

A new epacteriscid copepod (Calanoida: Epacteriscidae) from the Yucatan Peninsula, Mexico, with comments on the biogeography of the family

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Abstract.—The calanoid copepod family Epacteriscidae is represented by species from tropical marine and anchialine environments. Surveys of the anchialine invertebrate fauna of the Yucatan Peninsula, Mexico, have resulted in a number of interesting records of crustaceans during the last decade, but no records of Epacteriscidae. However, recent collections from hypogean environments of the Yucatan have yielded specimens of a new species of the previously monotypic genus *Balinella*. The specimens were included in this genus by having three outer spines on the third exopodal segment of legs 3 and 4, a biramous mandibular palp, and an antennal endopod longer than the exopod, among other characters. The new species, *B. yucatanensis*, is described on the basis of male and female specimens collected in caves associated with three different karstic sinkholes. The new species is distinguished from its only known congener, *B. ornata* Fosshagen, Boxshall and Iliffe, 2001, by the strong asymmetry of the caudal rami in females, a modified left fifth leg of the male in which the proximal and middle exopodal segments are attenuate at the point of origination of the outer spine, and by differences of the armature of mouthparts (mandibular palp, maxilla, maxilliped). This report extends the range of *Balinella* from anchialine caves of the Bahamas to hypogean waters of the Yucatan Peninsula. The introduction of epacteriscid copepods onto the Yucatan Peninsula may be an old event; diversification by genera into non-cave habitats appears to be secondary.

The family Epacteriscidae is one of the most representative copepod taxa in the anchialine and troglotic environments, together with the Ridgewayiidae (Fosshagen et al. 2001). The current distribution of the Epacteriscidae in geographically distant sites such as the Galapagos, Fiji, and the Bahamas seems to be related to a very old biogeographical pattern that may be linked to the Cretaceous period. A revision of the family was published by

Fosshagen et al. (2001), in which 9 new genera were described and a phylogeny of the known species of 12 genera was proposed. About the same time, Jaume & Humphreys (2001) described a new genus, *Bmderia*, from anchialine waters in northwestern Australia, and Boxshall & Jaume (2003) described the genus *Iboyella* from an anchialine cave in Cuba. Quite recently, Fosshagen & Iliffe (2004) described 3 additional monotypic genera

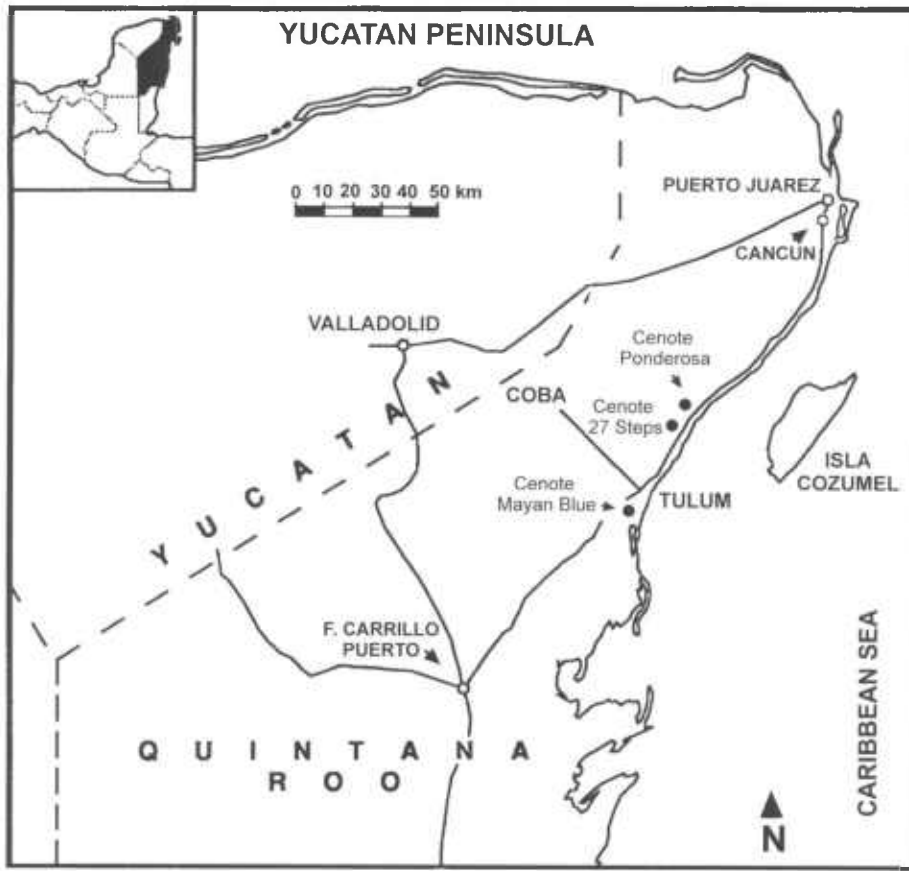


Fig. 1. The Yucatan Peninsula, showing the locations of the three sites at which *Balinella yucatanensis* was collected.

from caves of the Bahamas. In this paper we report a second species of *Balinella*, a genus known previously only from the Bahamas, on the basis of specimens collected in an hypogean anchialine habitat of the Yucatan Peninsula.

Materials and Methods

Epibenthic and zooplankton samples were collected by one of us (T.M.I.) from both epigeal and hypogean habitats of more than 20 sites in different areas of the Yucatan Peninsula during the summers of different years, as part of a biological survey to determine the composition, diversity, and distribution of the freshwater and anchialine fauna of the Yucatan

Peninsula. Open-water samples were collected using standard plankton nets with a mesh size of 60 μm . Littoral samples were obtained using a hand net or traps. Some specimens from these samples have been analyzed in previous reports (Suárez-Morales et al. 1996), but only freshwater forms have been reported to date. Samples from three of these sites (Fig. 1) contained a few specimens of a calanoid copepod assignable to the family Epactericidae.

In the laboratory, the copepods were sorted from the original sample and preserved in 70% ethanol. Specimens were prepared for taxonomic analysis by dissecting all appendages and staining each with chorazol black e in lactic acid.

Dissected and whole specimens were transferred to glycerin. Basic taxonomic observations were performed using bright-field or differential-interference-contrast microscopy. Illustrations were prepared with the aid of a camera lucida.

We use the interpretations and terminology by Huys & Boxshall (1991) for the maxillule and Ferrari & Ivanenko (2001) for the maxilliped.

