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Three new species of *Tisbe* (Copepoda: Harpacticoida) and a new record with complete redescription of *Tisbe monozota* from north-western Mexico

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Abstract: Representatives of the genus *Tisbe* were collected during two short-term studies examining the effects of organic enrichment on the abundance of meiofauna and diversity of harpacticoid copepods in two coastal systems in central and southern Sinaloa (north-western Mexico), and from an experimental culture of bullseye puffer (*Sphoeroides annulatus*). Three new species are described: *Tisbe antennulodenticulata* sp. nov., *T. brigittevolkmanna* sp. nov. and *T. puelloi* sp. nov.. Additionally *T. longisetosa* is relegated to a species inquirenda. Some specimens collected from experimental cultures of bullseye puffer turned out to belong to *T. monozota* known from a salt water aquarium in Florida. To the best of our knowledge, this is the first time that *T. monozota* is reported from the Tropical Eastern Pacific, and it is the second report of the species from salt water aquariums. A complete redescription of the species is provided.

Résumé : Trois nouvelles espèces de *Tisbe* (Copepoda : Harpacticoida), nouvelle signalisation et redescription complète de *Tisbe monozota* du nord-ouest du Mexique. Quelques représentants du genre *Tisbe* ont été récoltés pendant deux études à court terme concernant les effets de l'enrichissement organique sur l'abondance de la méiofaune et la biodiversité des copépodes harpacticoides de deux systèmes côtiers de Sinaloa central et méridional (nord-ouest du Mexique), et d'une culture expérimentale de *Sphoeroides annulatus*. Trois nouvelles espèces sont décrites, *Tisbe antennulodenticulata* sp. nov., *T. brigittevolkmanna* sp. nov., et *T. puelloi* sp. nov., et *T. longisetosa* est considérée comme species inquirenda. Des spécimens récoltés dans des cultures expérimentales de *Sphoeroides annulatus* appartiennent à l'espèce *Tisbe monozota*, connue d'un aquarium d'eau salée en Floride. A notre connaissance, c'est la première fois que *T. monozota* est signalée du Pacifique oriental tropical, et c'est la deuxième fois que l'espèce est signalée d'un aquarium d'eau salée. Une redescription complète de l'espèce est fournie.

Keywords: Copepoda, Harpacticoida, Tisbidae, *Tisbe*, Systematics, México

Introduction

Three new representatives of *Tisbe* Lilljeborg, 1853 were found in sediment samples taken during two short term

studies examining the effects of organic enrichment on the abundance of meiofauna and diversity of harpacticoid copepods in two brackish systems in central (Ensenada del Pabellón lagoon) and southern (Urías system) Sinaloa (north-western Mexico). Another species was found in an experimental culture of bullseye puffer *Sphoeroides annulatus* (Jenyns, 1842).

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The present contribution deals with the detailed taxonomic description of three new species of *Tisbe* and a complete redescription of *T. monozota* Bowman, 1962.

Material and methods

Triplicate sediment samples for meiofaunal analyses were taken during a number of sampling campaigns in two brackish systems (Ensenada del Pabellón lagoon and Urías system) in central and southern Sinaloa (north-western Mexico) during the early 1990s (see Gómez-Noguera & Hendrickx, 1997) and during 2001 and 2002 (Gómez, unpublished data). Harpacticoids were separated from the rest of the meiofauna using a stereomicroscope at a magnification of 40X. Also, specimens of *Tisbe* were collected from experimental cultures of bullseye puffer *Spherooides annulatus* at the Centro de Investigación en Alimentación y Desarrollo (CIAD-Unidad Mazatlán). The specimens were stored in 70% ethanol prior to further investigation. Observations and drawings were made from whole and then dissected specimens mounted in glycerine, at 1000X using a Leica microscope equipped with phase contrast and drawing tube. The type material of the three new species and the examined material of *T. monozota* were deposited in the collection of the Instituto de Ciencias del Mar y Limnología, Mazatlán Marine Station (EMUCOP-). The terminology proposed by Huys and Boxshall (1991) for the general description and the classification system for crustacean setae proposed by Watling (1989) were adopted. Abbreviations used in the text and tables are: A1, antennule; P1-P6, first to sixth swimming leg; EXP, exopod; ENP, endopod; CV, fifth copepodite; CIV, fourth copepodite; CIII, third copepodite; CII, second copepodite.

Systematics

Family TISBIDAE Stebbing, 1910

Genus *Tisbe* Lilljeborg, 1853

Tisbe antennulodenticulata sp. nov. (Figs 1-8)

Type locality. Urías estuary, southern Sinaloa, north-western Mexico (23°09'–23°13' N, 106°20'–106°25' W).

Type material. Female holotype deposited (EMUCOP-090301-162) and male allotype (EMUCOP-090301-163) preserved in alcohol, 1 dissected male (EMUCOP-090301-24) and 3 dissected female paratypes (EMUCOP-090301-23, EMUCOP-090301-50, EMUCOP-090301-161), 5 males, 3 females CV, 1 male CV and 1 female CIV paratypes (EMUCOP-090301-27), and 10 males, 4 females, 1 female CV, 2 males CV, 2 females CIV, 4 male CIV, 5 CIII, 1 CII paratypes (EMUCOP-090301-28) preserved in alcohol. Coll. S. Gómez.

Description

Female. Body fusiform, tapering posteriorly (Fig. 1A); greatest width at posterior margin of cephalic shield. Total body length ranging from 560 µm to 660 µm (holotype, 660 µm). Rostrum fused to cephalic shield. Cephalic shield and free thoracic somites with narrow plain hyaline frill. Dorsal surface of cephalic shield and free thoracic somites smooth. First urosomite (P5-bearing somite) with very narrow plain hyaline frill; dorsal surface smooth. Second and third urosomites (genital double-somite) completely fused dorsally and ventrally (Figs 1A; 2); with lateral chitinized strip and transverse row of minute spinules indicating former division between somites, dorsal surface smooth otherwise; abdominal half of genital double-somite (third urosomite) with semi-incised hyaline frill dorsally and ventrally (Figs 1A, C; 2); P6 represented by two setae in anterior half (Fig. 2). Dorsal and ventral surface of fourth urosomite with continuous semi-incised hyaline frill dorsally and ventrally. Fifth urosomite as previous somite except for a medial portion of crescent hyaline frill dorsally forming a pseudoperculum, and medial portion of plain frill ventrally (Figs 1A, C; 2). Anal somite narrow, often embedded in fifth urosomite; dorsal and ventral surface smooth; with small rounded anal operculum flanked by two distinct cones bearing one sensillum each. Caudal rami (Figs 1A, C; 2) about twice longer than wide, ornamented with small spinules at base of seta III and VI, and with an oblique row of inner spinules close to seta VII; with 7 setae in all; seta I arising ventrally to seta II, both nearly of the same length; seta III arising from cylindrical extension at outer distal corner, and as long as seta VI, the latter arising from smaller cylindrical extension at inner distal corner; seta IV shorter than seta V, the former with outer minute spinules in proximal half, the latter with few spinules (Fig. 1 D); seta VII small, as long as seta II, and located distally close to inner margin of ramus.

Antennule (Fig. 3A), 7-segmented; surface of segments smooth. Armature formula as follows: 1-(1), 2-(13), 3-(9), 4-(4+ae), 5-(2), 6-(8), 7-(6+acrothek). Acrothek consisting of aesthetasc and 1 seta.

Antenna (Fig. 3B-D). Basis ornamented with an anterior and a posterior row of spinules and armed with a dwarfed inner seta in distal fifth (see insert in Fig. 3D). Exopod (Fig. 3B, D) 4-segmented; first segment with one small and naked seta proximally and one bipinnate seta distally (the latter nearly three times longer); second segment with 1, third segment without seta; fourth segment with 3 setae and ornamented with long spinules. First endopodal segment ornamented with small spinules along inner margin, and armed with an inner bipinnate seta about 1/2 length of supporting segment. Second endopodal segment (Fig. 3C, D) ornamented with tiny spinules and fragile and long setules along inner and outer margin, respectively; with

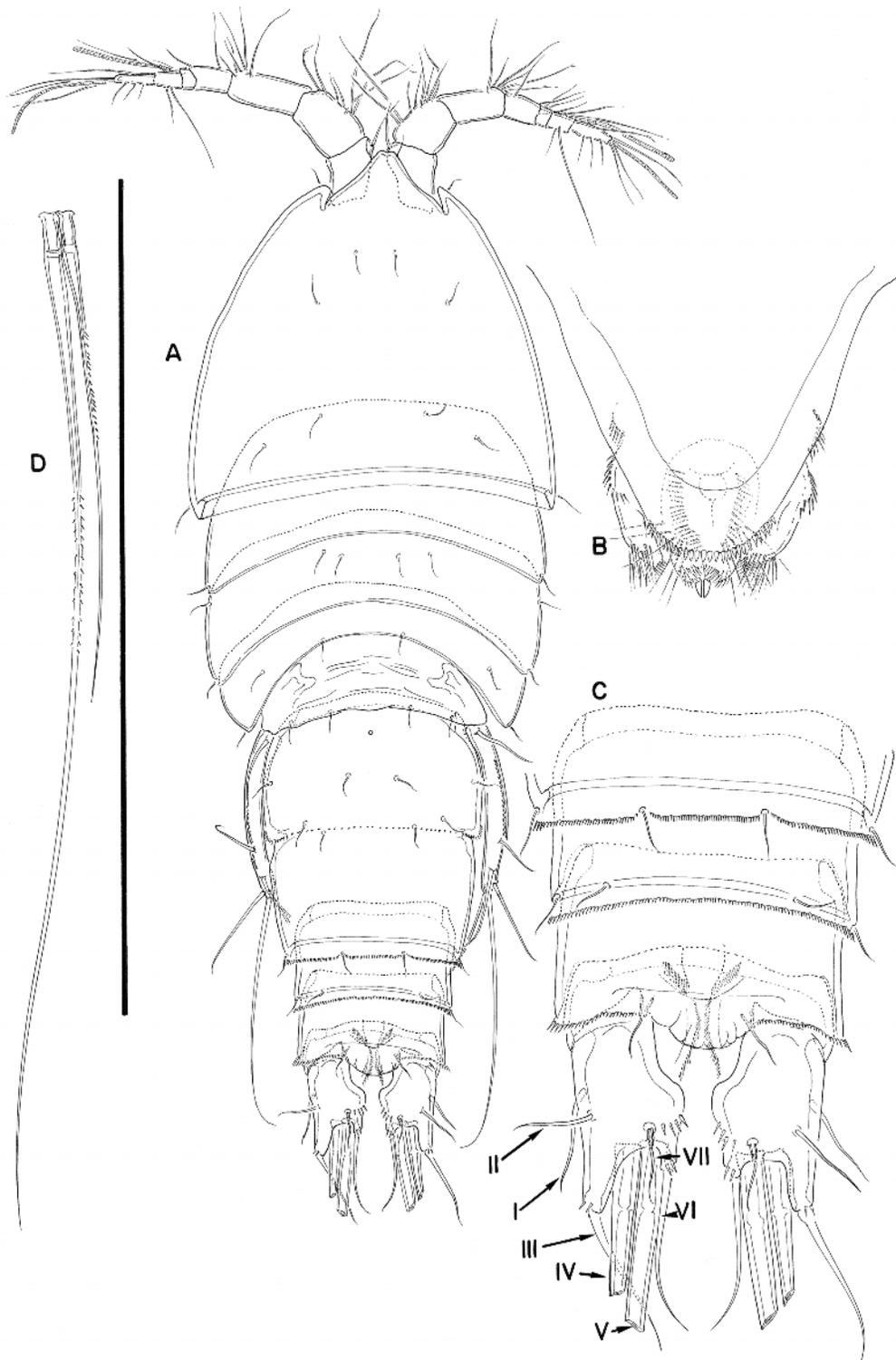


Figure 1. *Tisbe antennulodenticulata* sp. nov., adult female. **A, C-D**, holotype EMUCOP-090301-162; **B**, paratype EMUCOP-090301-23. **A.** habitus, dorsal; **B.** labrum and paragnaths; **C.** fourth and fifth urosomite, anal somite and caudal rami, dorsal; **D.** caudal setae IV and V. Scale bars: A, 500 μm ; B, 179 μm ; C, 250 μm ; D, 100 μm .

Figure 1. *Tisbe antennulodenticulata* sp. nov., femelle adulte. **A, C-D**, holotype EMUCOP-090301-162 ; **B**, paratype EMUCOP-090301-23. **A.** habitus, vue dorsale ; **B.** labrum et paragnathes ; **C.** quatrième et cinquième segments abdominaux, segment anal et furca, vue dorsale ; **D.** soies IV et V de la furca. Echelles : A, 500 μm ; B, 179 μm ; C, 250 μm ; D, 100 μm .

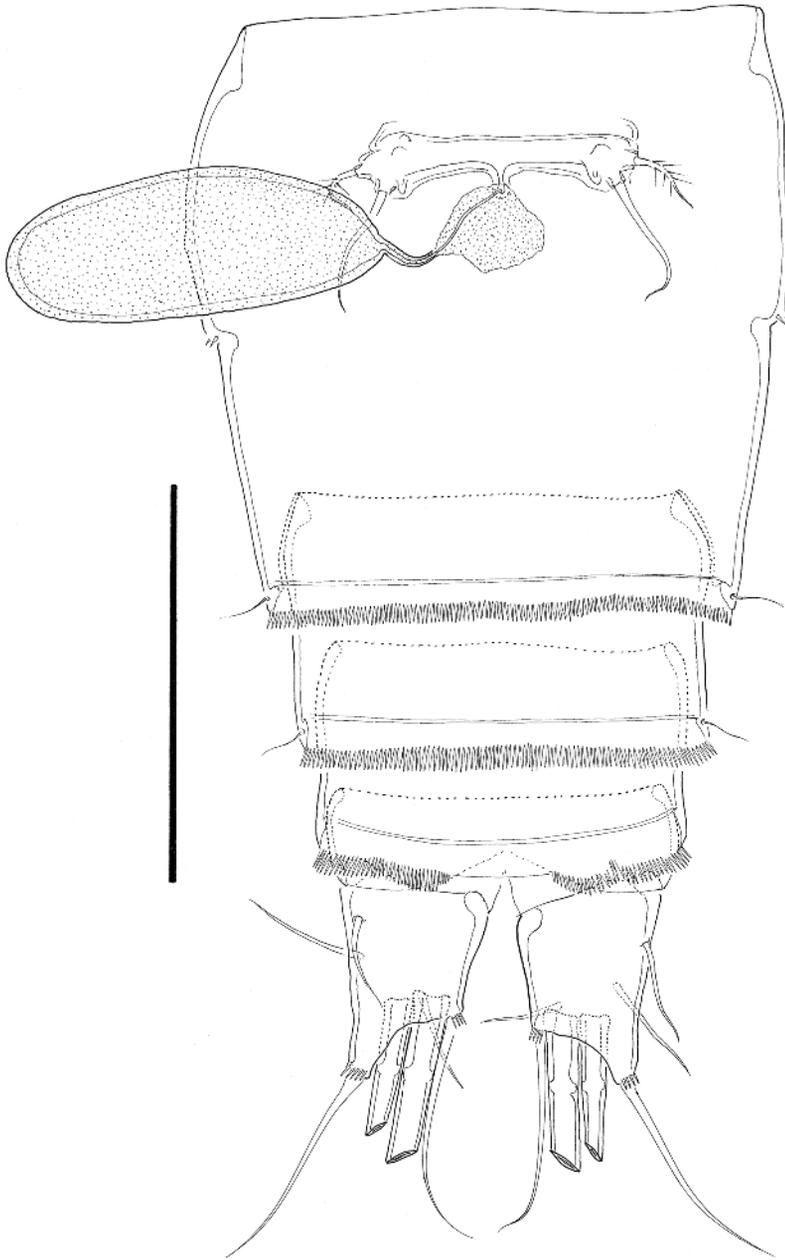


Figure 2. *Tisbe antennulodenticulata* sp. nov., adult female, paratype EMUCOP-090301-23. Urosome, ventral (P5-bearing somite omitted). Scale bar: 100 μ m.

Figure 2. *Tisbe antennulodenticulata* sp. nov., femelle adulte, paratype EMUCOP-090301-23. Urosome, vue ventrale (segment portant P5 omis). Echelle : 100 μ m.

subapical hyaline frill (arrowed in Fig. 3C, D), and armed with 2 lateral spines and 1 seta, and 4 geniculate elements and 3 slender setae distally (two of them fused).

Mandible (Fig. 4A-C), with well developed coxa ornamented with some spinules proximally. Gnathobase with bicuspidate teeth, row of long spinules, 2 spines and 1 pinnate seta (Fig. 4A, C). Basis ornamented with spinules,

without armature. Exopod 1-segmented, ornamented with transverse rows of spinules and armed with 2 apical setae of the same length. Endopod 1-segmented, ornamented with inner and outer spinules, armed with 3 lateral (two of them fused) and 6 apical slender setae (forming two sets of three fused setae) (Fig. 4A, B).

Maxillule (Fig. 4D-F). Arthrite of praecoxa ornamented with few spinules, and armed with 2 surface naked setae, 2 pinnate lateral and 6 distal elements (one of them, arrowed in Fig. 4 D, F, very small and difficult to see). Homologization of setae of the palp difficult to define, but most likely as follows: exopod represented by one well developed seta; endopod 1-segmented, armed with 3 setae (two of them fused at their base); with two basal endites, distal endite with 1 small and 1 well developed seta, proximal endite represented by 1 well developed setae; coxa with 3 (or 4?) setae (two of them fused at their base).

Maxilla (Fig. 4G) with one distal endite on syncoxa bearing 1 small and 1 well developed seta. Allobasis drawn out into strong claw with one accompanying seta.

Maxilliped (Fig. 4H), with robust syncoxa (suture between coxa and basis being not a functional articulation) ornamented with long and fragile elements proximally and with spinules medially and distally. Basis without ornamentation. Endopod 1-segmented, with long claw and 1 anterior and 1 posterior seta. Labrum and paragnaths as in Fig. 1B.

