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TULUWECKELIA CERNUA, A NEW GENUS AND SPECIES OF STYGOBIONT AMPHIPOD CRUSTACEAN (HADZIIDAE) FROM ANCHIALINE CAVES ON THE YUCATAN PENINSULA IN MEXICO

JOHN R. HOLSINGER

Department of Biological Sciences, Old Dominion University, Norfolk, Virginia 23529, U.S.A.

ABSTRACT

Tuluweckelia cernua, a new genus and species of stygobiont amphipod is described from six anchialine caves near the northeastern coast of the state of Quintana Roo on the Yucatan Peninsula in Mexico. The new genus is closely allied morphologically with *Mayaweckelia* Holsinger, which is also recorded from caves on the Yucatan Peninsula. Both taxa have probably evolved from marine ancestors since the late Tertiary.

ZUSAMMENFASSUNG

Tuluweckelia cernua, eine neue Gattung und Art stygobionten Amphipoden, in sechs anchialinen Höhlen an der Nordost Küste des Mexikanischen Bundeslandes Quintana Roo auf der Yukatan Halbinsel gefunden, wird hier aufgezeichnet. Die neue Gattung ist morphologisch *Mayaweckelia* Holsinger, welche auch aus Höhlen auf der Halbinsel Yukatan beschrieben ist, nahe verwandt. Beide Taxa stammen wahrscheinlich von einem gemeinsamen marinen Vorfahren aus dem späten Tertiär.

INTRODUCTION

Exploration of caves along the northeastern coast of the Yucatan Peninsula near the old Mayan city of Tulum by biologically trained cave divers in 1986-87 resulted in the discovery of a number of taxonomically diverse communities of stygobiont crustaceans. Most of the caves investigated contain deep, water-filled chambers and are thus explorable only by trained divers. Although these caves have entrances that open on dry land, they have subterranean connections to the nearby sea and are therefore, by definition, anchialine habitats. Yucatan caves in general are known locally as "cenotes" and many have well-like entrances (see Reddell, 1981: 55-56).

Among the various crustaceans collected by divers were specimens of the new genus and species of hadziid amphipod described below. Specimens of the closely related, sister genus *Mayaweckelia* Holsinger, which is composed of two species previously described from caves on the Yucatan Peninsula, were also collected from one cave. To facilitate critical comparsion of *Tuluweckelia* n. gen. and *Mayaweckelia*, a partial redescription of *Mayaweckelia cenoticola* Holsinger is given and the geographic distribution of both genera is plotted.

Tuluweckelia, new genus

Diagnosis. — Without eyes and pigment, of stygobiont (aquatic troglobitic) facies. Anterior region of body (including first 4 pereonites) bent downward at sharp angle. Head relatively small; lateral lobe small, cone-shaped; inferior antennal sinus shallow. Antenna 1 elongate, at least 75% length of body, longer than antenna 2; esthetascs on proximal primary flagellar segments; accessory flagellum 3-segmented. Antenna 2, segment 4 of peduncule little longer than 5. Upper lip symmetrical, apex rounded and unnotched. Mandibles: molar prominent, triturative; lacinia mobilis and molar seta present on both; palp absent. Outer lobes of lower lip strong, inner lobes small but fleshy. Maxilla 1: inner plate with few naked, apical setae; outer plate armed with 9 apical, serrate/pectinate spines; palps subequal, 2-segmented, with 8-10 bladespines. Maxilla 2: inner plate broader than outer plate, with oblique row of naked facial setae. Maxilliped: outer plate broader than inner plate, expanded distomedially, distal half of inner margin and apex with row of setae; palp normal, dactyl rather long and arcuate.

Gnathopods not sexually dimorphic. Gnathopod 1: propod subequal in length to carpus, palm long, oblique, armed with double row of unnotched spines; merus elongate, with prominent distoposterior lobe. Gnathopod 2: propod long and relatively narrow, subequal in length to carpus, palm long and oblique, armed with double row of unnotched spines. Coxal plates of gnathopods large, deeper than broad, margins with spines. Pereopods 3 & 4 subequal, except coxa of 4 much larger and expanded distally. Pereopod 6 longer than pereopods 5 or 7, at least 85% length of body; bases short and broad; dactyls proportionately elongate, bearing both setae and spines. Coxal gills large, with distinct peduncles, present on pereopods 2-6. Sternal gills absent. Brood plates narrow, sublinear, with numerous, long marginal setae. Distoposterior corners of pleonal plates 2 and 3 produced and rounded. Pleopods biramous, not sexually dimorphic, peduncles with 2 rather long coupling spines.

Uronites free (not fused), uronite 3 with 2 small dorsal spines. Uropods 1&2 not sexually dimorphic. Peduncle of uropod 1 without basofacial spine; outer ramus of uropod 2 distinctly shorter than inner ramus. Uropod 3 biramous, proportionately elongate; rami relative narrow, margins with setae/spines; outer ramus 1-segmented, little shorter than inner, outer margin with row of small spines but lacking setae. Telson relatively long, lobes completely separate and armed with both lateral and medial spines.

Type species. *Tuluweckelia cernua* Holsinger (by monotypy). Gender feminine.

Etymology. The generic name is derived by a combination of *Tulu*, which comes from the geographic place name Tulum, and *Weckelia*, the name of a potentially related Greater Antillean genus.