Systematic Account

Order Calanoida Sars, 1903

Family Epacteriscidae Fosshagen, 1973

Genus *Balinella* Fosshagen, Boxshall & Iliffe, 2001

Balinella yucatanensis, new species

Figs. 2–5

Material examined.—Holotype, one adult female, 12 January 1996 from Cenote (= sinkhole) Ponderosa (about 20°34.357'N, 87°11.280'W) in the central part of the eastern coast of the Yucatan Peninsula, state of Quintana Roo, Mexico. Specimen partly dissected, ethanol-preserved, vial and slides deposited in the collection of Zooplankton of El Colegio de la Frontera Sur (ECOSUR) in Chetumal, Mexico, under catalogue number ECO-CHZ-02358. Allotype, one adult male, collected on same date; Cenote Mayan Blue (Tulum; 20°11.641'N, 87°29.778'W), in the same general area of the Yucatan Peninsula, about 50 km from Ponderosa (Fig. 1). Specimen dissected, deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 1082690). Paratype, adult female collected on 17 March 1996 from Cenote 27 Steps (Akumal area) (20°24.190'N, 87°19.744'W); this sinkhole is located about midway between Ponderosa and Mayan Blue. Specimen dissected, mounted in permanent slide (USNM 1082691). All specimens were collected below the halocline in saline waters isolated from the sea. The halocline is

12–15 m below the overlying freshwater layer. These three cenotes are all located relatively close to the coastline (Fig. 1) and have a marine underground layer.

Description of adult female.—Mean length of prosome: 1.0 mm (N = 3); total length including caudal rami = 1.45 mm (N = 2). Body (Fig. 2A) with typical calanoid shape, relatively slender, prosome slightly wider anteriorly and widest at first prosome somite.

Prosome 5-segmented; 1st segment a complex of 5 cephalic somites and thoracic somites 1 and 2; 3–6 articulating. Rostrum wide, rostral points long, curved (Fig. 3A) and visible in lateral view (Fig. 2B). Sixth thoracic somite slightly asymmetrical and narrow, right side protruding slightly, with two rows of spiniform processes visible in lateral view (Figs. 2B, 3D); left side without cuticular processes. Arthroal membrane between 5th and 6th thoracic somites complete.

Urosome 4-segmented; first segment a complex of posterior thoracic somite and anterior urosomite. Urosome, excluding caudal rami, representing 28% of total body length; genital complex relatively large, 41% of urosome. Genital complex slightly asymmetrical, with right margin protruding as two bumps, left margin straight (Fig. 2A), and expanded ventrally both at proximal $\frac{1}{3}$, associated with oviduct opening, and at mid-section, associated with genital pore (Figs. 2B, 3D). Anal somite subrectangular, about 15% of urosome length, no cuticular ornamentations on dorsal and ventral surfaces.

Caudal rami (Figs. 2A, 3G) lamelli-form, asymmetrical, left ramus 1.3 times longer than right, about 2.5 times as long as wide; inner margin lightly setose on distal half. Right ramus about 2.8 times longer than wide; inner margin with tuft of short setae at mid-section. Each ramus with 1 dorsal, 1 subterminal, and 3 terminal setae. Middle terminal seta of left caudal ramus 1.7 times as long as body (Fig. 2A). All ramal setae plumose.

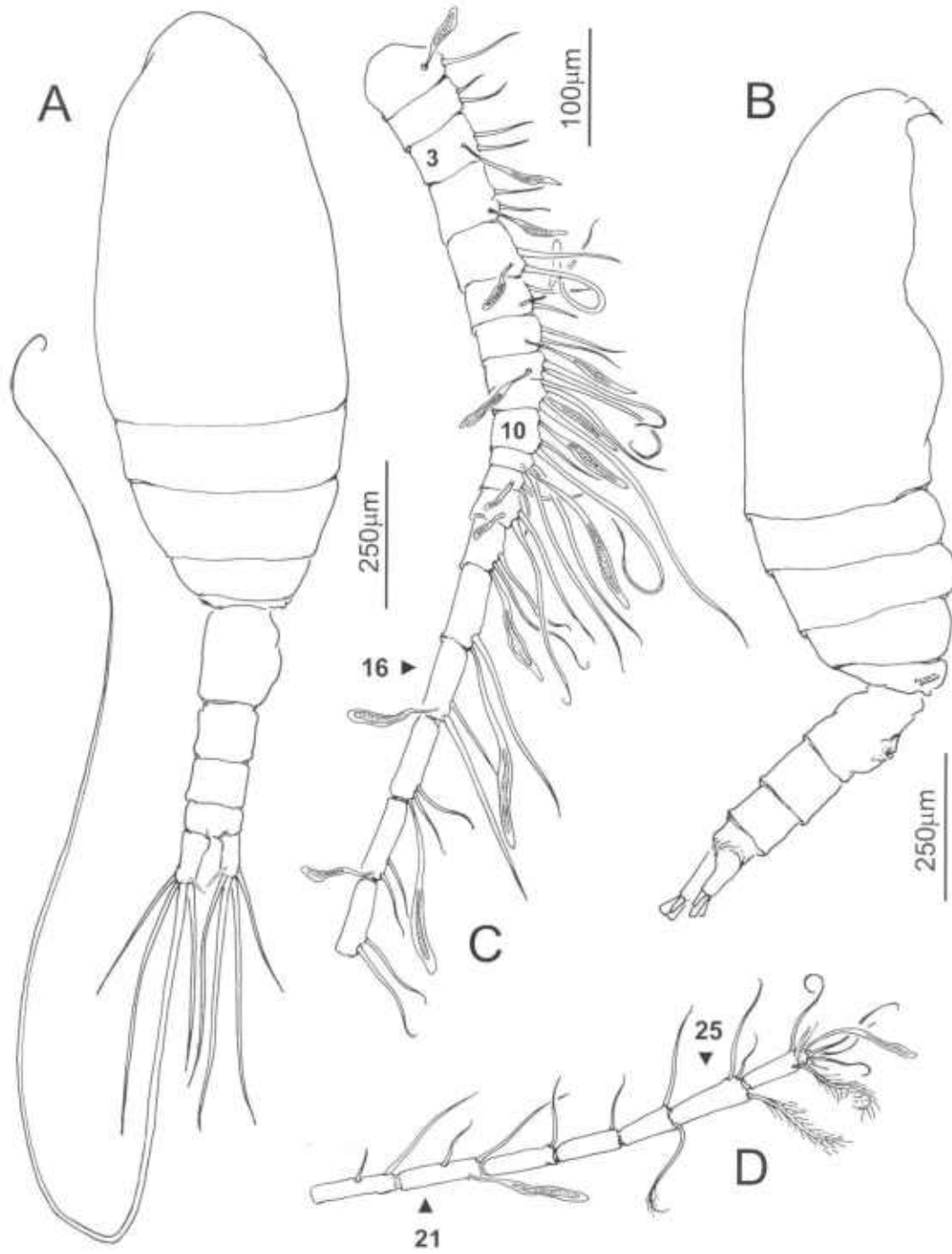


Fig. 2. *Balinella yucatanensis*, adult female. A, habitus, dorsal view; B, habitus, lateral view; C, antennule, segments 1-19; D, antennule segments 20-27.

