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A new *Speleophria* (Copepoda, Misophrioida) from an anchialine cave of the Yucatán Peninsula with comments on the biogeography of the genus

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ABSTRACT.—Misophrioid copepods are hyperbenthic or anchialine forms whose known distributional patterns appear to have a Tethyan origin and subsequent vicariant processes. A new misophrioid copepod, *Speleophria germanyanzei* n. sp., collected from an anchialine cave in Cozumel Island, Yucatán Peninsula (YP), is described based on male and female specimens. This is the second report describing a misophrioid copepod species from the Yucatán Peninsula, harboring a remarkably diverse anchialine crustacean fauna. The new species is the sixth of this anchialine genus. It differs from its congeners by a combination of characters including: the armature of leg 4 exopod, 21-segmented female antennule, 24-segmented male antennule, both with moderate proximal expansion, the male with the terminal antennular segments distinctively elongate. The fifth leg distal segment is armed with 3 elements in the female, 4 in the male. The female genital double-somite is furnished with long, slender spinules. The other members of *Speleophria* are distributed in Europe (Croatia, Spain), Bermuda, and Australia. Relationships among species of *Speleophria* have revealed amphiatlantic pairs of sister taxa. The new species has little affinity with its regionally closest congener from Bermuda; it appears to be most closely related to the Croatian *S. mestrovi* and could be its western Atlantic counterpart. The different misophrioid fauna between the YP and Cozumel Island and the more recent emergence of Cozumel with respect to that of the YP plate suggests either an ancestral Tethyan-related independent colonization or a relatively recent local dispersal through deep-sea crevicular habitats before emergence of these land masses.

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Misophrioid copepods include deep-sea hyperbenthic, a bathypelagic, and many anchialine forms that have been reported from different geographic regions (Boxshall and Roe 1980, Boxshall 1983, 1987, Boxshall and Iliffe 1986, 1990, Huys 1988, Jaume and Boxshall 1995, 1996a,b, 1997, 1998, Boxshall and Jaume 2000, Jaume et al. 2001, Boxshall et al. 2014), including the Yucatán Peninsula (YP) (Boxshall et al. 2014).

Previous records of misophrioids in the YP include a report of unidentified specimens of this group from cenotes (sinkholes) of the eastern coast of the YP (Jaume et al. 1998) and the description of *Mexicophria*, a new genus from the same area (Boxshall et al. 2014). The YP has been deemed as a clearly defined biotic province in the Neotropical region (Morrone 2014). It is an extensive karstic system with a wide variety of epigeal and subterranean aquatic systems, including anchialine systems (Schmitter-Soto et al. 2002, Pérez et al. 2011), which as defined by Bishop et al. (2015), merge with the marine system at the coast side and fresh groundwater inland. The geological history of the YP involves successive waves of marine invasions and regressions (Suárez-Morales et al. 2004); it has a highly diverse native aquatic biota as well as high levels of endemism of crustaceans (Fiers et al. 1996, Suárez-Morales et al. 2004, Mercado-Salas et al. 2013), and is clearly a hotspot for cave-related fauna. There are extensive areas of the YP whose copepod communities have not been explored; one of them is Cozumel, an island located off the northeast coast of the YP. During biological sampling of the anchialine caves of Cozumel, numerous copepods were collected, which were identified as misophrioids belonging to an undescribed species. The new species from Cozumel is described in full based on male and female specimens; it is compared with its known congeners and biogeographic comments are provided on the distribution of the genus.

METHODS

Sampling was performed on 6 July, 2014, from a sinkhole known as Cenote Tres Potrillos, Cozumel Island at 20°27'3.2"N, 86°59'14.4"W, Quintana Roo, Mexico. The cave entrance has a diameter of 3 m, followed by a 40 m long horizontal passage at 12 m of depth (Mejía-Ortiz et al. 2008, Yáñez-Mendoza et al. 2008). The total depth of this system is 38 m, with the halocline at 11 m overlying sulfidic fully marine water. Plankton samples were collected in the halocline by hauling a conical plankton net (50- μ m mesh). The collected material was fixed and preserved in 100% ethanol. The copepods were then transferred to glycerol and lightly stained with Methylene Blue for taxonomical analysis. The specimens were observed and analyzed in whole and then dissected with sharpened needles; the appendages were examined as temporary mounts in glycerine and later on, sealed with Entellan® as permanent mounts. Drawings were prepared using a camera lucida mounted on an E-200 Nikon compound microscope with Nomarski DIC at magnifications of 400 \times and 1000 \times . Morphological terminology followed Huys and Boxshall (1991). Body length was measured from the anterior margin of the rostrum to the posterior margin of the caudal rami. Two adult specimens (one male, one female) were prepared for SEM examination with a JEOL SM-6010 microscope at facilities of ECOSUR in Chetumal, Mexico. The process included dehydration in progressively higher ethanol solutions (60%, 70%, 80%, 96%, 100%) and drying with a treatment with hexamethyldisilazane (HMDS). The type specimens are deposited in the collection of zooplankton held at El Colegio de la Frontera Sur (ECOSUR), Chetumal, Quintana Roo, Mexico (ECO-CHZ) and in the Colección Nacional de Crustáceos (CNCR) held at the Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City. Original samples are held at the Universidad de Quintana Roo (UQROO) Campus Cozumel, Mexico.

