and Sket (2000) defined hotspots of subterranean biodiversity as those caves (or cave systems) with 20 or more cave-restricted species. Thus, the discovery of only one more new species may turn the system in the first hotspot of subterranean biodiversity in Africa, according to those authors. However, it is important to stand out that this number (20 species) is arbitrary, so that the WCS can be already considered a hotspot in South Africa.

Some of the previously mentioned species are considered Critically Endangered according to the IUCN Red List Categories criteria (1994). This includes the onychophoran *Peripatopsis alba* (Vulnerable) and the crustacean *Spelaeogriphus lepidops* since their known extent of occurrence is smaller than 100 km² (Sharratt et al. 2000).

With regards to the vulnerability of the WCS, Sharratt (1998) was one of the first researchers to highlight that the main threat to cave species in the Table Mountain area is human visitation. This threat is not only a concern due to trampling on fauna and the consequent alteration of micro-habitats, but also because of its potential to pollute terrestrial and aquatic environments with food scraps and waste (including batteries containing toxic chemicals). Additional risks include potentially disturbing the bat population and altering temperature and moisture conditions. Furthermore, Sharratt (1998) pointed out that although human visitation to Table Mountain caves was still relatively low, the steady increase in tourism levels was a cause for concern. Another factor mentioned by the latter author was the potential for introducing pesticides into the trophic cave webs through the feeding of fruit bats in the region that could start producing contaminated guano in the caves. Recently, the disturbance to caves was mentioned again in regards to the conservation of spiders listed on the South African National Red List (Foord et al. 2020), thus reinforcing the need to protect such habitats in the country.

In the same visit previously mentioned (October 2019), it was possible to verify several impacts in the cave interior, along the stretch considered the “Wynberg cave”, even considering the external landscape surrounding the cave is quite preserved (Fig. 2A). This is one of the most popular caves for visitors, given the easy access to one of the entrances (there is a well-marked trail from the main concrete pathway) (Fig. 2B). In addition to the graffiti on the walls (Fig. 2C), several passages are clearly overused, which is evidenced by the friable quartzite turned into sand after being trampled. It is important to note that several species shelter themselves under fallen blocks on the cave floor and therefore continuous trampling will almost certainly modify the micro-habitats inside the cave.

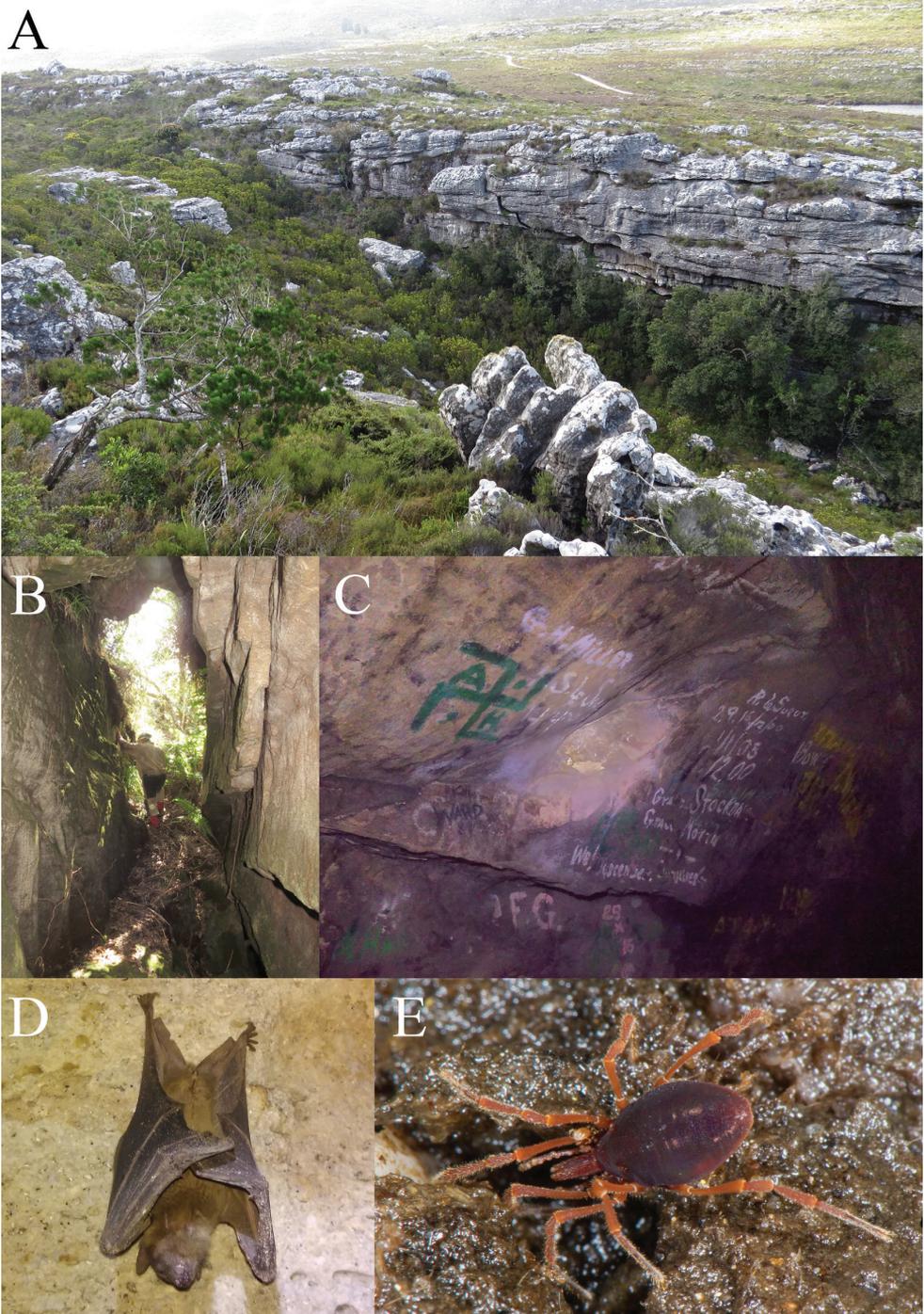


Figure 2. **A** External landscape surrounding the WCS **B** one of the entrances of the Wynberg cave **C** graffiti on the walls of Wynberg cave **D** Dead bat pending on the cave wall **E** *Purcellia argasiformis* with a parasitic mite attached to the first leg. Photographs **A**, **B** from Rodrigo Ferreira; photographs **C**, **D** from Oresti Ventouras; photograph **E** from Gonzalo Giribet.