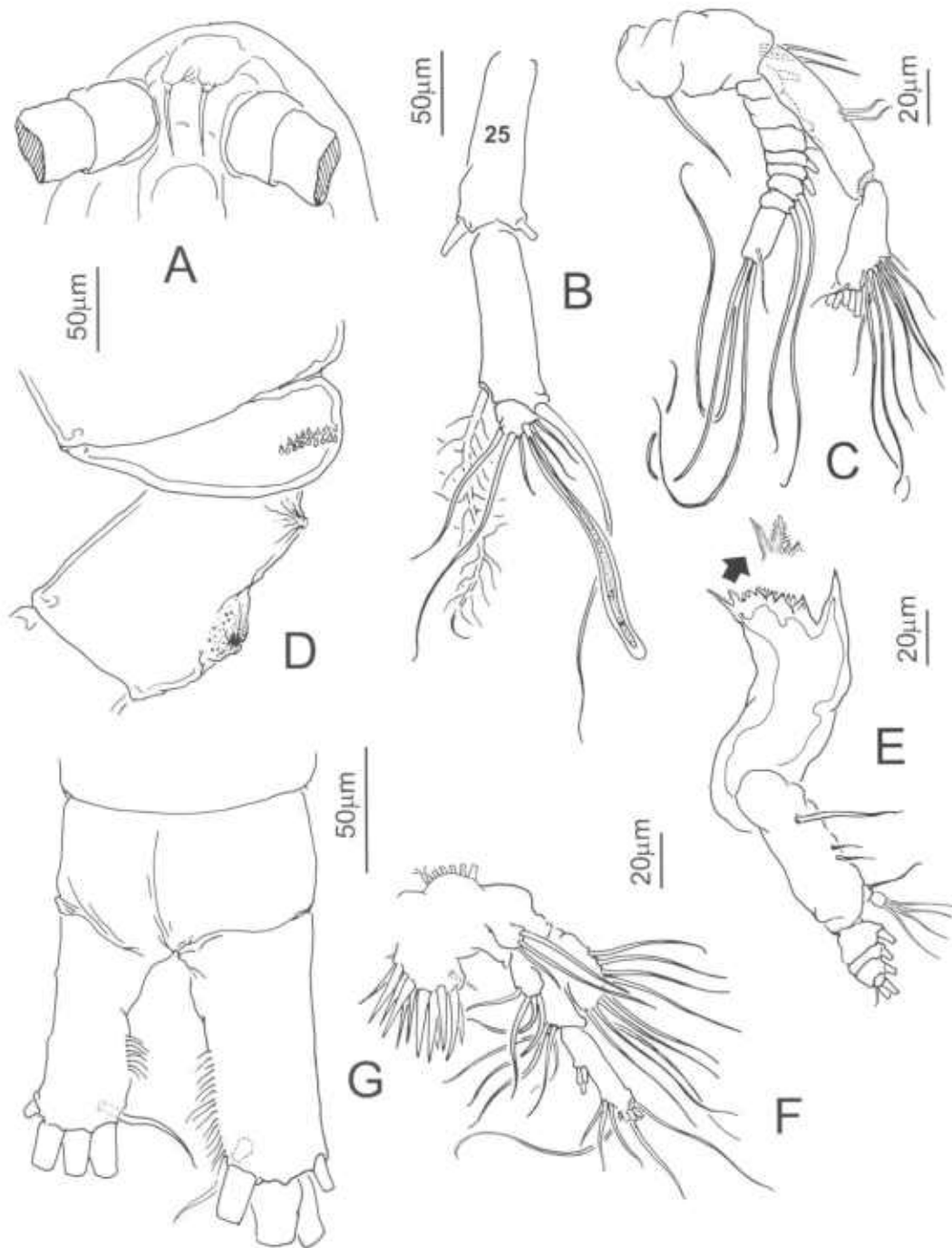


Fig. 3. *Balinella yucatanensis*, adult female. A, rostrum, ventral view; B, detail of distal three antennular segments; C, antenna; D, fifth thoracic somite and genital double-somite, lateral view; E, mandible with palp, detail of dorsal seta and tooth, arrowed; F, maxillule; G, caudal rami, ventral view.

Antennules (Fig. 2C, D) 27-segmented, reaching posterior margin of genital double-somite. Setae on segments 9, 10–13, 15, and 16 longest. Armature per segment as follows (numerals = segment, numerals in parentheses = number of setae, ae = aesthetasc): 1(1+ae), 2(2), 3–14 (2+ae), 15 (1+ae), 16 (2+ae), 17–18 (2+ae), 19 (2), 20(2), 21(2+ae), 22(1), 23(1), 24(2), 25(3), 26(2), 27(5+ae) (Figs. 2C, D, 3B).

Antenna (Fig. 3C) with exopod slightly shorter than endopod. Coxa with 1 long seta. Basis with 2 subequal setae on outer distal margin. Endopod 2-segmented, first segment long, with 2 setae inserted on distal half; distal portion of terminal segment with 2 lobes, proximal lobe with 9 anterior setae; distal lobe with single short, posterior seta plus 5 long terminal setae. Exopod 8-segmented with 1 seta on segments 1–7; distal segment small, with crown of 3 long, terminal setae, subequal in length and diameter, plus 1 shorter subdistal seta.

Mandible (Fig. 3E) gnathobase with 7–9 wide-based bicuspid or tricuspid teeth distinctly separated from large distal tooth. Proximal seta and adjacent tooth with spinules (arrow in Fig. 3E); basis of palp with 3 setae, 1 proximal and thick on proximal $\frac{1}{3}$ plus 2 small, slender setae at middle of margin. Endopod small, 2-segmented; proximal segment with 1 thin seta; distal segment subquadrate, with 4 terminal setae. Exopod 4-segmented, with 1, 1, 1, 3 setae.

