European Journal of Taxonomy 917: 152–169
https://doi.org/10.5852/ejt.2024.917.2395
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ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2024 · Suárez-Morales E.

Research article

urn:lsid:zoobank.org:pub:3C2B9600-0276-4B8E-A3FD-36653D7D79B6

Two new species of *Monstrilla* (Copepoda: Monstrilloida: Monstrillidae) from a protected reef system of the Mexican Caribbean

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Abstract. Several adult female monstrilloid copepods, collected in March 2022 from the protected reef area of Xcalak, on the southern part of the Mexican Caribbean coast, proved to belong to two undescribed species of *Monstrilla* Dana, 1849. They are described here as *M. xcalakensis* sp. nov. and *M. annulata* sp. nov., partly by use of scanning electron microscopy. Females of the two species are generally similar but differ in: (1) antennular segmental structure, (2) antennular armature and ornamentation, (3) structure and setation of the fifth leg, (4) number and modifications of the caudal setae, and (5) integumental ornamentation. Comparison with congeneric species revealed distinctive features for both species that support their status as new. These two species are interesting additions to the reef-dwelling monstrilloid copepod fauna of the Mexican Caribbean and confirm *Monstrilla* as the most diverse genus of monstrilloids in this area, now represented by nine species.

Keywords. Caribbean reef systems, parasitic copepods, monstrilloids, taxonomy, reef crustaceans, SEM.

Suárez-Morales E. 2024. Two new species of *Monstrilla* (Copepoda: Monstrilloida: Monstrillidae) from a protected reef system of the Mexican Caribbean. *European Journal of Taxonomy* 917: 152–169.
https://doi.org/10.5852/ejt.2024.917.2395

Introduction

As larvae, monstrilloid copepods are protelean endoparasites that infect different groups of benthic marine invertebrates (Huys *et al.* 2007; Suárez-Morales 2011, 2018; Suárez-Morales *et al.* 2014; Jeon *et al.* 2018a). The non-feeding reproductive adults, however, are frequently encountered in plankton samples. They are usually found in coastal and estuarine systems and can be highly diverse and abundant in reef-related waters (Suárez-Morales 2001; Grygier & Ohtsuka 2008). This copepod order is currently considered to include seven valid genera: *Monstrilla* Dana, 1849, *Cymbasoma* Thompson, 1888, *Monstrillopsis* G.O. Sars, 1921, *Maemonstrilla* Grygier & Ohtsuka, 2008, *Australomonstrillopsis* Suárez-Morales & McKinnon, 2014, *Caromiobenella* Jeon, Lee & Soh, 2018, and *Spinomonstrilla* Suárez-Morales, 2019 (Grygier & Ohtsuka 2008; Suárez-Morales & Gasca 2004; Suárez-Morales 2011, 2018, 2019; Jeon *et al.* 2018). Problems persist, however, concerning the distinctness and validity of *Maemonstrilla* and *Haemocera* Malaquin, 1896 with respect to *Monstrillopsis* (Jeon *et al.* 2018a, 2018b). At the species level, the taxonomic and nomenclatural history of the most diverse genera (viz, *Monstrilla*,

Cymbasoma, and *Monstrillopsis*) is also complex, and uncertainties remain (Grygier & Ohtsuka 2008; Suárez-Morales 2011, 2018; Grygier & Suárez-Morales 2018; Suárez-Morales & Grygier 2021). The re-examination of type specimens and the analysis of material from new sites using updated descriptive standards have been invaluable in our efforts to progressively solve some of these problems (Grygier 1994; Suárez-Morales 2000a, 2022a; Suárez-Morales & Gasca 2004) while also increasing our sum of knowledge of monstrilloid diversity.

Taxonomic examination of female monstrilloid copepods, obtained by light traps in March 2022 from the protected reef area of Xcalak, on the southern part of the Mexican Caribbean coast, revealed the presence of two undescribed species of *Monstrilla*, raising the known diversity of the reef-related monstrilloids of the Mexican Caribbean from eight species to ten. The previously known species of monstrilloids from these reef systems include *Cymbasoma quintanarooense* (Suárez-Morales, 1993), *Monstrilla mariaeugeniae* Suárez-Morales & Islas-Landeros, 1993, *M. careli* Suárez-Morales, 2001, *M. careloides* Suárez-Morales, 2001, *M. elongata* Suárez-Morales, 1994, *M. marioi* Suárez-Morales, 2003, *M. globosa* Suárez-Morales, 2003, and *M. mahahualensis* Suárez-Morales, 2022 (Suárez-Morales 2001, 2003, 2022b). The two new species are described herein, with comparisons to congeneric species.

Material and methods

Several female monstrilloids referable to the genus *Monstrilla* were isolated from light-trap samples collected in March 2022 from Xcalak, a protected reef system on the southern part of the Mexican Caribbean coast (approx. 18°16′ N, 87°50′ W). Detailed microscopic examination showed them to belong to two undescribed species of the genus, which are described here as much as possible by following the criteria proposed by Grygier & Ohtsuka (1995, 2008) for female monstrilloids. The descriptions of both species are partly based on SEM observations that provide insight into interesting morphological details. Two adult females of each species were prepared for SEM examination by dehydration of specimens in progressively stronger aqueous solutions of ethanol (70–100%), critical-point drying, and gold-coating following standard procedures. Observations were made with a JSM-6010LA microscope at El Colegio de la Frontera Sur, Chetumal, Mexico. The type specimens have been deposited in the Zooplankton collection (ECO-CHZ) at El Colegio de la Frontera Sur (ECOSUR) in Chetumal, Mexico. The new species were compared with their known congeners based on published literature.

Results

Phylum Arthropoda von Siebold, 1848
Subphylum Crustacea Brünnich, 1772
Superclass Multicrustacea Regier *et al.*, 2010
Subclass Copepoda Milne Edwards, 1840
Order Monstrilloida Sars, 1901
Family Monstrillidae Dana, 1849

Genus ***Monstrilla*** Dana, 1849

The two species studied here can be assigned to the genus *Monstrilla* by the presence of 1) a single urosomite between the genital double-somite and the anal somite, 2) well-developed fifth legs, with two ramal lobes usually carrying setae, and 3) six setae on each caudal ramus. This combination of characters is unique among the accepted genera of monstrilloids (Isaac 1975; Suárez-Morales & McKinnon 2014; Jeon *et al.* 2018).

Monstrilla xcalakensis sp. nov.
urn:lsid:zoobank.org:act:0C50D553-D29D-499E-A16A-93EFBE8EAC9B
Figs 1–3

Differential diagnosis

Medium- to large-sized female *Monstrilla* with elongate, cylindrical cephalothorax constituting more than 60% of body length and prominent oral cone situated one-third of way along ventral surface of cephalothorax. Antennule four-segmented and segments 1–4 separate. Outer exopodal spines of legs 1–4 long and acute. Genital double-somite with anterioventral expansion carrying pair of posteriorly directed ovigerous spines, these not reaching to tips of caudal rami. Fifth legs bilobed, both lobes of similar length and breadth (endopodal lobe slightly shorter) and fused to each other in distal half; endopodal lobe armed with single seta, exopodal lobe with three setae. Caudal rami each bearing six setae, with proximal ends of apical setae III and IV much swollen.

Etymology

The specific name, an adjectival Mayan toponym (+ Latin suffix '-*ensis*' = 'place'), refers to the reef system of Xcalak in the Mexican Caribbean, where this species was collected. The correct pronunciation of the species name starts with 'sh', followed by a strong 'ka'. Gender is feminine.

