

A NEW *EXUMELLA* (CRUSTACEA: COPEPODA: RIDGEWAYIIDAE) FROM ANCHIALINE WATERS OF THE WESTERN CARIBBEAN, WITH COMMENTS ON REGIONAL BIOGEOGRAPHY

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ABSTRACT

The calanoid copepod family Ridgewayiidae, with both demersal and cave-dwelling species, has representatives worldwide, but most have been known from the northwestern tropical Atlantic. Biological collections from anchialine cave environments of the Yucatán Peninsula, Mexico contained ridgewayiid copepods. These specimens were found to belong to an undescribed species of the genus *Exumella* Fosshagen. The new species of *Exumella* is distinguished by a combination of characters, including a relatively large anal somite, the presence of 24 antennular free segments in the female and 19 in the male right antennule, and by peculiar details of the structure of the male and female fifth legs. Although other ridgewayiids are present in the western Caribbean, this one represents the first record of the family in Mexico. The general distribution of the genus *Exumella* suggests a Tethyan pattern. The presence of ridgewayiids in the Yucatán anchialine systems probably results from an old biogeographic pattern derived of the presence and colonization of coastal marine ancestors. A key for the identification of the known species of *Exumella* is also included herein.

The family Ridgewayiidae is among the most representative copepod taxa in anchialine and cave environments (Fosshagen et al., 2001). Ridgewayiids have some exclusively cave-dwelling genera, but some species occur in epigeal environments such as corals, different types of shallow water demersal habitats, and at least one species has been known to be associated to an actiniarian (Humes and Smith, 1974; Ohtsuka et al., 1996). The highest diversity of this family is concentrated in the Caribbean area, but representatives of this group have been recorded in subtropical and tropical latitudes worldwide (Fosshagen and Iliffe, 1991, 2003).

There are no previous records of the family Ridgewayiidae in the Yucatán Peninsula (YP) area or in Mexico (Iliffe, 1992; Suárez-Morales and Rivera-Arriaga, 2000; Suárez-Morales et al., 2000). We (T.M.I.) collected epibenthic and zooplankton samples in hypogean habitats from several sites in different areas of the YP. Male and female specimens of copepods assignable to *Exumella* Fosshagen, 1970, one of the genera of the family Ridgewayiidae, were found in samples obtained in a large anchialine cave system of the YP. These specimens represent a new species, which is described herein. Comments on the regional distribution and biogeography of the genus are also included.

MATERIALS AND METHODS

Zooplankton samples were collected during the summer of different years (1996–2005) as part of a biological survey to determine the composition, diversity, and distribution of the freshwater and anchialine fauna of the westernmost sector of the Caribbean Basin, including the YP. One of these sites in the central part of the YP was positive for ridgewayiid copepods (Fig. 1). Biological samples were collected by SCUBA divers dragging a hand net with a fine

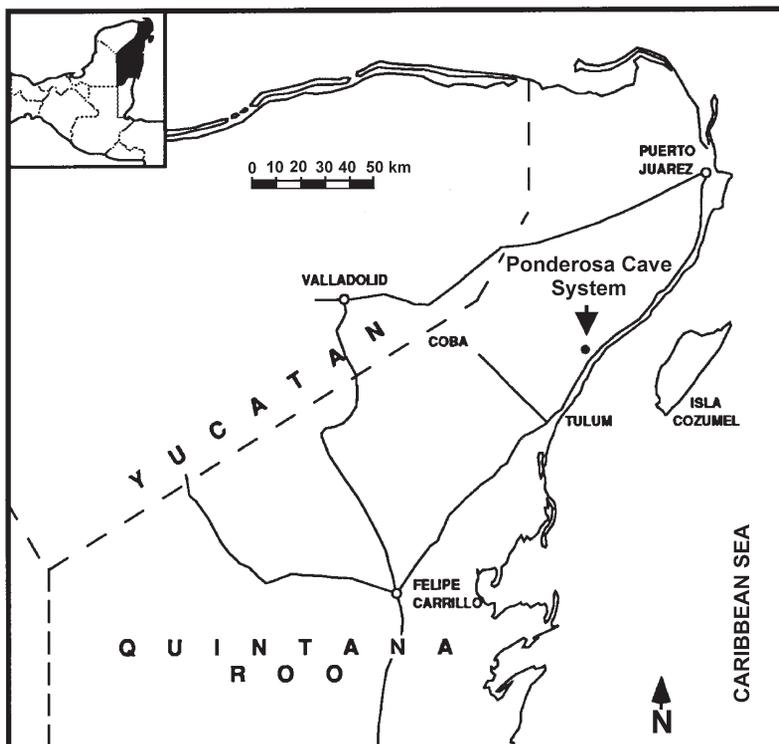


Figure 1. The Yucatán Peninsula with the location of the Ponderosa Cave System, the site in which *Exumella tsonot* n.sp. was collected.

mesh (100 μ m) through the water, or by meat-baited traps. The copepods were sorted from the original samples and preserved in 70% ethanol. Copepods were prepared for taxonomic analysis, which included dissection of the appendages and staining with Chorazol Black. The appendages were mounted using glycerine as a semi-permanent medium to perform the basic taxonomical examination. Illustrations were prepared with the aid of a camera lucida. Type specimens were deposited in the Collection of Zooplankton of El Colegio de la Frontera Sur (ECO-CHZ), Chetumal, Mexico.

STUDY AREA.—Cenote (= sinkhole) Edén is part of one of the largest known coastal karstic cave systems, the Ponderosa Cave System (see Fig. 2). It is located about 3 km south of the tourist complex of Puerto Aventuras on the central part of the eastern coast of the YP. This cenote is located 2 km inland from the coast; 15 km of cave passage, interconnecting 18 cenotes, have been explored to date. The main entrance, Cenote Edén, is a 60-m long by 40-m wide collapsed depression with a pool entirely covering the bottom. The cave water column consists of a surface freshwater layer underlain by a halocline at 10–12 m. The marine waters below the halocline are tidally influenced, yet isolated from the sea. A submerged cave passage extends 700 m from Cenote Edén to “La Capilla,” a partially air-filled chamber. All specimens were collected below the halocline in fully marine waters at depths of 10–16 m between Cenote Edén and La Capilla.