Maxillule (Fig. 3F) with precoxal (= protopodal segment proximal to coxa) arthrite bearing 14 spiniform setae [9 ventral, 4 posterior, 1 on anterior]. Coxal epipodite with 8 setae, coxal endite with 3 setae. Basis with proximal and distal endites bearing 4 setae each. Endopod reduced, 1 articulating segment with 2 groups of 3 setae each on ventral margin; 6 apical setae, including 1 dorsal, 1 ventral, and 4 terminal. Exopod oblong, with 9 subequal setae.

Maxilla (Fig. 4A) five-segmented, syn-coxa and basis fused; precoxal lobe with 5 setae, coxal lobe with 3 setae and basal spinules (arrowed in Fig. 4A), proximal and distal lobes of basis with 3 setae each. Proximal segment of 4-segmented endopod large, with 4 setae and spinules at insertion (arrowed in Fig. 4A), antepenultimate and penultimate segments small, also with 4 setae (3 on lobe) each, distal segment small, with 3 long, curved setae.

Maxilliped (Fig. 4B) with proximal, middle, and distal precoxal lobes with 1, 2, and 4 setae, respectively; coxal lobe with 4 setae. Basis with row of spinules on proximal $\frac{1}{5}$ of inner margin; neither proximal nor distal basal lobe developed, with 3, 2 setae, respectively. Endopod 5-segmented, armed as follows: proximal and succeeding segments with 4 ventral setae, middle segment with 4 ventral setae (1 thin), penultimate with 3 ventral and 1 outer setae, distal segment displaced dorsally, with 4 setae, 1 medial, 2 terminal, 1 lateral.

First swimming leg (Fig. 4C, D) with 3-segmented exopod and endopod; coxa with long seta on inner margin reaching beyond distal margin of basal segment. Basis with long, recurved seta on inner margin reaching middle of third endopodal segment and forming organ of Von Vaupel Klein with anterior knob of proximal endopodal segment; knob with a series of ridges anteriorly and posteriorly with 4 pores opening on the apex of different ridges (arrows in Fig. 4C). Second, third, and fourth legs with 3-segmented exopods and endopods (Figs. 4E, F, 5A–D). Third leg with stout, thick, outer spine on basis (Fig. 4F). For armature formula, see Table 1.

Description of adult male.—Total length: 1.39 mm (N = 1); length of cephalothorax: 1.01 mm. Slightly smaller than female; body relatively slender compared to female, with typical calanoid shape (Fig. 6D). Fifth thoracic somite as wide as succeeding somite; sixth thoracic

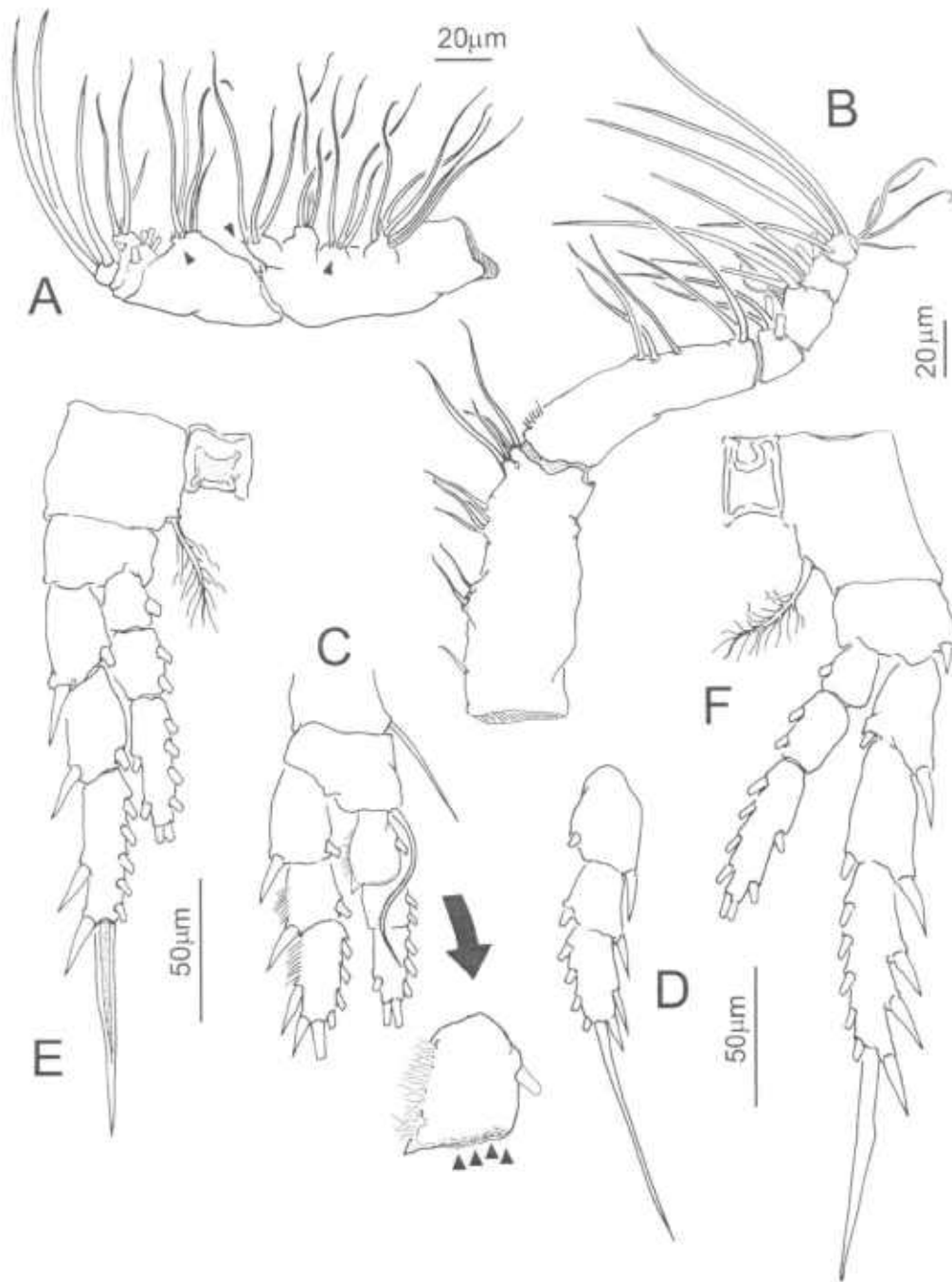


Fig. 4. *Balinella yucatanensis*, adult female. A, maxilla, spinules on base of endites, arrowed; B, maxilliped, some setae cut short; C, first swimming leg showing detail of distal pores (arrows) and related cuticular ridges on first endopodal segment; D, exopod of first swimming leg; E, second swimming leg; F, third swimming leg.