Material examined

Holotype

MEXICO • 1 ♀, undissected and mounted in glycerin on slide; Xcalak reef lagoon; 18°16′04.05″ N, 87°49′44.24″ W; depth 1–4 m; 3 Mar. 2022; L. Vásquez-Yeomans, J.A. Cohuo-Colli, J. López-May, and F. Andrade leg.; ECO-CH-Z 11812.

Paratypes

MEXICO • 4 ♀♀, undissected, mounted in glycerin on 4 slides; same collection data as for holotype; ECO-CH-Z 11813 to 11815 • 2 ♀♀, gold-coated and mounted together on one SEM stub; same collection data as for holotype; ECO-CH-Z 11817.

Other material

MEXICO • 1 ♀, undissected, glycerin-preserved in vial; same collection data as for holotype; author's collection at ECOSUR.

Type locality

Reef lagoon of Xcalak (18°16′04.05″ N, 87°49′44.24″ W), southern part of the Mexican Caribbean coast.

Description (♀)

Measurements. Body length of holotype 3.51 mm as measured from 'forehead' to posterior margin of anal somite, length range of paratypes 2.72–2.85 mm. Body tagmosis as usual in female *Monstrilla* (Isaac 1975; Suárez-Morales & Islas-Landeros 1993; Chang 2014).

Cephalothorax. Long, cylindrical, with straight margins, representing about 60% of total body length and fully incorporating first pedigerous somite. Oral cone prominent (oc in Fig. 3B), located 29% of way back along ventral surface of cephalothorax (Figs 1B, 3B). Cephalic region anteriorly subquadrate in dorsal view, 'forehead' flat with pair of small sensilla (arrowheads in Fig. 1A). Lateral cups of eye poorly developed, almost unpigmented (lc in Fig. 3B). Ventral cup relatively small (vcu in Fig. 3B), of nearly same diameter as lateral cups. Cuticular ornamentation of 'facial' region of cephalothorax consisting of

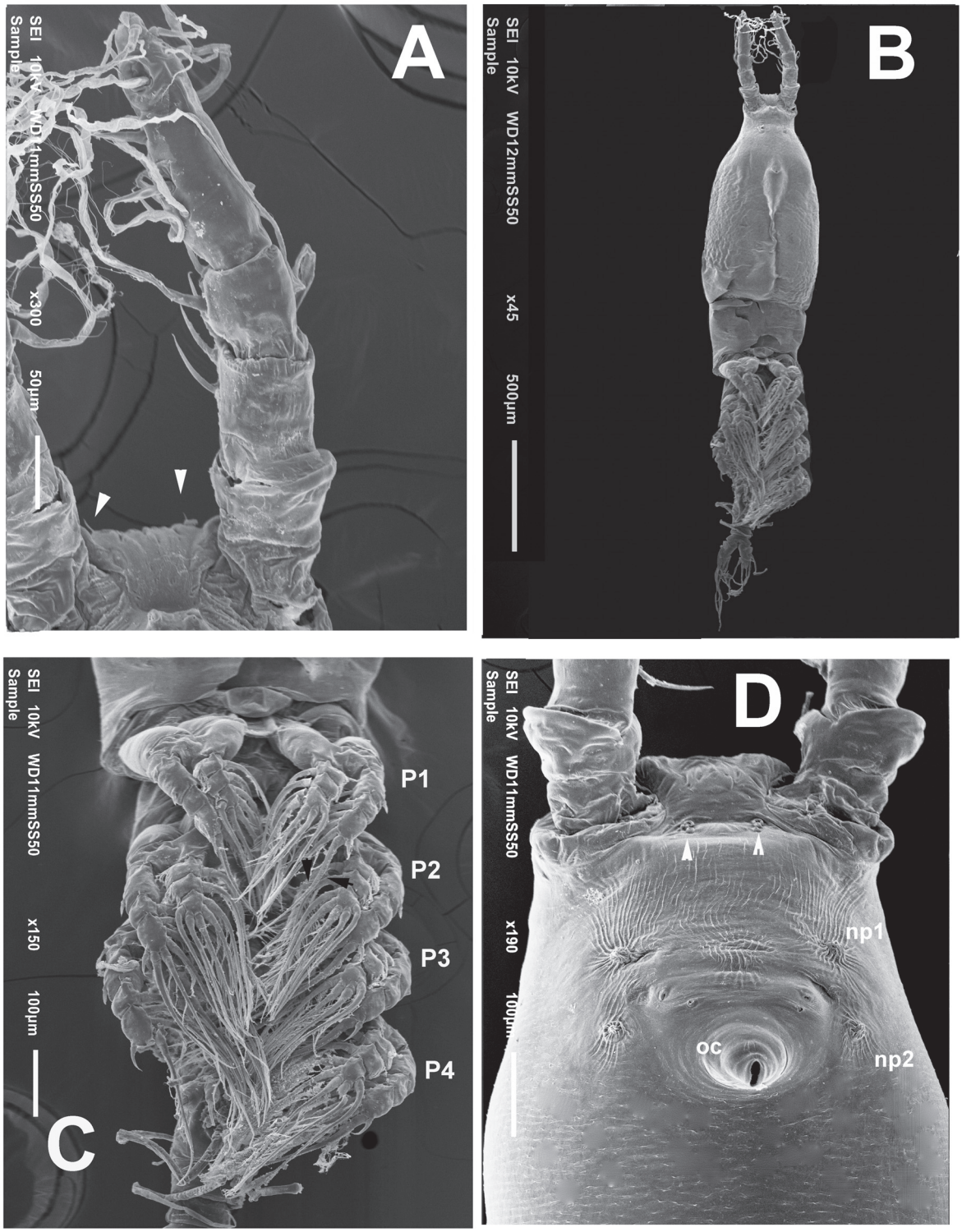

Fig. 1. *Monstrilla xcalakensis* sp. nov., paratype, ♀ (ECO-CH-Z 11814). **A**. Anterior cephalic region showing pair of sensilla, ventral view. **B**. Habitus, ventral view. **C**. Pedigerous somites 1–4 showing swimming legs, ventral view. **D**. Cephalic region showing oral cone (oc), paired nipple-like processes (np1,2), and integumental wrinkles. Arrowheads indicate sensilla (A) or pores (D).