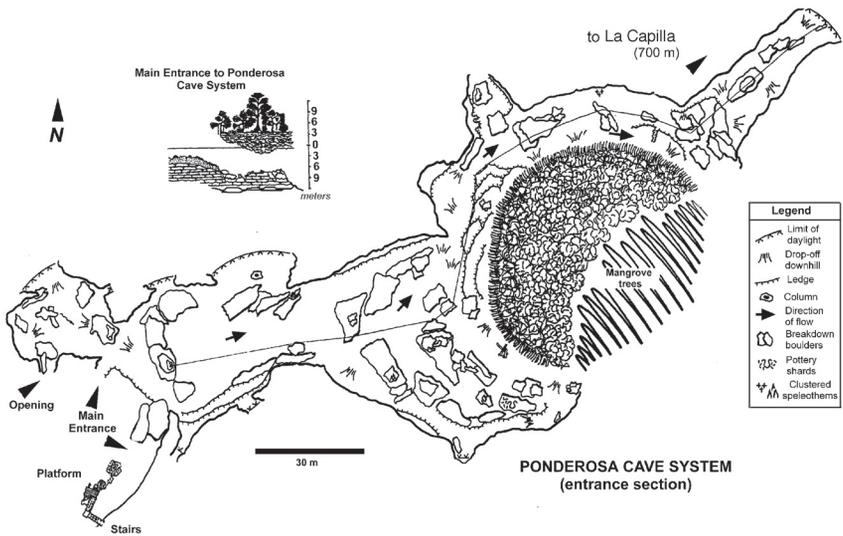


Figure 2. Cross-sectional and plan views of Cenote Edén, showing the main entrance to the Ponderosa Cave System (modified from map by Gary Walten, 1995).

SYSTEMATICS

Order Calanoida G.O. Sars, 1903

Family Ridgewayiidae M.S. Wilson, 1958 (emend. Fosshagen and Iliffe, 2003)

Genus *Exumella* Fosshagen, 1970

Exumella tsonot new species

(Figs. 3–7)

Material Examined.—Holotype, one adult female, collected by Thomas M. Iliffe, 18 June, 2004 from Ponderosa Cave System (Puerto Aventuras, Quintana Roo) (20° 29.498 N 87° 15.486 W) on the central part of the eastern coast of the YP, state of Quintana Roo, Mexico. Specimen dissected, on semi-permanent slide, deposited in the collection of Zooplankton of El Colegio de la Frontera Sur in Chetumal, Mexico, under number ECO-CHZ-02903. Allotype, one adult male, same locality and date, collected by Thomas M. Iliffe. Specimen partially dissected, ethanol-preserved, mouthparts on semi-permanent slides, ECO-CHZ-02904. Paratypes, five adult males, same locality and date, collected by Thomas M. Iliffe (ECO-CHZ-02905). Specimens undissected, ethanol-preserved.

Description.—Holotype adult female. Length of cephalothorax: 0.68 mm ($n = 1$); total length (TL) including caudal rami = 1.1 mm ($n = 1$). Body relatively slender, prosome slightly narrower anteriorly, body symmetrical (Fig. 3A). Rostrum strong, wide-based, triangular, rostral filaments paired, long, visible in lateral view, with pair of relatively large, oval integumental sensory vesicles and small sensillae on anterior surface. Last pedigerous somite symmetrical, both sides rounded, unornamented (Fig. 3A,B). Intersomite membrane between penultimate and last pedigerous so-