SYSTEMATICS

Order Misophrioida Gurney, 1933

Family Speleophriidae Boxshall and Jaume, 2000

Genus *Speleophria* Boxshall and Iliffe, 1986*Speleophria germanyanezi* new species

(Figs. 1–4)

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Type locality.—Cenote Tres Potrillos, Cozumel, Quintana Roo, Mexico; (location: 20°27'3.2"N, 86°59'14.4"W).

Material Examined.—Holotype: one adult female, dissected, mounted in glycerine sealed with Entellan (ECO-CHZ-09407). Collected 6 July, 2014, by G Yáñez-Mendoza and TM Iliffe. Allotype: adult male, specimen dissected, slide (ECO-CHZ-09408). Paratypes: three dissected adult females, two adult males, slides (ECO-CHZ-09409). Six adult males and two adult females, undissected, ethanol-preserved (90%), vial (ECO-CHZ-09410). Five paratype adult males and four adult females undissected, ethanol-preserved (90%), vial (CNCR-32596).

Description.—Adult female. Body (Fig. 1A) cyclopiform, moderately compressed laterally, with flat anterior margin, urosome relatively long, slender; prosome/urosome length ratio = 1.3. Body length ranging between 0.55 and 0.59 mm (average 0.58 mm, $n = 8$). Naupliar eye absent. Prosome 5-segmented, with first pedigerous somite incorporated into cephalothorax. Dorsal carapace-like extension on cephalosome absent. Rostrum strongly developed, fused to dorsal shield; projected frontally (Fig. 1A), with pair of medial sensilla (Fig. 3E). Posterolateral corners of pedigerous somites 1–4 moderately expanded posteriorly. Urosome 5-segmented (Fig. 1B, C); genital double somite elongate, proximal half weakly expanded, somite representing about 50% of urosome. Fifth pedigerous somite carrying fifth legs ventrally. Genital double-somite (Fig. 1B) with genital field located proximally in anterior 1/3; single midventral gonopore surrounded by transverse cuticular wrinkles; some specimens with attached pair of spermatophores with short tubules leading to copulatory pore (Fig. 4D). Ventral surface of somite ornamented with long, slender spinules unevenly distributed (Figs. 1C, 4B) or in a row (Fig. 4C). Anal somite shortest of urosome, about half the length of postgenital somite, with posterior ventral margin furnished with spinules (arrow in Fig. 4J).

Caudal rami subrectangular, about 1.25 times as long as wide; rami armed with 7 setae; caudal seta I vestigial, inserted anteroventrally on ramus, reduced to small spiniform element with minute spinules at insertion point (arrow in Fig. 4H, I). Seta II about as long as ramus, with spinules at insertion point. Seta IV second longest of ramus, with heteronomous ornamentation, proximal 2/3 of seta furnished with spinules on outer margin, distal 1/3 with setules, inner margin smooth. Caudal seta V longest, slightly longer than urosome; seta VI almost twice as long as ramus; dorsal seta VII as long as ramus (Fig. 1C).

Antennule (Fig. 1D) symmetrical, 21-segmented; reaching posterior margin of third pedigerous somite. First segment with proximal rounded expansion (arrowed

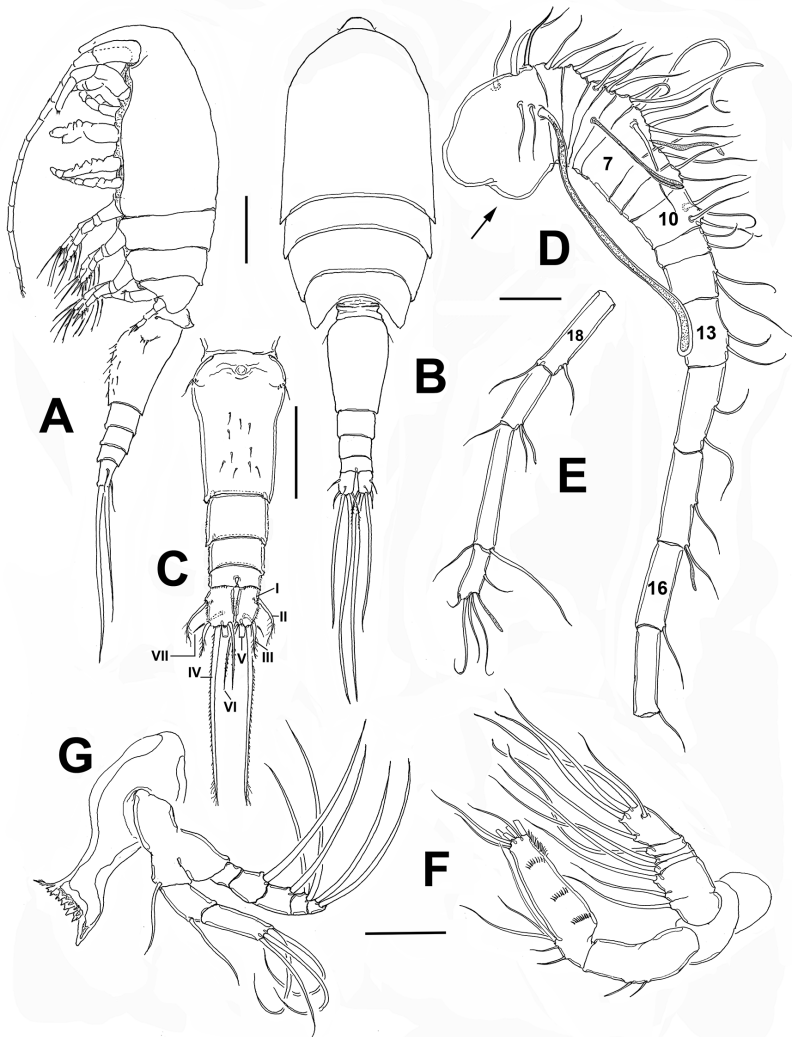


Figure 1. *Speleophria germanyanzei* n.sp., adult female holotype from Cozumel, Mexico. (A) habitus, lateral view, (B) same, dorsal view, (C) urosome, ventral view showing caudal setae I-VII, (D) antennule segments 1-17 showing rounded expansion on first segment (arrowed), (E) antennule segments 18-21, (F) antenna, (G) mandible with palp. Scale bars: A–C = 50 μ m, D–G = 20 μ m.