P1 (Fig. 5A). Coxa ornamented with transverse rows of small spinules on anterior surface, and with relatively longer spinules on posterior surface close to outer and inner margin. Basis ornamented with small spinules in anterior and posterior surface, and at base of outer and inner spine. Exopod 3-segmented; first and second segment about 1.5 times longer than wide, first segment armed with a long outer pinnate spine, second segment armed with a comparatively shorter bipinnate and flagellate outer spine ornamented with comparatively longer outer distal spinules; third exopodal segment visibly shorter, about 1.2 times as long as wide with 6 elements as follows: outer proximal spine similar to that of EXP 2, outer medial and distal bipinnate spine ornamented with long distal outer spinules, outer apical spine ornamented as preceding elements, inner apical seta ornamented with outer spinules and inner setules,

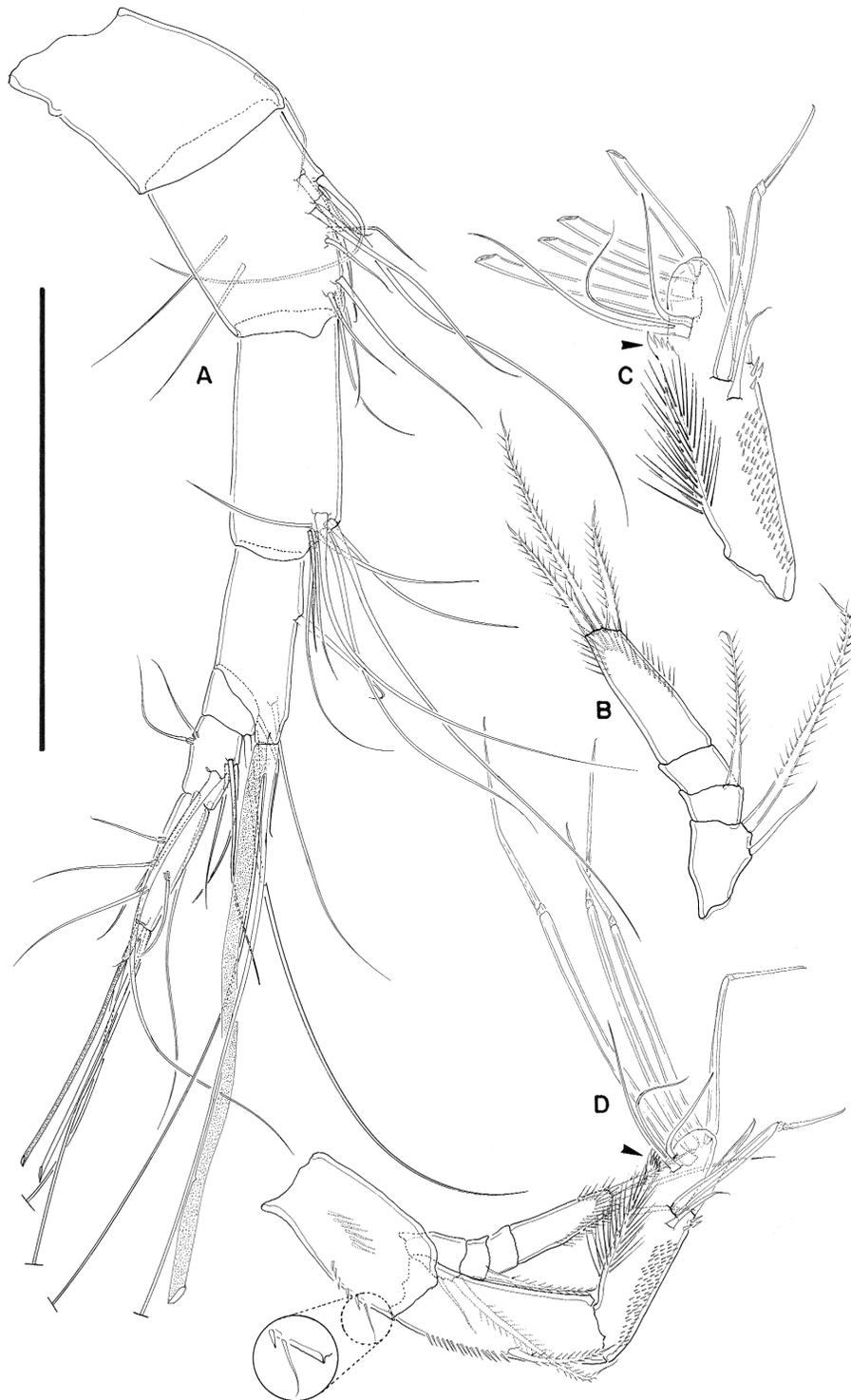


Figure 3. *Tisbe antennulodenticulata* sp. nov., adult female. **A**, paratype EMUCOP-090301-23; **B-D**, paratype EMUCOP-090301-161. **A**, antennule; **B**, exopod of antenna; **C**, second endopodal segment of antenna (hyaline frill arrowed); **D**, antenna (hyaline frill on second endopodal segment and inner seta of basis enlarged in figure). Scale bars: **A**, 100 μ m; **B-C**, 76 μ m; **D**, 108 μ m.

Figure 3. *Tisbe antennulodenticulata* sp. nov., femelle adulte. **A**, paratype EMUCOP-090301-23 ; **B-D**, paratype EMUCOP-090301-161. **A**, antennule ; **B**, exopode de l'antenne ; **C**, deuxième segment de l'endopode de l'antenne (membrane hyaline indiquée) ; **D**, antenne (membrane hyaline sur le deuxième segment de l'endopode et soie interne sur le basis agrandies). Echelles : **A**, 100 μ m ; **B-C**, 76 μ m ; **D**, 108 μ m.

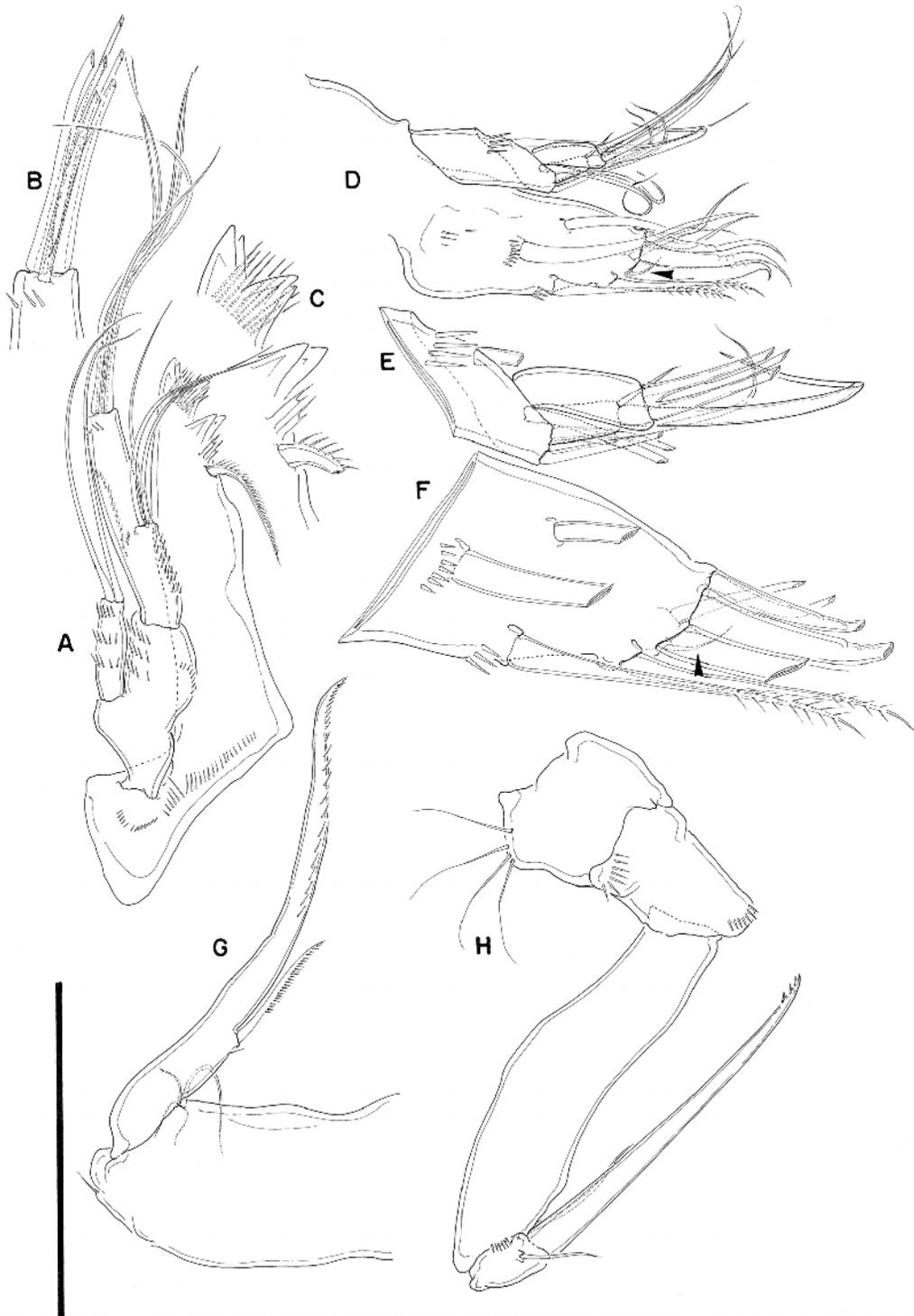


Figure 4. *Tisbe antennulodenticulata* sp. nov., adult female. **A-C**, paratype EMUCOP-090301-50; **D-G**, paratype 090301-161; **H**, paratype EMUCOP-090301-23. **A**. mandible; **B**. distal part of mandibular endopod; **C**. distal part of mandibular gnathobase; **D**. maxillule; **E**. distal part of maxillular palp; **F**. distal part of maxillular arthrite; **G**. maxilla; **H**. maxilliped. Scale bars: A, D, G, H, 50 μ m; B, C, E, F, 25 μ m.

Figure 4. *Tisbe antennulodenticulata* sp. nov., femelle adulte. **A-C**, paratype EMUCOP-090301-50 ; **D-G**, paratype 090301-161 ; **H**, paratype EMUCOP-090301-23. **A**. mandibule ; **B**. partie distale de l'endopode de la mandibule ; **C**. mandibule, partie distale ; **D**. maxillule ; **E**. maxillule, partie distale du palpe ; **F**. maxillule, arthrite, partie distale ; **G**. maxille ; **H**. maxillipède. Echelles : A, D, G, H, 50 μ m ; B, C, E, F, 25 μ m.

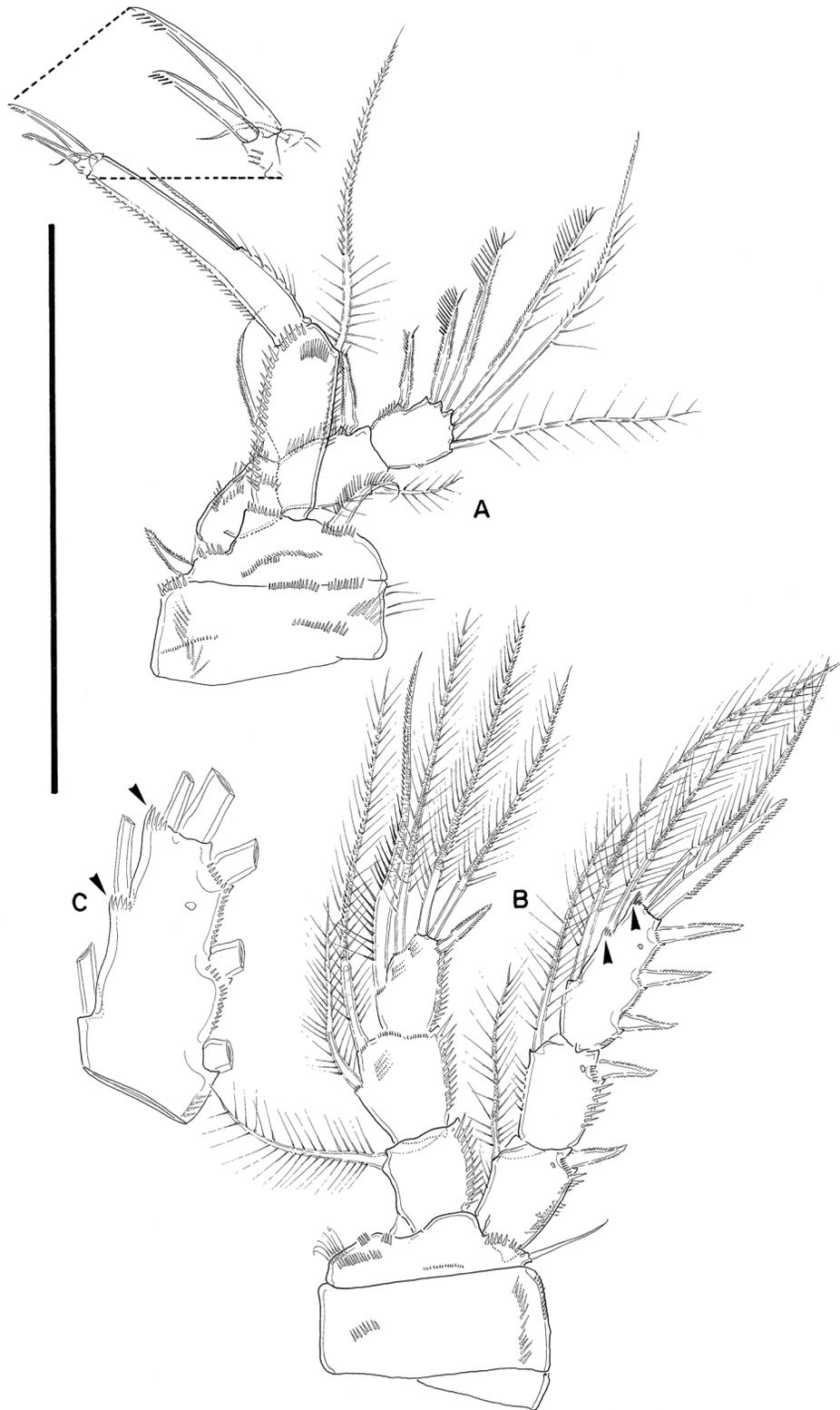
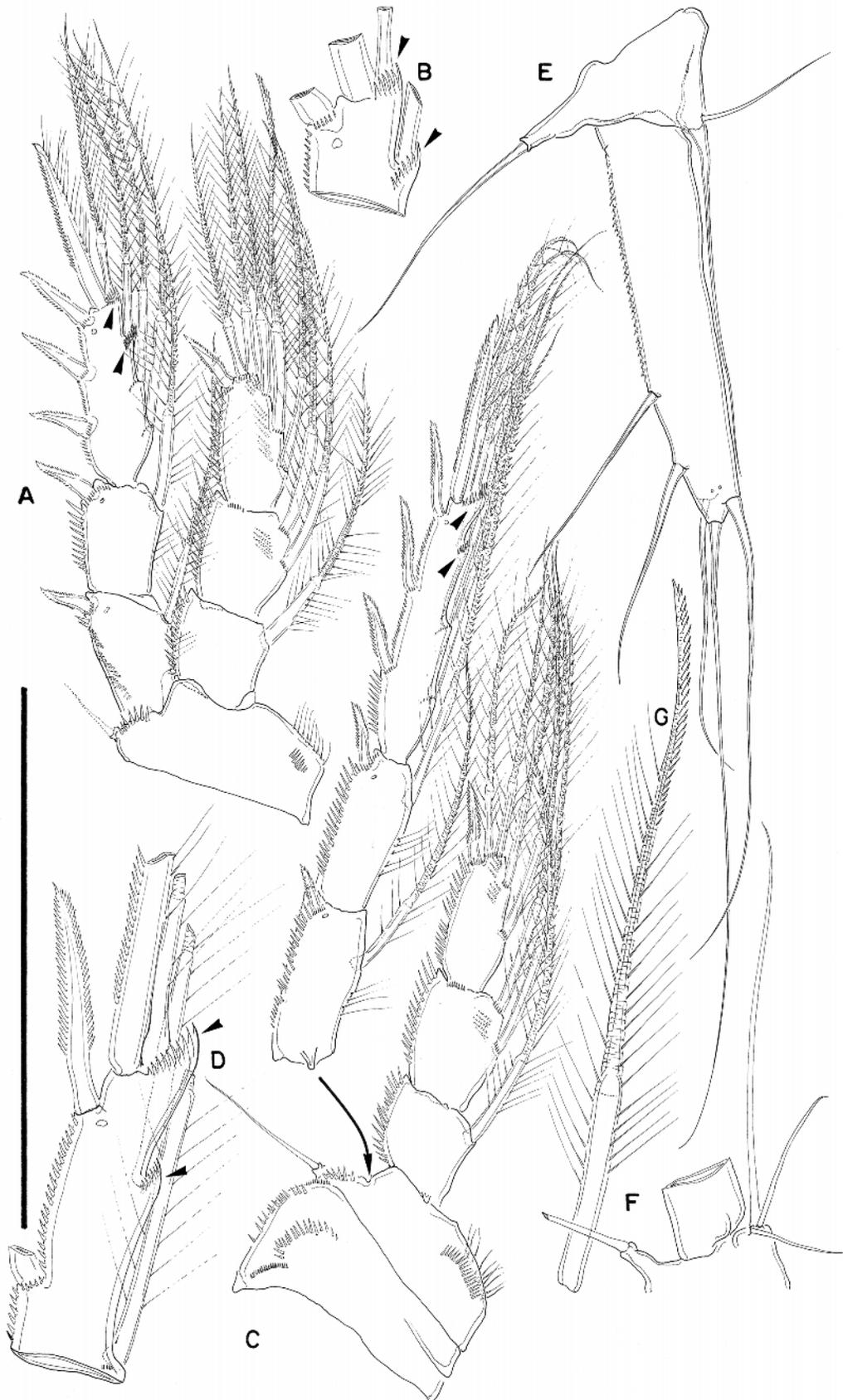


Figure 5. *Tisbe antennulodenticulata* sp. nov., adult female. Paratype EMUCOP-090301-23. **A.** P1; **B.** P2 (hyaline frills arrowed); **C.** third exopodal segment of P2 (hyaline frills arrowed). Scale bars: A, B, 200 μ m; C, 100 μ m.