One of the authors (O. Ventouras) attested that over the years speleologists have never seen Wynberg Cave in the state that it is in now. For the past three years, on every trip down into the cave they removed waste material (e.g. plastic bags, food remnants, and even discarded batteries). The area in which the majority of these items were observed is on the cave floor in the cave lowest level. This represents an important habitat (with flowing water) for the majority of the cave-restricted species inhabiting the WCS, although sometimes troglobitic species can be observed relatively close to the entrance. As an example, the velvet worm *Peripatopsis alba* is so rare that it has never been sighted by speleologists who have been visiting this cave for over 20 years. Furthermore, a noticeable reduction in bat colonies (Horseshoe Bats – *Rhinolophus capensis* and Egyptian Fruit Bats – *Rousettus aegyptiacus*) was observed within the last few years, which may be a result of uncontrolled visitation. These bats are extremely important to the cave trophic chain, directly contributing as food (guano) for many detritivorous species. During an excursion into the WCS, one of the authors (O. Ventouras) observed more than 10 dead bats within a stretch of 2–8 meters on the same sandy floor, as well as additional dead specimens still hanging on the cave walls (Fig. 2D).

Sharratt et al. (2000) suggested that management-orientated research, long-term population monitoring and the conservation of pseudokarst areas, were urgent requirements for the conservation of these rare and threatened isolated island-like habitats. However, as previously reported, most of those proposed actions were not implemented, which unfortunately resulted in an increased threat to the caves and its inhabitants. Considering the significant increase in the impacts arising from human visitation on the system in recent years, we would suggest two additional measures to the previous list presented by Sharratt et al. (2000). The first, which is a long-term goal, would be the implementation of environmental education programs for the visitors of the Table Mountain protected area, focusing on the caves and cave fauna. As indicated by Kastning and Kastning (1999), eliminating misconceptions and teaching well-established concepts in a clear and concise manner could considerably reduce environmental problems in cave ecosystems. Hence, such programs can directly contribute to the mitigation of impacts, since they increase the public's awareness on the importance of these environments for the unique fauna that depends on them. Such programs can include recurring lectures, booklets, pamphlets and other materials that can be released to visitors and to the larger human population (e.g. at schools, universities, etc.). Furthermore, it is highly recommended that the entire system is subjected to targeted studies linked to a management plan (as already recommended by Sharratt et al. 2000). Such plans are important in establishing visitation rules and restrictions in a given cave system. Such plans should indicate suitable areas for tourists (e.g. those without important bat colonies, troglobitic species populations or even with some dangerous species, as venomous spiders). Physical aspects should also be considered regarding the ease of access, the risk of injury and/or a boulder collapse, among others. Therefore, considering whether or not some parts of the WCS should be opened to tourism can only be determined following an environmental impact assessment.

Additionally, a short-term action (before a management plan is put in place) could be gating the caves to prevent uncontrolled visitation. Cave gates are steel structures

usually installed at a cave's entrances to protect their resources by keeping out human visitors, while allowing air, water, and wildlife to migrate without restrictions (Elliott 2004). Although cave gating has been used to eliminate human disturbance elsewhere (Martin et al. 2003), this is not a consensual procedure, since unsuitable cave gates can harm wildlife and cave resources (Elliott 2006). Furthermore, knowledge of the cave's ecology (especially bats) is required before gating can be considered (Elliott 2006). Among the "good reasons" to gate a cave, as mentioned by Elliott (2006), include: i) protecting the endangered species inhabiting the cave; ii) minimizing or even eliminating cave vandalism, and iii) cherishing the cave's important ecological value, which can best be studied and appreciated with a good permitting system combined with a gate. These criteria are currently applicable to WCS, thus justifying cave gating as a potential measure of protection. However, since the WCS has many entrances, the first step would be to determine which entrances could be the target of gating. Those most frequently accessed should be prioritized.

Finally, it is important to mention that further research should be undertaken in the WCS. The new species recorded in the cave in 2019 indicate that there are still unknown species awaiting to be discovered. This is quite plausible especially when considering the quartzite rock structure (highly fractured) which enables invertebrates to migrate or even use mesocavern spaces. Furthermore, ecological interactions, which were poorly explored in the previous studies, are another potential subject of further research, as is the case of parasitism in both vertebrates and invertebrates (Fig. 2E).

The Wynberg Cave System is of paramount importance, due to both its potential to become the first hotspot of subterranean biology in Africa. Emergency measures are required in order to ensure the conservation of this cave, threatened by the uncontrolled human impact.