in Fig. 1D). Segments 2–6 short, compacted. Segment 20 longest of antennule. Large aesthetascs on segments 1 and 5. Segmental armature showing setae (s), aesthetascs (ae) and ancestral segments (in Roman numerals) as: segment 1 (I–III) 5s+ae, 2 (IV) 2s, 3 (V) 2s, 4 (VI) 2s, 5 (VII) 2s+ae, 6 (VIII) 2s, 7 (IX–XII) 5s+ae, 8 (XIII) 2s, 9 (XIV) 2s, 10 (XV–XVI) 4s, 11 (XVII) 2s, 12 (XVIII) 2s, 13 (XIX) 2s, 14 (XX) 2s, 15 (XXI) 2s+ae, 16 (XXII) 1s, 17 (XXIII) 1s, 18 (XXIV) 2s, 19 (XXV) 2s+ae, 20 (XXVI) 2s, 21 (XXVII–XXVIII) 5s +ae.

Antenna (Fig. 1G) biramous, endopod 1.8 times as long as exopod. Coxa unarmed, basis separate, unarmed. Endopod 2-segmented; first segment shorter than second, armed with 2 short subequal setae inserted on medial margin. Second segment

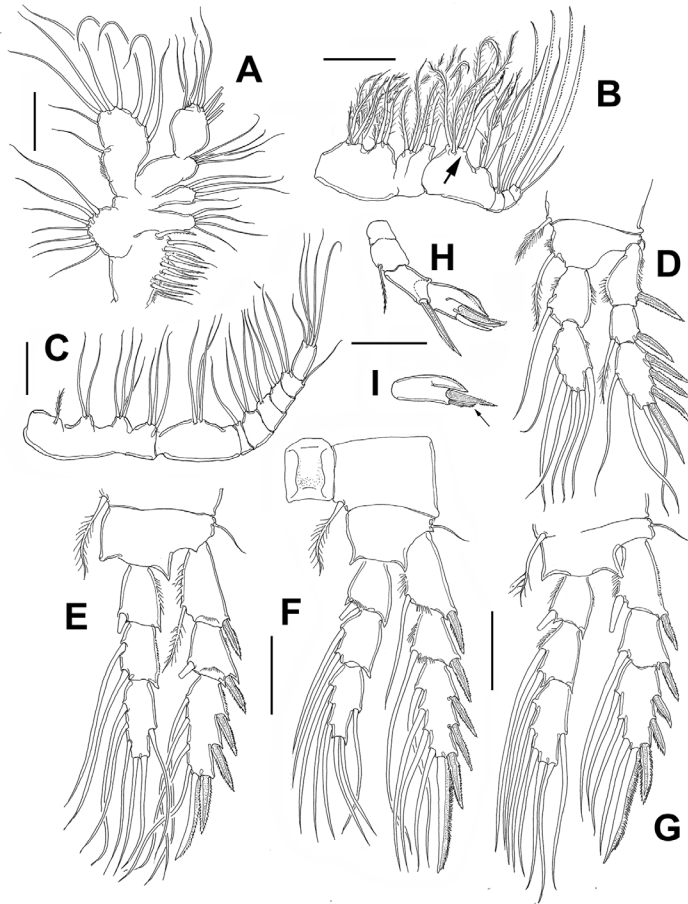


Figure 2. *Speleophria germanyanezi* n. sp., adult female holotype from Cozumel, Mexico. (A) maxillule, (B) maxilla, (C) maxilliped, (D) leg 1, (E) leg 2, (F) leg 3, (G) leg 4, (H) leg 5, (I) same, paratype specimen. Scale bars: A–I = 20 μ m.

elongate, armed with 2 proximal short setae and cluster of 3 setae on outer margin; with 7 setae on tip and ornamented with 3 transverse rows of spinules along inner margin plus additional subdistal longitudinal row of short setules (Fig. 1F). Exopod distinctly 6-segmented except for first segment with incomplete intersegmental suture; second segment longest of ramus. Armature of exopodal segments as: 1, 2, 1, 1, 1, 5.

Mandible comprising expanded coxal gnathobase and biramous palp (Fig. 1G); gnathobase with large, wide ventral tooth, separated by small diastema from row of 4 simple and 3 bicuspidate teeth; dorsal seta present, short. Mandibular palp slender, with basis about twice longer than wide, bearing 1 seta on inner margin; exopod indistinctly 5–6 segmented, apical segment shortest, probably representing two segments; setal formula of discernible segments as: 0, 1, 1, 2, 2. Endopod 2-segmented, proximal segment about 0.7 times as long as distal segment; armed with 1 seta. Second segment with 4 apical setae.