Figure 5. *Tisbe antennulodenticulata* sp. nov., femelle adulte. Paratype EMUCOP-090301-23. **A.** P1 ; **B.** P2 (membranes hyalines indiquées) ; **C.** troisième segment de l'endopode de P2 (membranes hyalines indiquées). Echelles : A, B, 200 μ m ; C, 100 μ m.



and inner plumose seta. Endopod 3-segmented; first segment robust, about 2.6 times as long as wide, and about 2/3 length of second segment, armed with an inner seta ornamented proximally with setules and medially and distally with spinules; second segment about 6 times as long as wide and armed with an inner pinnate seta 1/2 length of and not reaching the tip of supporting segment; third segment very small and armed with 1 small seta and 2 spines barely ornamented with minute spinules as depicted. P2 (Fig. 5B, C). Coxa ornamented with a short transverse row of small spinules on anterior surface close to inner margin, and with an anterior and posterior longitudinal row of spinules close to outer margin. Basis ornamented with few spinular rows anteriorly at the base of exopod and close to inner margin, and with fragile setules close to inner distal corner posteriorly. Rami 3-segmented. Endopod barely reaching the proximal third of third exopodal segment; first segment with inner non-annulate plumose seta; second segment with 1 inner proximal non-annulate plumose seta and 1 inner distal annulate plumose and fluted seta ornamented with inner spinules; third segment with 1 outer spine and 4 fluted setae as follows: inner proximal element very strong and armed with long spinules proximally, median spinules medially and small spinules distally, inner distal seta plumose, inner and outer apical setae plumose and ornamented with outer spinules. First and second exopodal segments armed with outer spine and inner annulate and fluted plumose seta; third segment with 3 outer spines, 1 outer apical spine and 1 inner apical annulate and fluted seta ornamented with setules and spinules along inner and outer margin, respectively, and 2 inner annulate and fluted plumose setae; with hyaline frill at base of inner distal and inner apical seta (arrowed in Fig. 5B, C).

P3 (Fig. 6A, B, G). Basis as in P2. Rami 3-segmented. Endopod barely reaching the middle of third exopodal segment; first segment with 1, second segment with 2 inner fluted and annulate plumose seta with spinules along inner margin; third segment with outer spine and 5 fluted and annulate setae as follows: inner proximal seta plumose and ornamented with spinules along inner margin, inner medial seta plumodenticulate and slightly thicker (Fig. 6G), inner distal seta plumose and ornamented with spinules along inner margin, inner apical seta plumose, outer apical seta

plumose with spinules along outer margin. First and second exopodal segments as in P2, except for spinules along inner margin of seta on P3 EXP 2; third exopodal segment with 3 outer spines, 1 outer apical spine and 1 inner apical fluted and annulate seta ornamented with setules and spinules along inner and outer margin, respectively, and 3 inner fluted and annulate setae as follows: inner proximal seta plumose, inner medial seta plumose with spinules along inner margin, inner distal seta plumose; third exopodal segment with hyaline frill at base of inner apical and inner distal seta (arrowed in Fig. 6A, B).

P4 (Fig. 6C, D). Coxa with transverse rows of spinules close to outer margin. Basis as in P2 and P3. Rami 3-segmented. Endopod barely reaching the proximal fifth of third exopodal segment; first segment with 1, second segment with 2 inner fluted and annulate plumose seta with spinules along inner margin; third segment with outer spine and 4 fluted and annulate setae as follows: inner proximal and distal setae plumose and ornamented with spinules along inner margin, outer apical setae plumose with spinules along outer margin, inner apical seta plumose. Exopodal segments comparatively longer than in P2 and P3; first and second segment equal in size and armed with outer spine and inner fluted and annulate plumose seta with outer spinules; third segment longest, nearly as long as first and second segments combined and about 4.6 times as long as wide, and armed with 3 outer spines, 1 outer apical spine, 1 inner apical fluted and annulate plumose seta with spinules along outer margin, and 3 inner fluted and annulate plumose setae with spinules along inner margin; third exopodal segment with hyaline frill at base of inner apical and inner distal seta (arrowed in Fig. 6C, D).

Armature formula of P1-P4 as follows:

	EXP	ENP
P1	I-0;I-1;III,I,1	0-1;0-1;I,I,1
P2	I-1;I-1;III,I,2	0-1;0-2;I,2,2
P3	I-1;I-1;III,I,3	0-1;0-2;I,2,3
P4	I-1;I-1;III,I,3	0-1;0-2;I,2,2

P5 (Fig. 6E, F) with triangular baseopod armed with 3 setae on inner lobe, without ornamentation. Exopod about



Figure 6. *Tisbe antennulodenticulata* sp. nov., adult female. **A, B, E, G**, paratype EMUCOP-090301-23; **C, D, F**, paratype EMUCOP-090301-161. **A**. P3 (hyaline frills arrowed); **B**. distal part of third exopodal segment of P3 (hyaline frills arrowed); **C**. P4 (hyaline frills arrowed); **D**. distal part of third exopodal segment of P4 (hyaline frills arrowed); **E**. P5; **F**. baseopod of P5 of another specimen; **G**. middle inner seta of third endopodal segment of P3. Scale bars: **A, C**, 200 µm; **B, G**, 100 µm; **D**, 83 µm; **E**, 127 µm; **F**, 134 µm.

Figure 6. *Tisbe antennulodenticulata* sp. nov., femelle adulte. **A, B, E, G**, paratype EMUCOP-090301-23 ; **C, D, F**, paratype EMUCOP-090301-161. **A**. P3 (membranes hyalines indiquées) ; **B**. exopode de P3, partie distale du troisième segment (membranes hyalines indiquées) ; **C**. P4 (membranes hyalines indiquées) ; **D**. exopode de P4, partie distale du troisième segment (membranes hyalines indiquées) ; **E**. P5 ; **F**. baseopod de P5 d'un autre spécimen ; **G**. endopode de P3, deuxième soie interne du troisième segment. Echelles : **A, C**, 200 µm ; **B, G**, 100 µm ; **D**, 83 µm ; **E**, 127 µm ; **F**, 134 µm.

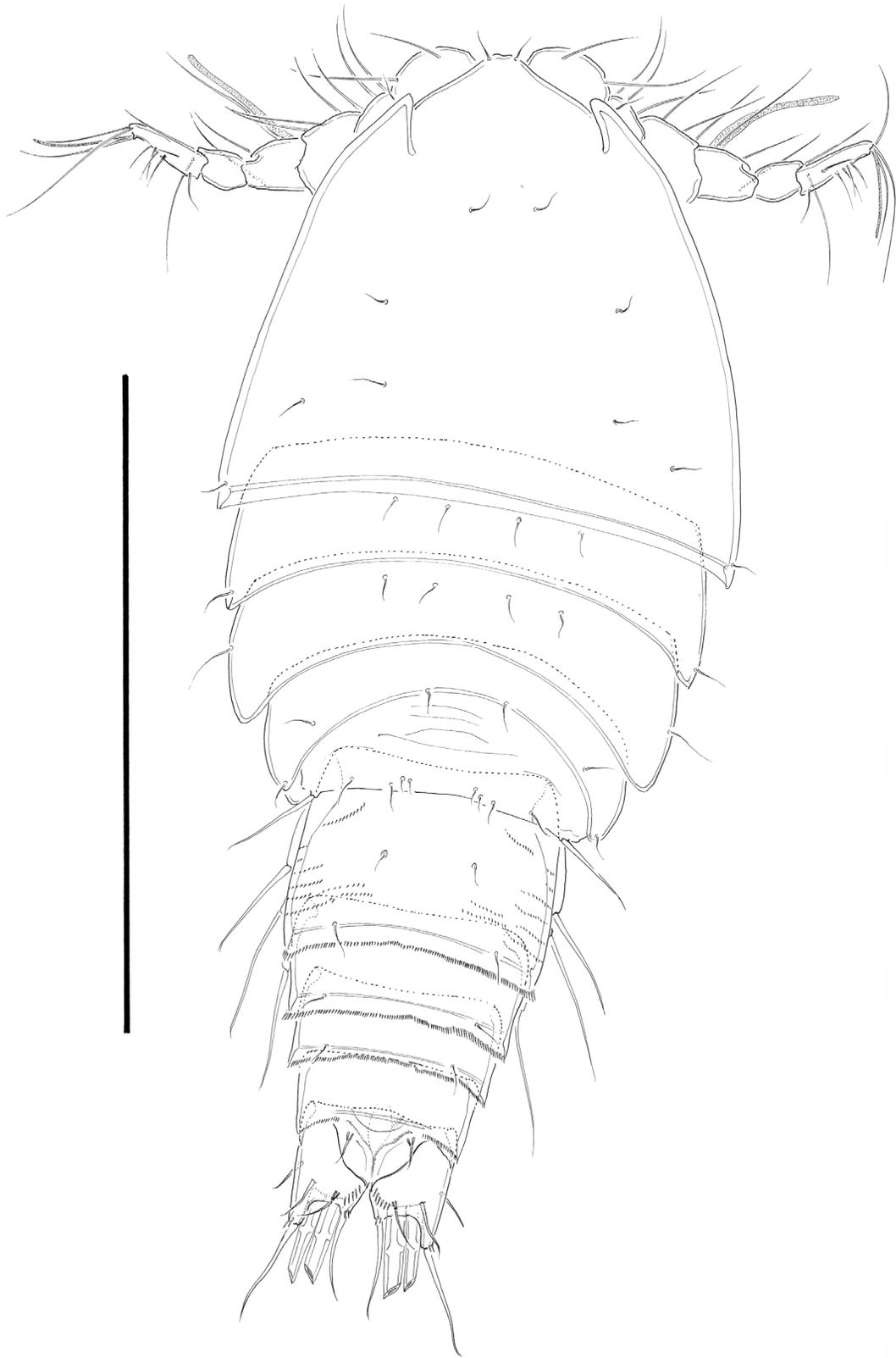


Figure 7. *Tisbe antennulodenticulata*. sp. nov., adult male. Allotype EMUCOP-090301-163. Habitus, dorsal. Scale bar: 200 μ m.

Figure 7. *Tisbe antennulodenticulata*. sp. nov., mâle adulte. Allotype EMUCOP-090301-163. Habitus, vue dorsale. Echelle : 200 μ m.

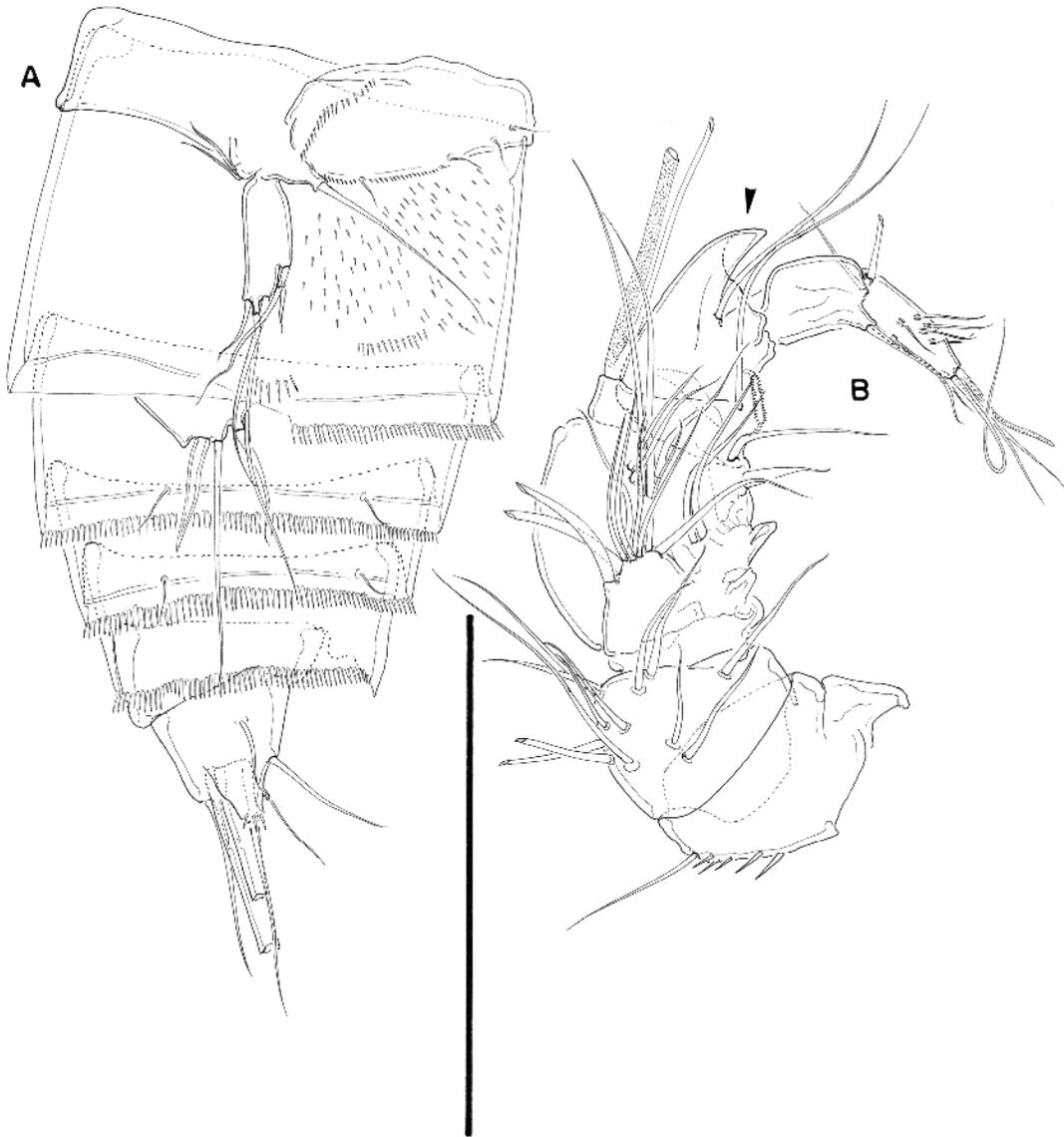


Figure 8. *Tisbe antennulodenticulata* sp. nov., adult male. Paratype EMUCOP-090301-24. **A.** urosome, lateral; **B.** antennule, ventral. Scale bars: A, 100 μ m; B, 92 μ m.

Figure 8. *Tisbe antennulodenticulata* sp. nov., mâle adulte. Paratype EMUCOP-090301-24. **A.** urosome, vue latérale ; **B.** antennule, vue ventrale. Echelles : A, 100 μ m ; B, 92 μ m.

5 times longer than wide, ornamented with tiny spinules along outer margin and armed with 3 outer, 1 apical and 1 inner seta. Relative length of exopodal and baseoendopodal setae as in Fig. 6E and F.

Male. General body shape as in female except for genital double-somite (Fig. 7). Total length measured from tip of rostrum to posterior margin of caudal rami ranging from 365 μ m to 390 μ m (allotype 375 μ m).

Antennule (Fig. 8B), subchirocer, 7-segmented; with aesthetasc on fourth and last segment; fifth segment with acute projection (arrowed in Fig. 8B).

P5 (Fig. 8A). Inner baseoendopodal lobe with 2 slender

setae. Exopod about 2.5 times longer than wide, and armed with 5 setae.

P6 (Fig. 8A) with 1 bare and 2 setae.

Etymology. The specific name refers to the acute projection on the male fifth antennular segment.

Tisbe brigittetvolkmannae sp. nov. (Fig. 9-15)

Type locality. Urías estuary, southern Sinaloa, north-western Mexico (23°09'-23°13' N, 106°20'-106°25' W).

Other localities. Ensenada del Pabellón lagoon, Sinaloa, Mexico (24°19'-24°35'N, 107°28'-107°45'W), stn. 2 (for details see Gómez-Noguera & Hendrickx, 1997).

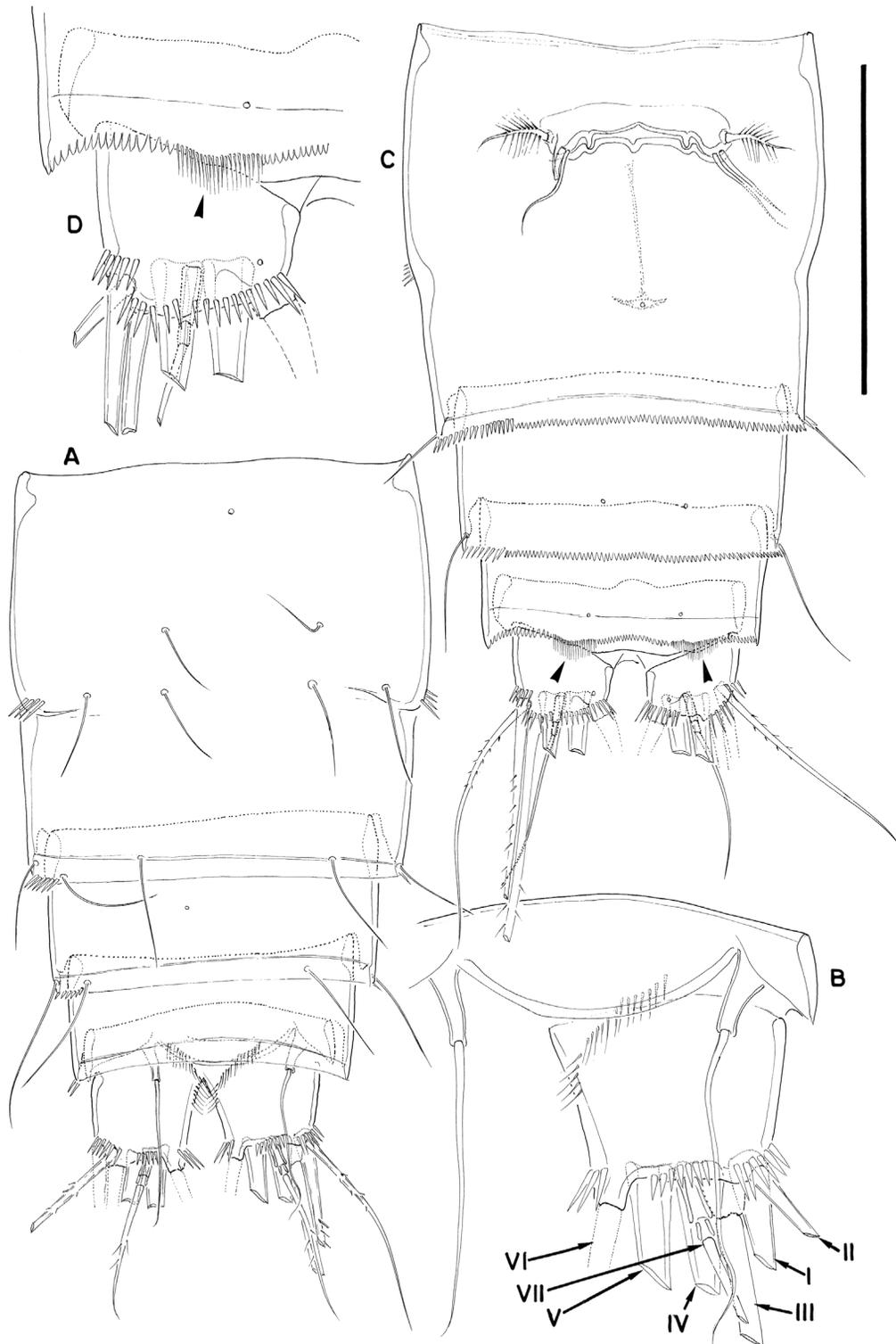


Figure 9. *Tisbe brigittvolkmannae* sp. nov., adult female. Paratype EMUCOP-090301-21. **A.** urosome, dorsal (P5-bearing somite omitted); **B.** anal somite and right caudal ramus, dorsal; **C.** urosome, ventral (P5-bearing somite omitted); **D.** anal somite and right caudal ramus, ventral. Scale bars: A, C, 100 μm ; B, D, 50 μm .