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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 Cenoteando'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, Tixkakil, 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 yucatanana* 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
<i>Barbouria cubensis</i> (von Martens, 1872)	Decapoda	von Martens 1872	Provincia de La Habana, Cuba	MNHB	No	saline water	ROO
<i>Creaseriella anops</i> (Creaser, 1936)	Isopoda	Creaser 1936	Cenote Sambulá (YUC)	UMLSA	Yes	fresh and saline water	YUC, ROO, CAM
<i>Antromysis cenotensis</i> Creaser, 1936	Mysida	Creaser 1936	Grutas de Balancanché (YUC)	UMLSA	Yes	fresh water	YUC, ROO
<i>Creaseria morleyi</i> (Creaser, 1936)	Decapoda	Creaser 1936	Cueva de San Isidro (YUC)	UMLSA	Yes	fresh water	YUC, ROO, CAM
<i>Typhlatya pearsei</i> Creaser, 1936	Decapoda	Creaser 1936	Grutas de Balancanché (YUC)	UMLSA	Yes	fresh water	YUC, ROO, CAM
<i>Stygiomysis holthuisi</i> (Gordon, 1958)	Stygiomysida	Gordon 1958	Devil's Hole, St. Martin, Lesser Antilles (France)	BMNH	No	fresh water	YUC, ROO
<i>Typhlatya mitchelli</i> H.H.III Hobbs & H.H.Jr. Hobbs, 1976	Decapoda	Hobbs and Hobbs 1976	Cenote Kabahchén (YUC)	USNM	Yes	fresh water	YUC, ROO
<i>Typhlatya campecheae</i> H.H.III Hobbs & H.H.Jr. Hobbs, 1976	Decapoda	Hobbs and Hobbs 1976	Grutas de Xtacumbilkunaán (CAM)	USNM	Yes	fresh water	CAM
<i>Mayaweckelia yucatanensis</i> Holsinger, 1977	Amphipoda	Holsinger 1977	Grutas de Xtacumbilkunaán (CAM)	USNM	Yes	fresh water	CAM*
<i>Mayaweckelia cenoticola</i> Holsinger, 1977	Amphipoda	Holsinger 1977	Cenote Xtacabihá (YUC)	USNM	Yes	fresh water	YUC, ROO, CAM
<i>Parhippolyte sterreri</i> (C.W.J. Hart & Manning, 1981)	Decapoda	Hart and Manning 1981	Tucker's Town Cave, Tucker's Town, Bermuda	USNM	No	saline water	COZ
<i>Metacirolana mayana</i> (Bowman, 1987)	Isopoda	Bowman 1987	Cueva Quebrada (COZ)	USNM	Yes	brakish and saline water	ROO, COZ
<i>Tulumella uidens</i> Bowman & Iliffe, 1988	Therosbaenacea	Bowman and Iliffe 1988	Cenote Naharon (ROO)	USNM	Yes	brakish and saline water	YUC, ROO
<i>Yagerocaris cozumel</i> Kensley, 1988	Decapoda	Kensley 1988	Cenote Areolito (COZ)	USNM	Yes	saline water	ROO, COZ
<i>Agostocaris bozanici</i> Kensley, 1988	Decapoda	Kensley 1988	Cenote Xcan-Ha (COZ)	USNM	Yes	saline water	COZ*
<i>Tuluweckelia cernua</i> Holsinger, 1990	Amphipoda	Holsinger 1990	Cenote Calavera (ROO)	USNM	Yes	brakish and fresh water	YUC, ROO
<i>Bahadzia bozanici</i> Holsinger, 1992	Amphipoda	Holsinger 1992	Cueva Quebrada (COZ)	USNM	Yes	saline water	ROO, COZ
<i>Bahadzia setodactylus</i> Holsinger, 1992	Amphipoda	Holsinger 1992	Cenote Xcan-Ha (COZ)	USNM	Yes	saline water	COZ
<i>Stygiomysis cokei</i> Kallmeyer & Carpenter, 1996	Stygiomysida	Kallmeyer and Carpenter 1996	Cenote Calavera (ROO)	USNM	Yes	fresh and brakish water	YUC, ROO
<i>Callasmata nobochi</i> Escobar-Briones, Camacho & Alcocer, 1997	Decapoda	Escobar-Briones et al. 1997	Crack House Cave, (ROO)	CNCR UNAM	Yes	saline water	ROO, COZ
<i>Haplolana boumani</i> 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
<i>Yucatalana robustispina</i> Botosaneanu & Iliffe, 1999	Isopoda	Botosaneanu and Iliffe 1999	Cenote Papakal (YUC)	ZMUA	Yes	fresh water	YUC
<i>Cirolana yunca</i> (Botosaneanu & Iliffe, 2000)	Isopoda	Botosaneanu and Iliffe 2000	Cenote Sabak Ha (YUC)	ZMUA	Yes	fresh water	YUC
<i>Cirolana yucatanana</i> Botosaneanu & Iliffe, 2000	Isopoda	Botosaneanu and Iliffe 2000	Cenote Dzonotilá (YUC)	ZMUA	Yes	fresh water	YUC*
<i>Procaris mexicana</i> von Sternberg & Schotte, 2004	Decapoda	Sternberg and Schotte 2004	Cueva Quebrada (COZ)	USNM	Yes	saline water	COZ
<i>Typhlatya dzilamensis</i> Álvarez, Iliffe & Villalobos, 2005	Decapoda	Álvarez et al. 2005	Cenote Buya Uno (YUC)	CNCR UNAM	Yes	saline water	YUC, ROO
<i>Triacanthoneus akumalensis</i> Álvarez, Iliffe, Gonzalez & Villalobos, 2012	Decapoda	Álvarez et al. 2012	Cenote Aak Kimin (ROO)	CNCR UNAM	Yes	saline water	ROO*
<i>Hyalella cenotensis</i> Marrón-Becerra, Hermoso-Salazar, Solís-Weiss, 2014	Amphipoda	Marrón-Becerra et al. 2014	Cenote Aktun Ha (ROO)	CNCR UNAM	Yes	fresh water	ROO*
<i>Cymadusa berrenae</i> Ortiz & Winfield, 2015	Amphipoda	Ortiz and Winfield 2015	Cenote Aerolito (COZ)	CNCR UNAM	Yes	brakish water	COZ*
<i>Agostocaris zabaletai</i> Mejía-Ortiz, Yañez & López-Mejía, 2017	Decapoda	Mejía-Ortiz et al. 2017	Cenote Chempita (COZ)	CNCR UNAM	Yes	saline water	COZ
<i>Anchialocaris paulini</i> Mejía-Ortiz, Yañez & López-Mejía, 2017	Decapoda	Mejía-Ortiz et al. 2017	Cenote Chempita (COZ)	CNCR UNAM	Yes	saline water	COZ*
<i>Mayaweckelia troglomorpha</i> Angyal, 2018	Amphipoda	Angyal et al. 2018	Cenote Dzonbakal (YUC)	CNCR UNAM	Yes	fresh water	YUC
<i>Curassanthura yucatanensis</i> 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	<i>Typhlatya dzilamensis</i>	Hobbs and Hobbs 1976	<i>Typhlatya mitchelli</i>
Álvarez et al. 2019	<i>Curassanthura yucatanensis</i>	Hobbs et al. 1977	genus <i>Typhlatya</i>
Angyal et al. 2018	<i>Mayaweckelia troglomorpha</i>	Hobbs 1979	genus <i>Typhlatya</i>
Botosaneanu and Iliffe 1997	<i>Haptolana bowmani</i>	Holsinger 1977	<i>Mayaweckelia cenoticola</i>
Botosaneanu and Iliffe 1999	<i>Yucatalana robustispina</i>	Holsinger 1990	<i>Tuluweckelia cernua</i>
Botosaneanu and Iliffe 2000	<i>Cirolana yunca</i> , <i>Cirolana yucatanana</i>	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	<i>Stygiomysis cokei</i>
Bowman 1966	family Cirolanidae	Kensley 1981	genus <i>Curassanthura</i>
Bowman 1977	genus <i>Antromysis</i>	Lowry and Myers 2013	suborder Senticaudata
Bowman and Iliffe 1988	<i>Tulumella unidens</i>	Meland et al. 2015	orders Mysida and Stygiomysida
Bowman et al. 1984	genus <i>Stygiomysis</i>	Melic 2015	order Thermosbaenacea
Bruce 1986	family Cirolanidae	Pérez-Aranda 1983a	<i>Typhlatya pearsei</i>
Bruce 2008	family Cirolanidae	Pérez-Aranda 1983b	<i>Creaseria morleyi</i>
Bruce and Humphreys 1993	family Cirolanidae	Pérez-Aranda 1984a	<i>Typhlatya mitchelli</i>
Bruce et al. 2017	family Cirolanidae	Pérez-Aranda 1984b	<i>Creaseriella anops</i>
Brusca et al. 1995	family Cirolanidae	Poore 2001	family Cirolanidae
Caroli 1937	family Cirolanidae	Rioja 1953	family Cirolanidae
Creaser 1936	<i>Antromysis cenotensis</i> , <i>Creaseriella anops</i> , <i>Creaseria morleyi</i> , <i>Typhlatya pearsei</i>	Tinnizi and Quddusi 1993	class Malacostraca
De la Fuente 1994	class Malacostraca	Wagner 1994	order Thermosbaenacea
Gordon 1960	<i>Stygiomysis holthuisi</i>		