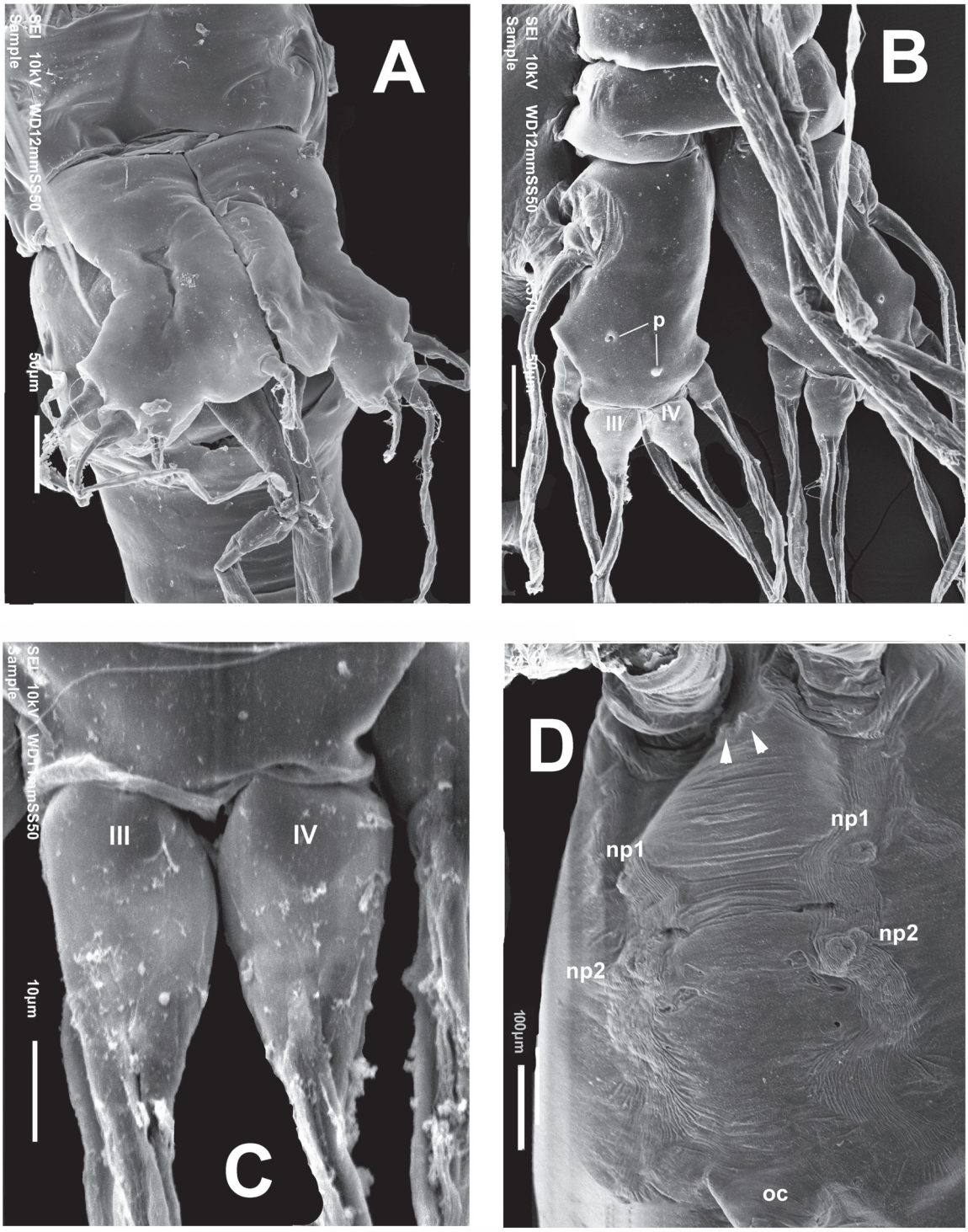

Fig. 2. *Monstrilla xcalakensis* sp. nov., paratype, ♀ (ECO-CH-Z 11813). **A**. Fifth legs, ventral view. **B**. Caudal rami and distal part of ovigerous spines, ventral view showing inflated caudal setae III and IV and large adjacent pores (p). **C**. Detail of proximally inflated caudal setae III and IV, ventral view. **D**. Preoral area, another specimen, ventral view, showing medial field of transverse striae, adjacent pairs of nipple-like integumental processes (np1,2), pair of pore clusters (arrowheads) at antennule bases, and oral cone (oc) with two pairs of preoral pores.

Table 1. Armature of swimming legs 1–4, including basipodites, endopodites, and exopodites, of *Monstrilla xcalakensis* sp. nov. and *M. annulata* sp. nov. (coxae lacking setae). Roman numerals indicate spiniform elements; Arabic numbers indicate setiform elements.

	Basipod	**Endopod**	**Exopod**
Leg 1	1–0	I–1;0–1;2.2,1	I–0;0–1; I,2,2
Legs 2–4	1–0	0–1;0–1;2,2,1	I–1;0–1; I,2,2,1

fields of longitudinal and oblique striae between oral cone and bases of antennules (Figs 1D, 3B); two clusters of three protruding pores each, these being located on anterioventral medial surface between antennule bases (Fig. 1D: white arrowheads); two pairs of nipple-like processes lateral and anteriolateral to oral cone, each with pore at apex, with additional indistinct pair between and slightly mesial to these (Fig 1D); and two pairs of minute pores at anteriolateral base of oral cone (Fig. 1D).

Antennules. Relatively short, about 22% as long as cephalothorax (Fig. 1B), distinctly four-segmented as usual in female monstrilloids, distal segment longest (Figs 1A, 3E). Length ratio of antennular segments (proximal to distal) 14.3 : 21.4 : 15.1 : 49.3 = 100 (Fig. 3A, C). Following Grygier & Ohtsuka's (1995) setal nomenclature for antennules of female monstrilloids, first segment with short, slender, spiniform setal element 1. Second segment bearing only four elements, including short elements $2d_{1-3}$ plus long seta IId, with ventral setation reduced, elements $2v_{1-3}$ being absent (Fig. 1A). Third segment with spiniform element 3 reaching to proximal third of succeeding fourth segment and lightly plumose setae IIId and IIIv. Fourth segment separated from third by well-defined suture, armed with setal elements $4d_{1,2}$ (short and spiniform), $4v_{1,2}$ ($4v_1$ shorter than $4v_2$), 4aes, IVv, IVd, Vm, Vv, Vd, 6aes, equally long spiniform apical elements 6_1 and 6_2, and subapical '*b*' setal group on outer margin comprising elements b_{1-3} and b_6 but lacking subdistal elements b_4 and b_5 (Figs 1A, 3E).

Thoracic somites. First pedigerous thoracic somite (incorporated into cephalothorax as noted above) and succeeding three free thoracic somites each bearing well-developed pair of biramous swimming legs (Figs 1C, 3D), all with exopodite longer than endopodite. Setal armature pattern (Table 1) as in *M. elongata* (see Suárez-Morales 2001). Basis of swimming legs 2–4 with short, slender outer seta, that on leg 3 longest and smooth; basipodal seta absent in leg 1. Outer apical spine of first and third exopodal segments of all legs noticeably long (arrows in Fig. 3D); outer apical spiniform seta of each distal exopodal segment with denticles along outer margin, sparse setules along inner margin (arrowheads in Fig. 3D); outer margin of endopodal segments 1 and 2 hirsute (Fig. 3D). All natatory setae lightly and biserially plumose.

Urosome. Consisting of four somites (Fig. 3A, C): fifth pedigerous somite carrying fifth legs, genital double-somite ventrally carrying paired ovigerous spines, one short, free preanal somite, and anal somite carrying pair of caudal rami. Length ratio of urosomites (from anterior to posterior) 31.7 : 36.8 : 14.7 : 16.8 = 100 (Fig. 3A, C). Fifth legs (Figs 2A, 3A, C) well developed, with square, undivided, unarmed protopod and pair of long, distally widening and distally confluent ramal lobes, proximal halves of which separated by narrow, tapered gap or crevice, appearing as an integumental depression; endopodal lobe slightly shorter than exopodal lobe, former armed with one seta, latter with three setae. Anterior half of genital double-somite weakly expanded, with incomplete transverse suture visible in dorsal and lateral view; ovigerous spines relatively short, reaching to midlength of caudal rami (Fig. 3C). Caudal rami subrectangular in dorsal view (Fig. 2B), 1.7 times as long as broad, each armed with six caudal setae. Seta I situated on proximal lateral margin, seta II subdistally along outer margin. Distalmost setae (III and IV) proximally expanded (Fig. 2B–C). Ventral surface of ramus with one large pore and two adjacent indistinct integumental structures on distal half (Fig. 2B).