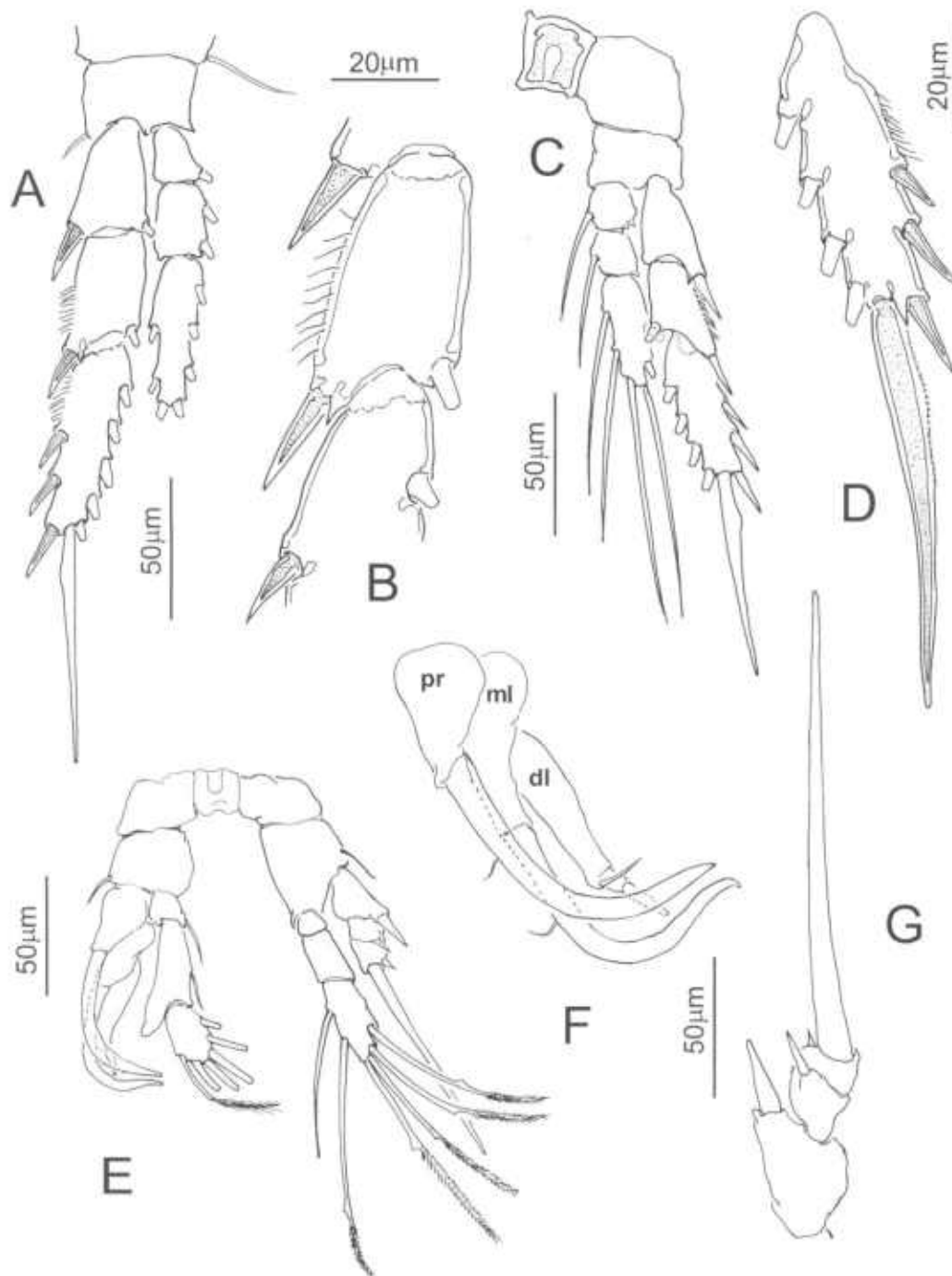


Fig. 5. *Balinella yucataensis*, A–D, adult female, E–G, adult male. A, fourth swimming leg; B, detail of exopod of fourth swimming leg; C, fifth swimming leg; D, distal exopodal segment of fifth swimming leg. E, fifth legs, posterior view; F, exopod of left fifth leg; G, exopod of right fifth leg.

Table 1.—Armature formula of swimming legs 1–5. Roman numerals indicate spines and Arabic numerals are setae. Numerals to the left of a comma or dash indicate lateral elements; numerals between two commas are terminal elements, and numerals to the right of a comma or dash are medial elements. (f = female; m = male; r = right leg; l = left leg).

	Coxa	Basis	Exopod	Endopod
leg 1	0-1	0-1	1-1; 1-1; II,1,4	0-1; 0-2; 1,2,3
leg 2	0-1	0-0	1-1; 1-1; II,1,5	0-1; 0-2; 2,2,4
leg 3	0-1	1-0	1-1; 1-1; III,1,5	0-1; 0-2; 2,2,4
leg 4	0-1	1-0	1-1; 1-1; III,1,5	0-1; 0-2; 2,2,3
leg 5f	0-0	0-0	1-0; 1-1; III,1,4	0-1; 0-1; 2,1,3
leg 5mr	0-0	1-0	1-0; 1-0; I,1	0-0; 0-0; 2,2,2
leg 5ml	0-0	1-0	1-0; 1-0; I,1	0-1; 0-1; 2,2,2

somite tapering posteriorly, slightly asymmetrical. Rostrum wide-based, rostral points slender, relatively shorter and thinner than in female, distally acute (Fig. 6C). Urosome relatively short, representing 23% of total body length, and 5-segmented. First urosomite slightly asymmetrical, with right lateral margin protuberant. Relative lengths of urosomites as: 26.6:20:17.3:22.6:13 = 100. Caudal rami relatively long, weakly asymmetrical with left caudal ramus 11% longer and slightly wider than right ramus (Fig. 6A). Armature of caudal rami as in female.

Left antennule 25-segmented, relatively longer than in female, when extended posteriorly. Right antennule with 22 segments, geniculated between segments 18 and 19 (Fig. 6B). Armature as follows: 1(1+ae), 2(6+2ae), 3-5(2+ae), 6(3), 7(2+ae), 8(1+ae), 9-17 (2+ae), 18(1+ae), 19(3+ae), 20(4+ae), 21(2), 22(5+ae). Longest setae on segments 7, 9, 11-16. Ventral seta of segment 18 and both ventral setae of segment 19 with broad base and appressed to a groove of the segment (arrows in Fig. 6B). Segment 20 with spiniform distal ventral attenuation; base almost $\frac{1}{3}$ as wide as the width of its segment, and reaching distal end of terminal antennule segment.