Figure 9. *Tisbe brigittvolkmannae* sp. nov., femelle adulte. Paratype EMUCOP-090301-21. **A.** urosome, vue dorsale (segment portant P5, omis) ; **B.** segment anal et furca, vue dorsale ; **C.** urosome, vue ventrale (segment portant P5, omis) ; **D.** segment anal et furca, vue ventrale. Echelles : A, C, 100 μm ; B, D, 50 μm .

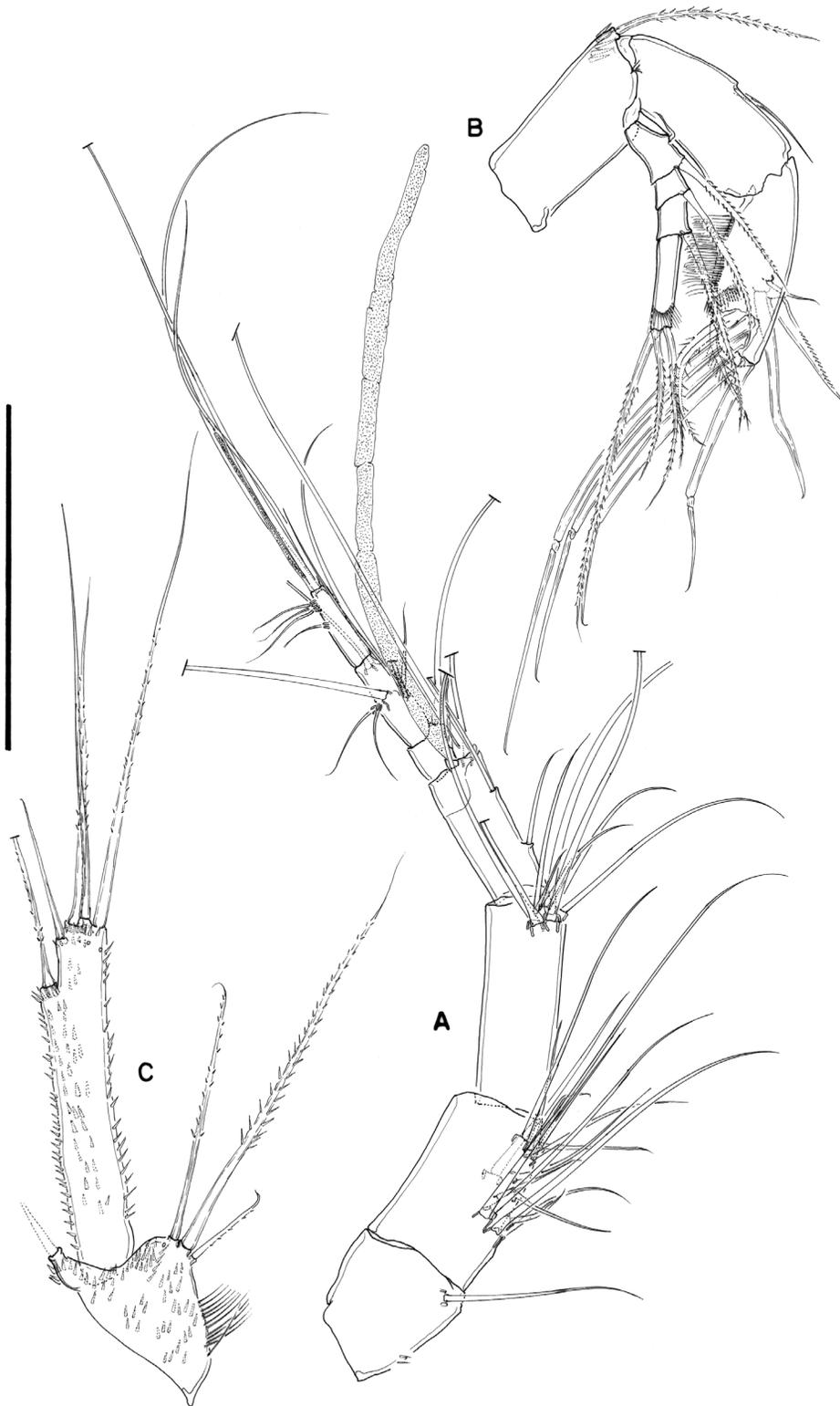
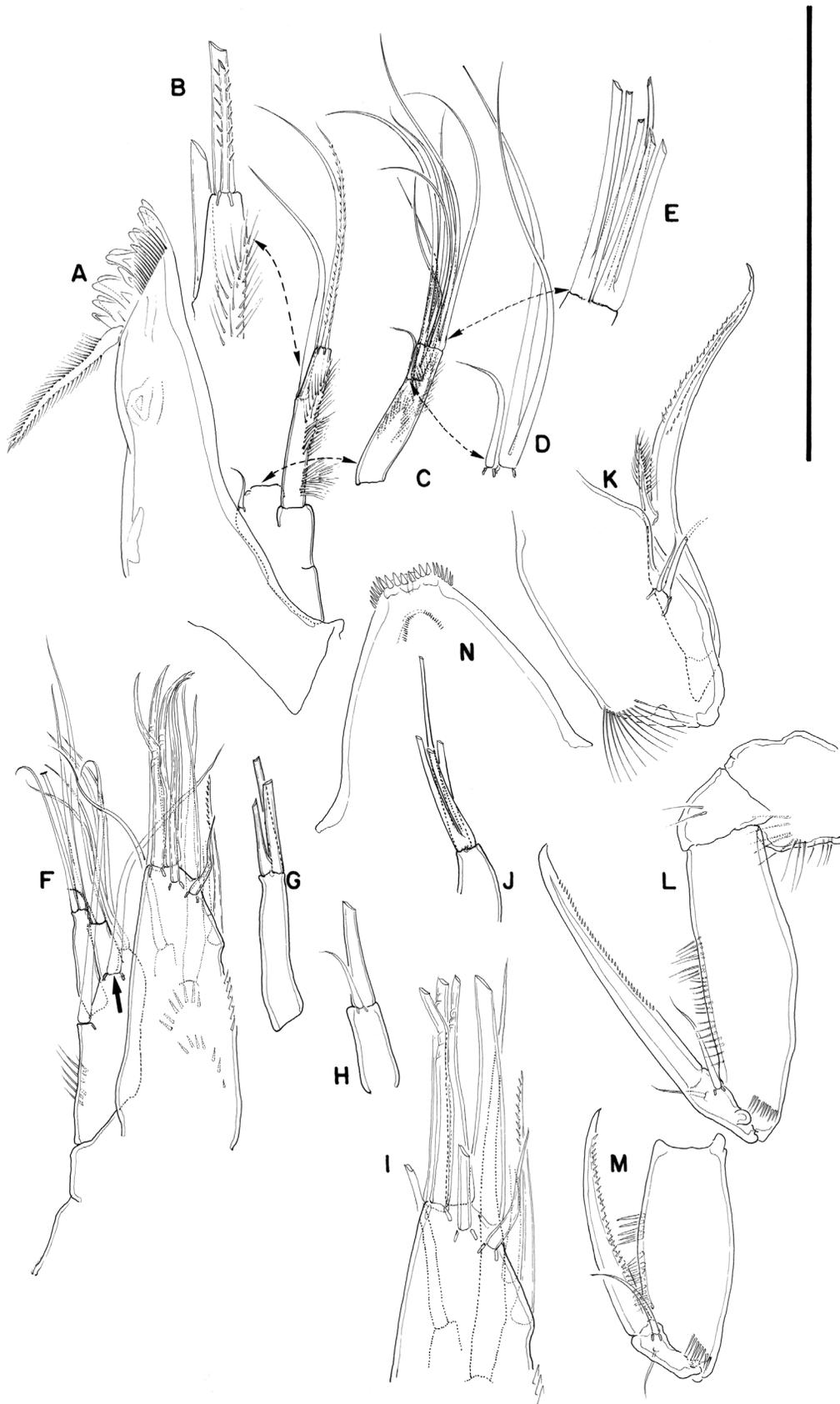


Figure 10. *Tisbe brigittevolkmannae* sp. nov., adult female. Paratype EMUCOP-090301-21. **A.** antennule, ventral; **B.** antenna; **C.** P5. Scale bars: A, C, 100 μ m; B, 83 μ m.

Figure 10. *Tisbe brigittevolkmannae* sp. nov., femelle adulte. Paratype EMUCOP-090301-21. **A.** antennule, vue ventrale ; **B.** antenne ; **C.** P5. Echelles : A, C, 100 μ m ; B, 83 μ m.



Type material. Female holotype (EMUCOP-090301-26) and male allotype (EMUCOP-090301-170) preserved in alcohol, 1 dissected female (EMUCOP-090301-21) and 3 dissected male paratypes (EMUCOP-010591-48, EMUCOP-010591-49, EMUCOP-090301-22), 5 paratypes preserved in alcohol (1 male, EMUCOP-090301-56, and 1 male CV, 1 female CV, and 2 females CIV, EMUCOP-090301-25). Coll. S. Gómez.

Description

Female. General body shape and somitic frills of cephalic shield and free thoracic somites as in *Tisbe antennulodenticulata* sp. nov. dorsally. Total body length of holotype 340 µm. Second and third urosomites (genital double-somite) completely fused dorsally and ventrally (Fig. 9A, C); with lateral chitinized strip ornamented with few spinules indicating former division between somites; dorsal and ventral surface smooth; with plain and semi-incised hyaline frill dorsally and ventrally, respectively. P6 represented by 1 strong, plumose outer seta and 2 slender, naked inner elements (Fig. 9C). Dorsal and ventral surface of fourth urosomite smooth, with plain hyaline frill dorsally and semi-incised ventrally. Fifth urosomite as previous somite except for frill with two parts where it is thinner and longer (arrowed in Fig. 9C, D). Anal somite narrow; dorsal and ventral surface smooth; with small rounded anal operculum flanked by two long distinct cones bearing one sensillum each (Fig. 9A-D). Caudal rami (Fig. 9A-D) nearly as long as wide, ornamented with small spinules at base of seta II, VI and VII dorsally; with spinules at base of I and III, and along posterior margin of ramus ventrally; with 7 setae in all; seta I located distally along outer margin of ramus and arising ventrally to seta II, both nearly the same length; seta III arising from cylindrical projection at outer distal corner; seta IV shorter than seta V, both ornamented with spinules (not shown); seta VII well developed, longer than supporting ramus and shorter than seta II, and located halfway along posterior margin of ramus.

Antennule (Fig. 10A), 7-segmented. Armature formula as follows: 1-(1), 2-(15), 3-(9), 4-(4+ae), 5-(2), 6-(8), 7-(6+acrothek). Acrothek consisting of aesthetasc and 1 seta.

Antenna (Fig. 10B). Basis ornamented with some spinules close to insertion site of inner distal seta, the latter

bipinnate and well developed. Exopod 4-segmented; first segment with one proximal small and naked seta and one bipinnate distal seta nearly five times longer than proximal element; second and third segments armed with 1 seta each; fourth segment ornamented with subapical row of spinules and armed with 3 setae, one of which is twice as long as the other two. First endopodal segment seemingly without spinular ornamentation and armed with a bipinnate seta about half length of the seta of basis. Inner margin of second endopodal segment without spinular ornamentation; with fragile, long outer setules; with subapical hyaline frill and armed with 2 lateral spines and 1 seta, 4 apical geniculate elements, and 3 slender setae (two of them fused).

Mandible (Fig. 11A-E), with well developed coxa (seemingly) without spinular ornamentation. Gnathobase with bicuspidate teeth, a row of slender spinules, and 1 pinnate seta. Basis (seemingly) without ornamentation and armed with 1 small inner seta. Exopod 1-segmented, ornamented with spinules and armed with 1 lateral and 2 apical setae (Fig. 11A, B). Endopod 1-segmented, ornamented with inner and outer spinules, armed with 3 lateral setae (two of them fused) (Fig. 11C, D) and 6 apical slender elements (forming two sets of three fused setae) (Fig. 11C, E).

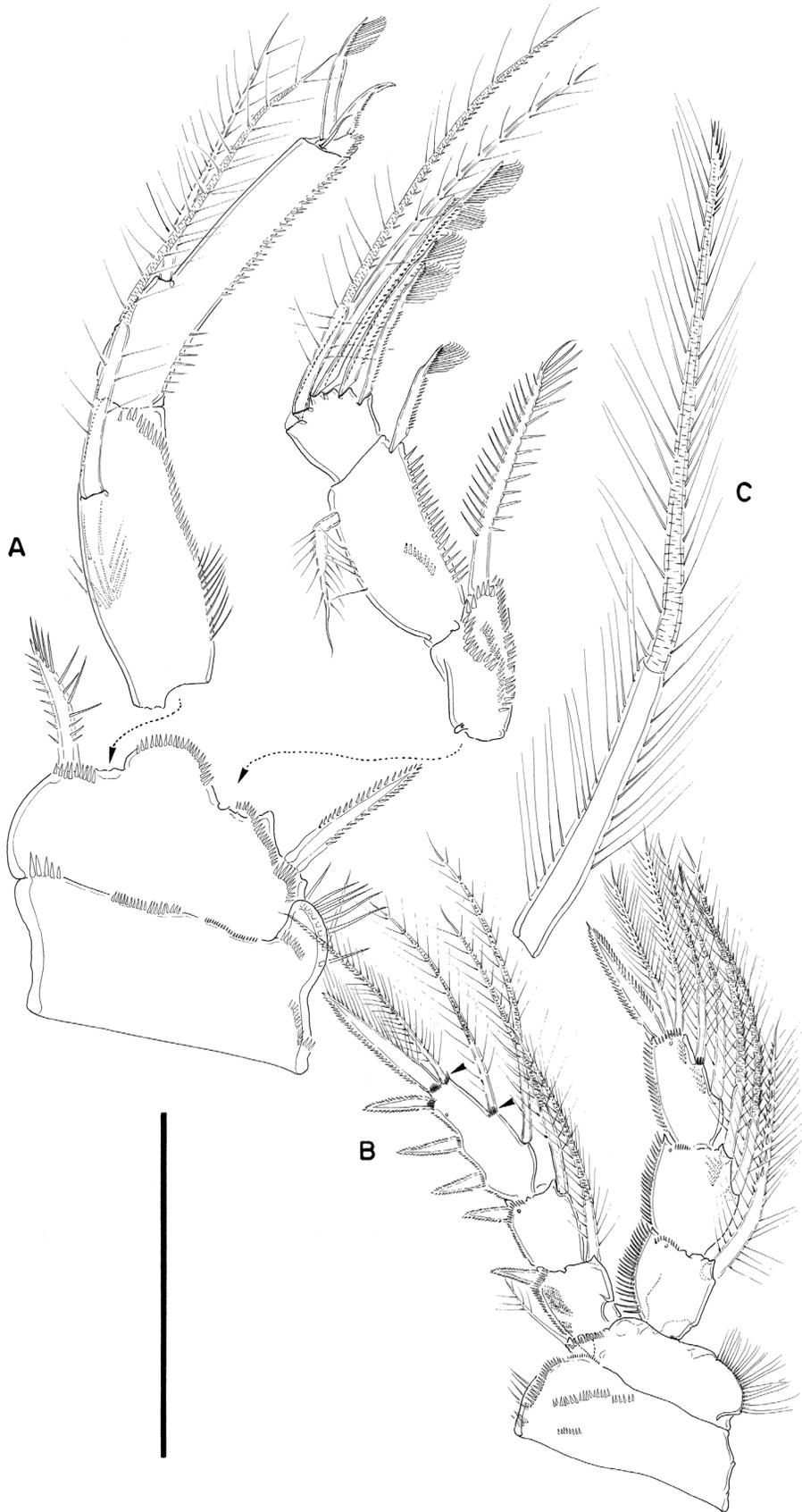
Maxillule (Fig. 11F-J). Arthritis of praecoxa ornamented with few surface spinules, and armed with 2 surface setae, 2 lateral and 6 distal elements (Fig. 11F, I). Homologization of setae of the palp difficult to define. Exopod represented by one well developed seta (Fig. 11F); endopod 1-segmented, armed with 3 setae (two of them fused at their base) (Fig. 11F, G); with two basal endites, distal endite with 1 small and 1 well developed seta (Fig. 11H), proximal endite with 1 well developed setae (arrowed in Fig. 11F); coxa with 2 pairs of setae fused at their bases (Fig. 11J).

Maxilla (Fig. 11K), syncoxa with one distal endite bearing 1 small and 1 well developed seta. Allobasis drawn out into strong claw with one accompanying seta.

Maxilliped (Fig. 11L). Syncoxa ornamented with long and fragile elements. Basis ornamented with some spinules along inner margin and with smaller spinules close to outer distal corner. Endopod 1-segmented; with claw and 2 accompanying setae. Labrum as in Fig. 11N.

Figure 11. *Tisbe brigittenvolkmanae* sp. nov. **A-L**, adult female, paratype EMUCOP-090301-21; **M, N**, adult male, paratype EMUCOP-090301-22. **A.** mandible; **B.** distal part of exopod of mandible; **C.** endopod of mandible; **D.** lateral setae of endopod of mandible, **E.** distal part of endopod of mandible; **F.** maxillule; **G.** endopod of maxillule; **H.** distal basal endite of maxillule; **I.** distal part of arthritis of praecoxa of maxillule; **J.** coxal setae of maxillule; **K.** maxilla; **L.** female maxilliped; **M.** male maxilliped; **N.** male labrum. Scale bars: A, K-M, 100 µm, B-E, 50 µm; F, 70 µm, G-J, 47 µm; N, 140 µm.