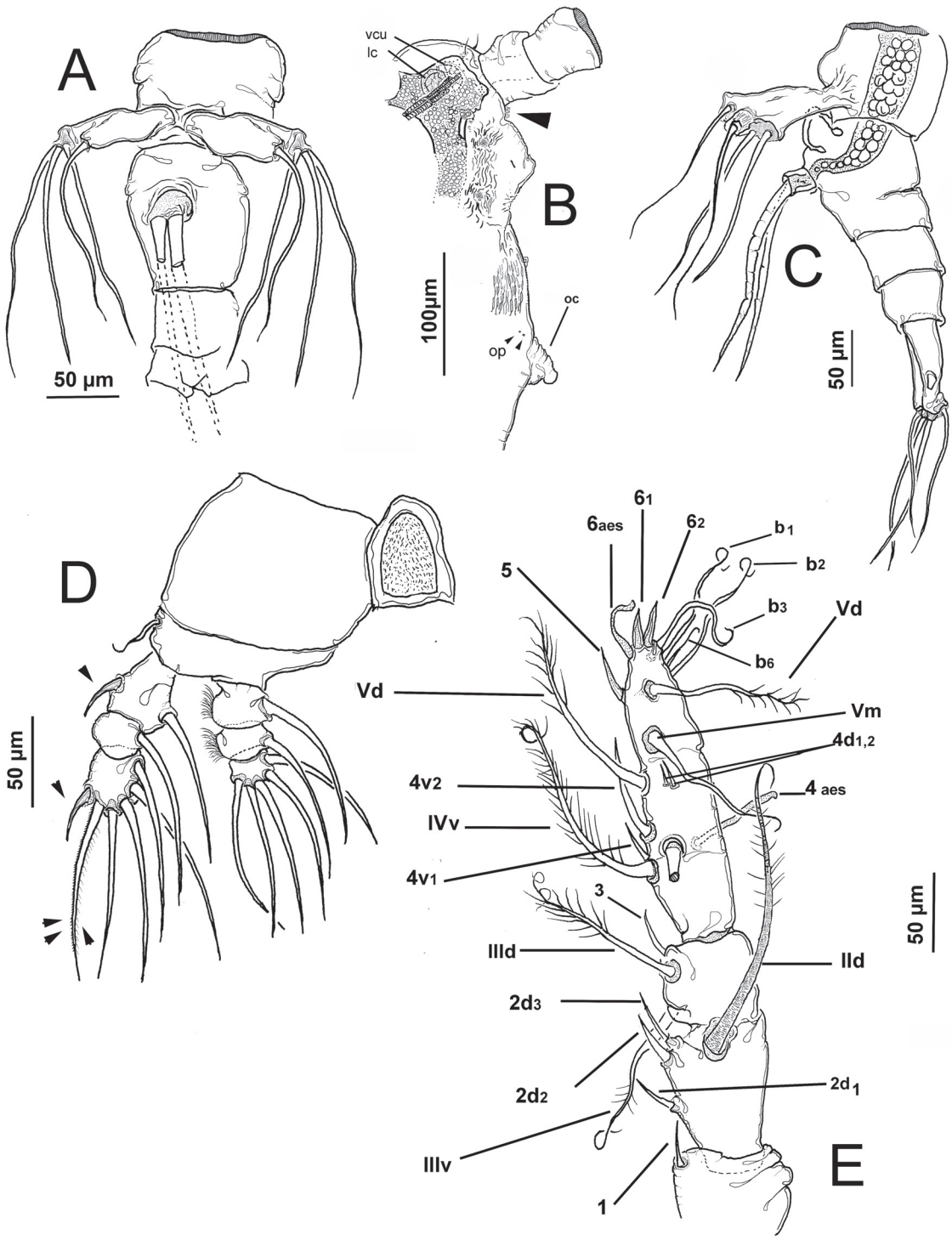

Fig. 3. *Monstrilla xcalakensis* sp. nov., holotype, ♀ (ECO-CH-Z 11812). **A**. Urosome showing fifth legs and insertion of ovigerous spines, ventral view. **B**. Cephalic morphology and ornamentation, lateral view, showing eye complex with naupliar eye medial cup (vcu), lateral cup (lc), cluster of three minite conical pores (large arrowhead), oral cone (oc), and pair of oral pores (op). **C**. Urosome, lateral view. **D**. Swimming leg 2 showing setation pattern with long exopodal spines (arrowheads) and hirsute outer margins of endopodal segments. **E**. Antennular armature with setal elements labelled following Grygier & Ohtsuka's (1995) nomenclature, dorsal view.

Justification for establishment of *M. xcalakensis* sp. nov.

Several species of *Monstrilla* have a well-developed, bilobed female fifth leg armed with one seta on the inner lobe and three on the outer, including some from the western Caribbean: *M. careli*, *M. careloides*, and *M. humesi* Suárez-Morales & Escamilla, 2001 (Suárez-Morales 2001; Suárez-Morales & Escamilla 2001). Such setation is a plesiomorphic character state that is seen in *M. grandis* Giesbrecht, 1891, *M. orcula* A. Scott, 1909, and *M. cymbula* A. Scott, 1909 as well (Scott 1909; Suárez-Morales 2000; Chang 2014). The new species differs from both *M. careli* and *M. careloides* in the strong development of the fifth leg's endopodal lobe, which is very reduced in *M. careloides* (cf. Suárez-Morales 2001: fig. 16) and weakly developed in both *M. careli* and *M. humesi*, barely reaching to the midlength of the exopodal lobe (cf. Suárez-Morales, 2001: fig. 6; Suárez-Morales & Escamilla, 2001: fig. 4d). The Caribbean *M. barbata* Suárez-Morales & Gasca-Serrano, 1992 also has a reduced endopodal lobe (cf. Suárez-Morales & Gasca-Serrano, 1992: figs 1d, 2f). Two western Caribbean species, *M. ciqroi* Suárez-Morales, 1993 and *M. rebis* Suárez-Morales, 1993, share with the new species the same armature of the fifth leg (i.e., 1, 3), but in both of them the endopodal lobe is much reduced, being represented only by a small protuberance (cf. Suárez-Morales 1993: figs 1d, 3d). In the Brazilian *M. brasiliensis* Suárez-Morales & Dias, 2000, the endopodal lobe is almost as long as the outer lobe, but is nonetheless more weakly developed and more slender (cf. Suárez-Morales & Dias, 2000: fig. 3c–d) than the strong, broad lobe of *M. xcalakensis* sp. nov. The fifth leg's endopodal lobe is wide and well-developed in *M. gibbosa* Suárez-Morales & Palomares-García, 1995 from the Gulf of California, but is not fused with the exopodal lobe (cf. Suárez-Morales & Palomares-García 1995: figs 2a, 3b). In addition, the antennular armature differs between these two species; in *M. gibbosa* the armature of the second segment includes elements $2v_{1-3}$ and $2d_{1,2}$, and element IId is absent, whereas in *M. xcalakensis* elements $2v_{1-3}$ are absent and IId is present. Also, *M. gibbosa* has branched setae in the 'b' setal group versus simple, unbranched 'b' setae in the new species (Fig. 3E).