Maxillule (Fig. 2A) with large praecoxal arthrite bearing 13 elements; coxa with single endite bearing 4 setae, and rounded epipodite armed with 7 setae; proximal

basal endite with 4 setal elements; distal endite incorporated into segment, represented by 4 long setae. Exopod 1-segmented, lamella-like, with 9 setae; endopod 3-segmented, armed with 3, 2, 6 setae.

Maxilla (Fig. 2B) robust, well developed, 6-segmented. Praecoxa and coxa each with two endites, setal formula of endites as: 4, 3, 3, 2. Allobasis with proximal basal endite well developed, drawn out distally into stout, curved medial claw with spinulate distal half (arrow in Fig. 2B); claw with 4 regular setae implanted around base. Distal basal lobe with 3 setae. Endopod 3-segmented, with setal formula 2, 2, 3.

Maxilliped (Fig. 2C) 8-segmented, long, slender. Precoxal endite with single seta; 3 coxal endites armed with 2, 4, 3 setae, respectively. Basis with 3 setae, followed by slender 6-segmented endopod; endopodal setal formula 1, 2, 2, 2, 2+1, 5; distal segment longest.

Legs 1 to 4 biramous (Fig. 2D–G), with 3-segmented rami except 2-segmented endopod of leg 1; exopodal ramus longer than endopod in legs 1–4. Members of each leg pair joined by subrectangular, smooth intercoxal sclerite. Distolateral corners of endopodal segments 1 and 2 of legs 2 to 4 produced into spinous processes. Distal margins of exopodal segments 1 and 2 of legs 3 and 4 with row of slender spinules. Inner margin of first exopodal segment of legs 1 to 4 ornamented with short setules. Spine and seta formula for legs 1 to 4 as follows:

coxa	basis	exopod	endopod
leg 1	0-1	I-1 I-0; I-1; III,I,3	0-1; 1,2,3
leg 2	0-1	1-0 I-1; I-1; II,II,4	0-1; 0-2; 1,2,3
leg 3	0-1	1-0 I-1; I-1; II,II,4	0-1; 0-2; 1,2,3
leg 4	0-1	1-0 I-1; I-1; II,II,3	0-1; 0-2; 1,2,3

Fifth leg (Fig. 2H) symmetrical, uniramous, intercoxal sclerite absent. Ramus 4-segmented; proximal segment short, subquadrate, representing the coxa, followed by slightly longer basal segment armed with single outer seta. Endopod absent. Exopod 2-segmented, proximal segment with stout, strong outer spiniform seta reaching well beyond distal margin of second exopodal segment. Distal segment bearing strong inner spiniform uniserially dentate process (Fig. 4A) arising from proximal margin plus two subequal spiniform distal elements. In some specimens the outermost apical element is clearly shorter than adjacent apical element (arrowed in Fig. 2I).

Adult male.—Body (Fig. 3D) as in female, including well-developed conical rostrum (Fig. 3E). Antenna, mouthparts and swimming legs 1–4 as in female. Sexually dimorphic in antennule segmentation and armature, legs 5 and 6, and in urosome segmentation and ornamentation. Body length as in female, ranging between 0.56 and 0.59 mm (average 0.57 mm) ($n = 10$). Urosome 6-segmented, with genital somite expanded ventrally, 1.3 times longer than wide, longest of urosome, representing 38% of urosome length. Spermatophores attached to some female specimens paired, elongate, reniform (Fig. 4D). Sixth legs each with 2 strong spiniform elements and long seta (Fig. 3G); spiniform elements remarkably longer and thicker than in female, with 2 reduced elements (Fig. 3I).