Figure 11. *Tisbe brigittenvolkmanae* sp. nov. **A-L**, femelle adulte, paratype EMUCOP-090301-21 ; **M, N**, mâle adulte, paratype EMUCOP-090301-22. **A.** mandibule ; **B.** mandibule, exopode, partie distale ; **C.** mandibule, endopode ; **D.** mandibule, soies latérales de l'endopode, **E.** mandibule, endopode, partie distale ; **F.** maxillule ; **G.** maxillule, endopode ; **H.** maxillule, endite distal ; **I.** maxillule, arthritis, partie distale ; **J.** maxillule, soies de la coxa ; **K.** maxilla ; **L.** maxillipède de la femelle ; **M.** maxillipède du mâle ; **N.** labrum du mâle. Echelles : A, K-M, 100 µm, B-E, 50 µm ; F, 70 µm, G-J, 47 µm ; N, 140 µm.



P1 (Fig. 12A). Coxa ornamented with rows of small spinules close to joint with basis on anterior surface and with small spinules and longer elements on proximal and distal outer corner posteriorly. Basis ornamented with small spinules at base of endopod, exopod, inner and outer spine. Exopod 3-segmented; first segment about 2 times as long as wide and armed with an outer spine ornamented with strong spinules; second segment about 3 times as long as wide and armed with 1 inner plumose seta and 1 outer penicillate spine; third exopodal segment nearly as long as wide and armed with 4 penicillate spines and 2 setae. Endopod 3-segmented; first segment robust, about 2.6 times as long as wide, and nearly as long as second segment, the latter about 5 times as long as wide; third segment very small and armed with 1 small seta, 1 claw-like and 1 penicillate spine.

P2 (Fig. 12B, C). Coxa ornamented with transverse rows of spinules close to outer margin anteriorly and with long spinules posteriorly. Basis ornamented with spinules at base of exopod, and with slender setules along margin of distal inner corner. Rami 3-segmented. Endopod barely reaching the proximal third of third exopodal segment; first segment with inner non-annulate plumose seta with 2 longitudinal rows of spinules; second segment with 2 inner fluted and annulate plumose seta ornamented with spinules along inner margin; third segment with 1 outer spine and 4 fluted setae as follows: inner proximal element plumodenticulate (Fig. 12C), inner distal seta plumose with spinules along inner margin, inner and outer apical setae plumose and ornamented with outer spinules. First and second exopodal segments armed with outer spine and inner annulate and fluted plumose seta with spinules along inner margin; third segment with 3 outer spines, 1 outer apical spine and 1 inner apical annulate and fluted seta ornamented with setules and spinules along inner and outer margin, respectively, and 2 inner annulate and fluted plumose setae; with hyaline frill at base of inner distal and inner apical seta (arrowed in Fig. 12B).

P3 (Fig. 13A). Coxa and basis as in P2. Rami 3-segmented. Endopod barely reaching the distal third of third exopodal segment; first segment with 1 strong plumose seta ornamented with 2 longitudinal rows of spinules, second segment with 2 inner fluted and annulate plumose setae with spinules along inner margin; third segment with outer spine and 5 fluted and annulate setae as follows: inner proximal and medial seta plumose and ornamented with spinules along inner margin, inner distal plumose seta, 2 apical plumose setae. First and second exopodal segments armed with outer spine and inner fluted and annulate plumose seta;

third exopodal segment with 3 outer spines, 1 outer apical spine, 1 apical fluted and annulate inner plumose setae, and 3 inner fluted and annulate plumose setae; third exopodal segment with hyaline frill at base of inner apical and inner distal seta (arrowed in Fig. 13A).

P4 (Fig. 13B). Coxa as in P3 anteriorly; densely covered with small spinules posteriorly close to outer margin. Basis as in P3. Rami 3-segmented. Endopod reaching the distal third of third exopodal segment; first segment with 1, second segment with 2 inner fluted and annulate plumose seta with spinules along inner margin; third segment with outer spine and 4 fluted and annulate setae as follows: inner proximal and distal setae plumose and ornamented with spinules along inner margin, outer apical setae plumose with spinules along outer margin, inner apical seta plumose. Exopodal segments comparatively longer than in P2 and P3; first segment slightly shorter than second segment, both segments armed with outer spine and inner fluted and annulate plumose seta; third segment longest, slightly longer than first and second segments combined and about 4.6 times as long as wide, and armed with 3 outer spines, 1 outer apical spine, 1 inner apical fluted and annulate plumose seta with spinules along outer margin, and 3 inner fluted and annulate plumose setae with spinules along inner margin; third exopodal segment with hyaline frill at base of inner apical and inner distal seta (arrowed in Fig. 13B).
Armature formula as in *T. antennulodenticulata* sp. nov.

P5 (Fig. 10C). Triangular baseoendopod ornamented with spinules and longer elements along inner margin, and armed with 3 setae on inner lobe. Exopod about 8 times longer than wide, ornamented with tiny spinules along inner and outer margin and on posterior surface, and armed with 3 outer, 1 apical and 1 inner seta. Relative length of exopodal setae as in Fig. 10C.

Male. General body shape as *T. antennulodenticulata* sp. nov. except for plain hyaline frill of urosomites dorsally (Fig. 14A). Total length measured from tip of rostrum to posterior margin of caudal rami ranging from 420 µm to 450 µm (allotype 445 µm). Caudal rami (Fig. 14 A-D) as in female.

Antennule (Fig. 15A), haplocer, 8-segmented; with aesthetasc on fourth and last segment.

Maxilliped (Fig. 11M) sexually dimorphic. Dimorphism expressed in comparatively shorter basis ornamented with stronger spinules along inner margin, and stronger claw of endopod.

←
Figure 12. *Tisbe brigittetvolkmannae* sp. nov. Adult female, paratype EMUCOP-090301-21. **A.** P1; **B.** P2 (hyaline frills arrowed); **C.** proximal inner seta of third endopodal segment of P2. Scale bars: A, 100 µm; B, 160 µm.

Figure 12. *Tisbe brigittetvolkmannae* sp. nov. Femelle adulte, paratype EMUCOP-090301-21. **A.** P1; **B.** P2 (membranes hyalines indiquées); **C.** endopode de P2, première soie interne du troisième segment. Echelles : A, 100 µm ; B, 160 µm.

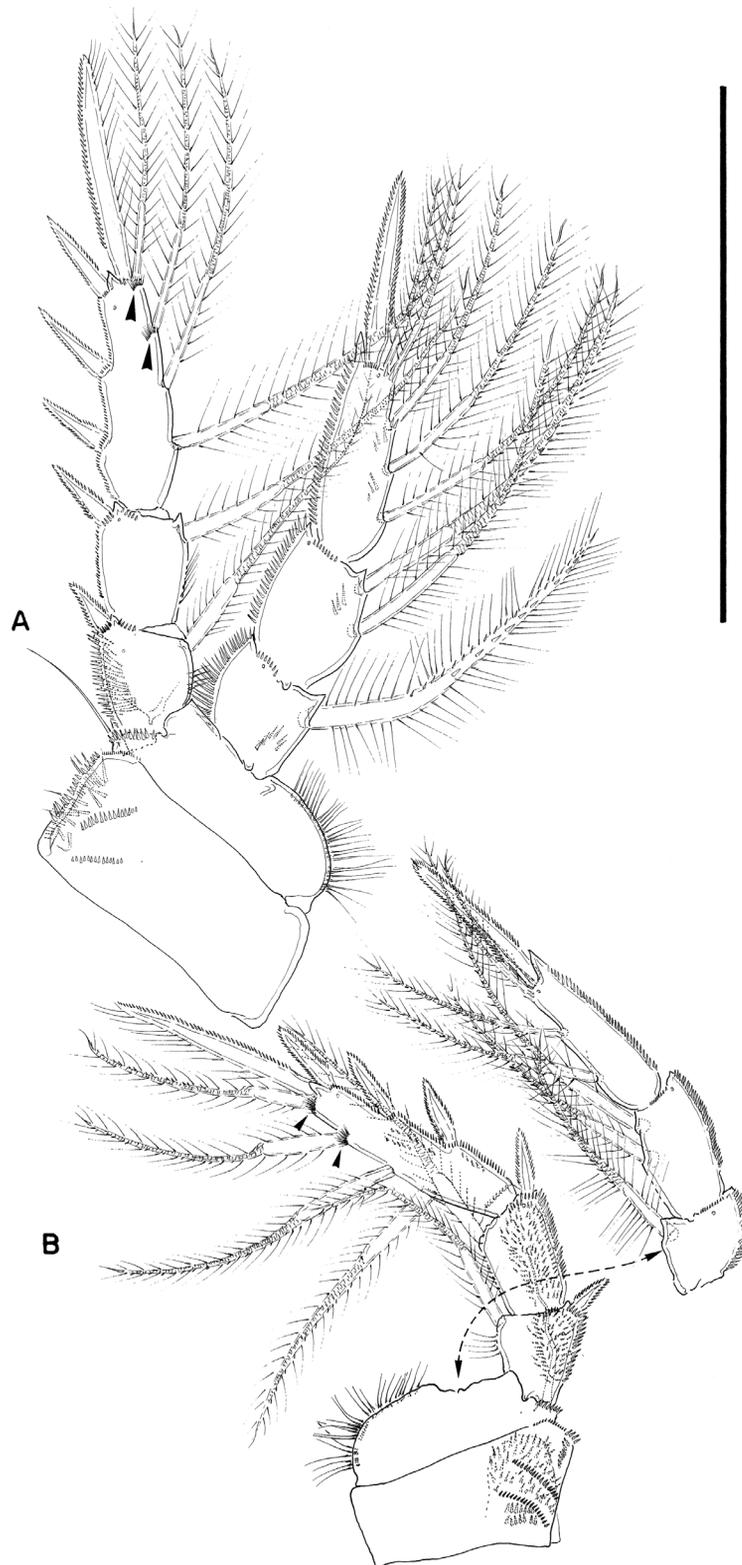


Figure 13. *Tisbe brigittevolkmannae* sp. nov. Adult female, paratype EMUCOP-090301-21. **A.** P3 (hyaline frills arrowed); **B.** P4 (hyaline frills arrowed). Scale bars: A, 200 μ m; B, 233 μ m.

Figure 13. *Tisbe brigittevolkmannae* sp. nov. Femelle adulte, paratype EMUCOP-090301-21. **A.** P3 (membranes hyalines indiquées) ; **B.** P4 (membranes hyalines indiquées). Echelles : A, 200 μ m ; B, 233 μ m.

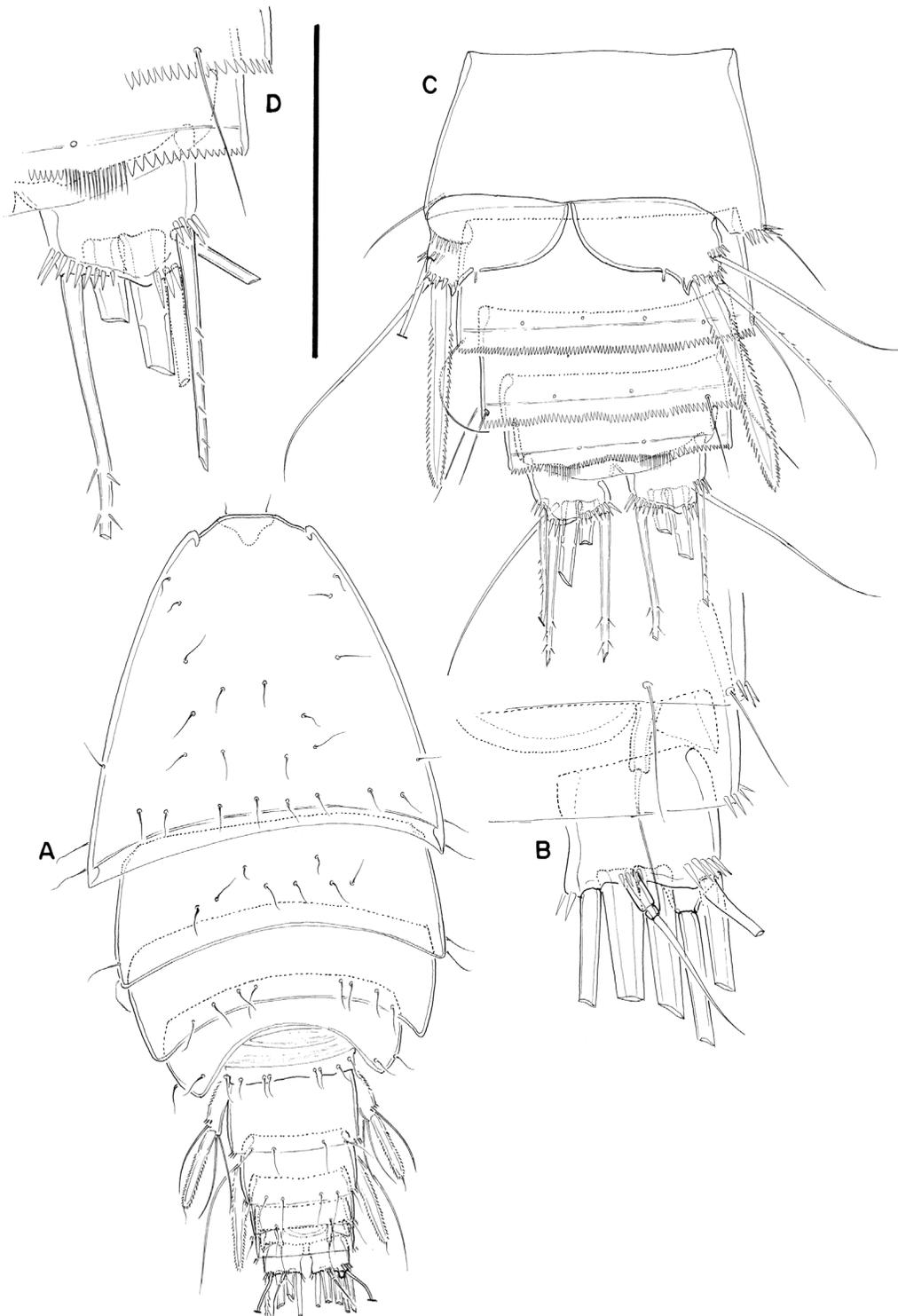


Figure 14. *Tisbe brigitttevolkmannae* sp. nov. Adult male. **A, B**, allotype EMUCOP-090301-170; **C, D**, paratype EMUCOP-090301-22. **A.** habitus, dorsal; **B.** right caudal ramus, dorsal; **C.** urosome, ventral (P5-bearing somite omitted); **D.** left caudal ramus, ventral. Scale bars: A, 197 μ m; B, 49 μ m; C, 100 μ m; D, 50 μ m.

Figure 14. *Tisbe brigitttevolkmannae* sp. nov. Mâle adulte. **A, B**, allotype EMUCOP-090301-170 ; **C, D**, paratype EMUCOP-090301-22. **A.** habitus, vue dorsale ; **B.** furca, vue dorsale ; **C.** urosome, vue ventrale (segment portant P5, omis) ; **D.** furca, vue ventrale. Echelles : A, 197 μ m ; B, 49 μ m ; C, 100 μ m ; D, 50 μ m.

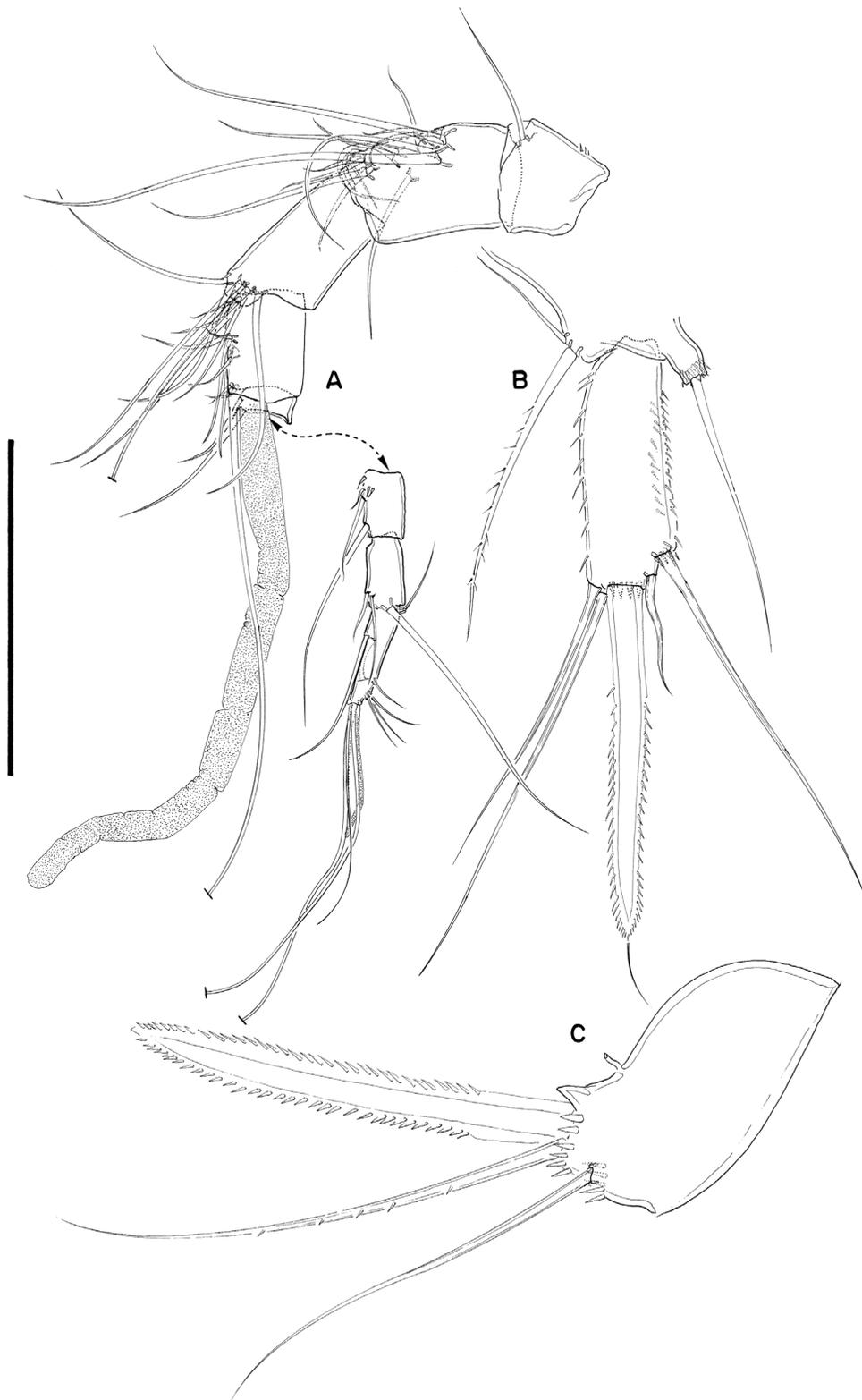


Figure 15. *Tisbe brigittevolkmannae* sp. nov. Adult male, paratype EMUCOP-090301-22. **A.** antennule; **B.** P5; **C.** P6. Scale bars: A, 100 μ m; B, C, 50 μ m.