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

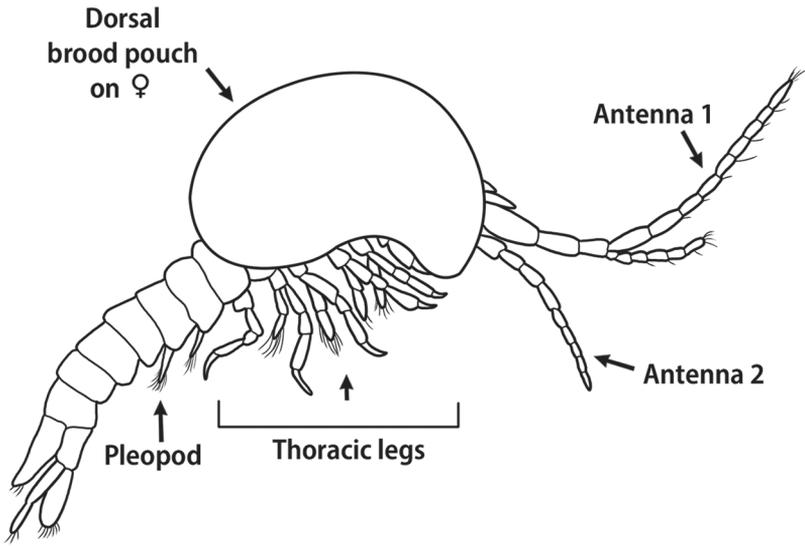


Figure 1. Thermosbaenacea, schematic drawing.

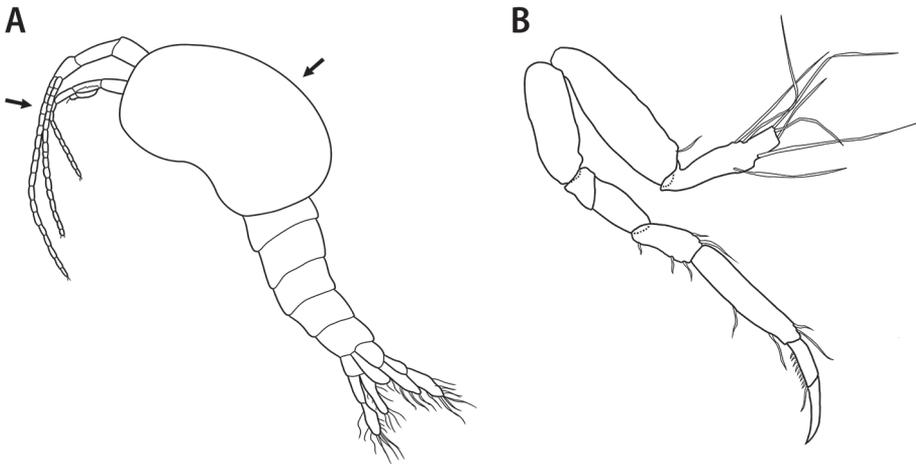


Figure 2. **A** *Tulumella unidens* habitus simplified drawing **B** *T. unidens* pereopod VI.

(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).

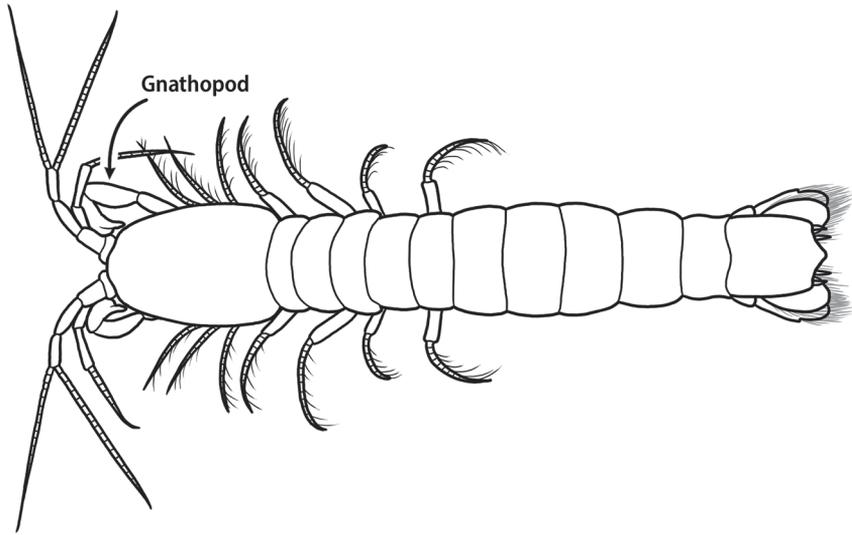


Figure 3. Stygiomysida, schematic drawing.

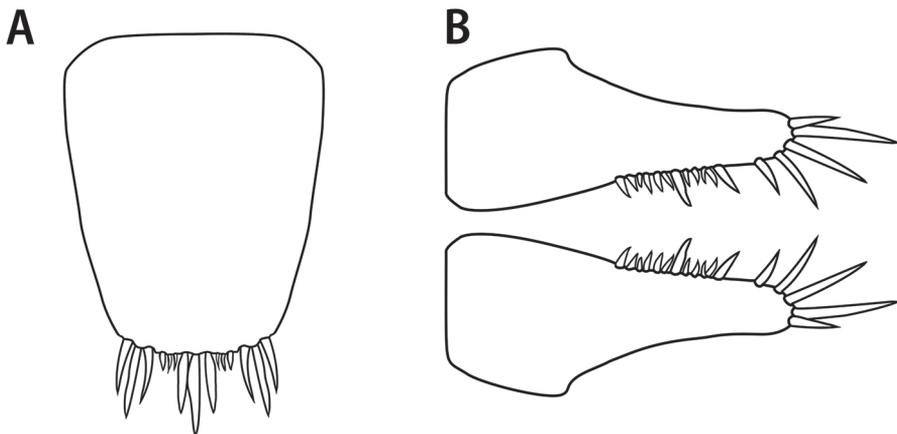


Figure 4. A *Stygiomysis holtbuisi* telson **B** *S. holtbuisi* uropod protopodal process.