Mouthparts and swimming legs 1-4 as in female.

Fifth legs biramous (Fig. 5E-G). Right basis with short, slender seta inserted distally on outer margin. Endopod 3-

segmented; proximal and middle segments unarmed, distal segment with 6 setae, 2 outer, 2 terminal, 2 inner. Exopod 3-segmented, proximal segment with thick outer spine, middle with outer spine, distal with 1 small spine in subdistal position, plus 1 long, terminal stout seta (Fig. 5G); middle and distal segments imperfectly separated. Left fifth leg (Fig. 5E, F) with basis subquadrate, bearing small, slender seta on outer margin. Endopod 3-segmented, first segment short, with slender seta on inner margin; second with short inner seta, outer margin produced into thumb-like process reaching mid-section of third endopodal segment; third segment oblong, with 6 setae, 2 outer, 2 terminal, 2 inner. Exopod of left leg 3-segmented (Fig. 5F). Proximal and middle segments attenuate laterally at insertion of outer spine; each spine with short, slender dorsal seta. Distal segment elongate, with 2 setae; cylindrical subdistal spine tapering gradually to acute point; distal spine blade-like (Fig. 5F).

Etymology.—This species' epithet refers to the Yucatan Peninsula, the huge karstic zone in which these specimens were collected.

Remarks.—Despite the large number of genera of Epacteriscidae recently added by Fosshagen et al. (2001), Jaume & Humphreys (2001), Boxshall & Jaume (2003), and Fosshagen & Iliffe (2004), a clear set of synapomorphies for the

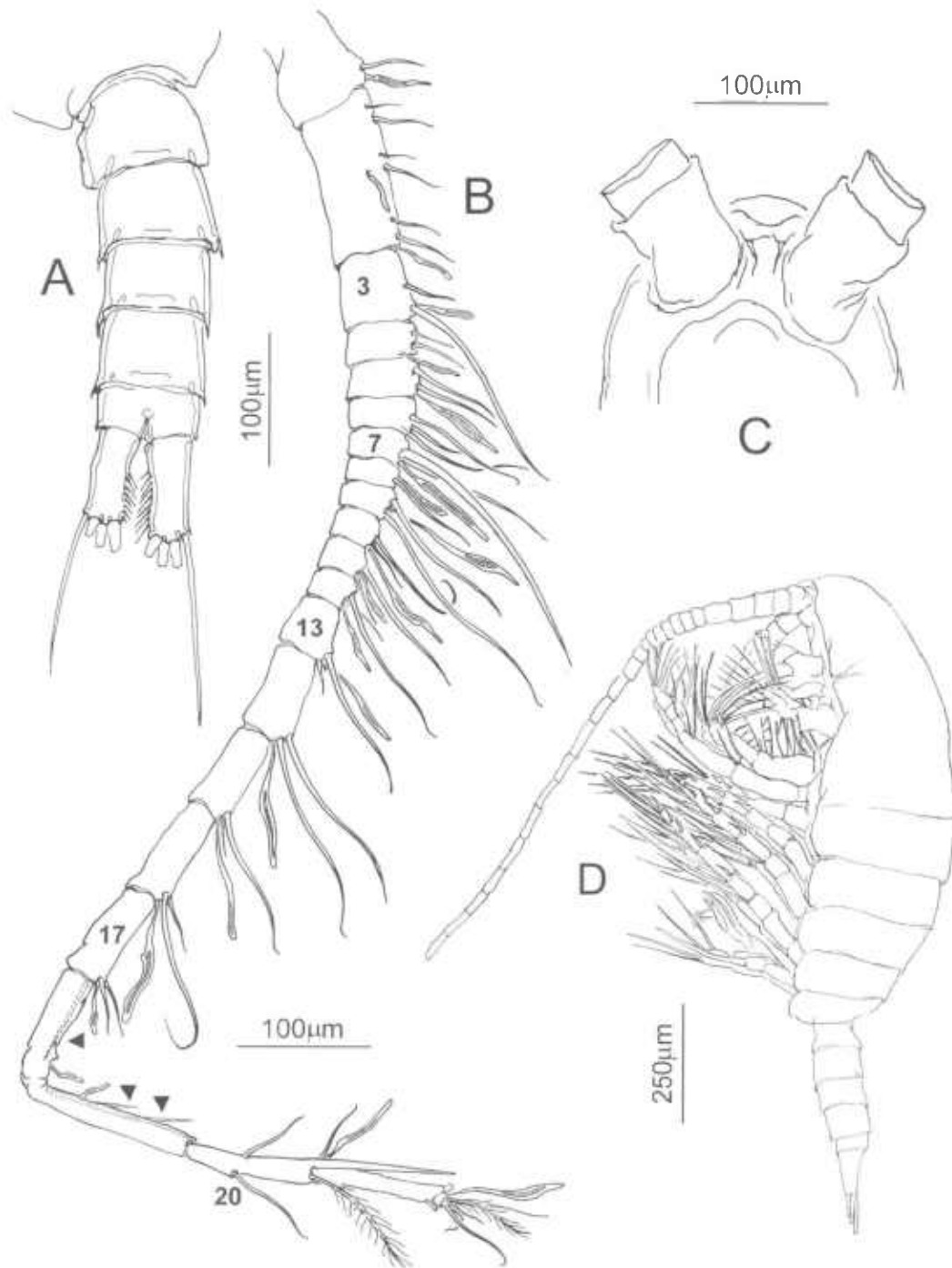


Fig. 6. *Balinella yucatanensis*, adult male. A, urosome, ventral view; B, geniculate right antennule, arrows indicate setae on segments 18 and 19 that fit in a cuticular groove; C, rostrum, ventral view; D, habitus, lateral view.

family or genera is still needed in order to define details of their phylogenetic relations. Fosshagen et al. (2001) split the family into two subfamilies, Erebonectinae and Epacteriscinae. There are 17 genera known in the family (Fosshagen et al. 2001, Boxshall & Halsey 2004, Fosshagen & Iliffe 2004), but only two, *Erebonectes* and *Erebonectoides*, belong to the relatively primitive subfamily Erebonectinae. The new species is included in the formerly monotypic genus *Balinella*, among the most primitive genera of the subfamily Epacteriscinae (Fosshagen et al. 2001), based on the following observations.