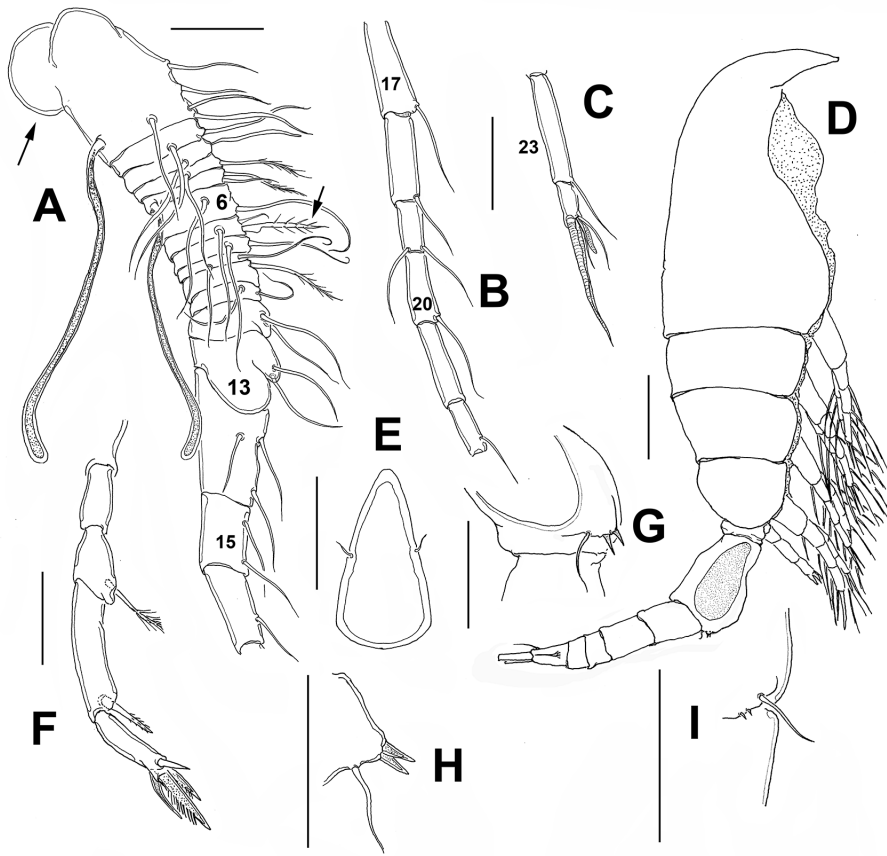


Figure 3. *Speleophria germanyanezi* n. sp., adult male allotype from Cozumel, Mexico, (A) antennule segments 1–16, rounded expansion on first segment and modified setae on segment 7 arrowed, (B) antennule segments 17–22; (C) same, segments 23–24; (D) habitus, lateral view, (E) rostrum, frontal view, (F) fifth leg, (G) posterior part of genital somite showing sixth leg, lateral view, (H) detail of sixth leg, (I) adult female sixth leg. Scale bars: A–C, E, F = 20 μ m, D = 50 μ m; G–I = 10 μ m.

Caudal rami with seta I vestigial as in female (arrow in Fig. 4H) and spinules at insertion of caudal seta II (inclined arrow in Fig. 4I), dorsal seta VII annulate, shorter than in female (transverse arrow in Fig. 4I).

Antennules (Figs. 3A–C, 4E, F) bilaterally symmetrical, similar to female in general aspect, distinctly 24-segmented with segments 2 to 11 compacted; segment 1 with dorsolateral margin moderately swollen, forming low protuberance proximally. Segmentation and armature as follows: segment 1 (I–III) 5s+ae, 2 (IV) 2s, 3 (V) 1s+ae, 4 (VI) 2s, 5 (VII) 2s+ae, 6 (VIII) 2s, 7 (IX) 3s, 8 (X) 2s, 9 (XI) 2s, 10 (XII) 1s, 11 (XIII) 2s, 12 (XIV) 2s, 13 (XV) 2s, 14 (XVI–XVII) 3s, 15 (XVIII) 2s, 16 (XIX) 1s, 17 (XX) 1s, 18 (XXI) 1s, 19 (XXII) 2s, 20 (XXIII) 1s, 21 (XXIV) unarmed, 22 (XXV) 1s, 23 (XXVI) 1s, 24 (XXVII–XXVIII) 4s +ae. Segment 7 with modified stout, basally expanded element (arrowed in Fig. 3A), segment 13 cup-shaped with proximal lobe-like process. Terminal segment with partially fused apical setae appearing as fusiform expansion of segment (Fig. 4F).