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 pereopods. Ventral brood pouch enclosed by large, flexible oostegites present on females. Fourth pleopod longer than others in males and has a specialized reproductive function. Statocysts on uropods present.

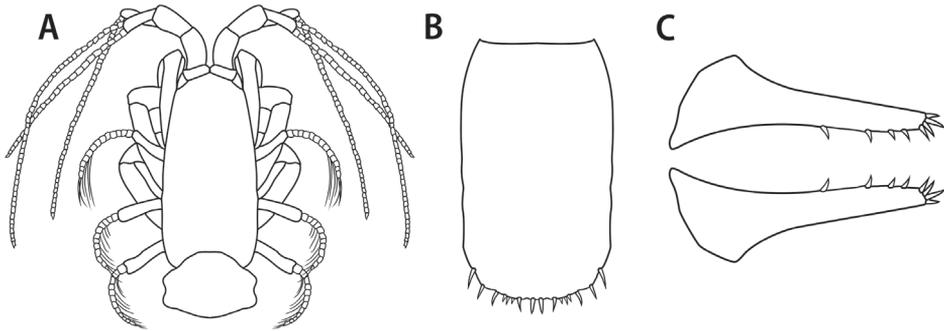


Figure 5. **A** *Stygiomysis cokei* carapace with appendages **B** *S. cokei* telson **C** *S. cokei* uropod protopodal process.

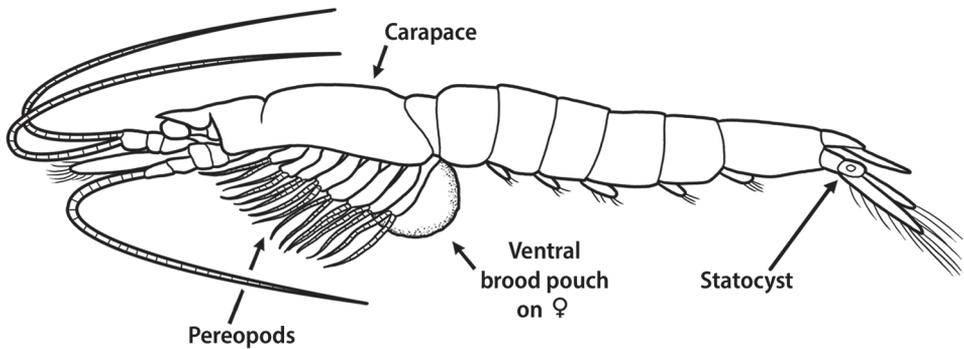


Figure 6. Mysida, schematic drawing.

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.

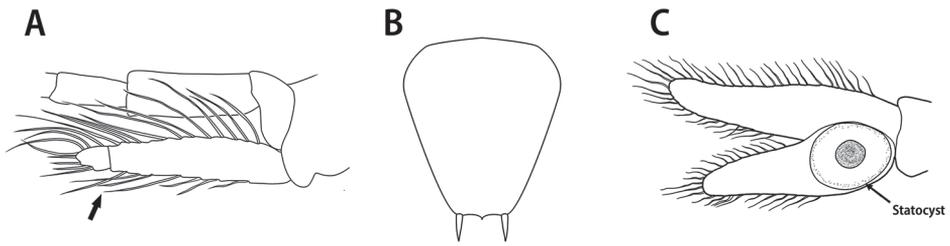


Figure 7. **A** *Antromysis cenotensis* scale of antenna 2 **B** *A. cenotensis* telson **C** *A. cenotensis* uropod with statocyst.

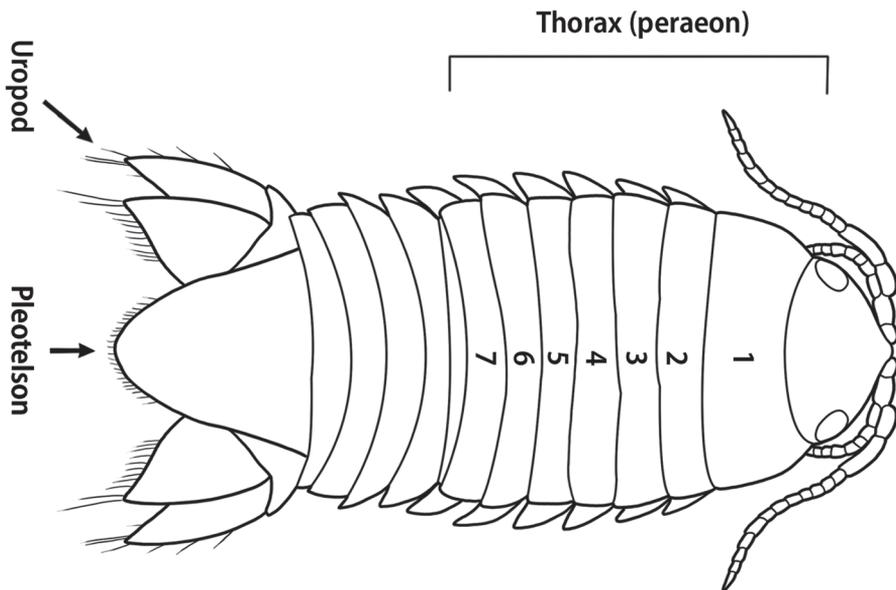


Figure 8. Isopoda, schematic drawing.