Overall, the Korean species *M. ilhoii* Lee & Chang, 2016 most closely resembles *M. xcalakensis* sp. nov. It shares with the new species some important features: a large body size, exceeding 3 mm in total length; the same peculiar structure of the fifth leg, with a strong, broad endopodal lobe that largely is fused with the exopodal lobe; and proximally expanded terminal caudal setae (cf. Lee & Chang 2016: figs 1E, 2D). The two species nonetheless differ in several respects. Nearly the entire body surface of *M. ilhoii*, including the antennules, caudal rami, and legs 1–4, is finely sculptured with a polygonal pattern (cf. Lee & Chang 2016: fig. 4b–d), which *M. xcalakensis* wholly lacks. The cephalothorax of *M. ilhoii* constitutes 53% of the total body length, versus slightly more than 60% in the new species. The oral cone is more strongly protuberant in *M. ilhoii* (cf. Lee & Chang 2016: figs 1b, 4b) than in *M. xcalakensis* (Fig. 3B). Antennular segments 3 and 4 are completely fused in *M. ilhoii*, together forming a long distal segment that represents 69% of the antennular length (cf. Lee & Chang 2016: fig. 2a), whereas all four antennular segments are distinct and separate in the new species (Fig. 1A). Finally, according to Lee & Chang (2016), the ovigerous spines of *M. ilhoii* are long, reaching well beyond the tips of the caudal setae, while they are much shorter in the new species, not reaching the distal end of the caudal rami (Fig. 3A). The differences observed from the other known species of *Monstrilla*, and especially from *M. gibbosa* and *M. ilhoii*, appear to be sufficient to warrant the proposal of a new species for the present specimens.

Monstrilla annulata sp. nov.
urn:lsid:zoobank.org:act:6AFE4500-1C37-4AC0-87B5-AF4D511B8842
Figs 4–6

Differential diagnosis

Medium- to large-sized female *Monstrilla* with long cephalothorax. Antennule 4-segmented, with reduced setal armature: segment 1 unmodified; segment 2 lacking all elements of '2v' group (i.e., $2v_{1-3}$); segment 3

with usual armature and 3 weak integumental constrictions; and segment 4 with 5–7 deep integumental constrictions making it appear multi-annulate, with apex modified into diagonally truncate tip forming flat, disc-like structure with reduced armature, i.e., lacking usual apical elements 6_1 and 6_2 but retaining reduced 6aes. Fifth legs weakly bilobed, with endopodal lobe represented by short, flat protuberance on proximal inner margin of exopodal lobe, latter represented by large, subrectangular plate with incised inner margin, distinctively pilose outer margin, and one distal and one subdistal seta. Ovigerous spines not reaching to distal margins of caudal rami. Surface of caudal rami and other appendages, including proximal parts of ovigerous spines and urosomites (Fig. 6E), densely sculptured with fine, thread-like undulate patterns. Caudal rami each bearing five setae.

Etymology

The specific name is a Latin adjective with a feminine suffix to match the gender of the genus, meaning 'ringed' in reference to the worm-like appearance of the integumental constrictions of antennular segments 3 and 4.

Type material

Holotype

MEXICO • ♀, undissected glycerin-preserved in vial; Xcalak reef lagoon; 18°16′04.05″ N, 87°49′44.24″ W; depth 2.5 m; 3 Mar. 2022; L. Vásquez-Yeomans, J.A. Cohuo-Colli, J. López-May, and F. Andrade leg.; plankton light-trap; ECO-CH-Z 11810.

Paratypes

MEXICO • 3 ♀♀, 1 ♀ of them undissected, mounted in glycerine on slide, sealed with acrylic varnish; same collection data as for holotype; ECO-CH-Z 11811 • 2 ♀♀, two partly dissected, gold-coated, mounted on single SEM stub; same collection data as for holotype; ECO-CH-Z 11818.

Other material

MEXICO • 2 ♀♀, undissected in vial with glycerol; same collection data as for holotype; author's collection at ECOSUR.

Type locality

Reef lagoon of Xcalak (18°16′04.05″ N, 87°49′44.24″ W), southern part of the Mexican Caribbean coast.

Description (adult ♀)

Measurements. Body length of holotype 1.96 mm measured from 'forehead' to posterior end of anal somite, three paratypes 2.00, 2.12, and 2.25 mm long, two non-type individuals 2.0 and 2.1 mm long. Body tagmosis as usual in female *Monstrilla* (Isaac 1975; Suárez-Morales & Islas-Landeros 1993; Chang 2014).

Cephalothorax. Relatively robust, representing about 63% of total body length and fully incorporating first pedigerous somite. Oral cone prominent, located 30% of way back along ventral surface of cephalothorax. Cephalic region anteriorly subquadrate in dorsal view, 'forehead' flat, sensilla not observed. Nauplius eye as in *M. xcalakensis* sp. nov. except for lateral cups being almost unpigmented. Cuticular ornamentation of cephalothorax including medial cluster of minute, crater-like pores between antennule bases (Fig. 5A), two pairs of nipple-like processes between oral cone and antennule bases, and field of transverse striae adjacent to oral cone (Fig. 6C).

Antennules. About 40% as long as body, almost 65% as long as cephalothorax, four-segmented as usual in female monstrilloids, with second and third segments separate from each other and fourth

(longest) segment separated from third by well-defined suture (Fig. 4A–B). Length ratio of antennular segments (proximal to distal) 8.3 : 22.2 : 13.9 : 56.1 = 100. Following Grygier & Ohtsuka's (1995) setal nomenclature for antennules of female monstrilloids, first segment lacking spiniform setal element 1. Second segment bearing elements $2d_{1-3}$ (dots in Fig. 4A), but dorsal seta IId not observed. Third segment with short, spiniform element 3 and slender ventral seta IIIv (Fig. 4A), but dorsal seta IIId absent. Third and fourth segments with three and five to seven regular ring-like constrictions respectively; annulation more clearly expressed in fourth segment (Fig. 4A–C). Fourth segment armed with setal elements $4v_{1-3}$ (arrowheads in Fig. 4A), 4aes, IVd, IVv, Vm, 5 (broken), Vv, Vd, 6aes, 6_1, 6_2 (both vestigial) (Fig. 4B, D), and subapical 'b' setal group on outer margin comprising only four elements (b_{1-4}, thus lacking b_5 and b_6) (Fig. 4A–B). Antennular surface densely sculptured with fine, undulate thread-like patterns (Fig. 4C).

Thoracic somites. Swimming legs 1–4 on posterior cephalothorax and first three free pedigerous somites armed as in *M. xcalakensis* sp. nov. (Table 1).

Urosome. As usual in *Monstrilla*, urosome consisting of four somites (Fig. 3A, C): fifth pedigerous somite carrying fifth legs, genital double-somite with anterior half expanded and bearing pair of posteriorly-directed ovigerous spines, one short free somite, and anal somite. Length ratio of urosomites (from anterior to posterior) 25.3 : 26.6 : 31.4 : 16.6 = 100. Fifth legs well developed, bilobed, with finely sculptured integument. Endopodal lobe reduced, unarmed, fused to outer lobe. Outer lobe large, subrectangular, plate-like, with hirsute outer margin (Fig. 5B–C), three to four diagonal incisions on inner margin (Fig. 5C–D), and one apical and one subapical seta. Ovigerous spines (Fig. 5B) relatively short, not reaching tips of caudal rami. Caudal rami subrectangular, 1.7 times as long as broad in dorsal view, armed with five caudal setae (Fig. 6F), with setae II, III and IV grooved along lateral surfaces (Fig. 6D, F).