Relationship. Although *Tuluweckelia* is closely allied with *Mayaweckelia*, a number of major differences clearly warrant its recognition as a separate genus. Whereas the overall structural similarity of the mouthparts, gnathopods, uropods, and telson of these genera suggest a close morphological and phylogenetic alliance, *Tuluweckelia* differs significantly in 8 or 9 characters. These include: the peculiar anterior bending of the body; supernumerary esthetascs on flagellum of antenna 1; relatively spinose peduncle segment 4 of antenna 2; gnathopods not sexually dimorphic; short, broadened bases and elongate spinose dactyls of pereopods 5-7; produced distoposterior corners of pleonal plates 2&3; and proportionately long, relatively narrow 3rd uropod.

Tuluweckelia cernua, new species (Figs. 1-3)

Material examined. — MEXICO. Quintana Roo: Temple of Doom Cenote, 1.5 km NW of Tulum, holotype ♀ and 2 ♀ paratypes, J. Yager, 20 Sept. 1987. Additional paratypes from Quintana Roo as follows: Temple of Doom Cenote, 1 juv., D. Williams, 20 June 1986, and 1 ♂ and 1 juv., T. Iliffe, 10 Nov. 1986; Cueva de la Calavera, Rancho San Carlos, 1 juv., T. Iliffe, 8 Nov. 1986; Carwash Cenote, 8 km NW of Tulum, 1 ♂ and 4 ♀,

J. Bozanic, 18 Feb. 1986, and 4 ♀, D. Williams, 19 June 1986; Mayan Blue Cenote 3 km S of Tulum, 4 ♀, J. Yager, 19 Sept. 1987, and 1 ♂, 7 ♀ and 7 juvs., T. Iliffe, 7 Nov. 1986, and 1 ♀, M. Madden, 2 Oct. 1987; Cenote Mojara, Pamul, 1 ♂ and 6 ♀, T. Iliffe, 14 Nov. 1986; Naharon (= Najaron) Cenote, 3 km SW of Tulum, 4 ♀, J. Bozanic, 17 Feb. 1986, and 7 ♀ and 2 juvs., T. Iliffe, 11 Nov. 1986.

The holotype and 2 paratypes are deposited in the National Museum of Natural History (Smithsonian Institution) (USNM 253530, 253531); paratypes are deposited in the Zoölogisch Museum, Amsterdam (ZMA Amph. 108.691), and in the collection of the author.

Diagnosis. — With the characters of the genus. Readily distinguished from all other hadziid amphipods by the anterior region of the body, which is markedly bent downward. Largest males, 5.0 mm; largest female, 8.0 mm (but rarely exceed 7.5 mm).

Description. — Sexes generally similar, except mature female larger than mature male. Antenna 1, 75-85% length of body, about 50% longer than antenna 2; peduncle segment 1 nearly equal to combined length of segments 2&3; primary flagellum with up to 54 segments, 2 to 3 esthestascs on proximal 18-20 flagellar segments; accessory flagellum 3-segmented. Antenna 2: peduncular segments 3-5 sparsely armed with spines; flagellum with 13-15 segments. Mandible: molar large, palp absent; incisor broad, with strong teeth; lacinia mobilis of left mandible 5-dentate, that of right mandible 3-dentate; 6 rather long, curved accessory spines in spine row. Lower lip: outer lobes high; inner lobes distinct; lateral processes short and bluntly rounded apically. Maxilla 1: inner plate with up to 5 coarse, naked setae and approximately 6 fine setae on apex; outer plate with 9 apical spine teeth; palp with row of 8-10 bladespines distally on inner margin. Maxilla 2: inner and outer plates with numerous apical setae; inner plate also bearing oblique row of 21 or 22 naked facial setae and row of setae on inner margin. Maxilliped: inner plate bearing 2 short, thick spines, 2 longer spines, and several naked setae apically, and short row of naked setae on inner margin distally; outer plate with stiff setae on inner margin and apex; face of palp dactyl with row of fine setae.

Propod of gnathopod 1 broadest distally; palm oblique, armed with double row of 6 or 7 distally unnotched spine teeth and few long setae; posterior margin rather short, with single seta; medial setae few. Segment 5 (carpus) of gnathopod 1 subequal in length to propod, richly setose on distal and anterior margins; segment 4 (merus) longer than carpus, produced distally into conspicuous lobe that is pubescent on lower half of inner face. Coxal plate of gnathopod 1 almost 2 × deeper than broad, ventral margin with 4 spines and few short setae. Propod of gnathopod 2 longer than that of first propod; palm nearly 3 × length of posterior margin, armed with double row of 10-11 distally unnotched spine teeth and several long setae; defining angle with 3 long spine teeth on inside, 2 on outside; anterior margin setose. Dactyl of gnathopod 2 narrowly subtriangular in shape, densely setose distoposteriorly. Coxal plate of gnathopod 2 nearly 2 × deeper than broad, margin with 7 or 8 spines. Coxal plate of pereopod 4 as deep as broad, expanded distally, with bluntly rounded distoposterior lobe, ventral margin with few very short setae. Pereopod 6 longer than pereopods 5 or 7, about 85% length of body. Pereopods 5&7 subequal in length, about 65% length of body. Bases of pereopods 5-7 as broad as deep, posterior margins broadly convex, anterior margins with row of short spines. Dactyls of pereopods 5-7 comparatively long, those of 5&7 approximately 50-52% length of corresponding propods, that of pereopod 6 approximately 40% length of corresponding propod; dactyls bearing few spines and setae on upper and lower margins. Coxal gills suboval, largest on gnathopod 2 and pereopods 3&4. Brood plates decreasing in length from gnathopod 1 to pereopod 5, bearing numerous long setae toward distal end.