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 margin deeply depressed

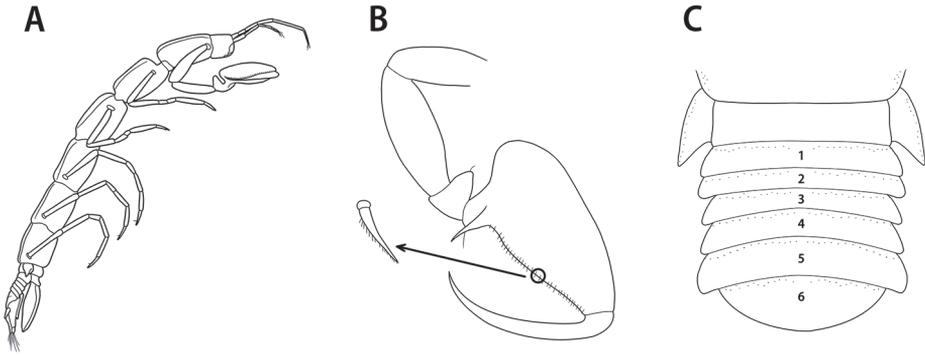


Figure 9. **A** *Curassanthura yucatanensis* habitus **B** *C. yucatanensis* propodus of pereopod I **C** *C. yucatanensis* pleonites. Drawings were adapted from Álvarez et al. 2019.

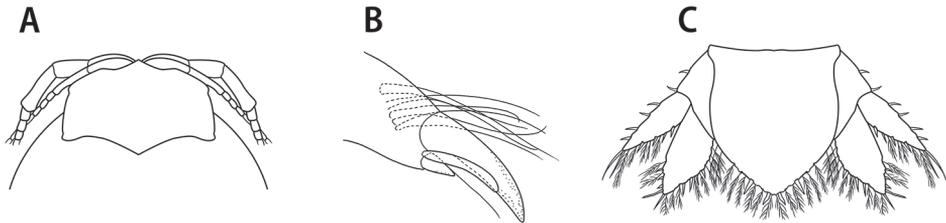


Figure 10. **A** *Cirolana yunca* cephalon with rostrum **B** *C. yunca* nails of pereopod III dactylus (adapted from Botosaneanu & Iliffe 2000) **C** *C. yunca* pleotelson and uropods.

(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 yucatanana (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

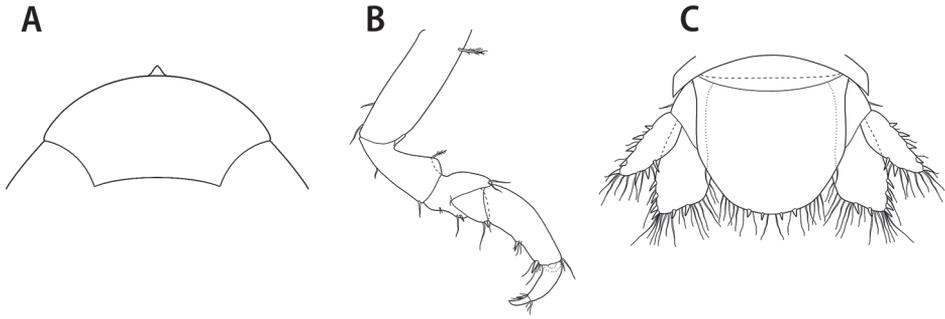


Figure 11. **A** *Cirolana yucatanana* cephalon **B** *C. yucatanana* pereopod II **C** *C. yucatanana* pleotelson and uropods. Drawings were adapted from Botosaneanu & Iliffe 2000.

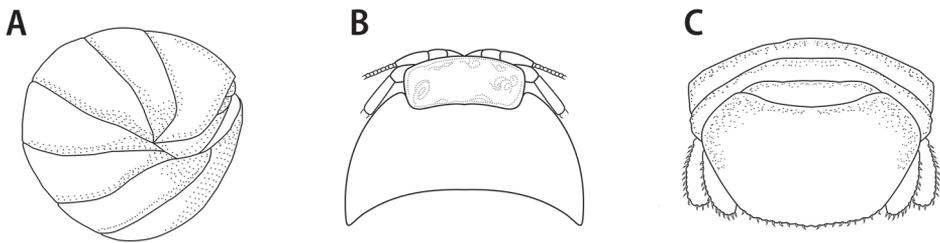


Figure 12. **A** *Creaseriella anops* rolled position **B** *C. anops* cephalon **C** *C. anops* pleotelson and uropods.

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).

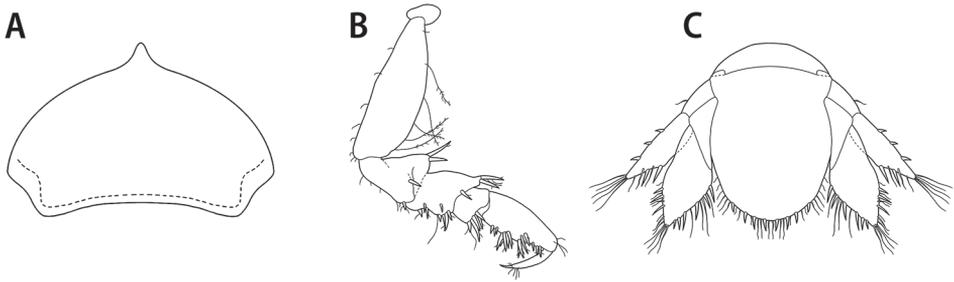


Figure 13. **A** *Haptolana bowmani* cephalon with rostrum **B** *H. bowmani* pereopod III **C** *H. bowmani* pleotelson and uropods. Drawings were adapted from Botosaneanu & Iliffe 1997.

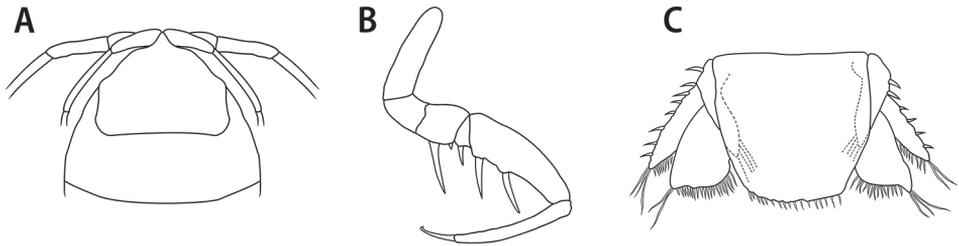


Figure 14. **A** *Yucatalana robustispina* cephalon with rostrum **B** *Y. robustispina* pereopod I **C** *Y. robustispina* pleotelson and uropods.

Order: AMPHIPODA Latreille, 1816

Figure 15

Body laterally compressed, slightly arched. Thorax of seven somites (pereaeon), 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 cenotocola 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).