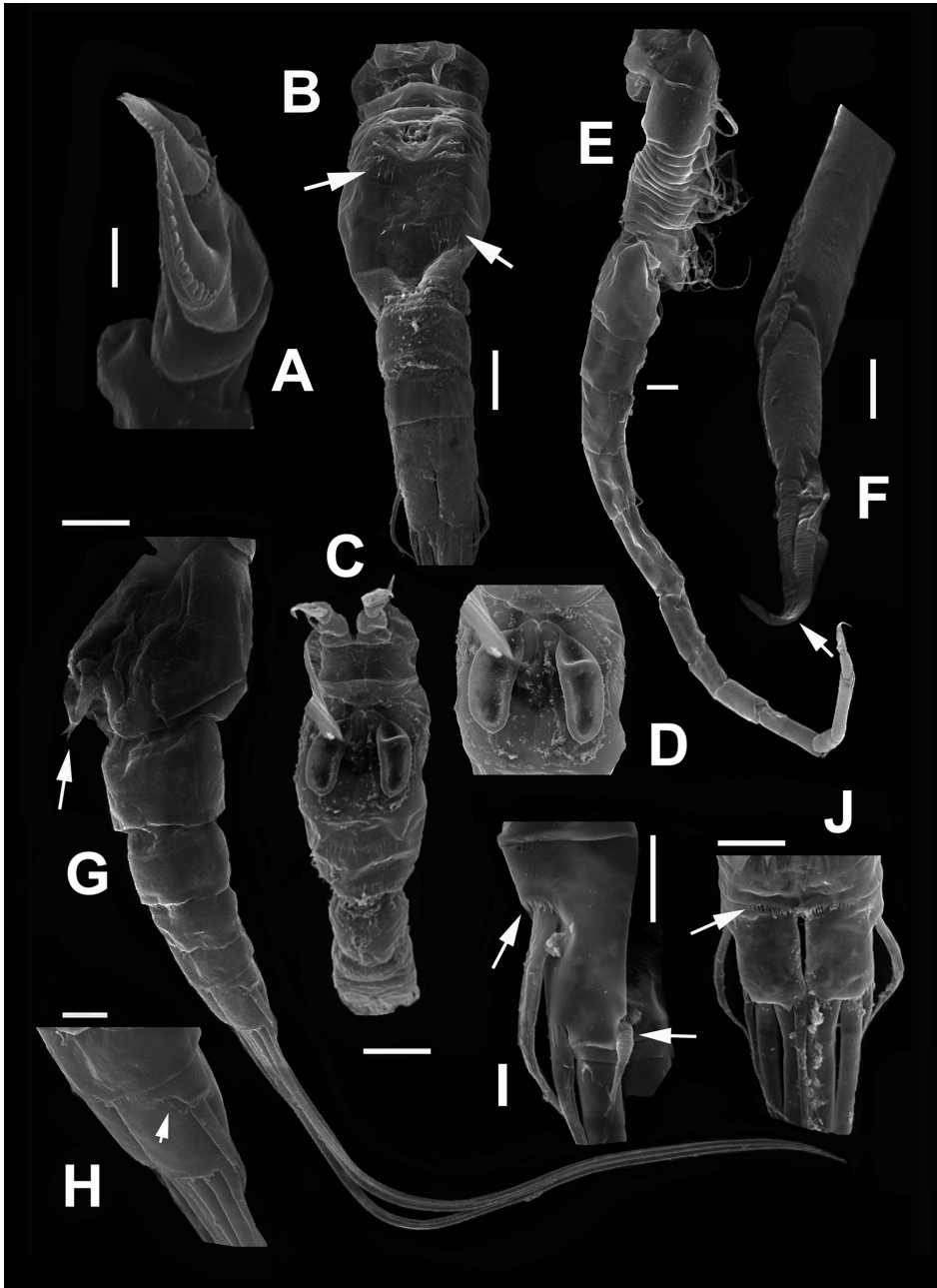


Figure 4. *Speleophria germanyanezi* n.sp. from Cozumel, Mexico, SEM-processed adult specimens. Adult female. (A) fifth leg showing ornamentation of subdistal spiniform process, (B) urosome, ventral view, hair-like elements on surface arrowed, (C) urosome, specimen with attached paired spermatophores, showing ventral row of long, slender spinules, (D) detail of reniform spermatophore with short tubules; Adult male. (E) antennule, (F) detail of last two antennular segments, (G) urosome, lateral view showing spiniform elements of sixth legs (arrowed), (H) detail of caudal ramus showing vestigial caudal seta I (arrowed), (I) caudal ramus, dorsal view showing caudal seta VII (arrowed), (J) caudal ramus, ventral view showing spinulate posterior margin of anal somite. Scale bars: A, D–F, H = 10 μ m, B, C, G, I, J = 25 μ m.

Fifth legs symmetrical, uniramous (Fig. 3F). Fifth leg more slender, relatively longer than in female, coxa also longer than in female, unarmed. Basis armed with single basipodal seta. First exopodal segment elongate, about twice as long as preceding basal segment; armed with spiniform setal element shorter and narrower than in female, barely reaching midlength of second exopodal segment. Second exopodal segment with 4 elements including subapical spiniform process narrower than in female plus 3 apical spiniform elements (Fig. 3F).

Etymology.—The species is named after Germán Yáñez, a Mexican cave diver who has enthusiastically collaborated in the collection and knowledge of the anchialine fauna of the Yucatán Peninsula.

Remarks.—The new species was identified as a species of *Speleophria* by possession of a lobate proximal segment of the antennule, with a maxillary allobasis armed with 5+3 setal elements, 2-segmented leg 1 endopod, and endopod of fifth leg absent (Jaume et al. 1998, Boxshall and Halsey 2004). One of the characters included in the genus definition is the absence of a precoxal seta on the maxilliped but it is present in the new species and also in other species of *Speleophria* (Jaume et al. 2001, Kršinić 2008). Another originally proposed generic character with variations is the number (4) of inner elements on leg 4 third exopodal segment, most known species have 3 (see Table 1).

Currently, five nominal species of *Speleophria* are known: *Speleophria bivexilla* Boxshall and Iliffe, 1986 from Bermuda, *Speleophria gymnesica* Jaume and Boxshall, 1996 from the Balearic Islands, *Speleophria bunderae* Jaume, Boxshall and Humphreys, 2001 from north-western Australia, *Speleophria mestrovi* Kršinić, 2008 from Croatia, and *Speleophria nullarborensis* Karanovic, 2009 from southern Australia (Jaume et al. 2001, Kršinić 2008, Karanovic and Eberhard 2009). Males are known only for *S. bunderae* and *S. mestrovi*. The new species, *S. germanyanezi* differs from all other members of the genus by a combination of characters. The presence of a proximal bulb-shaped process on the first antennular segment is a character shared by most of its congeners, but it has its strongest expression in *S. mestrovi* (Kršinić 2008, fig. 2D) and absent in *S. bivexilla* (Boxshall and Iliffe 1986) and *S. nullarborensis* (Karanovic and Eberhard 2009); the process is weak in *S. gymnesica* (Jaume and Boxshall 1996a, fig. 5A) and in male and female *S. bunderae* (Jaume et al. 2001, fig. 10A, B) but it is moderately developed in both sexes of the new species (Figs. 1D, 3A, 4E). Particularly, the new species differs from the Australian *S. nullarborensis* by its possession of a 2-segmented leg 1 endopod; this character is shared with most of its congeners except for *S. nullarborensis* which is distinguished by its 3-segmented leg 1 endopod (Karanovic and Eberhard 2009). In addition, the female fifth leg of the new species from Cozumel has relatively short, thick apical elements vs long, slender elements in *S. nullarborensis* (Karanovic and Eberhard 2009, fig. 20). The outer spine on the second segment of the fifth leg is slender in *S. nullarborensis*, barely reaching the distal margin of the succeeding segment whereas this element is remarkably stout, thick and longer, reaching well beyond the distal margin of the third segment (Fig. 2H). The anal somite is distinctively constricted in *S. nullarborensis* (Karanovic and Eberhard 2009, figs. 7–9), a feature absent in the new species. The new species has some affinities with *S. bivexilla*, like the armature of the mandibular palp and the maxillule (see Table 1), but it is easily distinguished from *S. bivexilla* because this species has 4 short elements on the distal segment of the female fifth leg (Boxshall

and Iliffe 1986, fig. 1D) and 22 segments in the female antennule; these are unique characters not found in any other species of this genus. Also, the new species has 3 inner setae on leg 4 third exopodal segment, thus differing from the 4 setae present in *S. bivexilla* and *S. gymnesica*, and the 3 spines found in *S. bunderae* and *S. mestrovi* (see Table 1).