Pleonal plates: distoposterior corners rather narrowly rounded, usually with 1 short seta

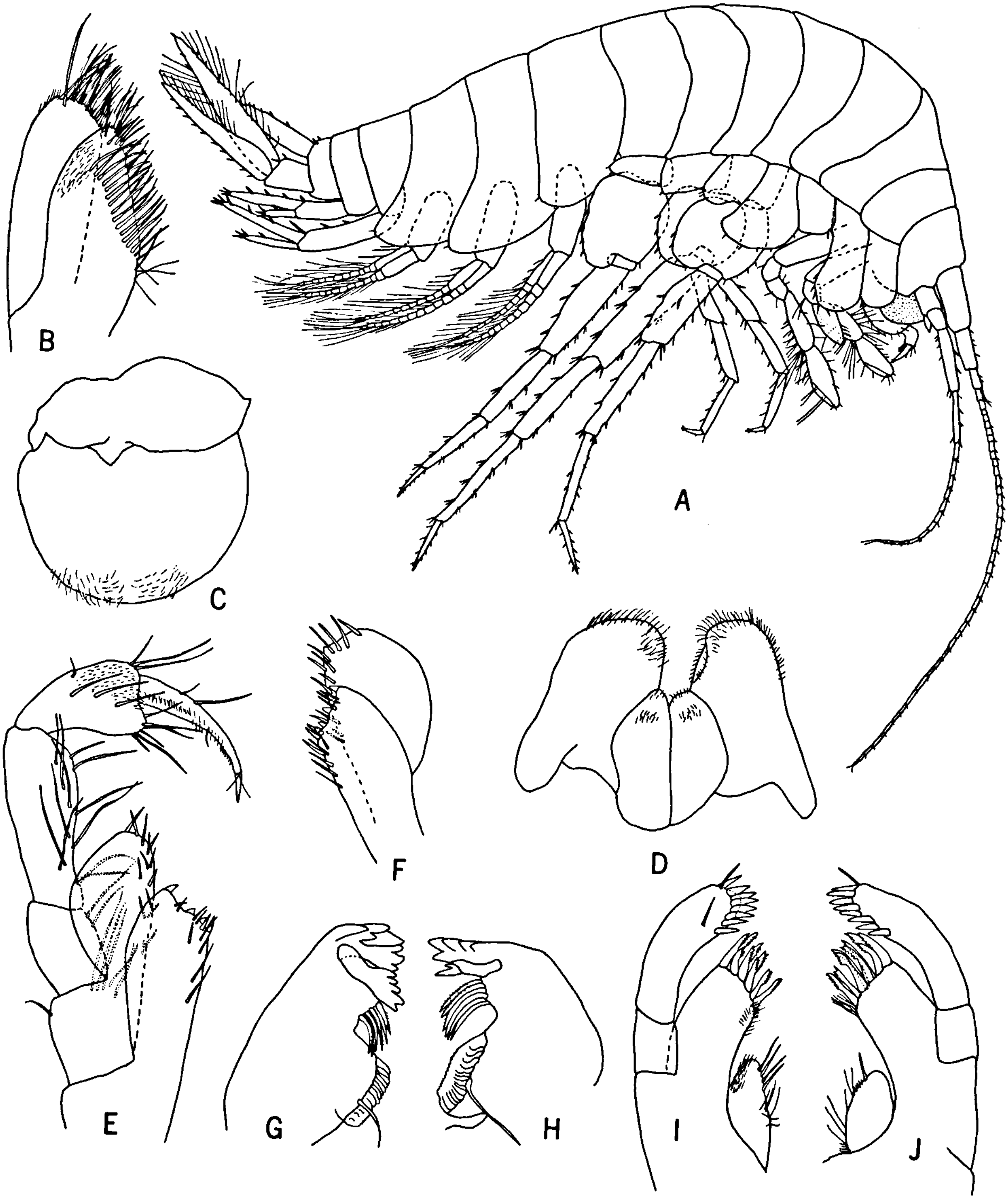

Fig. 1. *Tuluweckelia cernua* n. sp., female paratype (6.8 mm), Carwash Cenote, Quintana Roo, Mexico: A, entire animal from right side; B, maxilla 2; C, upper lip; D, lower lip; E, left maxilliped; F, inner and outer plates of right maxilliped; G, H, left and right mandibles; I, J, left and right maxillae 1. (Mouthparts to same scale except maxilliped, which is drawn to slightly larger scale.)