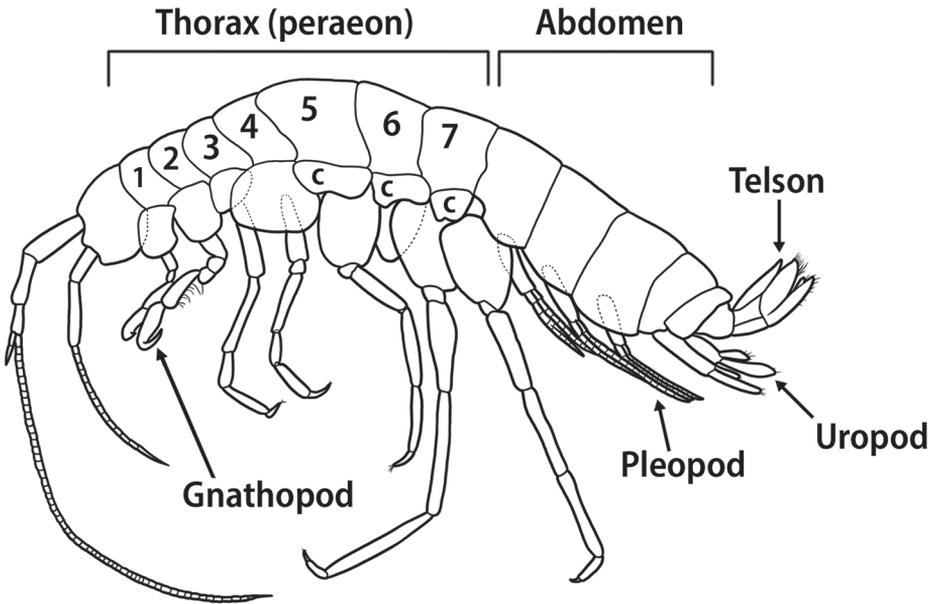


Figure 15. Amphipoda, schematic drawing.

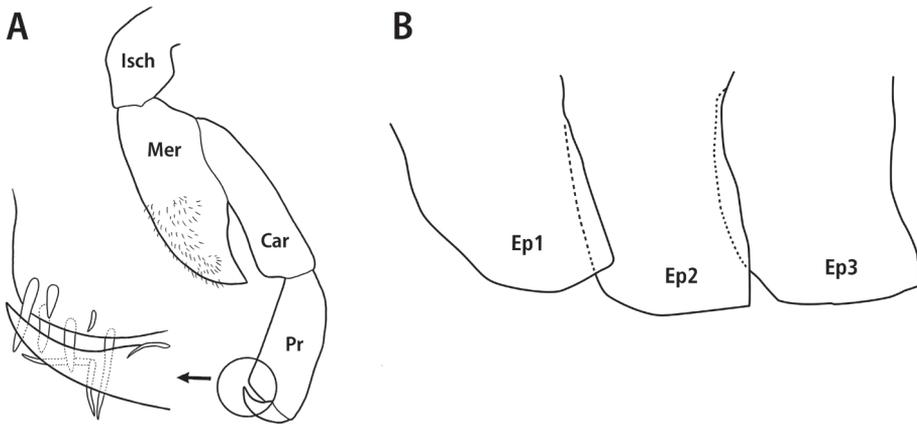


Figure 16. A *Mayaweckelia cenoticola* propodus of gnathopod 1 (Ish = ischium, Mer = merus, Car = carpus, Pr = propodus) **B** *M. cenoticola* epimeral plates 1-3 (Ep = epimeral plates).

***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

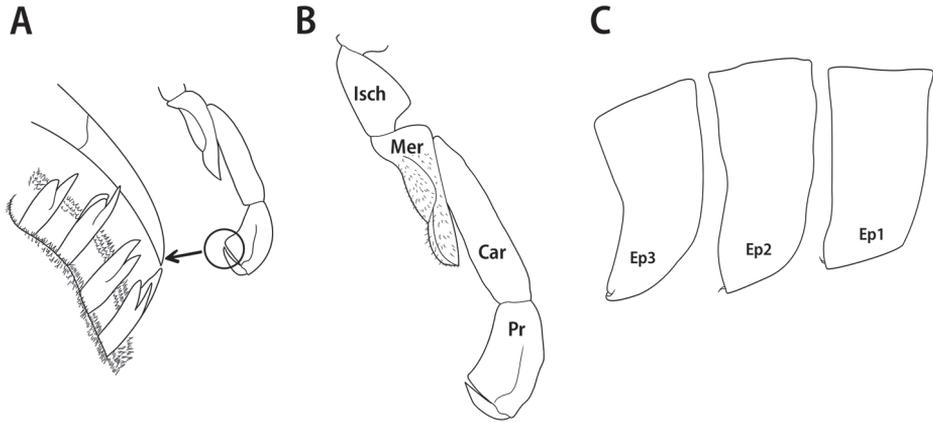


Figure 17. A *Maya weckelia troglomorpha* notched spine teeth of gnathopod 1 propodus **B** *M. troglomorpha* gnathopod 1 schematic drawing (Ish = ischium, Mer = merus, Car = carpus, Pr = propodus) **C** *M. troglomorpha* epimeral plates 1-3 (Ep = epimeral plates).

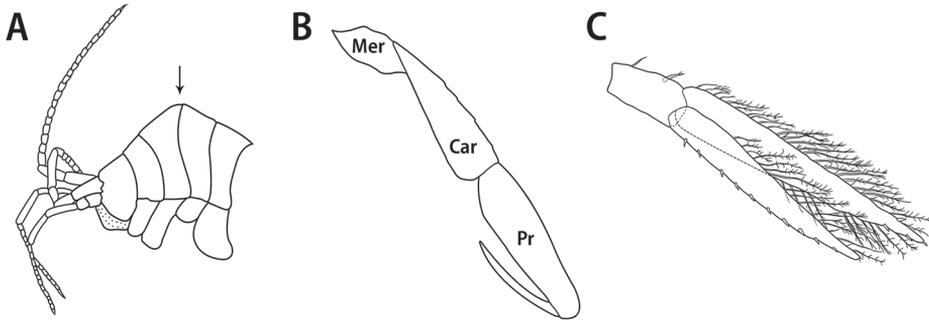


Figure 18. A *Tuluweckelia cernua* anterior body part **B** *T. cernua* gnathopod 2, schematic drawing (Mer = merus, Car = carpus, Pr = propodus, C = coxa) **C** *T. cernua* uropod III.