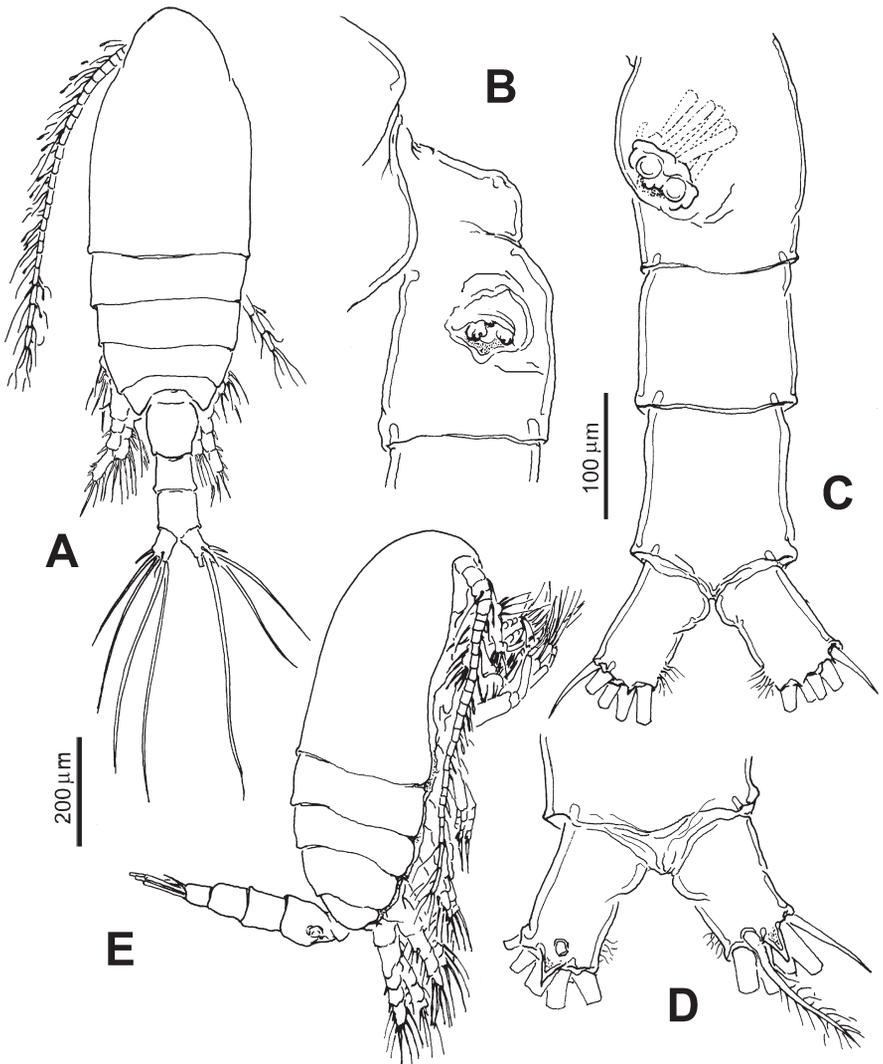


Figure 3. *Exumella tsonot* n.sp. from the Yucatán Peninsula, Mexico, adult female. A. Habitus, dorsal view; B. Genital somite, lateral view showing genital field; C. Urosome and caudal rami, ventral view; D. Caudal rami, dorsal view; E. Habitus, lateral view.

mites complete. Urosome, excluding caudal rami, representing 28% of total body length; urosome formed by three somites (Fig. 3C,E). Genital double-somite relatively large, representing 45% of urosome length, slightly asymmetrical, with left margin straight, right margin slightly protuberant. Genital double-somite asymmetrical, not expanded ventrally but laterally at mid-section, latter process associated with genital pore and genital operculum on right lateral surface (Fig. 3B,C). Anal somite subrectangular, relatively large, representing about 28% of urosome length, cuticular ornamentations absent on dorsal and ventral surfaces of urosomites.

Caudal rami (Fig. 3D) lamelliform, subquadrate, symmetrical, about $0.75 \times$ length of anal somite; with distal spiniform process on dorsal surface, near insertion of dorsal seta. Inner margin naked except for distal tuft of hair-like epicuticular ornamen-

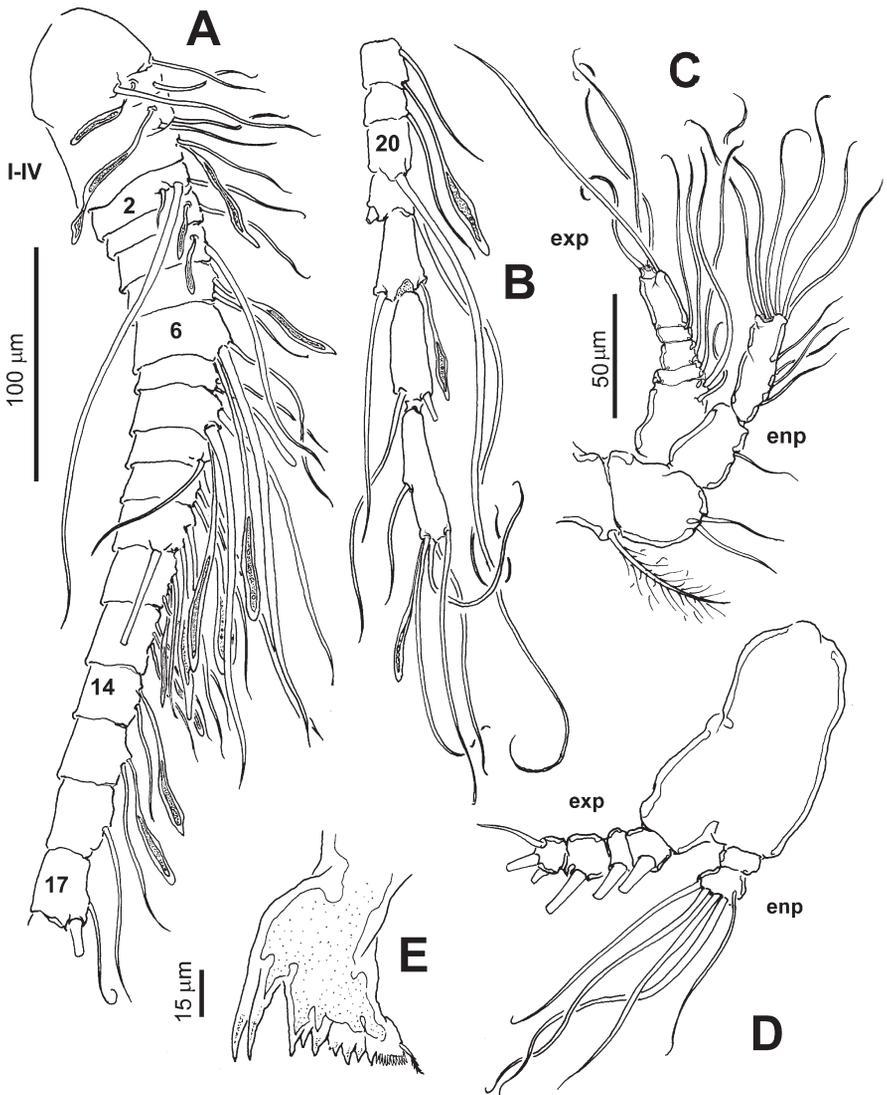


Figure 4. *Exumella tsonot* n.sp. from the Yucatán Peninsula, Mexico, adult female. A. Right antennule, anterior view, free segments 1–17; B. Same, free distal segments 18–24. Roman numbers indicate ancestral antennular segments of fusions; C. Antenna; D. Mandible with palp; E. Mandible blade. Enp = endopod, exp = exopod.

tations. Each caudal ramus with four terminal, one dorsal, and one outer spiniform seta. Dorsal seta almost as long as caudal ramus. Caudal seta V (sensu Huys and Boxshall, 1991) on left ramus slightly longer than corresponding seta on right ramus. All terminal caudal setae plumose.