The new species has several affinities with the Croatian species *S. mestrovi*, including a female fifth leg with 3 elements on the distal segment and the male fifth leg with 4, a similar setation pattern of legs 1–4, except for the lack of modified spiniform setae on the exopods and endopods of legs 3 and 4 (Kršinić 2008, fig. 4C, D) and a similar structure and armature of the mouthparts, except for the armature of the mandible palp (see Table 1). Both species share a long innermost caudal seta which is longer than the outermost seta. These two species can be easily distinguished by the size of the postgenital somite which is remarkably long in *S. mestrovi*, about 1.5 times as long as the succeeding preanal somite (Kršinić 2008, fig. 1C); this somite is as long as the preanal somite in the new species. Also, the male genital somite is strongly globose in *S. mestrovi* (Kršinić 2008, fig. 5A) and relatively elongate and ventrally expanded in the new species (Fig. 3D). The spermatophores have been depicted only for *S. mestrovi*, it is a single one with a relatively long tubule (Kršinić 2008, fig. 2A), thus contrasting with the short tubules observed in the pair of spermatophores observed in the new species (Fig. 4C, D). In addition, the inner spiniform process on the female fifth leg is strongly curved outwards (Kršinić 2008, fig. 4E) vs straight in the new species and the outer element on the first exopodal segment is shorter and narrower than in the new species. Overall, the new species can be readily distinguished from its congeners by the presence of slender spinules on the ventral surface of the female genital double-somite (arrowed in Fig. 4B). In all other known species, the ventral surface of this somite is unornamented.

The male of the new species differs from that of *S. bunderae* by its 22-segmented antennules; the new species has 24, sharing this character also with *S. mestrovi* (Kršinić 2008). In addition, it has 4 elements on the fifth leg vs. only three present in *S. bunderae*. The sixth leg of the new species, with two short spiniform and one long outer setal elements (Figs. 3H, 4G) differs from that of the two other species for which males are described: *S. mestrovi*, armed with three long setae (Kršinić 2008, fig. 5C) and *S. bunderae*, with three unequally long elements of which the innermost is longest (Jaume et al. 2001, fig. 9E). Additional comparative characters of the new species and its known congeners are presented in Table 1.

DISCUSSION

Several contributions about the distributional patterns of misophrioid copepods point to the notion that shallow benthic ancestors of these anchialine taxa dwelled around the coastal and hyperbenthic habitats of the Tethys Sea during the Mesozoic and that these ancestral populations were separated by processes related to plate tectonics. The most speciose misophrioid genera each display a remarkable disjunct distribution with species known from anchialine habitats in at least two ocean basins (Boxshall et al. 2014). Hence, their current extremely disjunct distributional pattern is best explained by vicariant processes; the resulting populations were able to colonize new anchialine habitats or they were already colonized (Boxshall and Jaume 2000, Boxshall and Halsey 2004). In the Northwestern Tropical Atlantic (NWTA),

the YP (Maya Block) shared the same origin with the Florida-Bahamas plate during the separation of the Pangaea (160 MYA) but were separated later (100 MYA) so both remained isolated for a very long period (Iturralde-Vinent and MacPhee 1999). A further diversification of the subterranean crustacean fauna took place 96-85 MYA (Bauzá-Ribot et al. 2012). These events appear to be related to both the origin of the ancestral misophrioid fauna in the NWTa and its eventual divergence and diversification at the genus level. It is generally assumed that these resulting fractions, almost confined to anchialine conditions, have very reduced potential for dispersal and are thus deemed highly endemic. The two Australian species of *Speleophria* are not the most closely related; one of them resembles the Mediterranean *S. gymnesica* (Karanovic and Eberhard, 2009). This is also true when comparing the YP *Speleophria* with its closest congener, *S. bivexilla* from the Bermuda, they have many differences in important characters as discussed above and shown in Table 1. In addition, Bermuda has different geological origin and conditions (i.e., volcanic, emerged 33 MYA, caves dry 0.18 MYA) (Coates et al. 2013) when compared with the YP. These regional divergences add to the idea of intra-regional isolation among species of this genus.

According to Boxshall et al. (2014), relationships among species of *Speleophria* revealed the amphiatlantic pair *S. gymnesica* (Mediterranean)–*S. bivexilla* (Bermuda) as sister taxon of *S. bunderae* from western Australia. The new species appears to be most closely related to the Croatian *S. mestrovi*, a basal species in the genus together with the Australian *S. nullarborensis* (Boxshall et al. 2014). This affinity suggests *S. germanyanzezi* as the NWTa counterpart of *S. mestrovi* and thus would support the disjunct amphiatlantic distributional pattern of morphologically close forms among misophrioids.