Justification for establishment of *M. annulata* sp. nov.

The new species *Monstrilla annulata* sp. nov. has two distinctive features that make it readily distinguishable among its congeners and support its status as a new member of the genus *Monstrilla*. First is the modified antennule with integumental constrictions appearing as rings, particularly in segments 3 and 4. A generally similar pattern is known in *Spinomonstrilla spinosa* Suárez-Morales, 2019, but in that species the annulated appearance is imparted by arcuate protruding scales, not by simple circular constrictions (cf. Suárez-Morales 2019: fig. 2d–e). Also, the antennules are remarkably elongate and narrow in *S. spinosa*, with the setal groups of segments 2–4 being more widely separated from each other than in *M. annulata*.

Other antennular modifications are found among species of *Monstrilla*, such as the absence of any intersegmental articulations in *M. mariaeugeniae*, with the segmental divisions only being marked by segmental constrictions (cf. Suárez-Morales & Islas-Landeros 1993: fig. 1b) and a similar pattern involving only segments 2–4, described in *M. humesi* from the Gulf of Mexico (cf. Suárez-Morales & Escamilla 2001: fig. 3b). An inflated margin of some antennular segments has been reported in *M. brasiliensis* (now in *Caromiobenella* Jeon, Soh & Lee, 2018; see Cruz Lopes da Rosa *et al.* 2021), *M. grygieri* Suárez-Morales, 2000a, and *M. inserta* A. Scott, 1909 (for both, see Suárez-Morales 2001).

The second distinctive feature of *M. annulata* sp. nov. is the uniquely modified exopodal lobe of the female's fifth leg; no other member of *Monstrilla* has a fifth leg combining an indented inner margin and a heavily hirsute outer margin. A lightly hirsute outer margin is known only in the female *Caromiobenella brasiliensis* (Suárez-Morales & Dias 2000), in which, however, the exopodal lobe carries three seta and the endopodal lobe is cylindrical and narrow (cf. Suárez-Morales & Dias 2000: fig. 3d), thus differing from *M. annulata*. A spinulose outer margin of the fifth leg is present in the poorly described *M. dakinensis*

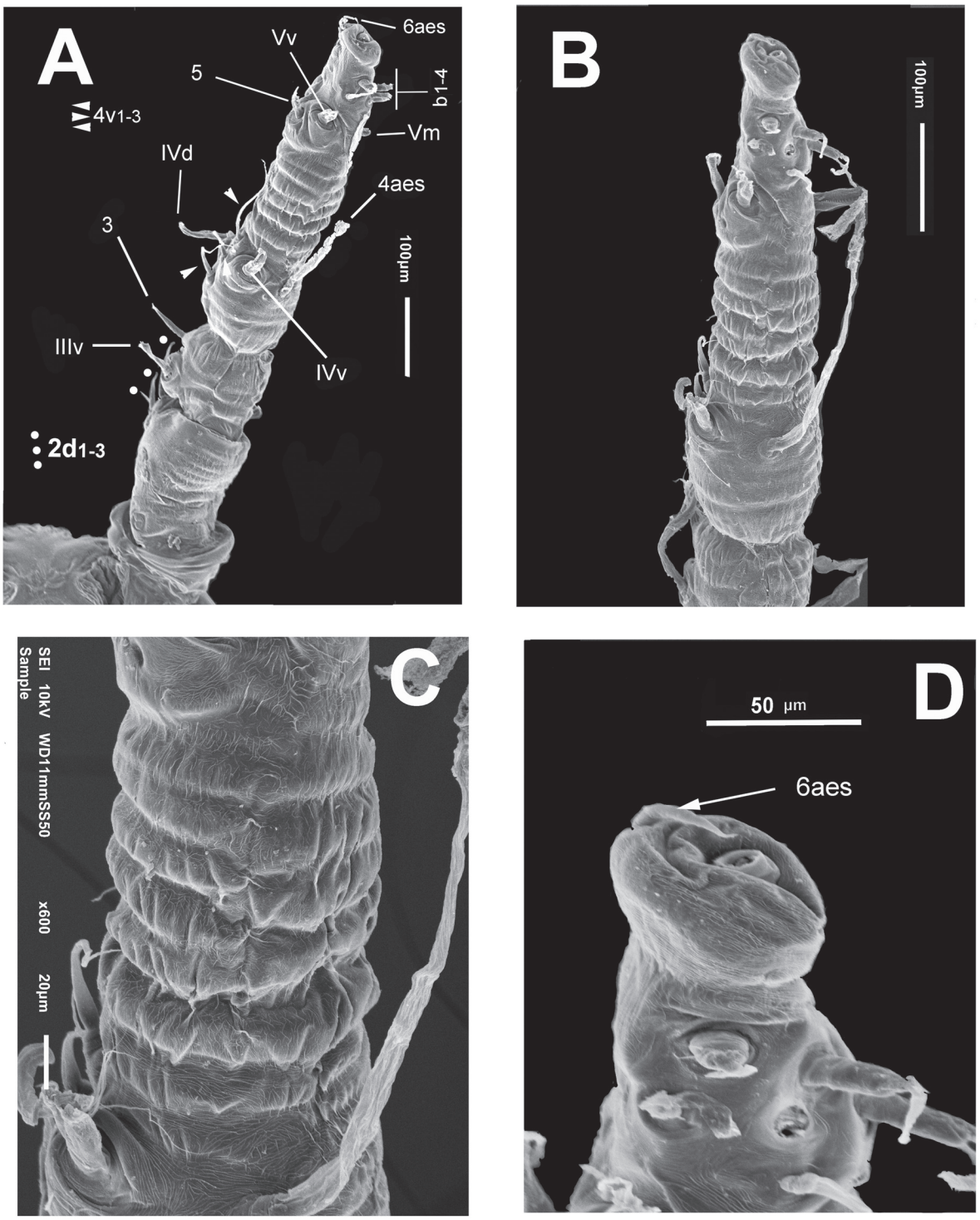

Fig. 4. *Monstrilla annulata* sp. nov., paratype, ♀ (ECO-CH-Z 11818). **A**. Left antennule with some setal elements or setal groups (v.gr., $2v_{1-3}$, $2d_{1-3}$) labeled following Grygier & Ohtsuka's (1995) nomenclature, ventral view. **B**. Distal (fourth) segment of right antennule, ventral view, showing truncate, disc-like apical modification. **C**. Detail of ring-like constrictions of fourth antennulary segment, ventral view. **D**. Truncate, disc-like apical process of antennule, showing reduced aesthetasc 6aes and absence of usual apical elements 6_1 and 6_2 (sensu Grygier & Ohtsuka 1995).

Davis, 1949 from Australia (Dakin & Colefax 1940), which shares with *M. annulata* the same armature of two setae on the exopodal lobe and a reduced endopodal lobe, but differs in lacking the indentations in the exopodal lobe's inner margin that help to define the new species. An exopodal lobe with two setae is also known in the Caribbean *M. elongata*, but the lobe is bulbous, not plate-like, and the antennules are unsegmented (cf. Suárez-Morales 1994: fig. 1c–d, g), unlike in the new species *M. annulata*.