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: Atyidae 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). Exoskeleton 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

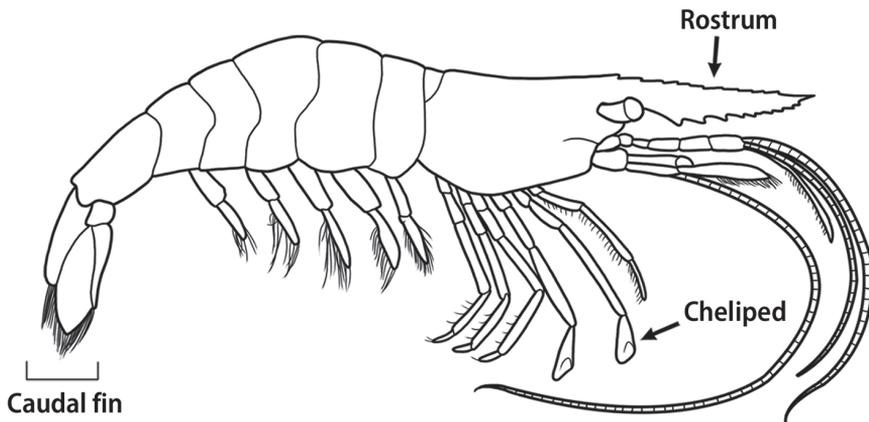


Figure 19. Decapoda, schematic drawing.

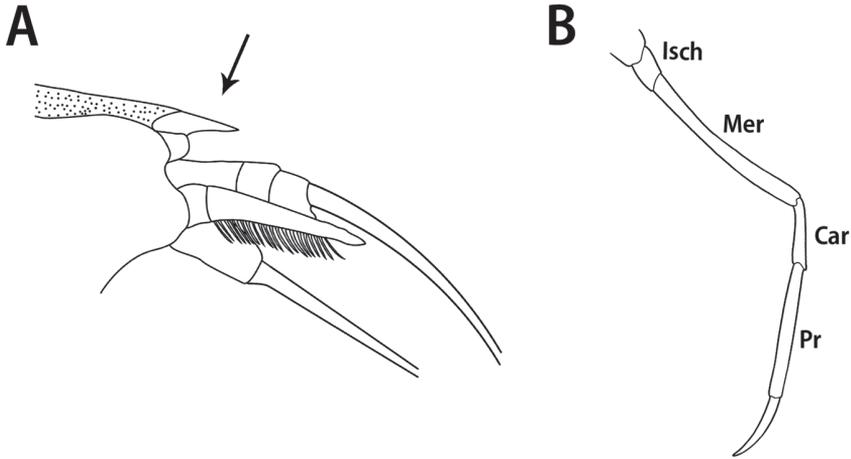


Figure 20. **A** *Typhlatya pearsei* rostrum and eyestalk **B** *T. pearsei* pereopod V schematic drawing.

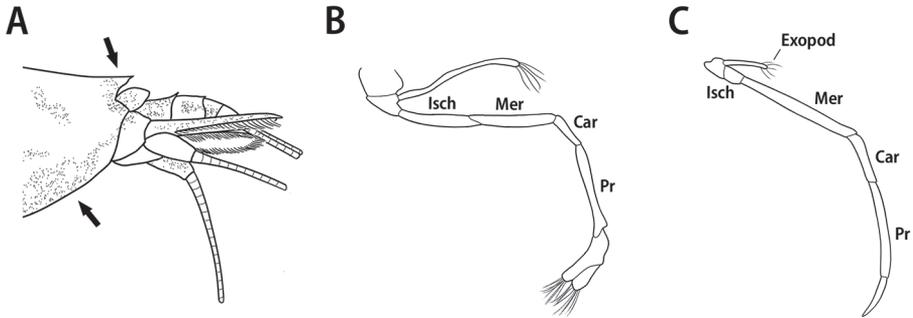


Figure 21. **A** *Typhlatya mitchelli* rostrum and eyestalks **B** *T. mitchelli* pereopod II schematic drawing **C** *T. mitchelli* pereopod V schematic drawing.

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

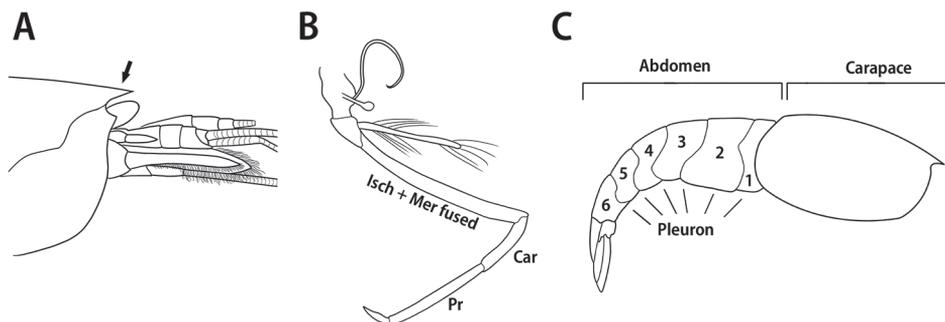


Figure 22. **A** *Typhlatya dzilamensis* rostrum and eyestalks **B** *T. dzilamensis* pereopod III schematic drawing **C** *T. dzilamensis* carapace and abdomen schematic drawing.

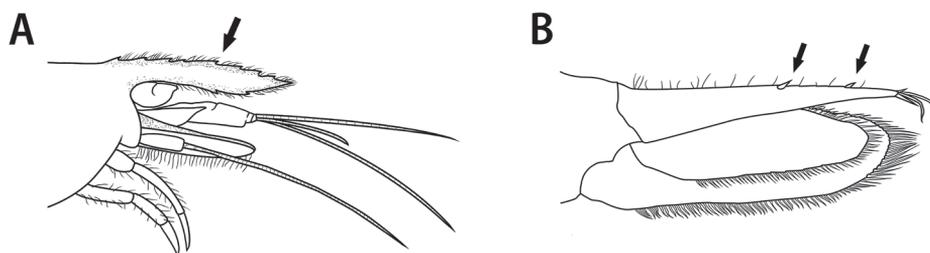


Figure 23. **A** *Creaseria morleyi* rostrum and eyestalks **B** *C. morleyi* telson and uropods.

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) yucatanana* 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 yucatanana* (Botosaneanu & Iliffe, 2000).

There are four monotypic, highly endemic genera (*Tuluweckelia* Holsinger, 1990; *Creaseriella* Rioja, 1953; *Yucatalana* Botosaneanu & 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. cenotocola* are due primarily 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 sinkholes (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 identification 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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