The history of Cozumel Island is partially independent from that of the geologically old YP, a massive karstic plate that remained submerged or partially submerged for about 200 MY; the complete plate emerged about 2.8 MYA (Pliocene) (Vázquez-Domínguez and Arita 2010) and the younger northeastern coast surfaced 1.8 MYA. In contrast, Cozumel Island emerged relatively recently (0.12 MYA) as a block of land pushed upward between two fault lines of Pleistocene origin deposited over older Miocene and Pliocene bedrock. The timing difference in the geological history of these two areas suggests that the finding of this new *Speleophria* in Cozumel Island would result either from local dispersal and secondary vicariant processes of misophrioid YP ancestors or from older Tethyan-related processes followed by regional (NWTa) dispersal through deep-sea crevicular passages.

Jaume et al. (1998) detected an undescribed species of *Speleophria* from the central eastern coast of the YP; considering the different geological history of Cozumel and the YP mainland and the low dispersal abilities of these anchialine forms, it is assumed that the species from Cozumel is not the same as that mentioned by these authors. However, it is likely that these two populations had common ancestors that dwelled in the hyperbenthic community while both landmasses were submerged. The YP main body emerged long before Cozumel so both faunas remained isolated and eventually diverged. Relatively recent local or regional dispersal through crevicular passages is a likely process to explain how misophrioids established in the YP colonized adjacent crevicular or cave habitats including the submerged island of Cozumel. Because of the isolation of the marine caves by the overlying freshwater lens during the marine regressions, the anchialine forms had dispersal opportunities

Table 1. Comparative characteristics of the known species of *Speleophria*; based on Juame et al. (2001), with additions from the present study.

Characteristics	<i>Speleophria bivexilla</i>	<i>Speleophria gymnesica</i>	<i>Speleophria bunderae</i>	<i>Speleophria mestrovi</i>	<i>Speleophria nullarboensis</i>	<i>Speleophria germanyanezi</i> n.sp.
Body size (mm)	0.37–0.40	0.57–0.64	0.56–0.63	0.60–0.72	0.49	0.56–0.59
Antennule (female)						
No. of segments	22	21	21	21	21	21
Expansion of 1 st segment	absent	present, weak	present, weak	present, strong	absent	present, moderate
Caudal ramus						
Length innermost seta/ramus	2.0	1.0	1.0	3.5	4.3	1.7
Antenna						
End/exp length ratio	1.4	2.2	2.1	1.6	2.0	1.8
End-1	clearly shorter than end-2	about as long as end-2	about as long as end-2	longer than end-2	about as long as end-2	shorter than end-2
End-2, no. of proximal setae	3	5	4	5	5	4
Mandible						
No. of setae on basis	1	0 (?)	1	1	1	1
No. of setae on palp end-1	1(?)	3	3	3	3	1
No. of setae on palp end-2	4	7	7	7	6	4
End-2	subquadrate	long, slender	long, slender	subrectangular	subrectangular	long, slender
Maxillule						
No. of setae on coxal epipodite	7	7 (?)	8	8	8	7
No. of setae on exopod	8	9	9	9	9	9
Maxilla						
No. of setae on prox praecoxal endite	7	6 (?)	5	6	5	5
Maxilliped						
Praecoxal seta	absent (?)	absent (?)	present	present	present	present
No. of setae on end-1	2 (?)	1	1	1	1	1
Caudal seta I	well developed	well developed	vestigial	well developed	vestigial	vestigial

Table 1. Continued.

Characteristics	<i>Speleophria bivexilla</i>	<i>Speleophria gymnesica</i>	<i>Speleophria bunderae</i>	<i>Speleophria mestrovi</i>	<i>Speleophria nullarborensis</i>	<i>Speleophria germanyanzei</i> n.sp.
Leg 1						
Segments of enp	2	2	2	2	3	2
Leg 2						
End-3 outer armature	spine	seta	seta	seta	seta	seta
Leg 4						
Exp-3 inner armature	4 setae	4 setae	3 spines	3 spines	1 spine+2 setae	3 setae
End-2 armature	spine+seta	2 setae	2 setae	2 setae	2 setae	2 setae
End-3 distal armature	2 spines	2 spines	2 setae	2 spines	2 setae	2 setae
Female leg 5						
No. of distal elements	4	3	3	3	3	3
Seta on exp-1	shorter than segment	as long as segment	as long as segment	longer than segment	as long as segment	longer than segment
Apical exp seta	shorter than segment	longer than segment	longer than segment	as long as segment	longer than segment	as long as segment
Exopodal spiniform process	short, thick	short, thick	long, slender	long, curved	short, slender	short, thick
Male leg 5						
No. of distal elements	?	?	3	4	?	4
Male leg 6 (elements)	?	?	3 unequal setae	3 subequal setae	?	1 setiform, 2 spiniform

during marine transgressions only, as suggested by the regional distribution of ridgewayiid and epacteriscid anchialine copepods (Suárez-Morales and Iliffe 2005, Suárez-Morales et al. 2006).

After analysis of regional geological evidence, Karanovic and Eberhard (2009) concluded that the presence of *Speleophria* in northern and southern Australia can be explained mainly by dispersal, or by a significant extension of the Tethyan track down to the southern coastal margin of Australia. If it is assumed that dispersal is weak among these anchialine forms, it is unlikely that it explains a disjunct pattern implying a distance of 2000 km, thus contrasting with the distance between the YP coast and Cozumel (approximately 17 km), which could make the dispersal hypothesis more likely between the YP and Cozumel. The misophrioid fauna of the YP is probably more diverse than previously thought and it is assumed that its analysis will reveal interesting details on the biogeographic origin of regional anchialine faunas. In agreement with Boxshall et al. (2014) it is recognized that molecular analysis should be the next step to disentangle these intriguing patterns and determine the regional links of this group of stygobitic copepods.

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