Antennule (Fig. 4A,B) moderately long, with 24 free segments, reaching posterior margin of third pedigerous somite. Proximal ancestral segments (indicated by Roman numerals in Fig. 4) I–IV partially fused. Setae on free segments 2, 4, 6, 8, 10, 20, and 21–23 longest. Armature per free (not ancestral) segments as follows (Arabic

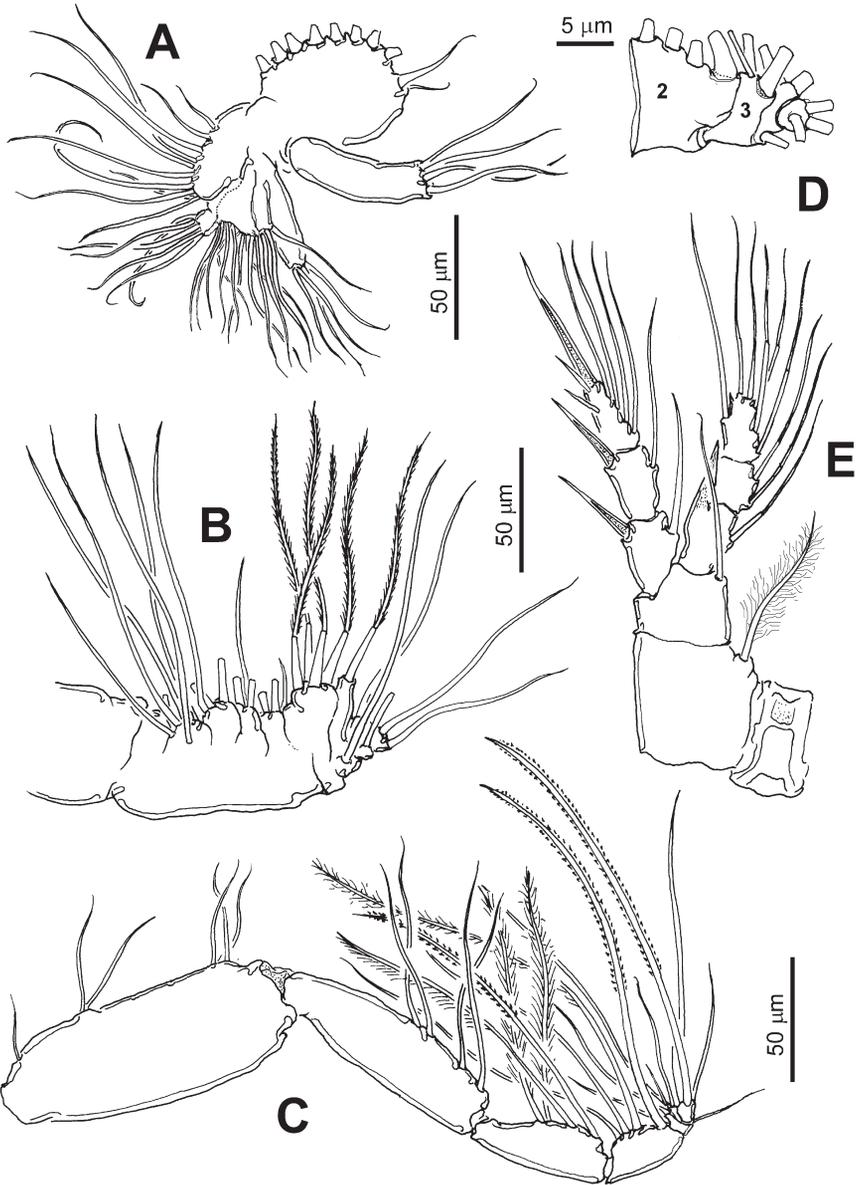


Figure 5. *Exumella tsonot* n.sp. from the Yucatán Peninsula, Mexico, adult female. A. Maxillule; B. Maxilla; C. Maxilliped; D. Detail of distal endopodal segments of maxilliped; E. First leg, anterior view.

numerals = segment, Arabic numerals in parentheses = number of setae, ae = aesthetasc): 1(6 + 3ae), 2(3), 3–5 (1 + ae), 6 (2 + ae), 7 (1 + ae), 8(2 + ae), 9 (2), 10(1 + ae), 11–13 (2 + ae), 14 (1 + ae), 15 (1 + ae), 16(1), 17 (2), 18 (1 + ae), 19 (1), 20(1), 21(2), 22(1 + ae), 23(2), 24(5 + ae).

Antenna (Fig. 4C) with exopod about 0.25 longer than endopod. Coxa with one long, biserially plumose seta. Basis with two short subequal setae on inner distal

margin. Endopod two-segmented. First segment short, robust, with one outer seta inserted on midlength. Terminal segment reduced, with one distal lobe armed with six terminal setae; medial margin of endopodal segment bearing four setae. Exopod six-segmented, with two setae on first segment, one on segments 2–5. Distal segment shortest, with three long terminal setae subequal in length and breadth.

Mandible (Fig. 4D,E) with basis of palp naked. Mandibular palp with endopod two-segmented, proximal segment short, unarmed; distal segment subquadrate, with five terminal setae, distolateral seta smallest. Exopod four-segmented, with 1, 1, 1, 3 setation pattern, respectively. Gnathobase with 9–10 wide-based medial teeth, most of them unicuspidal, one bicuspidal. Distal teeth paired, strong, both clearly separated from outermost remaining teeth by a diastema. Proximal part with serrated blade-like set of teeth next to short dorsal seta.