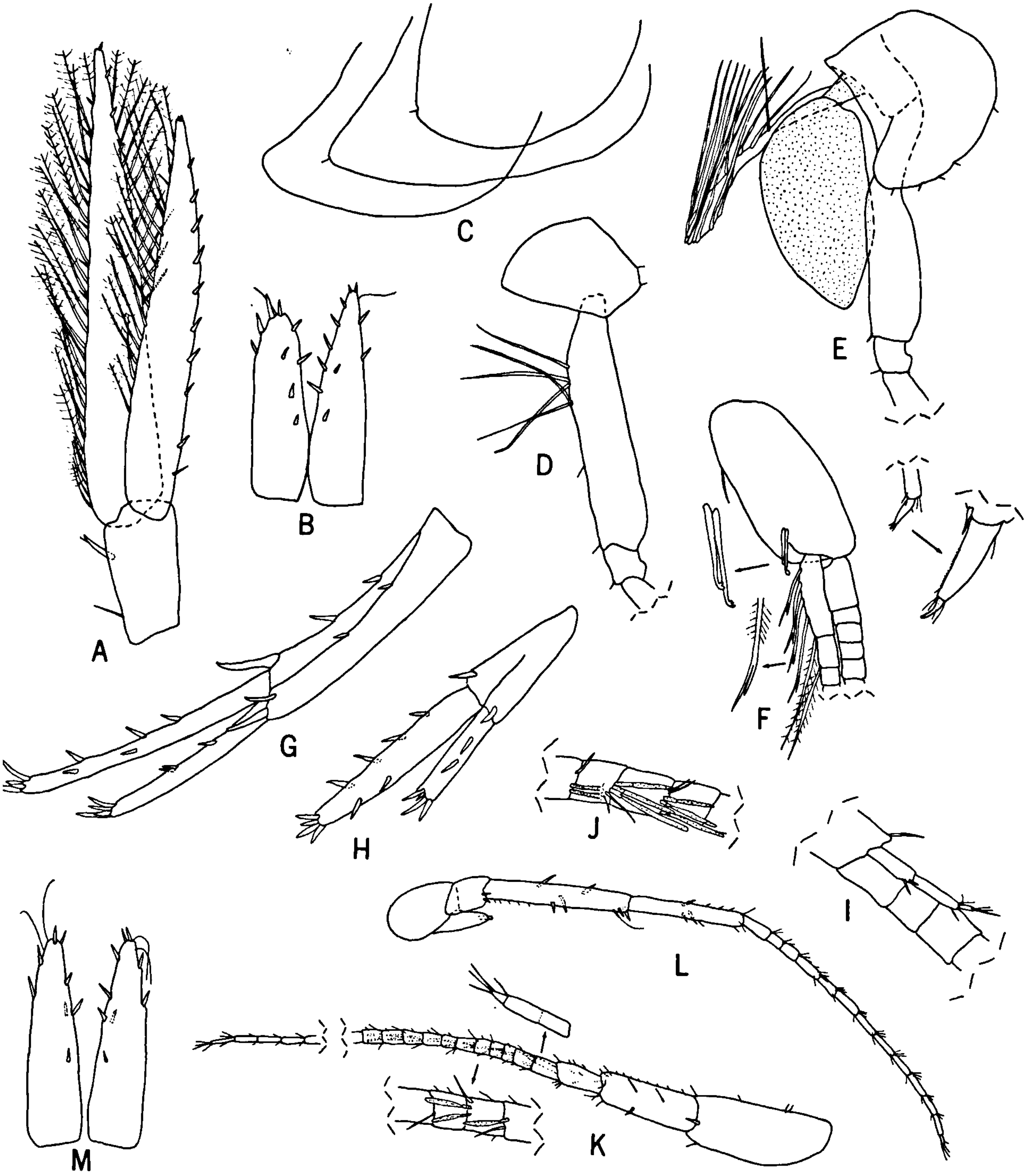

Fig. 2. *Tuluweckelia cernua* n. sp., paratypes, Carwash Cenote, Quintana Roo, Mexico. Female (8.0 mm): A, uropod 3; B, telson; C, pleonal plates; D, pereopod 3 (in part); E, pereopod 4 (in part) (dactyl enlarged); F, pleopod 1 (in part); G, H, uropods 1 and 2; I, accessory flagellum of antenna 1 (medial view); J, proximal segments of antenna 1 with esthetascs (medial view). Female (6.8 mm): K, antenna 1 (accessory flagellum and several esthetascs enlarged in medial view); L, antenna 2. Female (5.0 mm): M, telson. (All structures to same scale except pereopods 3 and 4 to slightly smaller scale, esthetascs and accessory flagellum to much larger scale, and telson of 5.0 mm female to larger scale.)