Figure 15. *Tisbe brigittevolkmannae* sp. nov. Mâle adulte, paratype EMUCOP-090301-22. **A.** antennule ; **B.** P5 ; **C.** P6. Echelles : A, 100 μ m ; B, C, 50 μ m.

P5 (Fig. 15B) with 2 setae on inner baseoendopodal lobe. Exopod about 2.7 times as long as wide; ornamented with inner and outer spinules and armed with 2 lateral setae (distalmost smaller), 1 strong flagellate spine and 1 seta apically, and 1 inner seta.

P6 (Figs 13C; 15C) ornamented with spinules at the base of outer seta, and at the base of apical seta and apical spine, the latter with acute projection at its base, and reaching the caudal ramus; with inner tube pore.

Etymology. The species is named in honour to Brigitte Volkmann for her outstanding work on the genus *Tisbe*.

Tisbe puelloi sp. nov. (Figs 16-20)

Type locality. Urías estuary, southern Sinaloa, north-western Mexico (23°09'–23°13' N, 106°20'–106°25' W).

Type material. Dissected female holotype (EMUCOP-090301-131). Coll. S. Gómez.

Description

Female. Body badly damaged during sample processing. General body shape and somitic frills as in *Tisbe brigittetvolkmannae* sp. nov. Approximate total body length of holotype, 750 µm. Second and third urosomites (genital double-somite) distinct dorsally and completely fused ventrally; without spinular ornamentation except for some lateral spinules close to posterior margin of first and second genital somites, with lateral chitinized strip indicating former division between somites (Fig. 16A, B); dorsal and ventral surface smooth; with plain and semi-incised hyaline frill dorsally and ventrally, respectively. P6 represented by 1 long and 2 small setae (Fig. 16B). Dorsal and ventral surface of fourth and fifth urosomite smooth, with plain hyaline frill dorsally and semi-incised ventrally. Anal somite narrow; dorsal and ventral surface smooth; with small rounded anal operculum flanked by two long distinct cones bearing one sensillum each. Caudal rami nearly as long as wide, without spinular ornamentation close to seta VI and VII; with spinules at base of seta I and III; with 7 setae in all; seta I arising ventrally to seta II, and located halfway along outer margin of ramus; seta II longer than seta I; seta III arising from outer distal corner, nearly as long as seta VI; seta IV shorter than seta V, both ornamented with minute spinules along inner and outer margin (Fig. 18C); seta VII well developed, as long as supporting ramus, located halfway along posterior margin of ramus, close to insertion site of seta VI.

Antennule (Fig. 17A), 7-segmented. Armature formula as follows: 1-(1), 2-(14), 3-(9), 4-(4+ae), 5-(2), 6-(8), 7-(6+acrothek). Acrothek consisting of aesthetasc and 1 seta.

Antenna (Fig. 17B). Basis ornamented with some spinules close to insertion site of inner distal seta, the latter bipinnate and well developed. Exopod 4-segmented; first segment with 1 proximal small and naked seta and one

bipinnate distal seta nearly 6.4 times longer than proximal element; second and third segment armed with 1 seta each; fourth segment ornamented with row of spinules and armed with 3 setae, one of which is twice as long as the other two. First endopodal segment (seemingly) without spinular ornamentation, and armed with a very small and naked seta in anterior third. Inner margin of second endopodal segment with some spinules close to inner margin; with outer fragile and long setules, and armed with 2 lateral spines (one of which seems to be geniculate) and 1 seta, 4 apical geniculate elements, and 3 spinulose setae (two of them fused); with distal hyaline frill.

Mandible (Fig. 17C), with well developed coxa (seemingly) without spinular ornamentation. Gnathobase with bicuspidate teeth, a row of slender spinules, one multicuspidate spine and one strong seta. Basis (seemingly) without ornamentation and armed with one well developed seta. Exopod 1-segmented, ornamented with transverse rows of spinules and armed with 3 setae. Endopod 1-segmented, ornamented with outer spinules, armed with 3 lateral setae (two of them fused) and two sets of three fused setae.

Maxillule (Fig. 18A). Arthrite of praecoxa ornamented with few surface spinules, and armed with 2 surface setae, 2 lateral and 5 (or 6?) distal elements. Exopod represented by one well developed seta. Endopod 1-segmented and armed with 3 setae (two of them fused at their bases). With two basal endites, distal endite with 2 well developed seta, proximal endite with 1 well developed setae; coxa with 3 (or 4?) setae (two of them fused at their bases).

Maxilla (Fig. 18B), syncoxa with one distal endite bearing 1 small and 1 well developed seta. Allobasis ornamented with some spinules; drawn out into strong claw with one accompanying seta.

Maxilliped (Fig. 18D), basis ornamented with some inner and outer spinules, with some spinules close to joint with endopod, and without armature. Endopod 1-segmented, with long claw and 2 accompanying setae. Labrum as in Fig. 18E.

P1 (Fig. 19A). Coxa ornamented with transverse spinular rows in the middle and close to joint with basis on anterior surface and with longer spinules on proximal and distal outer corner posteriorly. Basis ornamented with spinules at base of endopod, exopod, inner and outer spine. Exopod 3-segmented; first segment about 2 times as long as wide and armed with an outer spine ornamented with strong spinules; second segment about 3 times as long as wide and armed with 1 inner plumose seta and 1 outer penicillate spine; third exopodal segment nearly as long as wide and armed with 4 penicillate spines and 2 setae. Endopod 3-segmented; first segment robust, about 3 times as long as wide, and nearly as long as second segment, the latter about 4 times as long as wide; third segment very small and armed with 1 small seta, 1 claw-like and 1 penicillate spine.

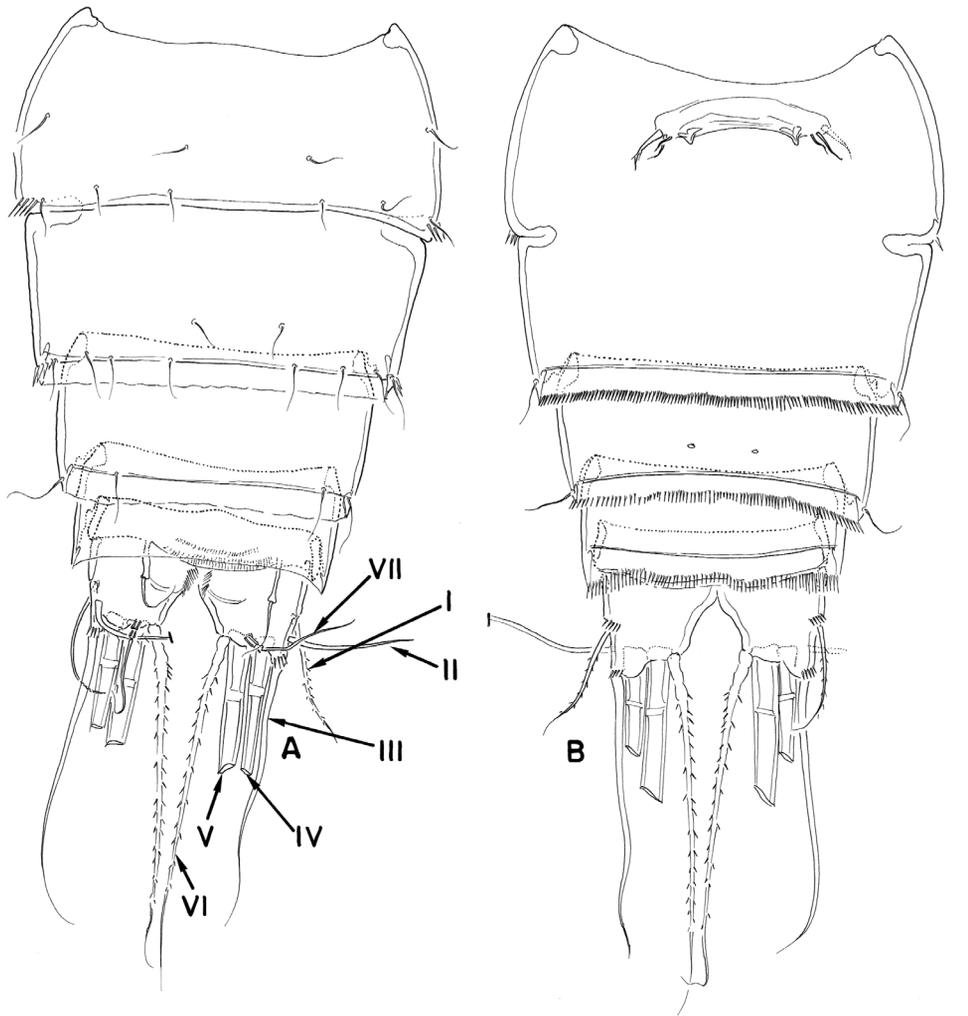


Figure 16. *Tisbe puelloi* sp. nov. Adult female. Holotype EMUCOP-090301-131. **A.** Urosome, dorsal (P5-bearing somite omitted); **B.** Urosome, ventral (P5-bearing somite omitted). Scale bar: 100 μ m.

Figure 16. *Tisbe puelloi* sp. nov. Femelle adulte. Holotype EMUCOP-090301-131. **A.** Urosome, vue dorsale (segment portant P5, omis) ; **B.** Urosome, vue ventrale (segment portant P5, omis). Echelle : 100 μ m.

P2 (Fig. 19B). Coxa with transverse spinular rows in the middle and close to outer margin anteriorly, with long spinules close to outer distal corner posteriorly. Basis with spinules at base of exopod, and with slender setules along margin of distal inner corner. Rami 3-segmented. Endopod longer than exopod; first segment with inner non-annulate plumose seta with spinules; second segment with 2 inner fluted and annulate plumose seta with spinules along inner margin; third segment with 1 outer spine and 4 fluted setae as follows: inner proximal element plumodenticulate as in *T. brigittevolkmannae* sp. nov. (see Fig. 12C), inner distal seta plumose with spinules along inner margin, inner and outer apical setae plumose and ornamented with outer spinules. First and second exopodal segments armed with outer spine and inner annulate and fluted plumose seta with

spinules along inner margin; third segment with 3 outer spines, 1 outer apical spine and 1 inner apical annulate and fluted seta ornamented with setules and spinules along inner and outer margin, respectively, and 2 inner annulate and fluted plumose setae; with hyaline frill at base of inner distal and inner apical seta (arrowed in Fig. 19B).

P3 (Fig. 20A). Coxa and basis as in P2. Rami 3-segmented. Endopod longer than exopod; first segment with 1 strong plumose seta ornamented with spinules, second segment with 2 inner fluted and annulate plumose setae with spinules along inner margin; third segment with outer spine and 5 fluted and annulate setae as follows: inner proximal and medial seta plumose and ornamented with spinules along inner margin, inner distal plumose seta with spinules, 2 apical plumose setae with spinules along outer margin.

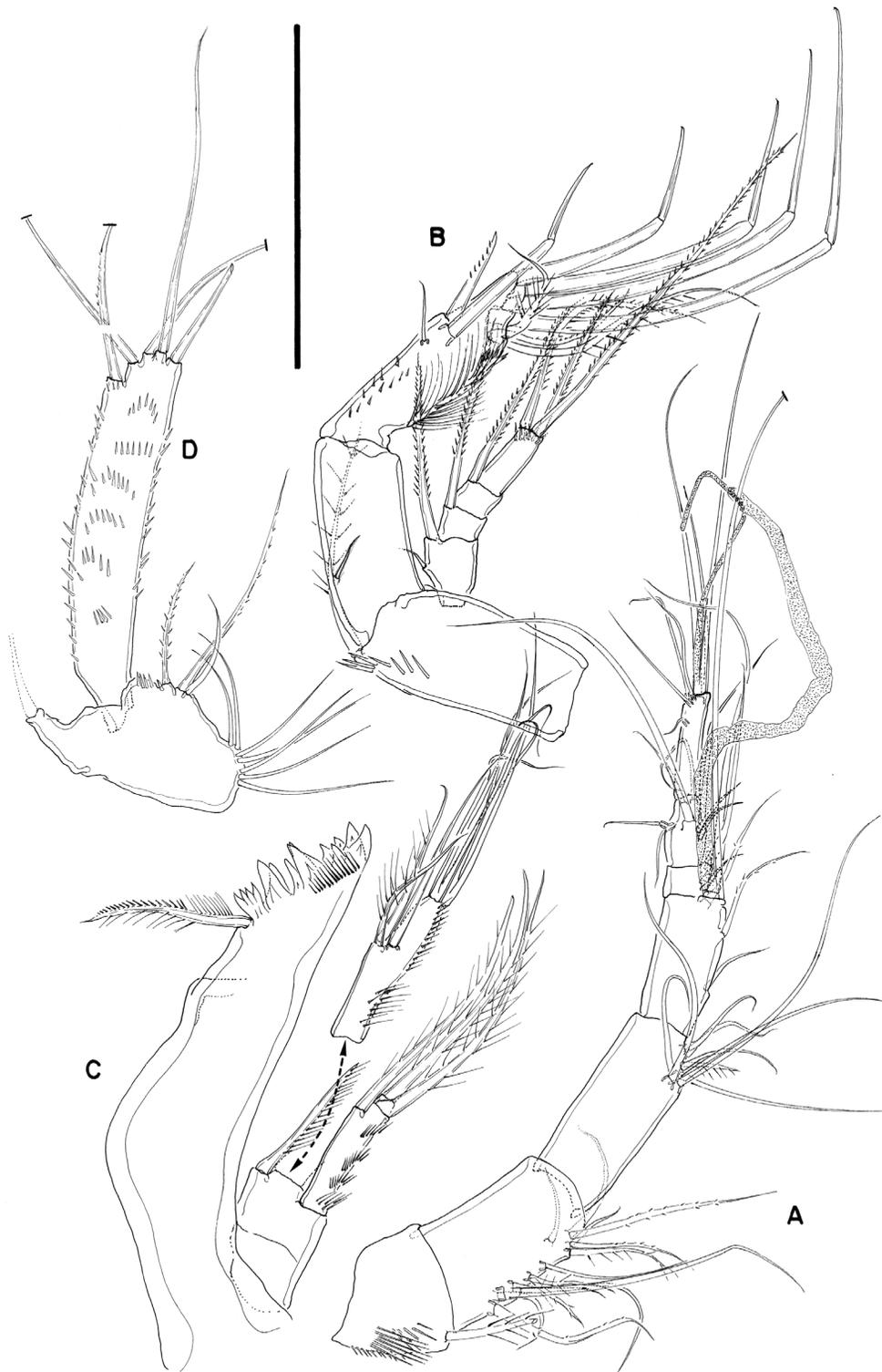


Figure 17. *Tisbe puelloi* sp. nov. Adult female, holotype EMUCOP-090301-131. **A.** antennule, ventral; **B.** antenna; **C.** mandible; **D.** P5. Scale bars: A, D, 100 μ m; B, C, 71 μ m.

Figure 17. *Tisbe puelloi* sp. nov. Femelle adulte, holotype EMUCOP-090301-131. **A.** antennule, vue ventrale ; **B.** antenne ; **C.** mandibule ; **D.** P5. Echelles : A, D, 100 μ m ; B, C, 71 μ m.

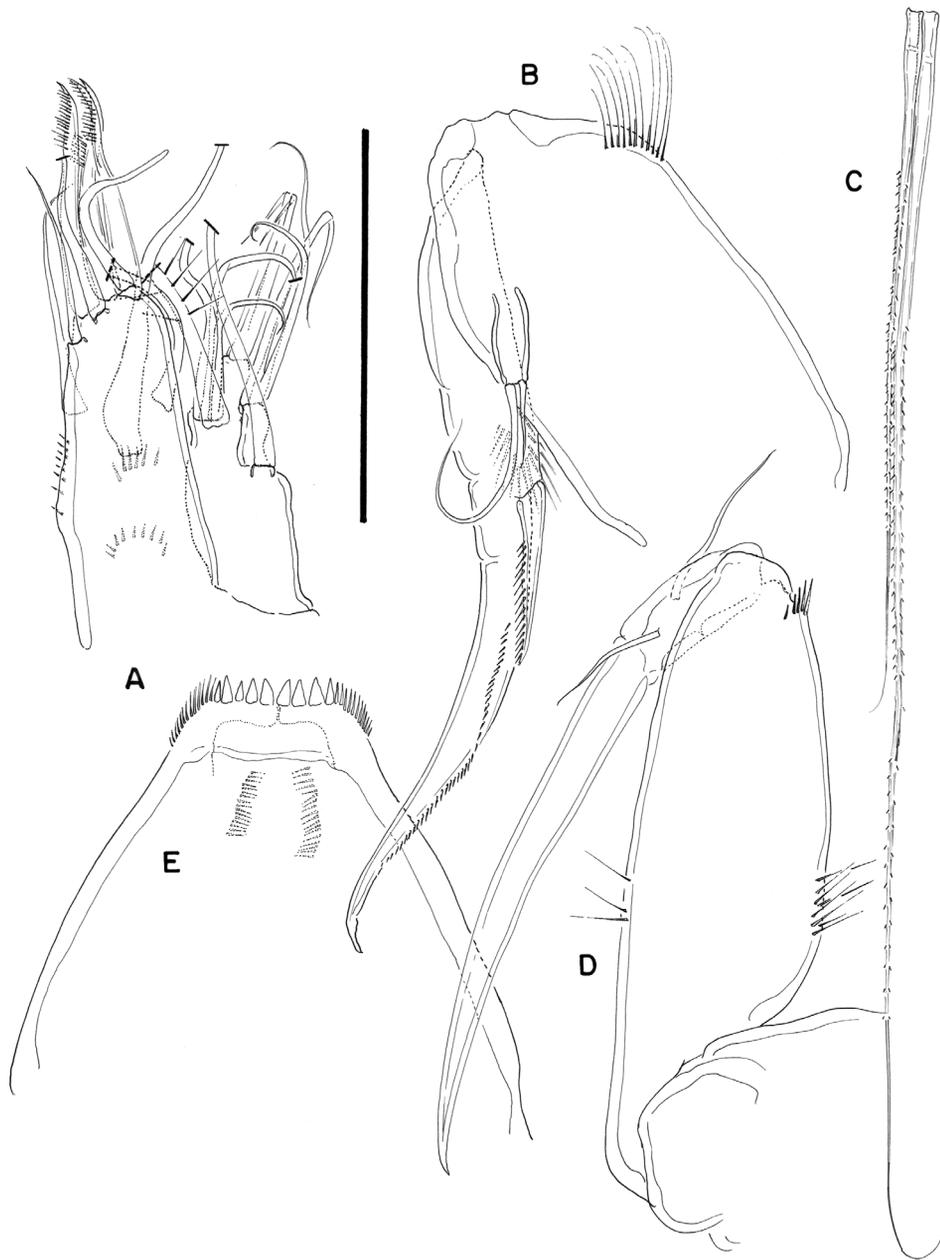


Figure 18. *Tisbe puelloi* sp. nov. Adult female, holotype EMUCOP-090301-131. **A.** maxillule; **B.** maxilla; **C.** caudal setae IV and V; **D.** maxilliped; **E.** labrum. Scale bars: A, B, D, 50 μ m; C, 200 μ m; E, 71 μ m.