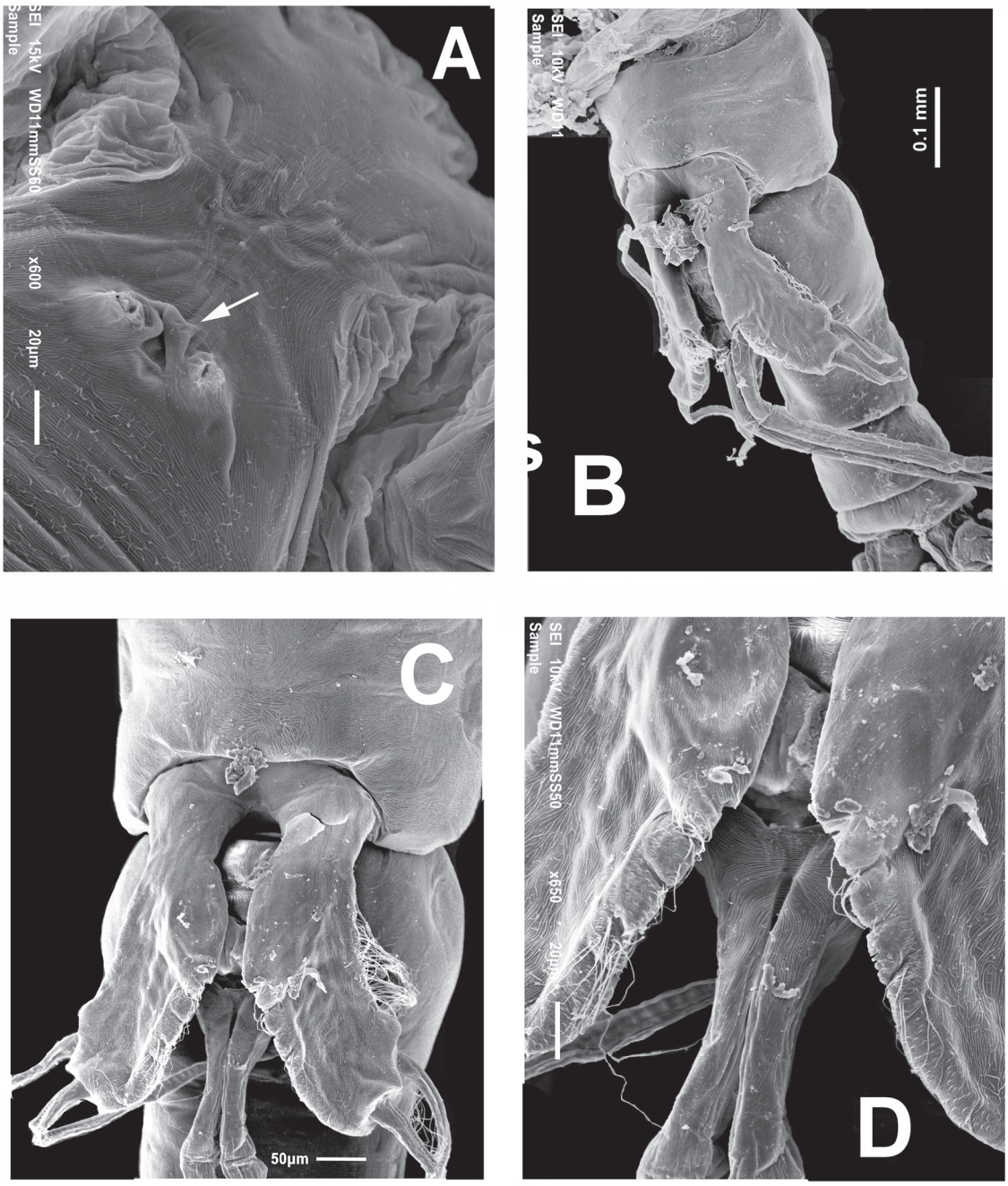

Fig. 5. *Monstrilla annulata* sp. nov., paratype, ♀ (ECO-CH-Z 11818). **A**. Cluster of three crater-like pores (arrow) between the antennule bases, ventral view. **B**. Urosome, showing fifth leg and short ovigerous spines, semi-lateral view. **C**. Fifth leg showing fine integumental sculpturing and hirsute outer margin, ventral view. **D**. Detail of inner margin of fifth leg's exopodal lobe showing diagonal incisions, ventral view.