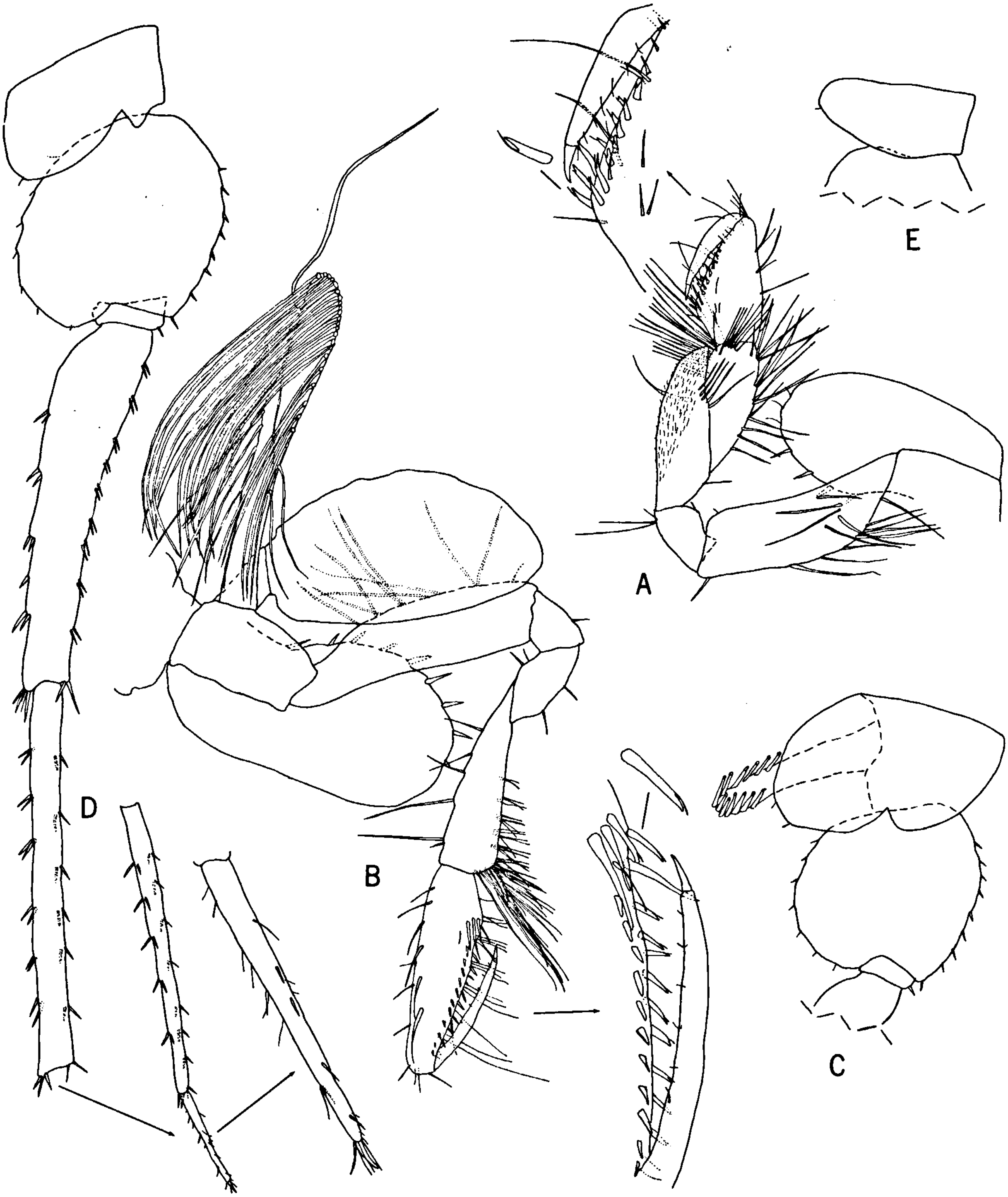

Fig. 3. *Tuluweckelia cernua* n. sp., female paratype (8.0 mm), Carwash Cenote, Quintana Roo, Mexico: A, B, gnathopods 1 and 2 (propod palms enlarged); C, pereopod 5 (in part); D, pereopod 6 (dactyl greatly enlarged); E, coxal plate of pereopod 7. (Gnathopods drawn to slightly larger scale than pereopods.)

each; ventral margins without spines. Pleopods 1&2 subequal in length, 3 slightly shorter. Uropod 1: inner ramus longer than outer ramus and peduncle, armed with 9 or 10 spines; outer ramus with 7 or 8 spines; peduncle bearing 7 spines. Uropod 2: inner ramus almost 50% longer than outer ramus, bearing about 10 marginal spines; outer ramus bearing about 6 spines; peduncle with 2 distal spines. Uropod 3 about 33% length of body; rami narrowing distally, inner little longer than outer, inner and outer margins with short spines and plumose setae; outer ramus with few short spines and plumose setae on inner margin, with spines only on outer margin. Telson in 2 separate, relatively long and narrow halves (lobes); outer (lateral) margins with 2 short, singly inserted spines each near distal end; inner (medial) margins and surfaces each bearing 5-7 short spines; apices with 2 spines and 1 or 2 setae each.

Variation. — The peculiar bending of the anterior region of the body is more pronounced in juvenile specimens, ca. 3-4 mm in length. The angle decreases to some extent in larger specimens. In specimens between 5 and 7 mm, the proximal flagellar segments of antenna 1 bear 1 or 2 esthetascs each, whereas in the largest specimens (ca. 7.5-8.0 mm), most of these segments bear 3 esthetascs (see fig. 2J). The accessory flagellum is 3-segmented in larger males (>5.0 mm) and females (7.0-8.0 mm) but sometimes only 2-segmented (or faintly 3-segmented) in smaller females (<6.8 mm).

Type-locality. — Temple of Doom Cenote, located 1.5 km NW of Tulum and the junction of highways 307 and 180, is an anchialine cave situated about 9 km from the east coast of Quintana Roo, Mexico (see fig. 5) (see also Bowman, 1987).

Etymology. — The epithet *cernua* is from the Latin adjective *cernuus*, meaning "facing earthward," "drooping," or "nodding."

Distribution and ecology. — To date this species has been collected from six caves, all anchialine, in the vicinity of Tulum just inland from the northeastern coast of Quintana Roo (fig. 5). Most specimens of *Tuluweckelia cernua* have been collected from the fresh to weakly brackish (oligohaline) water zone above a halocline at depths of <13-26 m. However, a few specimens have been taken in mesohaline water at depths below 18-20 m. Out of a total of 56 specimens collected to date, 40 are females, 4 are males, and 12 are juveniles (<4.0 mm), strongly suggesting a highly disproportionate sex ratio favoring females in this species. Some of the larger females had setose brood plates but none was ovigerous.

In February 1986 this species was taken in the freshwater zone of Carwash Cenote with 16 specimens of the stygobiont amphipod *Mayaweckelia cenoticola* (see partial redescription and remarks below). *Bahadzia* n. sp. (ms. in preparation by the author), another stygobiont amphipod, was also collected from this cave, but from below the halocline at a depth of 21-23 m in euhaline water (35 ppt salinity).