Figure 18. *Tisbe puelloi* sp. nov. Femelle adulte, holotype EMUCOP-090301-131. **A.** maxillule ; **B.** maxille ; **C.** soies IV et V ; **D.** maxillipède ; **E.** labrum. Echelles : A, B, D, 50 μ m ; C, 200 μ m ; E, 71 μ m.

First and second exopodal segments armed with outer spine and inner fluted and annulate plumose seta; third exopodal segment with 3 outer spines, one outer apical spine, one apical fluted and annulate inner plumose setae with spinules along outer margin, and 3 inner fluted and annulate plumose setae; third exopodal segment with hyaline frill at base of inner apical and inner distal seta (arrowed in Fig. 20A).

P4 (Fig. 13B). Coxa and basis as in P3. Endopod reaching the distal third of third exopodal segment; first segment with 1, second segment with 2 inner fluted and annulate plumose seta with spinules along inner margin; third segment with outer spine and 4 fluted and annulate setae as follows: inner proximal and distal setae plumose and ornamented with spinules along inner margin, outer and

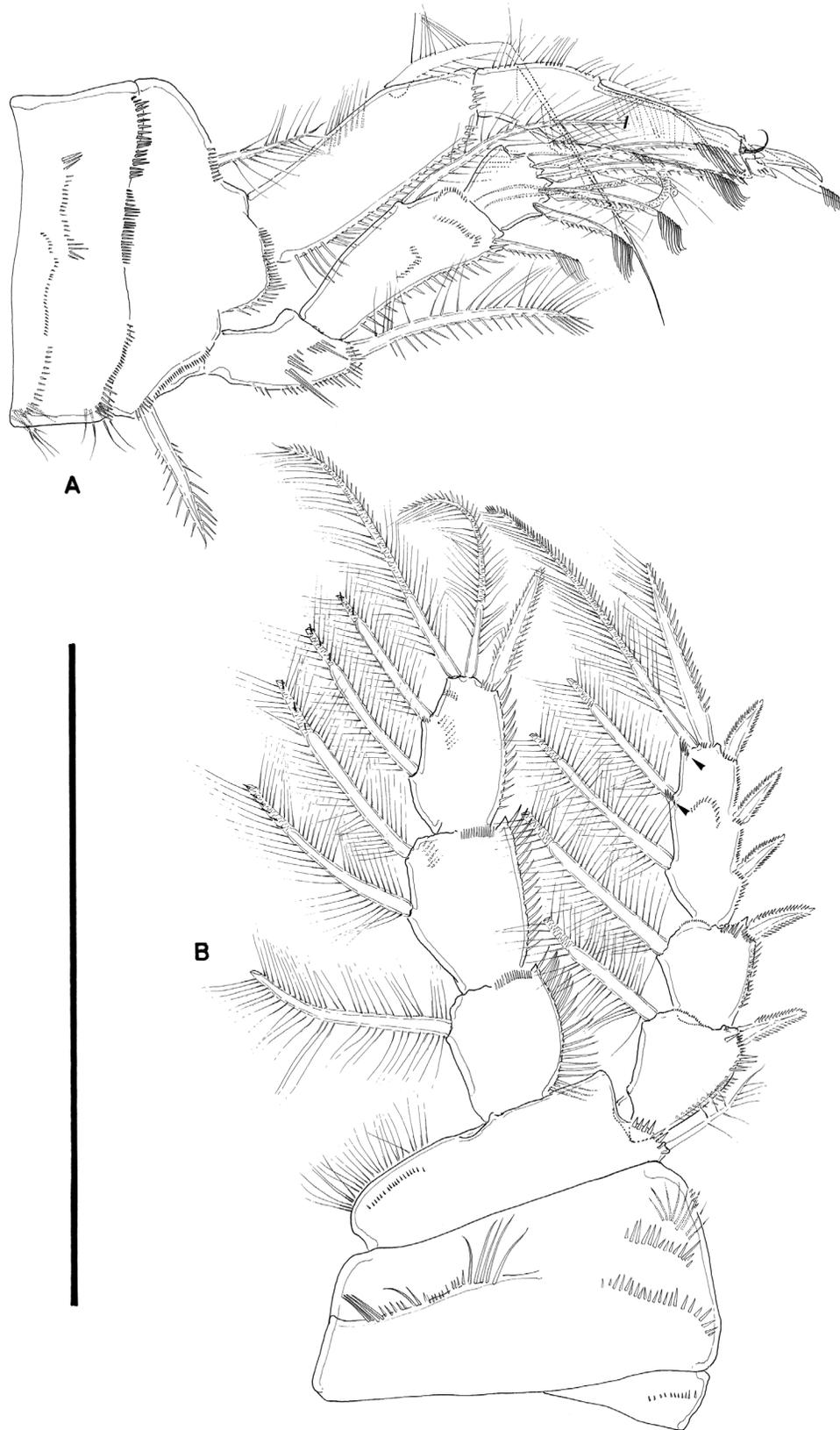


Figure 19. *Tisbe puelloi* sp. nov. Adult female, holotype EMUCOP-090301-131. **A.** P1; **B.** P2. Scale bar: 200 μ m.
Figure 19. *Tisbe puelloi* sp. nov. Femelle adulte, holotype EMUCOP-090301-131. **A.** P1 ; **B.** P2. Echelle : 200 μ m.

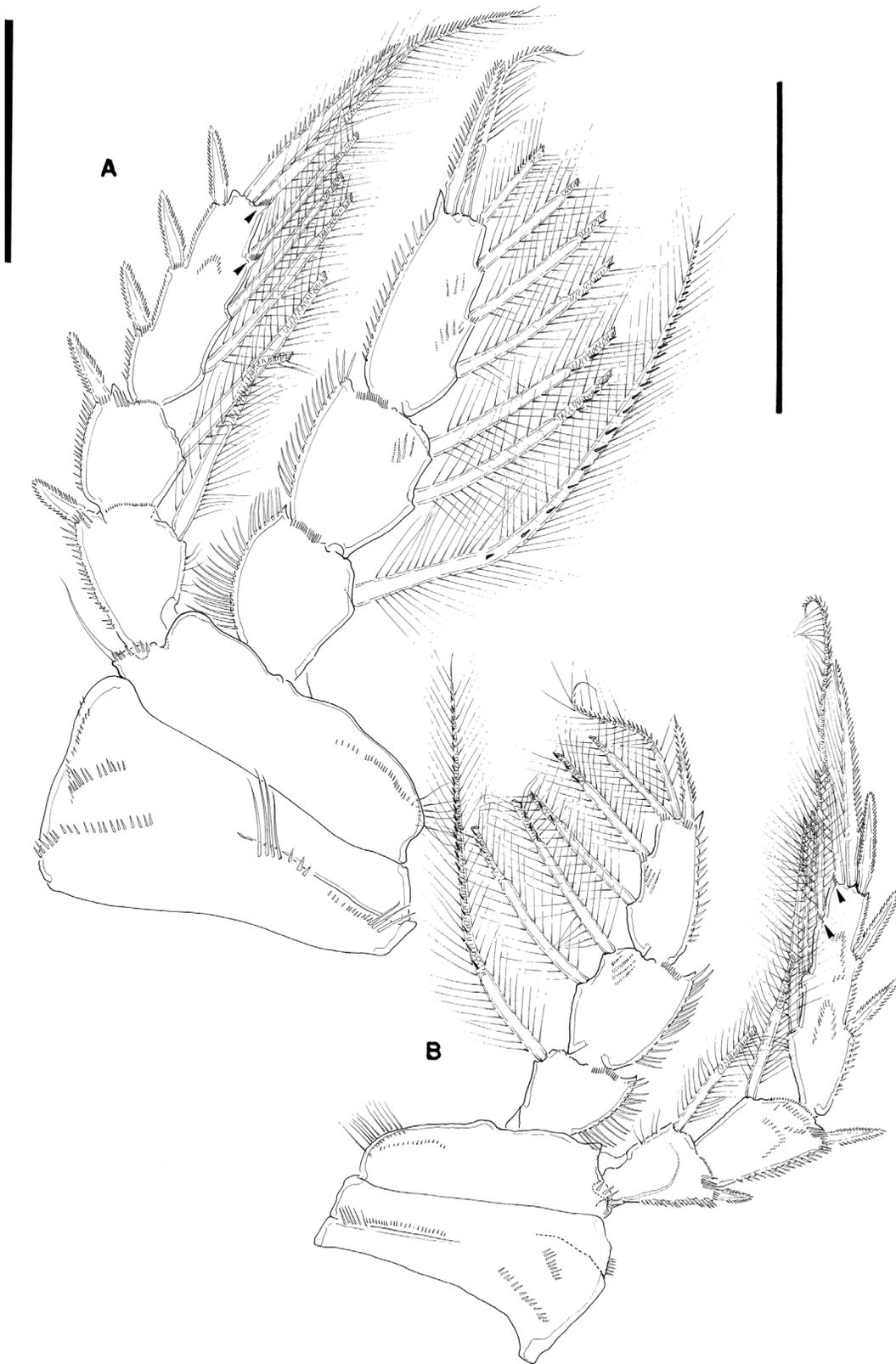


Figure 20. *Tisbe puelloi* sp. nov. Adult female, holotype EMUCOP-090301-131. **A.** P3; **B.** P4. Scale bars: A, 100 μ m; B, 125 μ m.
Figure 20. *Tisbe puelloi* sp. nov. Femelle adulte, holotype EMUCOP-090301-131. **A.** P3 ; **B.** P4. Echelles : A, 100 μ m ; B, 125 μ m.

inner apical setae plumose with spinules along outer margin. Exopodal segments comparatively longer than in P2 and P3; first segment slightly shorter than second segment, both segments armed with outer spine and inner fluted and annulate plumose seta; third segment longest, slightly longer than first and second segments combined and about 3.5 times as long as wide, and armed with 3 outer spines, 1 outer apical spine, 1 inner apical fluted and annulate plumose seta with spinules along outer margin, and 3 inner fluted and annulate plumose setae; third exopodal segment with hyaline frill at base of inner apical and inner distal seta (arrowed in Fig. 20B).

Armature formula as in *T. antennulodenticulata* sp. nov.

P5 (Fig. 17D) with triangular baseoendopod ornamented with spinules and longer setules along inner margin, and armed with 3 setae on inner lobe. Exopod about 5.6 times longer than wide, ornamented with spinules, and armed with 3 outer, 1 apical and 1 inner seta. Relative length of exopodal setae as in Fig. 17D.

Male. Unknown.

Etymology. The species is named in fond memory of Dr. Alfonso Puello.

Tisbe monozota Bowman, 1962 (Figs 21-28)

Distribution. U.S.A.: Between Virginia Key and Biscayne Key, Biscayne Bay, Dade County, Florida (Bowman, 1962); Mexico: the material examined here was found in experimental cultures of bullseye puffer (*Sphoeroides annulatus*); the water used in such cultures was taken from El Yugo estuary, Sinaloa, North-western Mexico (23°18.14'N, 106°29'W).

Citations. Bowman (1962), Volkmann (1974, 1979b).

Material examined. 41 females and 18 males preserved in alcohol (EMUCOP-010602-02), 3 dissected females (EMUCOP-010602-01, EMUCOP-010602-03, EMUCOP-010602-04) and 2 dissected males (EMUCOP-010602-05, EMUCOP-010602-06). Colls. A. C. Puello-Cruz, B. González-Rodríguez.

Redescription

Female. Body tapering posteriorly with maximum width in posterior margin of cephalic shield (Fig. 21A). Total body length ranging from 740 µm to 840 µm. With plain somitic frill in posterior margin of cephalic shield and free thoracic somites. Second and third urosomites (genital double-somite) distinct dorsally, with transverse row of minute spinules on posterior margin of abdominal half of genital double-somite (Fig. 22); completely fused ventrally (Fig. 21B); dorsal and ventral surface smooth; with semi-incised hyaline frill dorsally and ventrally (Figs 21A, B; 22). P6 (Fig. 21B) represented by 1 plumose seta and 2 small and naked elements (innermost smallest). Dorsal and ventral surface of fourth and fifth urosomite smooth, with semi-

incised hyaline frill dorsally and ventrally; fifth urosomite with two ventral parts of semi-incised frill seemingly longer and thinner (arrowed in Fig. 21B). Anal somite narrow; dorsal and ventral surface smooth; with small rounded anal operculum flanked by two distinct cones bearing one sensillum each; seemingly without somitic frill (Figs 21A, B; 22). Caudal rami (Figs 21A, B; 22) nearly as long as wide, ornamented with inner row of small spinules close to insertion site of seta VI, with long spinules at base of seta VII, and with smaller spinules close to insertion site of seta I and II; with 7 setae in all; seta II located laterally close to outer distal corner of ramus, about twice as long as seta I, the latter located ventrally in distal third of ramus; seta III arising from outer distal corner; seta IV shorter than seta V; seta VI arising from inner distal corner; seta VII well developed, as long as supporting ramus and located halfway along posterior margin of caudal ramus.

Antennule (Fig. 23A), 7-segmented. Armature formula as follows: 1-(1), 2-(14), 3-(9), 4-(4+ae), 5-(2), 6-(8), 7-(6+acrothek). Acrothek consisting of aesthetasc and 1 seta.

Antenna (Fig. 23B). Basis ornamented with minute spinules close to outer margin, with longer spinules at base of distal inner seta, and with transverse row of strong spinules close to inner margin; distal inner seta well developed, nearly as long as supporting segment. Exopod 4-segmented; first segment with one proximal well developed and naked seta and one bipinnate distal seta, the former as long as first and second exopodal segments combined; second and third segment with 1 seta each; fourth segment ornamented with subapical spinules and armed with 3 setae, one of which is noticeably smaller. First endopodal segment with small spinules along inner margin and armed with a naked seta about 1/2 length of the seta of basis. Inner margin of second endopodal segment with inner small spinules and with outer fragile and long setules; with subapical hyaline frill (arrowed in Fig. 23B), and armed with 2 lateral spines and 1 seta, 4 apical geniculate elements, and 3 spinulose setae (two of them fused).

Mandible (Fig. 24A), with well developed coxa ornamented with strong spinules proximally. Gnathobase with bidentate teeth, a row of slender spinules, and 1 pinnate and strong seta. Basis ornamented with few spinules and armed with 1 small inner seta. Exopod 1-segmented, ornamented with rows of spinules and armed with 1 lateral and 2 apical setae. Endopod 1-segmented, ornamented with inner and outer spinules, armed with 3 lateral setae and 6 apical slender elements forming 2 sets of fused setae with 3 elements each.

Maxillule (Fig. 24B), with long arthrite of praecoxa ornamented with spinules, and armed with 2 surface strong setae, 2 lateral (one of them very small) and 7 distal elements. Exopod represented by one well developed seta. Endopod 1-segmented and armed with 3 setae (two of them

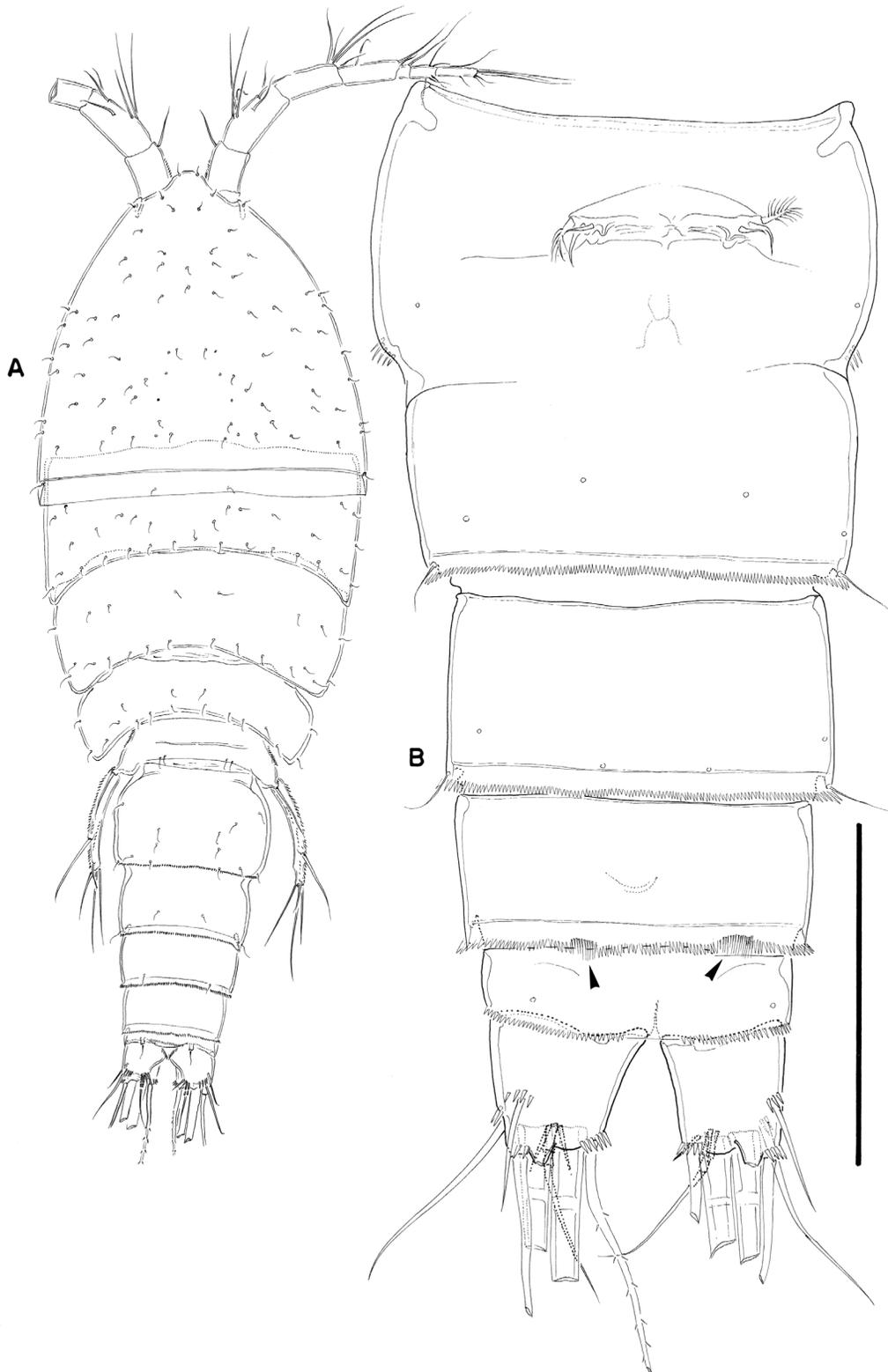


Figure 21. *Tisbe monozota* Bowman, 1962. Adult female. **A**, EMUCOP-010602-05; **B**, EMUCOP-010602-03. **A**. habitus, dorsal; **B**. urosome, ventral (P5-bearing somite omitted). Scale bars: **A**, 333 μ m; **B**, 100 μ m.