Setation on the precoxal lobes of the maxilliped is 1, 2, 4 in the following epacteriscid genera: *Azygonectes*, *Balinella*, *Buuderia*, *Cryptonectes*, *Edaxiella*, *Euantronia*, *Euantronoides*, *Euautiosis*, *Erebonectes*, *Erebonectoides*, and *Miunonectes* (Fosshagen et al. 2001, Fosshagen & Iliffe 2004). In the other known genera (*Gloiella*, *Oiuella*), the number of setae is fewer; usually the seta on the proximal precoxal lobe is missing, but in a few genera, setae from the middle or middle and distal lobes also are missing. Among the genera listed above, an antennal exopod with 8 segments and 3 setae on the distal segment, and 1 seta each on the remaining segments is the state for *Erebonectes*, *Erebonectoides*, *Balinella*, and *Buuderia*. In all other genera of Epacteriscidae except *Epacteriscus*, the exopod is 10-segmented and at least 1 segment bears no seta. The exopod of *Epacteriscus* is 8-segmented and 2 segments bear no seta. Of the above genera, only *Balinella* has a 2-segmented mandibular endopod with 1 and 4 setae; this character is present in our specimens. *Buuderia*, on the other hand, has an apparently 2-segmented mandibular endopod with 1 and 4 setae, but the proximal segment lacks a proximal arthrodial membrane and so does not articulate with the basis (Jaume & Humphreys 2001).

The structure and armament of swimming legs 1–4 are similar in *B. ornata* and in the new species, including a thick outer spine on the basis of leg 3. Both species share the same general structure of male fifth legs with unmodified endopods, although both left and right exopod of the new species are 3-segmented. In both species, the exopod of the left leg bears curved spines and the right exopods show similar morphologies (see Fosshagen et al. 2001: 290, fig. 26J).

As in most epacteriscids, including *Balinella*, the middle terminal caudal seta is elongate (seta V in Fosshagen et al. 2001). In the new species, as in *Balinella ornata* as recently amended by Fosshagen & Iliffe (2004) from the original description (Fosshagen et al. 2001), the elongate seta is on the left ramus of both genders. The gender-specific location of this seta was considered an autapomorphy of *Balinella* by Fosshagen et al. (2001), differentiating the genus from several other epacteriscid genera (*Bouburiella*, *Edaxiella*, *Euautiosis*, *Euantronia*, *Epacteriscus*, and *Erebonectoides*) which have an elongate seta on the left ramus of both genders, as does *B. yucatanensis*. The slight asymmetry reported for *Balinella* (Fosshagen et al. 2001) on the right caudal ramus has a much stronger expression in the new species. The location of asymmetrical structures, but not their morphology, in the Epacteriscidae may be similar to the pattern found in the Metridinidae. In the latter family, asymmetry has been studied extensively in *Pleuromamma* (Ferrari 1984) and location appears to have evolved several times so that the phylogenetic information available from the location of asymmetrical structures is particularly difficult to interpret.

Overall, the main differential characters used to include this species in *Balinella* are: 3 outer spines on the third exopodal segment of legs 3 and 4; mandibular gnathobase not projected frontally; mandibular palp biramous; a wide labrum,

rounded distally; female antennule with no modified setae; and endopod of antenna slightly longer than exopod.

Balinella yucatauensis also differs from *B. ornata* in the structure of several presumed secondary sex characters. A cluster of spinules present on the fifth pedigerous somite of the new species is absent in *B. ornata*. The female genital double-somite is not produced in *B. ornata*, whereas it is produced asymmetrically as 2 small bulges on the right side of *B. yucatauensis*. A coxal seta is absent on the female fifth leg in the new species but is present in *B. ornata*; the armature of distal exopodal segment is 2,1,3 in the new species; it is 2,2,2 in *B. ornata*. The distal attenuation on the antepenultimate segment of the male right antennule extends to the distal segment of *B. ornata* (Fosshagen et al. 2001, fig. 26B) but beyond the distal segment of the new species.

There are many additional differences in segmental and setal morphology of the male fifth leg exopods, among which are: the distal exopodal segment of the left leg appears as an unarmed trapezoidal structure in *B. ornata* vs. an elongate, dactyli-form structure in the new species; the dorsal margin of the left middle endopodal segment is only slightly produced in *B. ornata* but forms a thumb-like extension in the new species; the distal endopodal segment of the right ramus extends beyond the terminal spine of the exopod of *B. ornata* (see Fosshagen et al. 2001, fig. 26J) but does not reach beyond the midlength of the terminal exopodal spine of the new species (Fig. 5E–G). In addition, the two species diverge in several other characters. The rostral filaments of *B. ornata* are relatively shorter and stronger (see Fosshagen et al. 2001, fig. 28D) than in the new species, in which these structures are long, slender. The antennules of *B. ornata* appear 26-segmented in the female (segments 26–27 intersegmental articulation incomplete)

but are 27-segmented in the female of the new species. The antennary exopod distal segment is fused to the penultimate segment in the new species, whereas the segments are separate in *B. ornata*. The mandibular basis has 3 setae in the new species vs. 2 in *B. ornata*; also, the maxillule of the latter species has a characteristic set of spinule rows that are absent in the new species. In *B. yucatauensis* the maxilla has 5 setae on the proximal coxal endite and the maxilliped bears 4 setae on the distal exopodal segment; this armature diverges from that found in *B. ornata* (6 and 3 setae, respectively). The male right antennule of the new species has ancestral segments II–IV fused vs. a II–III fusion in *B. ornata*. The female rostrum is different in both species: the filaments are stout and relatively short in *B. ornata* but longer and more slender in *B. yucatauensis*.

Discussion

The anchialine crustacean fauna of the Yucatan Peninsula includes a number of species: 8 cyclopoid copepods, 2 ostracods, 10 decapods, 6 isopods, 5 amphipods, 2 mysids, 1 remipede, and 1 thermosbaenacean (Iliffe 1992, Yager 1987, Suárez-Morales & Rivera-Arriaga 2000). The wide distribution and relatively high diversity of epacteriscid copepods in the tropical northwestern Atlantic Ocean (Barr 1984, Fosshagen et al. 2001, Fosshagen & Iliffe 2004) suggest that species of this family should be present in the anchialine caves of the Yucatan. *Balinella yucatauensis* is the first such calanoid copepod recorded in the Yucatan Peninsula and represents the first record of the Epacteriscidae in Mexico (see Suárez-Morales et al. 2000).