Tuluweckelia cernua has been collected from several caves with significant stygobiont faunas consisting primarily of crustaceans. In Temple of Doom Cenote it has been taken together with the cirolanid isopods *Bahalana mayana* Bowman and *Creaseriella anops* (Creaser), the mysid *Antromysis cenotensis* Creaser, and the decapod shrimps *Creaseria* sp. and *Typhlatya* sp. (see Bowman, 1987). Sightings of remipedes (*Speleonectes*) and thermosbaenaceans (*Tulumella*) have also been recorded from the this cave by J. Yager (pers. comm.).

In Carwash Cenote, in addition to the two other amphipods already mentioned, *T. cernua* has been taken with the remipede *Speleonectes tulumensis* Yager, the thermosbaenacean *Tulumella unidens* Bowman, *Creaseriella anops*, *Typhlatya* sp., mysids, and the brotulid cave fish *Ogilbia* (= *Typhlias*) *pearsei* (Hubbs) (see Yager, 1987). Some of these taxa, however, such as the remipedes and *Bahadzia*, occur below the halocline and at greater depths than *Tuluweckelia*. Many of the same taxa recorded from Carwash Cenote have been collected from Naharon Cenote as well, including *Speleonectes*, *Tulumella*, *Tuluweckelia*, *Creaseriella*, *Typhlayta*, and *Ogilbia* (see Bowman&Iliffe, 1988).

Mayaweckelia Holsinger

Mayaweckelia Holsinger, 1977: 15-16 [type species by original designation, *Mayaweckelia yucatanensis* Holsinger, 1977]. — Holsinger & Longley, 1980: 9-10. — Barnard & Barnard, 1983: 646-647. — Stock, 1985: 391. — Holsinger, 1986: 99-100. — Holsinger et al., 1986: 99-100.

Remarks. — This genus was described by Holsinger (1977) on the basis of two stygobiont species from freshwater caves on the Yucatan Peninsula. A second detailed diagnosis of the genus was given by Barnard & Barnard (1983); its geographic distribution is shown on a map in Holsinger (1986, fig. 10).

Mayaweckelia cenoticola Holsinger (Fig. 4)

Mayaweckelia cenoticola Holsinger, 1977: 19-24, figs. 4-6 [type-locality: Cenote Xtacabiha, state of Yucatan, Mexico]. — Wilkens, 1979: 265. — Reddell, 1981: 101-102. — Wilkens, 1982: 240. — Barnard & Barnard, 1983: 646-647. — Stock, 1986: 508.

Range. — Recorded from 11 caves on the Yucatan Peninsula of Mexico (see Holsinger, 1977; Reddell, 1981). New locality records (since Holsinger, 1977) based on material examined in the present study, are: Carwash Cenote, Quintana Roo, 8 km NW of Tulum, 1 ♂, 12 ♀ and 2 juv., J. Bozanic, 18 Feb. 1986, and 1 ♀, T. Iliffe, 12 Nov. 1986; and Cenote X-Keken, Yucatan, ca. 7 km W of Valladolid, 1 juv., T. Iliffe, 9 Nov. 1986.

Remarks. — Small to medium-sized stygobiont species, distinguished by the characters described by Holsinger (1977) and additional diagnostic features shown in fig. 4 of the habitus of the female specimen. Characters noted since the original description include: distal 10-12 flagellar segments of antenna 1 with esthetascs (1 each); pereopod 6 up to 15% longer than pereopod 7; dactyls of pereopods 5-7 with row of fine setae (pubescence) on distal half of upper margin and 2 sets of 2 setae each on lower margin. Largest males, 4.0 mm; largest female, 6.0 mm.

Mayaweckelia cenoticola is closely allied morphologically with *M. yucatanensis* Holsinger, which is recorded from a single cave in the state of Campeche, on the western side of the Yucatan Peninsula (fig. 5). Although new data are not available for the latter species, it should be noted that its original description (see Holsinger, 1977: 16-19) was based on what appear to be submature specimens, therefore raising the strong possibility that the differences noted between the two species of *Mayaweckelia* are due primarily to age. If further study shows this to be the case, these species should be synonymized. Meanwhile, this problem cannot be resolved without examination of adult specimens of *M. yucatanensis.*

DISCUSSION

Because *Mayaweckelia* has taxonomic affinities with marine forms and occurs at present in areas of old marine embayments, I have suggested that it probably evolved from a marine ancestor by "stranding" in newly developing subterranean freshwater habitats following regression of sea water from the Yucatan Peninsula in late Tertiary or early Quaternary times (Holsinger, 1977, 1986). Several populations of *Mayaweckelia* occur very close to a putative Pliocene shoreline (see Wilkens, 1982, 1986; Holsinger, 1986), whereas others occur in an area situated between Pliocene and Pleistocene shorelines (Wilkens, 1982). *Mayaweckelia* is predominately a freshwater inhabitant, and only two or three of its 11 known populations are recorded from cave waters that are, at most, weakly brackish.

In contrast, *Tuluweckelia* lives in cave waters that are often at least weakly brackish, and its range, as presently known, is restricted to a small number of anchialine caves near the northeastern coast of Quintana Roo (fig. 5). The geographic distribution and ecology of *Tuluweckelia* suggest that its orgin from putative marine ancestors is more recent than that of *Mayaweckelia.* The colonization of Yucatan Peninsula caves by marine ancestors of *Tuluweckelia* may be related to the recession of a high sea stand during the Pleistocene.