Maxillule (Fig. 5A) with praecoxal arthrite bearing nine stout spiniform setae plus relatively short simple seta. Coxal epipodite with 10 setae, subequal in size and width, coxal endite elongated, with four setae. Proximal basal endite lobe bearing four setae, distal lobe with three setae. Endopod reduced, one-segmented, with five distal setae. Exopod with 10 subequal setae.

Maxilla (Fig. 5B) indistinctly segmented, coxa and praecoxa partially fused, with four lobes, two praecoxal and two coxal; first lobe with six setae, one relatively short, about half the length of other four; second to fourth lobes each with three setae. Basal segment with well-developed basal lobe bearing four plumose setae. Endopod three-segmented, first segment protuberant, with two setae; second and third segments with two setae each.

Maxilliped (Fig. 5C,D) well developed. Syncoxa armed with six setae distributed in three groups along medial margin, proximalmost with one small, slender seta, second with two setae, third, distal group with three subequal setae. Basis elongated, with four long, subequal setae on inner margin, two inserted at middle of segment, two on distal third. Endopod five-segmented. First segment elongated, bearing four setae aligned on distal half of segment. Second segment shorter than first; with four setae; third segment with three setae; fourth endopodal segment with two terminal plus one dorsal seta; last segment with three distal setae.

First leg (Fig. 5E) with three-segmented exopod and endopod, coxa with large, biserially plumose coxal seta on internal margin, reaching beyond distal margin of first endopodal segment. Basipod with long, curved seta on distal inner margin reaching beyond distal end of second endopodal segment. First endopodal segment with outer margin forming strong spiniform process reaching beyond proximal margin of third endopodal segment. Legs 2–5 each with three-segmented exopods and endopods (Fig. 6A–C). Third leg with small lateral spine on basis. Fifth leg endopod with first segment produced, forming distolateral bicuspidate protuberance on outer margin (Fig. 6D); exopod modified, second segment produced laterally, armed with strong, serrate spiniform seta; third segment inserted on middle inner margin of second, armed with four lateral and terminal strong spiniform setae subequal in length. Fifth leg endopod with equal structure in both legs, with first segment bearing outer process distally bilobed. Armature formula (Roman numerals indicate spiniform elements, Arabic numerals indicate setae) of swimming legs:

Leg	Coxa	Basis	Exopod	Endopod
1	0-1	0-1	I-1;I-1;II,1,4	0-1;0-2;1,2,3
2	0-1	0-0	I-1;I-1;II,1,5	0-1;0-2;2,2,4
3	0-1	1-0	I-1;I-1;III,1,5	0-1;0-2;2,2,4
4	0-1	0-1	I-1;I-1;III,1,5	0-1;0-2;2,2,3
5	0-0	0-0	I-1;I-1;III,1,3	0-1;0-1;2,2,2

Male.—Habitus similar to female (Fig. 7D) with TL range of male specimens: 0.94–0.98 mm; mean length: 0.97 mm ($n = 7$). Length of cephalothorax: 0.69–0.74 mm, urosome 0.25–0.29 mm. Body relatively slender, smaller compared with that of the female. Fourth pedigerous somite as wide as succeeding somite; fifth pedigerous somite tapering posteriorly, symmetrical, rounded. Rostrum strong, subtriangular, rostral filaments paired, slender, rostral integumental sensory vesicles similar to those found in female (Fig. 7C). Urosome representing 24%–26% of total body length, symmetrical, four-segmented (Fig. 7D). Relative lengths of urosomites as: 21:24:25:30 = 100. Caudal rami relatively short, about 0.75 the length of anal somite. Caudal rami symmetrical, caudal seta V symmetrical on both caudal rami. Armature of caudal rami as in female, except for dorsal seta, relatively shorter than in female.

Left antennule 24-segmented, relatively longer than in female, when stretched posteriorly, last segment of male left antennule reaching posterior margin of fourth urosomite, armature as in female. Right antennule geniculate, with 19 free segments (Figs. 7A,B), ancestral segments II–IV partially fused, X–XI and XII–XIII fused. Armature of free segments as follows: 1(1 + ae), 2(4 + ae), 3(1), 4–6 (1 + ae), 7(2 + ae), 8 (2 + 2ae), 9(3 + ae), 10–14 (2 + ae), 15(1), 16 (2 + ae), 17 (3 + ae), 18(2), 19 (5 + ae). Longest setae on free segments 3, 7–10, and 15. Mouthparts and swimming legs 1–4 as described for female, except for males having only four setae on distal endopodal segment of mandibular palp instead of five as in female.

Fifth leg biramous, asymmetrical (Fig. 7E,F). Both legs with coxa elongated, unarmed, joined to quadrate intercoxal plate. Basis subquadrate, with relatively long, slender basipodal seta inserted on middle of lateral outer margin. Right fifth leg (Fig. 7E) with endopod three-segmented, shorter than exopod of same leg; first segment unarmed, outer margin of first endopod with large digitiform process projected laterally; second segment with single inner seta; third segment armed with six setae. Exopod two-segmented, first segment cylindrical, elongated, with short outer spiniform seta, second with three elements, two terminal spiniform seta armed with spinules, inner one largest, about three times longer than outer seta, distally blunt. Third element represented by long, slender spiniform process expanded from inner distal corner of segment, with hyaline membrane from distal half of segment to tip of process.