Epacteriscids frequently co-occur with remipedes in different tropical areas of the world (Yager 1991, 1994; Jaume & Humphreys 2001). This co-occurrence

and the fact that remipedes are the oldest crustaceans known was considered by Fosshagen et al. (2001) as evidence for an ancient origin of the Epacterisidae. In the Yucatan Peninsula, the presence of the remipede *Speleonectes tulumensis* Yager, 1987 and the thermosbaenacean *Tulumella midens* Bowman & Iliffe, 1988 in the same area as *B. yucatanensis* supports this association and deduction. The distribution of hypogean thermosbaenaceans in the West Indies, Yucatan, the Canary Islands, and the Mediterranean region has been taken to indicate their post-Jurassic, Tethyan origin (Cals & Monod 1988, Iliffe 1992). The occurrence of *Balinella* with its primitive morphology (Fosshagen et al. 2001) supports an ancient origin and isolation of the anchialine fauna of the Yucatan Peninsula.

The geological history of the Yucatan Peninsula is associated in many ways with that of the Caribbean and Central America. The Yucatan crustacean troglobitic fauna is clearly linked to that known from the Bahamas (at least 8 genera) and Bermuda (4 genera) (see Holsinger 1986, Iliffe 1992). Geological evidence indicates that the Greater Antilles were associated closely with North America via Yucatan (Coney 1982). The oldest rocks known in the Yucatan Peninsula are from the Paleozoic, and the Yucatan Peninsula has been influenced by episodes of marine regressions and transgressions of variable intensities. All of the Yucatan Peninsula was submerged during the Cretaceous. A later regression in the Paleocene-Eocene exposed the central core of the Yucatan Peninsula, but another complete transgression occurred in the middle Eocene. In the Upper Oligocene-Lower Miocene, only the eastern coast, where the new *Balinella* was recorded, remained above sea level. In the Early Pliocene, this coast was covered once again. Finally, the current littoral perimeter of the Yucatan Peninsula was reached during the Late

Pliocene-Pleistocene (Weyl 1966, López-Ramos 1975); epigeal waters and systems along the epicontinental fringe were colonized by freshwater forms (Suárez-Morales et al. 2004).

If the ancestors of the epacteriscids were epigeal marine forms that progressively invaded the cave environments, as were the ancestors of most other known marine stygobionts (see Holsinger 2000), the current distribution of epacteriscids (Fig. 7) may be a result of different events of colonization and diversification. Wilkens (1982) suggested that the evolution of the Yucatan troglobitic marine fauna started in coastal caves of the Pliocene shoreline, along the central axis of the peninsula. Epacteriscids have not been recorded in areas related to this oldest core of the Yucatan Peninsula, perhaps because their marine ancestors living in the submerged parts of the peninsula did not adapt to the fluctuating epigeal conditions. The karst's hydrographic structure in this core is different from the hydrography along the eastern coast, the latter with a subjacent layer of marine water below a surficial lens of freshwater. During the Pleistocene, when the eastern coast emerged, some Yucatan Peninsula populations that were already established in caves became isolated by the overlying freshwater lens. Succeeding marine transgressions may have promoted periodic dispersal of some of these species. Therefore, the present Yucatan Peninsula epacteriscid populations may represent secondary invasions, and probably became established in caves along the present coastline of the Yucatan only after the Pleistocene, and in younger epicontinental anchialine systems. In the Caribbean region, including the Yucatan Peninsula, the successive marine transgressions followed by regressions promoted dispersal followed by isolation or strandings, respectively. The current distribution of the most primitive epacteriscid genera, including *Balinella*, *Erebo-*

nectes, and *Erebonectoides*, probably represents the oldest biogeographic pattern in the region. They may result from different invasive events, as has been hypothesized for many demersal and freshwater copepods (Boxshall & Jaume 2000).

All genera of the family Epacteriscidae have been collected from caves, but two species of *Epacteriscus* and *Enantiosis*, with many apomorphies, also have been recorded outside cave systems and presumably are more likely to be dispersed. The most primitive genus, *Erebonectes*, to which *Balinella* seems to be closely related (Fosshagen et al. 2001), is known only from remote, isolated parts of caves. Surprisingly, *Enantiosis belizensis* and the two species of *Epacteriscus* found on the adjacent coast of Belize do not appear to be closely related to *Balinella* (Fosshagen et al. 2001). The differences between the Belizean epacteriscid fauna and that of the Yucatan Peninsula may result from 1) the dispersal of *Epacteriscus-Enantiosis*, both living in habitats outside of cave systems; and 2) the radiation and divergence of relatively isolated populations of the primitive genus *Balinella* before dispersal of the relatively modern *Epacteriscus-Enantiosis* to Belize. Geological data supporting this faunistic divergence may be represented in the fault dividing Belize into a northern and a southern part (Bateson and Hall 1972). All of the Belize species were recorded in reef-related caves along the fault, but not inland. During the Pliocene, when the main invasions of caves may have taken place (Wilkens 1982), the southern part of Belize had emerged while the Yucatan Peninsula remained submerged under marine water. The southern part of Belize, initially above sea level during the Paleocene, submerged in the Late Oligocene and re-emerged during the Middle Miocene (Weyl 1966, Iturralde-Vinent & McPhee 1999). During these events, geological differences between the Yucatan Peninsula and Belize may have prevented or

delayed the invasion of ancestral epacteriscids into this area; their presence probably results from a secondary invasion into the Belizean reef caves. Similar cases are represented by the divergence of the single species of *Iboyella* and of *Gloinella* in Cuba, and by the Yucatan epacteriscid. Although these two areas were in contact during the Paleocene, prior to the displacement of the Greater Antilles to the east, the Yucatan Channel was in existence long before the Late Eocene and represents a continuous deep-water barrier to dispersal of a shallow-water fauna (Iturralde-Vinent & McPhee 1999).

So far, the Bahamas and Bermuda have the most diversified epacteriscid fauna, with 10 and 3 species recorded, respectively. The western Caribbean, including Belize, Cuba, and now the eastern coast of the Yucatan Peninsula constitutes, in general, a relatively rich zone, with six species. Most of the other genera and species are represented in isolated areas of the Pacific or the eastern Tropical Atlantic (Fig. 7). A phylogenetic analysis of the Epacteriscidae (Fosshagen et al. 2001) resulted in a cladogram that separates different clusters. One of the most interesting is that formed by the diverse *Enantiosis*, with species in different geographic zones (Bermuda, Belize, Galapagos, Palau, Fiji). The diversification of *Enantiosis*, the most speciose epacteriscid genus, could be related to its dispersal capabilities, although part of this pattern could be related to the Tethyan distribution of the epacteriscid ancestors. This genus formed two clusters of species, one of three Indo-Pacific species and the other with four species, three of which are known from the greater Caribbean region.

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