Primarily because of the absence of mandibular palps and a second (terminal) segment

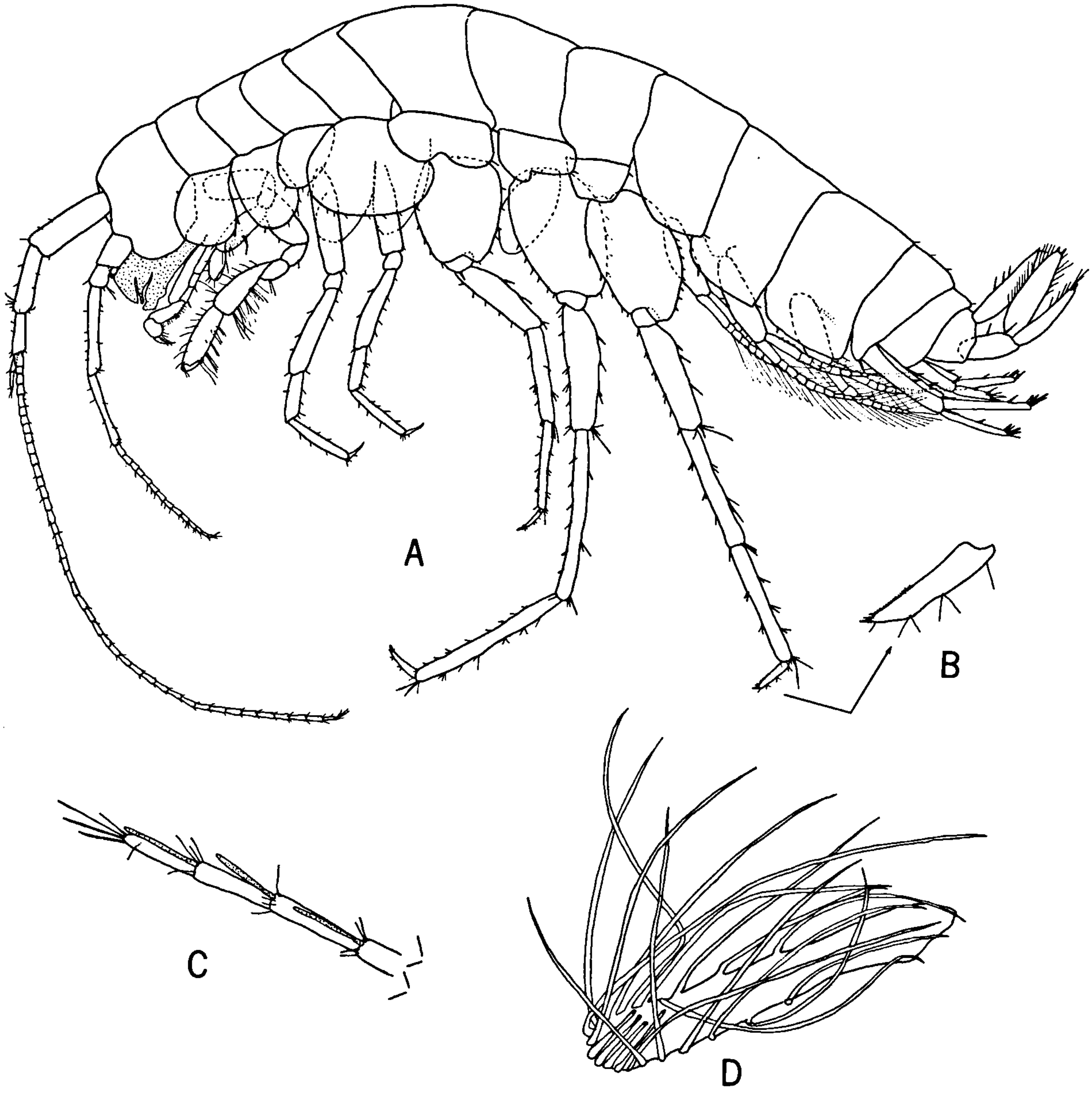

Fig. 4. *Mayaweckelia cenoticola* Holsinger, female (6.0 mm), Volcán de los Murciélagos (11 km E of Conhuas), Campeche, Mexico: A, entire animal from left side; B, dactyl of pereopod 7 (enlarged). Female (6.0 mm), Carwash Cenote, Quintana Roo, Mexico: C, terminal segments of antenna 1 with esthetascs; D, brood plate from pereopod 4. (Each drawing to different scale.)

on the outer ramus of uropod 3, *Mayaweckelia* has been assigned to the weckeliid group of Hadziidae (Holsinger & Longley, 1980; Holsinger, 1986). This group includes a number of subterranean freshwater genera found in southcentral Texas, northern Mexico, Cuba, Puerto Rico, and Haiti (see Holsinger & Longley, 1980; Barnard & Barnard, 1983; Stock, 1985; Holsinger, 1986). All are believed to be marine relicts. The close relationship of *Mayaweckelia* and *Tuluweckelia* makes the latter a candidate for membership in the weckellid