Left fifth leg (Fig. 7F) with endopod three-segmented, first segment unarmed, with distolateral margin produced in subtriangular process. Second segment armed with medial seta; third segment armed with six setae, two outer, two terminal, two inner. Exopod of left leg two-segmented, modified. First segment elongated, distomedial margin with rounded protuberance, with strong distolateral spiniform seta armed with spinules on outer margin only; spiniform seta reaching beyond apex of second exopod segment. Distal segment of exopod tapering to acute point armed with row of spinules on inner margin; short strong distolateral spiniform process and disto-

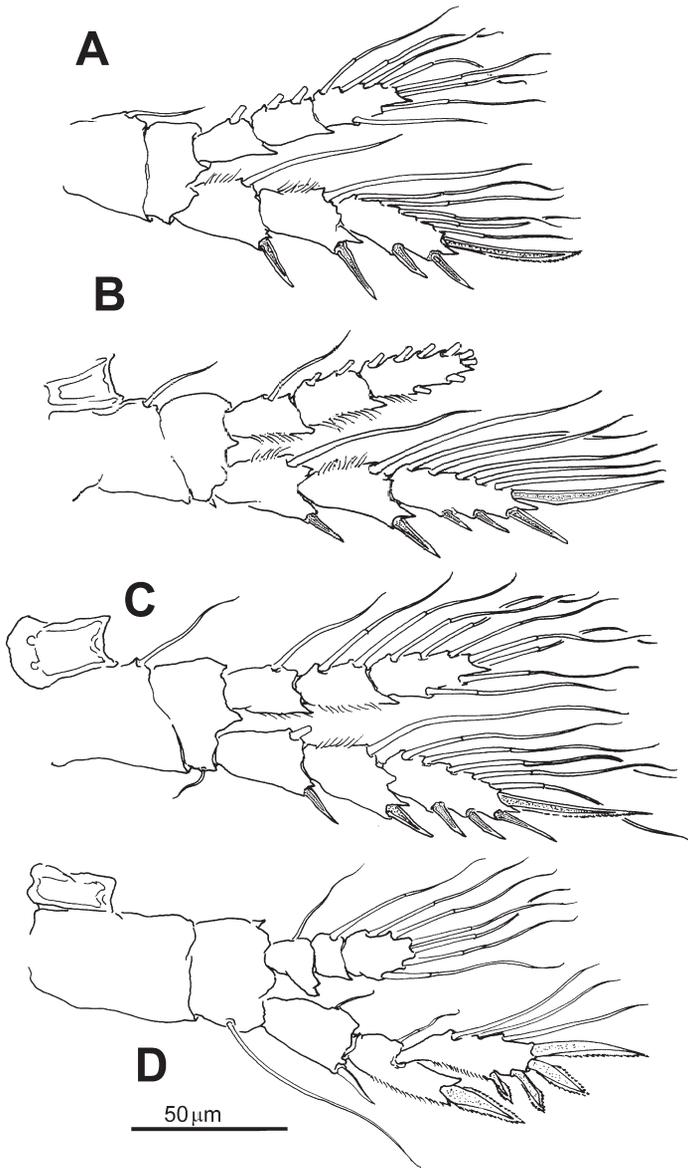


Figure 6. *Exumella tsonot* n.sp. from the Yucatán Peninsula, Mexico, adult female. A. Second leg; B. Third leg; C. Fourth leg; D. Fifth leg. All appendages in anterior view.

medial process narrowing distally, bifid at apex; process not articulated with bearing segment.

Etymology.—This species epithet is a noun in apposition derived from the Mayan term *ts'onot* meaning sinkhole; it is also the root of the Spanish word *cenote*. It makes reference to the type of environment in which this species was recorded.

Remarks.—The new species was assigned to the ridgewayiid genus *Exumella* for the following reasons: body not compressed laterally, female urosome three-segmented, male with four urosomites, a strong pointed rostrum with a pair of filaments, a well-