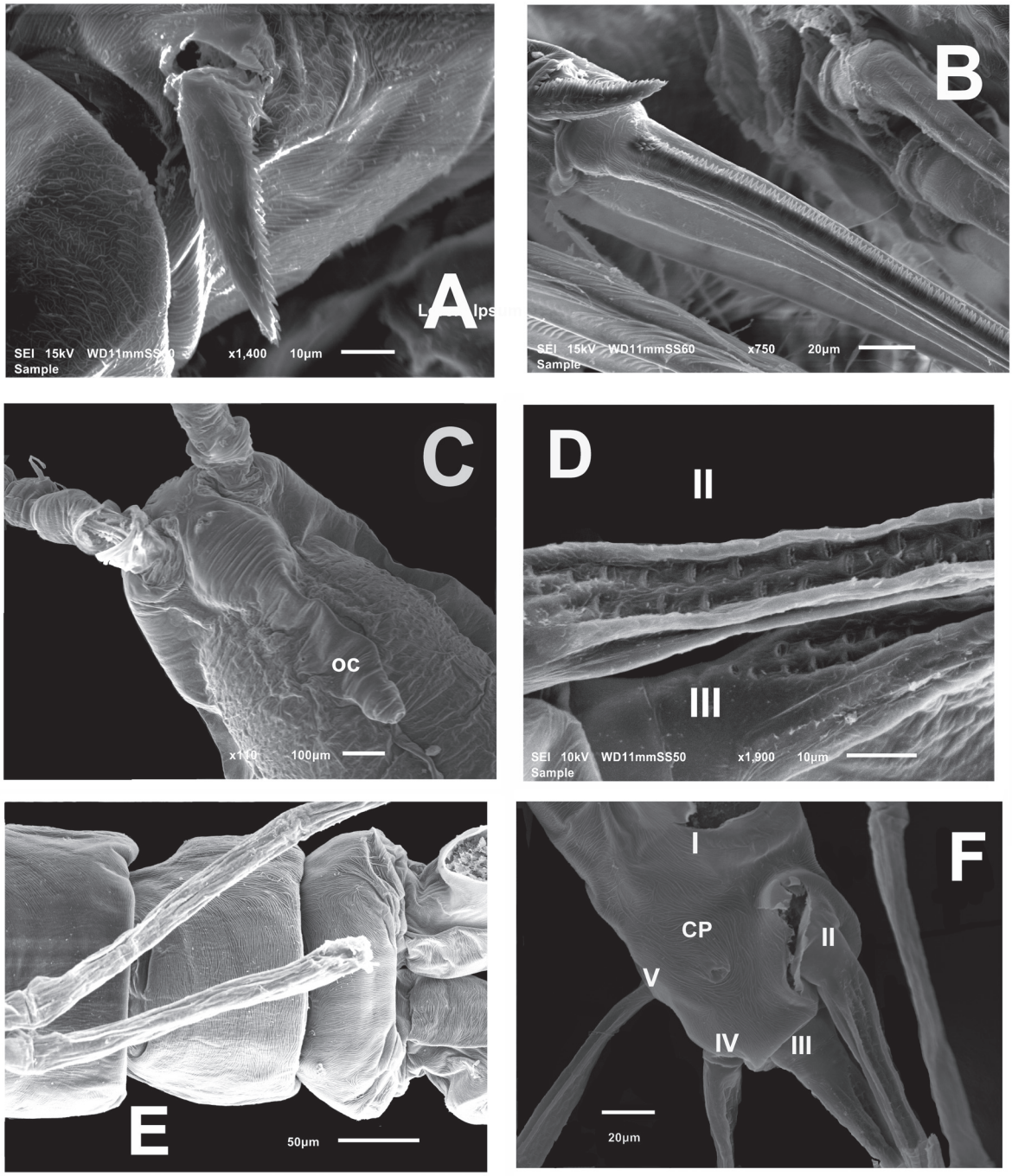

Fig. 6. *Monstrilla annulata* sp. nov., paratype, ♀ (ECO-CH-Z 11818). **A**. Leg 2, outer spine of first exopodal segment, showing ornamentation. **B**. Leg 1, outer spine of third exopodal segment and outer apical spiniform seta, both showing ornamentation. **C**. Anterior half of cephalothorax showing oral cone (oc) and preoral ornamentation, ventral view. **D**. Detail of caudal setae II and III, lateral view, showing grooves. **E**. Last urosomites showing dense pattern of fine, undulate thread-like integumental sculpturing, ventral view. **F**. Caudal rami showing large ventral pore (CP) and modified caudal setae II, III, and IV, with lateral grooves.

Discussion

No other species of *Monstrilla* besides the new species *M. xcalakensis* sp. nov. and *M. ilhoii* has a fifth leg showing distal fusion of the endopodal and exopodal lobes. The developmental stages of monstrilloids have been studied in some detail by Huys *et al.* (2007), focusing on the antennules and caudal rami of males, but the possible ontogenetic origin of ramal fusion in the female's fifth leg requires closer attention. According to Huys & Boxshall (1991), this leg is biramous, both rami are fused to the protopodal part of the limb, and the protopods of the left and right members of the leg pair are not connected by an intercoxal sclerite. An account of the development of the female fifth leg from the CIII stage to the preadult CV in an unidentified species of *Monstrilla* (Suárez-Morales *et al.* 2014) revealed that at the CIII stage, the fifth leg is represented by a single lobe, which progressively splits into a pair of distal lobes. Before this, the fifth legs were very likely a pair of unarmed buds. Completion of the final setation pattern is attained at the CIV stage, while separation of the lobes is still in progress. The endopodal lobe then becomes clearly separated from the exopodal lobe by the time the copepod exits its host as a preadult CV. It seems more likely that the unusual fifth legs of *M. xcalakensis* and *M. ilhoii* are the result of incomplete separation of the lobes in ontogeny, not a secondary but incomplete re-fusion of fully-formed lobes during the copepodite phase of development. The juvenile development of both species needs to be studied and compared to confirm this.

The structure of crustacean setae is highly variable, being defined by their function. In Garm & Watling's (2013) categorization of the known types of arthropod setae, none displays the type of grooved structure found in some of *M. annulata*'s caudal setae. Since such grooves do not occur in any recognized setal type, their function and origin remain speculative. It is also possible that the grooves are shrinkage artifacts resulting from the dehydration and critical point drying procedures employed prior to SEM observation. Caudal setae of other specimens of the type series examined by light microscopy had a row of setule scars but no obvious grooves.

The student who initially sorted the samples from Xcalak assumed that the female specimens of *Monstrilla xcalakensis* sp. nov. and *M. annulata* sp. nov. belonged to a single species, as they generally resemble each other. Superficial examination of plankton samples, particularly in highly diverse habitats for monstrilloids like coral reefs (Sale *et al.* 1986; Suárez-Morales 2001, 2003; Grygier & Ohtsuka 2008), can fail to distinguish among morphologically similar species. As many as eight species of monstrilloids had been described or reported from different reef zones of the Mexican Caribbean coast before the present study. This coast, which is part of the Mesoamerican Barrier Reef System (MBRS), supports a wide variety of aquatic habitats, including northern (Puerto Morelos = PM) and southern (Mahahual-Xcalak = MXK) reef sectors and Banco Chinchorro (BCH), an oceanic atoll. The species reported from these areas are *M. mariaeugeniae* (PM), *M. elongata* (PM, BCH), *M. mahahualensis* (PM, MXK), *M. xcalakensis* (MXK), *M. annulata* (MXK), *M. careli* (BCH), *M. careloides* (BCH), *M. marioi* (BCH), *M. globosa* (BCH), and *Cymbasoma quintanarooense* Suárez-Morales, 1994 (BCH) (Suárez-Morales 1994, 1996, 2003, 2022b). *Monstrilla* is clearly the most diverse genus of monstrilloid copepods in Mexican Caribbean reef areas, thus providing a contrast with other coastal and estuarine habitats like those in Brazilian waters, where the monstrilloid diversity is relatively low and mainly confined to coastal, transitional, and estuarine areas (Suárez-Morales & Dias in prep.), or in the southern Gulf of Mexico and northern coast of the Yucatan Peninsula, where only three species, *M. humesi*, *C. quintanarooense*, and *C. chelemense* Suárez-Morales & Escamilla, 1997, have been reported (Suárez-Morales 1993; Suárez-Morales & Escamilla 1997, 2001), all from shallow, low-salinity coastal systems. The diversity of monstrilloids has been underestimated in western Caribbean marine habitats, and the list is expected to grow as new sampling programs are undertaken.

The males of both new species described herein remain unknown. One of the main problems in monstrilloid taxonomy has been to reliably match both sexes of a species (Suárez-Morales 2010, 2011,

2018; Jeon *et al.* 2018b), a task that is particularly difficult in highly diverse habitats like coral reefs. The Mexican Caribbean reef system harbors at least three species of *Monstrilla* with males that have a genital complex like that of *M. conjunctiva* Giesbrecht, 1893 (see Suárez-Morales 2022b) and crater-like processes on antennular segments 2–4 (Suárez-Morales 1996, 1998, 2022). Members of this group are now known to be distributed in three different reef areas of the Mexican Caribbean, PM, MXK (*M. mahahualensis*), and BCH (*M. elongata*), but females are known only for *M. elongata*. It is possible that one or both of the present new species, currently known only from females, will eventually be matched by means of life-history studies or molecular systematics to one or the other of this region's current male-only species.

Acknowledgments

I thank my institution, El Colegio de la Frontera Sur (ECOSUR-Chetumal), for full support during the collection and taxonomic analysis of these samples. José Angel Cohuo deposited and catalogued the type series of these species in the collection of Zooplankton at ECOSUR-Chetumal. My dear colleague Lourdes Vásquez-Yeomans provided the samples from which these specimens were isolated, and Manuel Elías-Gutiérrez and J.A. Cohuo guided me in the use of ECOSUR's SEM equipment. An anonymous referee provided extensive constructive comments and suggestions that are deeply appreciated. This input allowed a significant improvement of the originally submitted manuscript.

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Manuscript received: 29 March 2023
Manuscript accepted: 28 August 2023
Published on: 12 January 2024
Topic editor: Magalie Castelin
Section editor: Fabio Stoch
Desk editor: Pepe Fernández

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum national d'histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic.

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Digitale Literatur/Digital Literature

Zeitschrift/Journal: European Journal of Taxonomy

Jahr/Year: 2024

Band/Volume: 0917

Autor(en)/Author(s): Suarez-Morales Eduardo

Artikel/Article: Two new species of Monstrilla (Copepoda: Monstrilloida: Monstrillidae) from a protected reef system of the Mexican Caribbean 152-169