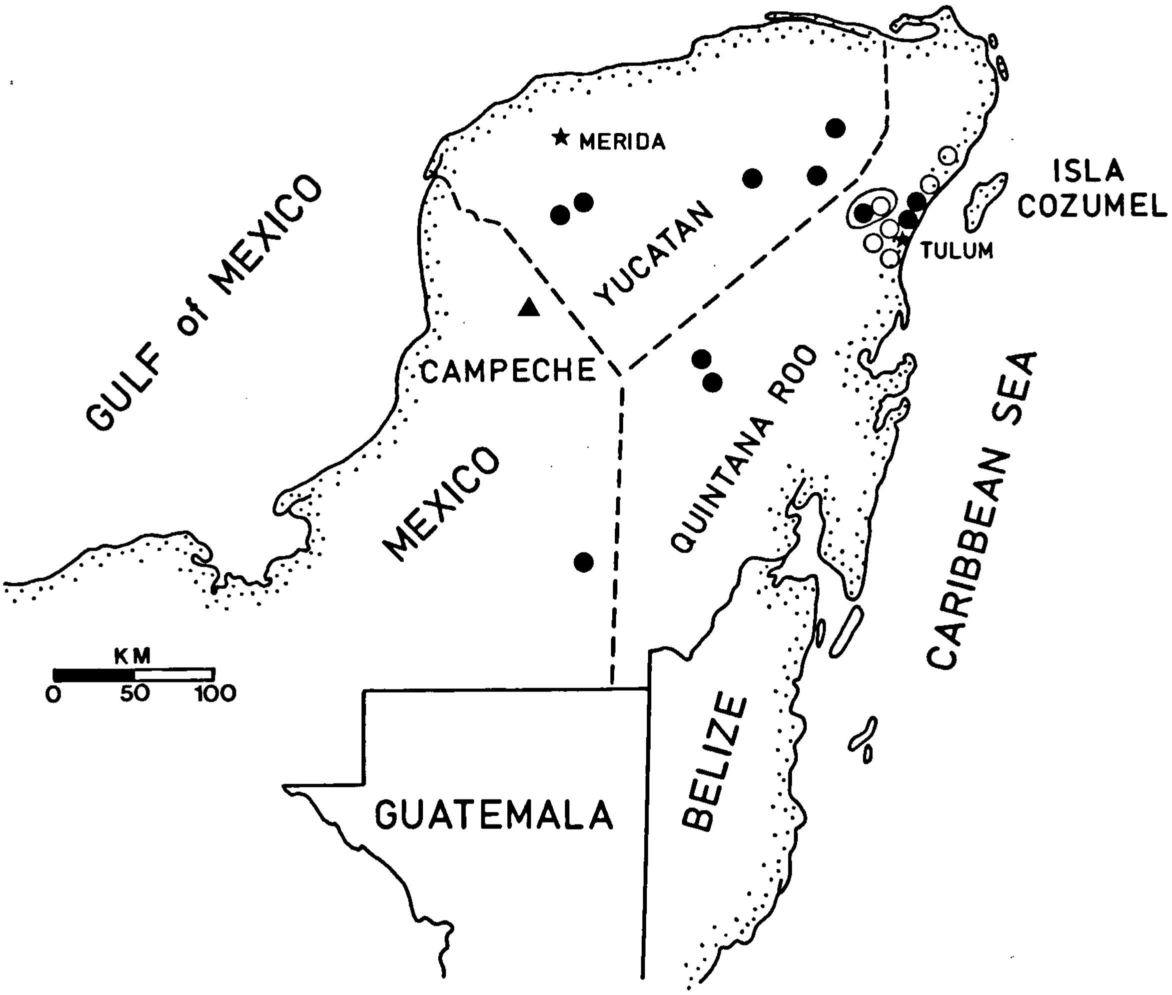

Fig. 5. Distribution of *Tuluweckelia* and *Mayaweckelia* on the Yucatan Peninsula of Mexico. Open circles indicate recorded localities for *T. cernua*, solid circles for *M. cenoticola*, and closed triangle for *M. yucatanensis*. The two symbols enclosed in a circle indicate two taxa from Carwash Cenote.

group as well. However, the relationship between these Yucatan genera and the other weckeliids may not be as close as previously indicated.

For example, a re-evaluation of the phylogenetic relationships of *Mayaweckelia* and *Tuluweckelia* with other weckeliid genera, indicates a different (more distant?) relationship than that which is shown on the cladogram in Holsinger (1986, fig. 9). In table 4 of that paper, the apomorphic state of character 10 (posterior margin of segment 5 of gnathopod 1) should read "with distinct lobe;" the states for character 11 (segment 4 of gnathopod 1) are reversed, although the apomorphic state (enlarged, with lobe) is shown correctly on the *Mayaweckelia* clad in figure 9; and the apomorphic state of character 18 (number of basofacial spines of peduncle of uropod 1) does not occur in *Mayaweckelia*, as is shown incorrectly on the cladogram in figure 9. Both *Mayaweckelia* and the newly described *Tuluweckelia*, unlike all other genera previously assigned to the weckeliid group of Hadziidae, lack basofacial spines on uropod 1 altogether. On a revised cladogram that incorporates the above changes and corrections (Holsinger, in preparation), the Yucatan weckeliids move to the position of an "outgroup" on the left of all other genera.

The possibility that the Yucatan weckeliids may be more closely allied with the West Indian, stygobiont genus *Bahadzia* than with other weckellids has also been suggested (see Stock, 1985; Holsinger et al., 1986). This possibility is undergoing further study (Holsinger, in preparation).

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Institute of Taxonomic Zoology (Zoölogisch Museum), University of Amsterdam,
P.O. Box 4766, 1009 AT Amsterdam, the Netherlands