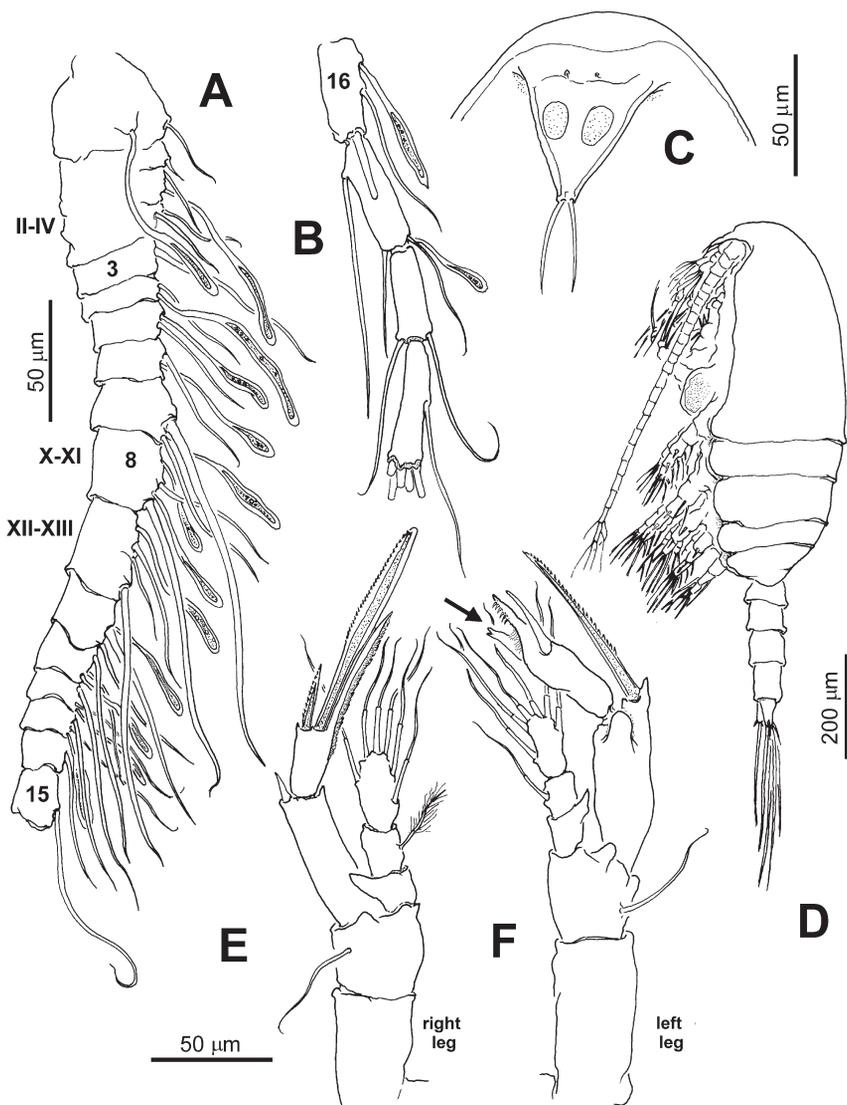


Figure 7. *Exumella tsonot* n.sp. from the Yucatán Peninsula, Mexico, adult male allotype. A. Right antennule segments 1–15, anterior view; B. Same, distal segments 16–19. Roman numbers indicate ancestral segments of fusions; C. Rostrum, ventral view; D. Habitus, lateral view; E. Right fifth leg; F. Left fifth leg.

developed maxilliped with two extremely elongate setal elements on the endopod, and both rami of the fifth legs of the female three-segmented, whereas the male has a two-segmented, elongated fifth leg exopod with long spines. Apex of male left exopod modified.

Hitherto, there were three nominal species recognized within the genus *Exumella*, *E. polyarthra* Fosshagen, 1970, *E. tuberculata* Grahame, 1979, and *E. mediterranea* Jaume and Boxshall, 1995. The new species differs from its other congeners as follows. A tuberculated process is absent on the fifth thoracic somite; this character

is exclusive of *E. tuberculata*. The new species has 24-segmented antennules in the female instead of 25 in *E. tuberculata* (see Grahame 1979), 26 in *E. polyarthra* (see Fosshagen, 1970), and 27 in *E. mediterranea* (see Jaume and Boxshall, 1995). This is among the most reduced condition of the antennule segmentation within the family.

The new species also differs from its congeners in having a reduced number of setae (10) on the second segment of the antennal endopod; this character is shared with *E. mediterranea*, whereas the figure is 11 in *E. polyarthra* and 14 in *E. tuberculata*. The new species differs from *E. mediterranea* by having one seta on the first segment of the antennal endopod, vs two in the latter species; also, *E. mediterranea* bears two distinctive brush-like scales on the second segment of the antennal endopod (Jaume and Boxshall, 1995).

The setation pattern of the terminal endopodal segment of the mandibular palp is different in three of the species; there are four setae in *E. tuberculata*, six in *E. polyarthra* and *E. mediterranea*, and five in the new species. The ventralmost teeth of the gnathal blade are unicuspidal in *E. tuberculata* and in the new species, whereas they are bifurcated in *E. polyarthra* and multi-cuspidal, brush-like in *E. mediterranea*.

The swimming legs 1–4 have few distinctive characters. The new species has a relatively large, subacute outer spiniform process on the first endopodal segment of the first leg. This process is absent in *E. tuberculata* and relatively short in both *E. polyarthra* and *E. mediterranea*; the process is clearly rounded in the latter species (see Jaume and Boxshall, 1995).

The fifth legs of the female are, in general, very similar in these four species, with the spines of the third exopodal segment increasing in size towards the distal margin and with an outer process on the first endopodal segment. However, in the new species the latter process is bifurcate at apex (see Fig. 6D), whereas it is subtriangular, distally simple, in the other three species.

The male fifth leg of *E. tsonot* n.sp. also has the same basic structure found in the other species; differences are subtle but helpful in separating the species (see Jaume and Boxshall, 1995). The right leg has a long, cylindrical first exopod with a small outer spine and the second segment is about half the length of the first one. It carries three elements distally, one short, stout outer spine, a long, distally blunt middle spine, and a slender, curved process with a hyaline lamella on the inner margin. The new species shows differences in these structures. The first, outer distal spine is longest in the new species, it reaches beyond the proximal third of the middle spine (Fig. 7E); this spine does not reach the proximal 0.2 in the other known species of *Exumella* (see Jaume and Boxshall, 1995, figs. 5E, 8D,F). The inner spiniform process is clearly curved inwards in *E. polyarthra*, *E. tuberculata*, and *E. mediterranea*, whereas it is straight in the new species.

The left male fifth leg shows additional distinguishing characters. One of them is the relative length of the outer spiniform seta on the first exopodal segment; it reaches beyond the distal end of the third exopod (see Fig. 7F), whereas it is shorter in the three other species, not reaching the distal end of the exopod (Grahame, 1979, fig. 5b; Fosshagen, 1970, fig. 7c; Jaume and Boxshall, 1995, fig. 5C). The new species has a pronounced protuberance on the distal end of the first exopodal segment. This structure is absent in the other known species of *Exumella*. Also, the innermost projection of the third exopodal segment is different in the four species; terminally truncate in *E. polyarthra* and *E. mediterranea*, with an acute end in *E. tuberculata*, and bifid in the new species. Also, the basipodal seta is shortest in the new species.

The male right antennule has 19 free segments in both *E. tuberculata* and the new species; it has 20 in both *E. polyarthra* and *E. mediterranea*. These differences seem to be evidence enough to separate *E. tsonot* as a new species.

DISCUSSION

Representatives of *Exumella* have been recorded from different epigeal and hypogean habitats, including a plankton trawl in de-oxygenated turbid water (Grahame, 1979), sandy bottoms and mixed sand and algal bottoms (Fosshagen, 1970), and from anchialine caves (Jaume and Boxshall, 1995; this survey). The marine ancestors of the cave-dwelling calanoid copepods, such as epacteriscids and ridgewayiids, were probably hyperbenthic forms that became adapted to the oligoxic conditions present in anchialine, hypogean systems (Jaume and Boxshall, 1995). This hypothetical preadaptation would explain the occurrence of at least two species of *Exumella* (*E. mediterranea*, *E. tsonot* sp. nov.) as colonizers of the challenging inland subterranean habitats. The only two other ridgewayiids known in the western Caribbean are both from Belize: *Ridgewayia klausruetzleri* Ferrari, 1995 from a coral reef system, and *Brattstromia longicaudata* Fosshagen and Iliffe, 1991 from an anchialine cave.

The stygobitic and anchialine crustacean fauna of the YP includes a number of cyclopoid copepods, mostly cyclopids (Fiers et al., 1996, 2000). Hitherto, there is only one other record of a calanoid found in the anchialine environments of the Yucatán, a species of the epacteriscid genus *Balinella* (E. Suárez-Morales and F. Ferrari, National Museum of Natural History, Smithsonian Institution, unpubl. data). The regional distribution of the family Ridgewayiidae in the tropical northwestern Atlantic (mostly in the Caribbean area; Fosshagen, 1970; Fosshagen and Iliffe, 1991, 2003) suggested that members of this group could well be present in the anchialine caves of the YP, in the northwestern sector of the Caribbean Basin. The new species of *Exumella* represents the first record of the family Ridgewayiidae in Mexico (see Suárez-Morales et al., 2000). The other species of *Exumella* are known from Jamaica (*E. tuberculata*; Grahame, 1979) and the Bahamas (*E. polyarthra*; Fosshagen, 1970). *Exumella mediterranea* represents the only representative of the genus known outside the Caribbean region; it was described from specimens recorded in anchialine caves of the Balearic Islands and Sardinia, Mediterranean Sea. *Exumella tsonot* n.sp. is the only species of the genus found in a continental, coastal anchialine system; a species of the ridgewayiid genus *Brattstromia* was recorded from a non-continental anchialine system in Belize (Fosshagen and Iliffe, 1991).

The general distribution of ridgewayiids, with most species in the northwestern tropical Atlantic, but with representatives worldwide is taken to indicate a Tethyan distribution (Cals and Monod, 1988; Iliffe, 1992); the exploration of caves is slowly revealing these old patterns. It is speculated that the discovery of *E. tsonot* n.sp., in the YP is in agreement with the old origin and early isolation of the anchialine fauna of the Yucatán.

The geological history of the YP is strongly linked with that of the Caribbean and Central America. The YP crustacean stygobitic fauna has clear affinities to that known from the Bahamas and Bermuda (see Holsinger, 1986; Iliffe, 1992) and the presence of the ridgewayiid *Exumella* in the YP confirms this biogeographic link.

The natural history of the YP has been influenced by episodes of marine regressions and transgressions of variable intensities. In the Upper Oligocene-Lower Miocene, part

of the eastern coast, where both epacteriscid and ridgewayiid copepods were recorded, remained emerged but most was a shallow marine area, an environment in which these forms could have initiated the colonization of hypogean, brackish habitats. Because of the isolation of the marine caves by the overlying freshwater lens during the marine regressions, the anchialine forms had dispersal opportunities during marine transgressions only. The current distribution of ridgewayiids in the region is a result of different events of colonization and diversification.

Both the continent-island vicariance theory of Rosen (1976) and the model of island-island vicariance (Iturralde-Vinent and MacPhee, 1999) might explain the current distributional pattern of *Exumella* and other ridgewayiids in the Caribbean area. Under the premises of the first theory, the ancestors of ridgewayiids were present in the shallow seas around the Maya Block, which came in contact first with the Florida-Bahamas Block and later on with the drifting proto-Antilles. The coastal edges of these ancient islands were colonized by marine benthic or epibenthic marine forms that were tectonically transported eastwards to their current position. For Iturralde-Vinent and MacPhee (1999), the continental Maya Block, to which the YP belongs, had an early contact with western Jamaica, but contact with the Lesser Antilles was only brief; this would explain the presumed absence of ridgewayiids in the Lesser Antilles, although this could be an effect of the lack of specific surveys in the area. Hence, for *Exumella* and probably for other ridgewayiids as well, the oldest regional populations might have been those connected to the continental mainland (YP). The discovery of *E. tsonot* as a representative of the continental lineage of ridgewayiids supports Rosen's (1976) continent-island vicariance mechanism. Remipedes, the oldest crustaceans known, are present in the same area of the YP where this new ridgewayiid was found (Yager, 1987, 1991). This also suggests an old origin of this species in the Caribbean. The discovery of *E. mediterranea* in the eastern Atlantic could be explained as part of this pattern by speculating that after the break up of the Pangaea, ancestral forms of these copepods were already present and populations were separated tectonically.

KEY FOR THE IDENTIFICATION OF THE KNOWN SPECIES OF *EXUMELLA*

- 1A Fifth thoracic somite with conspicuous protuberances, 25 antennular segments on female, 14 setae on second segment of antennal endopod *E. tuberculata* Grahame, 1979
- 1B Fifth thoracic somite without protuberances, more than 25 antennular segments, <14 setae on second antennal endopod 2
- 2A Inner process on first endopodal segment of first leg short, distally rounded; second exopod of male right fifth leg with outer spine short, not reaching proximal third of middle spine; male right antennule with 20 free segments. Innermost projection of third exopodal segment of male left leg distally truncated..... 3
- 2B Inner process on first endopodal segment of first leg long, distally acute, first exopod of male right fifth leg with outer spine reaching proximal third of succeeding segment; male right antennule with 19 free segments. Innermost projection of third exopodal segment of male left leg distally bifurcated..... *E. tsonot* n.sp.
- 3A Ventral teeth of mandibular blade bicuspidal; second segment of antennal endopod with pair of distinctive brush-like scales..... *E. mediterranea* Jaume and Boxshall, 1995
- 3B Ventral teeth of mandibular blade brush-like; without scales on second segment of antennal exopod *E. polyarthra* Fosshagen, 1970

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