Figure 21. *Tisbe monozota* Bowman, 1962. Femelle adulte. **A**, EMUCOP-010602-05 ; **B**, EMUCOP-010602-03. **A**. habitus, vue dorsale ; **B**. urosome, vue ventrale (segment portant P5, omis). Echelles : **A**, 333 μ m ; **B**, 100 μ m.

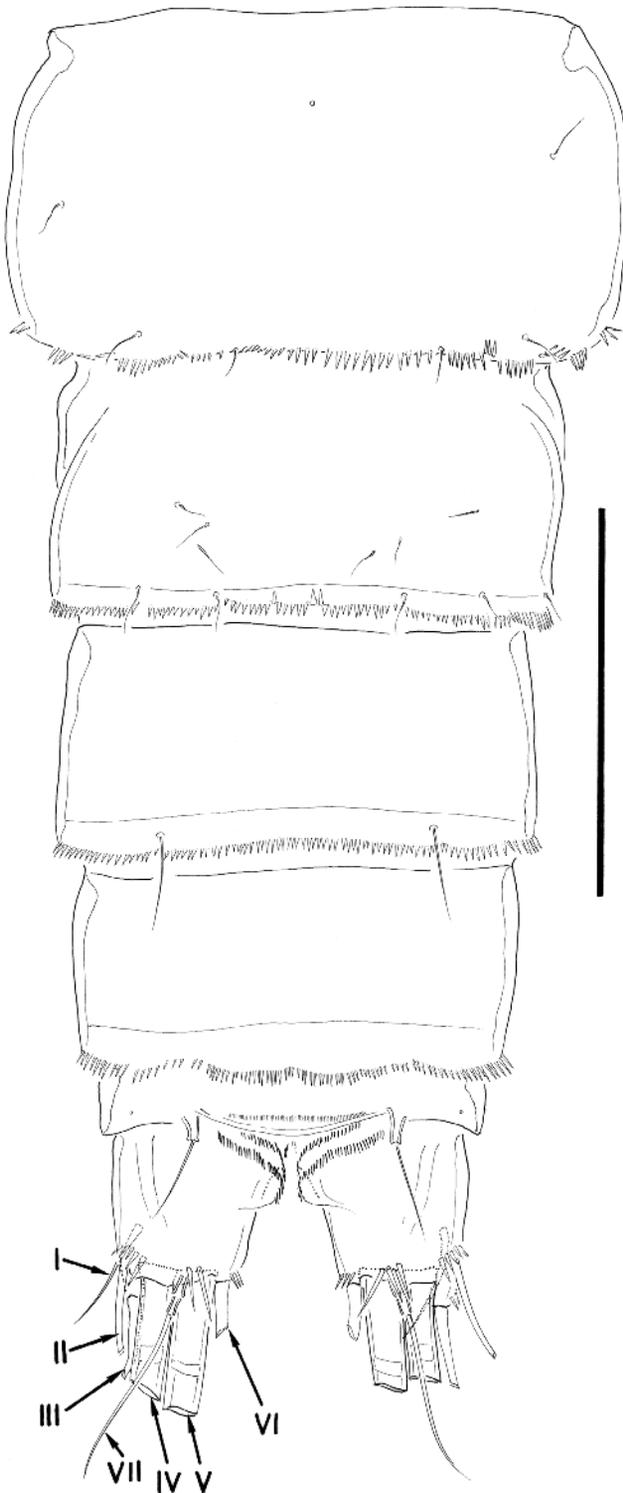


Figure 22. *Tisbe monozota* Bowman, 1962. Adult female. EMUCOP-010602-04. Urosome, dorsal (P5-bearing somite omitted). Scale bar: 100 μ m.

Figure 22. *Tisbe monozota* Bowman, 1962. Femelle adulte. EMUCOP-010602-04. Urosome, vue dorsale (segment portant P5, omis). Echelle : 100 μ m.

fused at their bases). With two basal endites, distal endite with 2 well developed seta, proximal endite with 1 well developed setae; coxa with 4 setae.

Maxilla (Fig. 24C) with one distal endite bearing 1 small and 1 well developed seta. Allobasis drawn out into strong claw with one accompanying seta and a tube pore (the latter arrowed).

Maxilliped (Fig. 24D). Syncoxa ornamented with small spinules. Basis with strong spinules close to outer margin anteriorly and posteriorly, and with row of long and short spinules along inner margin, and with some smaller spinules close to joint with endopod, the latter 1-segmented, with long claw and 3 accompanying seta (one of them longer and strong). Labrum as in Fig. 24E.

P1 (Fig. 25A). Coxa ornamented with transverse spinular rows in the middle and close to joint with basis on anterior surface and with longer spinules on proximal and distal outer corner posteriorly. Basis ornamented with spinules at base of endopod, exopod, inner and outer spine anteriorly, and with long spinules close to distal inner corner posteriorly. Exopod 3-segmented; first segment about 2 times as long as wide and armed with an outer spine ornamented with strong spinules; second segment about 2.7 times as long as wide and armed with 1 inner plumose seta and 1 outer spine; third segment with 3 outer spines, 1 outer spine and 1 inner fluted and annulate seta distally, and 1 fluted and annulate inner seta; spines of second and third exopodal segments with 1 long and strong, and 1 small spinule distally. Endopod 3-segmented; first segment about 0.7 times as long as second segment, the latter with small seta midway along inner margin; third segment very small, with 1 slender and small seta and 2 claw-like spinules.

P2 (Fig. 25B). Coxa ornamented with transverse spinular rows anteriorly, and with longer and slender spinules posteriorly along outer margin. Basis with spinules in the middle, at base of outer seta and close to inner distal corner anteriorly; with slender and longer setules along inner distal corner. Rami 3-segmented. Endopod reaching about distal third of third exopodal segment; first segment with inner non-annulate plumose seta with spinules; second segment with 2 inner fluted and annulate plumose seta with spinules along inner margin; third segment with 1 outer spine and 4 fluted setae as follows: inner proximal element plumodenticulate, inner distal element, and inner and outer apical setae plumose with outer spinules. First and second exopodal segments armed with outer spine and inner annulate and fluted plumose seta; third segment with 3 outer spines, 1 outer apical spine and 1 inner apical annulate and fluted seta ornamented with setules and spinules along inner and outer margin, respectively, and 2 inner annulate and fluted plumose setae; with hyaline frill at base of inner distal and inner apical seta (arrowed in Fig. 25B).

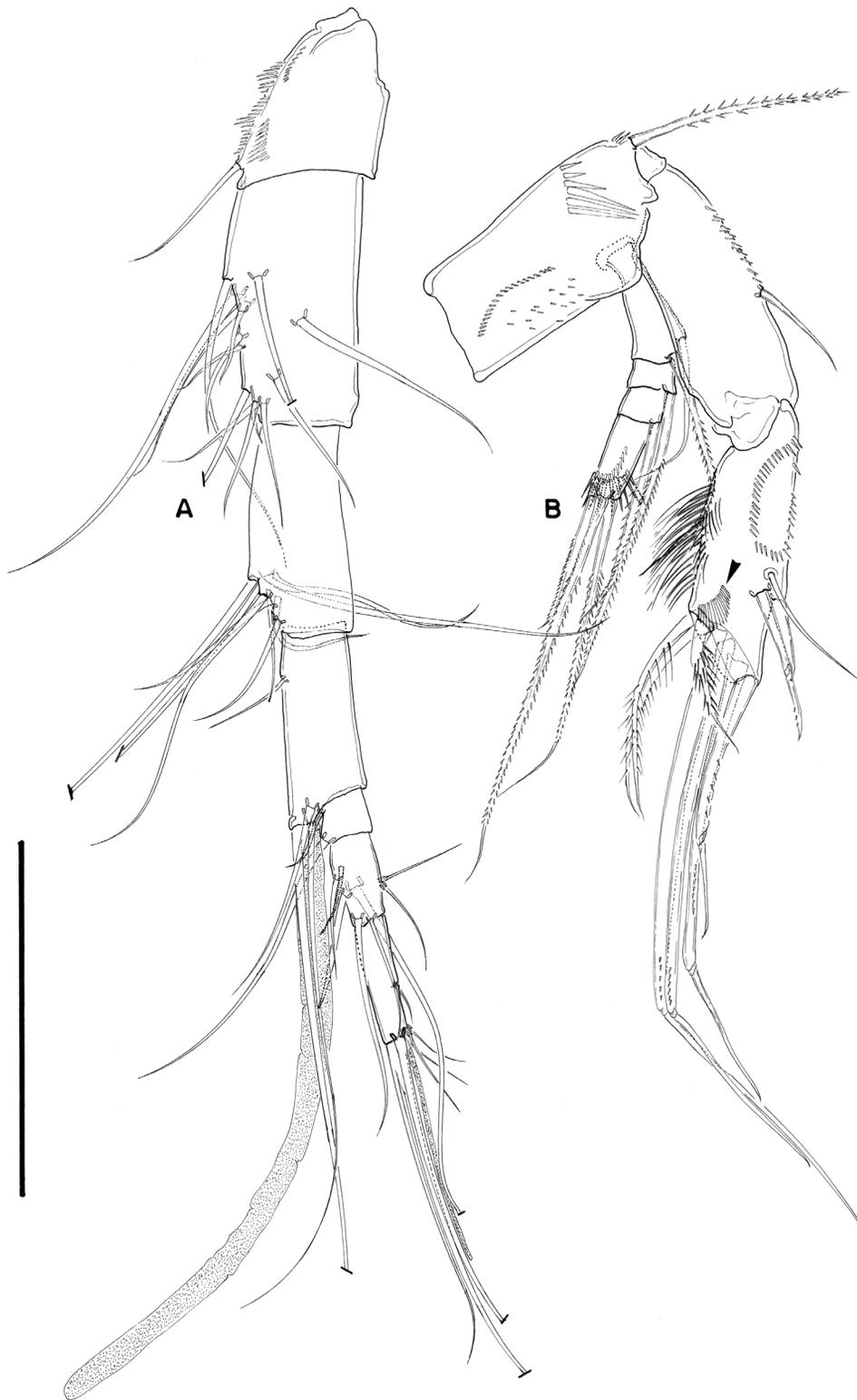


Figure 23. *Tisbe monozota* Bowman, 1962. Adult female. EMUCOP-010602-03. **A.** antennule; **B.** antenna (hyaline frill of second endopodal segment arrowed). Scale bars: A, 100 μ m; B, 71 μ m.

Figure 23. *Tisbe monozota* Bowman, 1962. Femelle adulte. EMUCOP-010602-03. **A.** antennule ; **B.** antenne (membrane hyaline du deuxième segment de l'endopode indiquée). Echelles : A, 100 μ m ; B, 71 μ m.

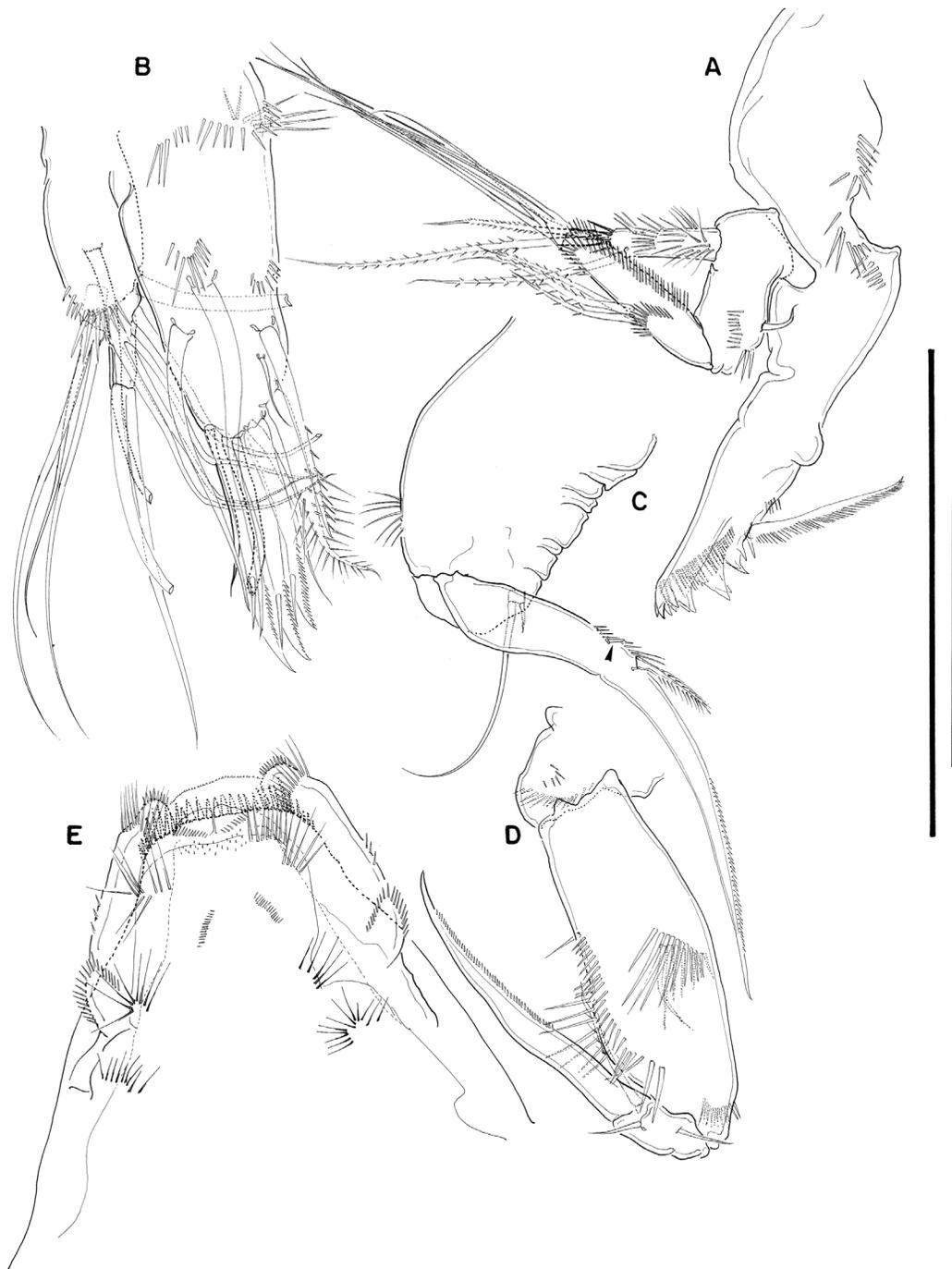


Figure 24. *Tisbe monozota* Bowman, 1962. Adult female. **A, C, D**, EMUCOP-010602-03; **B**, EMUCOP-010602-01; **E**, EMUCOP-010602-04. **A**, mandible; **B**, maxillule; **C**, maxilla; **D**, maxilliped; **E**, labrum and paragnaths. Scale bars: **A, C, D, E**, 100 μm ; **B**, 69 μm .

Figure 24. *Tisbe monozota* Bowman, 1962. Femelle adulte. **A, C, D**, EMUCOP-010602-03 ; **B**, EMUCOP-010602-01 ; **E**, EMUCOP-010602-04. **A**, mandibule ; **B**, maxillule ; **C**, maxille ; **D**, maxillipède ; **E**, labrum et paragnathes. Echelles : **A, C, D, E**, 100 μm ; **B**, 69 μm .

P3 (Fig. 26A). Coxa and basis as in P2. Rami 3-segmented. Endopod reaching distal third of last exopodal segment; first segment with 1 strong plumose seta

ornamented with spinules, second segment with 2 inner fluted and annulate plumose setae with spinules along inner and outer margin; third segment with outer spine and 5



fluted and annulate setae as follows: 3 inner setae plumose and ornamented with spinules along inner and outer margin, 2 apical plumose setae with spinules along outer margin. First and second exopodal segments armed with outer spine and inner fluted and annulate plumose seta; seta of first segment without, of second segment with additional spinules; third exopodal segment with 3 outer spines, 1 outer apical spine, 1 apical fluted and annulate inner plumose setae with spinules along outer margin, and 3 inner fluted and annulate plumose setae with spinules along inner and outer margin; third exopodal segment with hyaline frill at base of inner apical and 2 distalmost inner setae (arrowed in Fig. 26A).

P4 (Fig. 26B). Coxa and basis as in P3. Endopod reaching the middle of third exopodal segment; first segment with 1 inner fluted and annulate plumose seta with inner spinules, second segment with 1 inner fluted and annulate plumose seta with inner spinules and 1 inner distal plumose, fluted and annulate seta with spinules along inner and outer margin; third segment with outer spine and 4 fluted and annulate setae as follows: inner proximal and distal setae plumose and ornamented with spinules along inner margin, outer and inner apical setae plumose with spinules along outer margin. Exopodal segments comparatively longer than in P2 and P3; first segment slightly shorter than second segment, both segments armed with outer spine and inner fluted and annulate plumose setae; third segment longest, as long as first and second segments combined and about 3.5 times as long as wide, and armed with 3 outer spines, 1 outer apical spine, 1 inner apical fluted and annulate plumose seta with spinules along outer margin, and 3 inner fluted and annulate plumose setae with spinules along inner margin; third exopodal segment with hyaline frill at base of inner apical and inner distalmost setae (arrowed in Fig. 26B).

Armature formula as in *T. antennulodenticulata* sp. nov.

P5 (Fig. 25C) with triangular baseoendopod ornamented with spinules at base of outer seta; inner lobe of baseoendopod armed with 3 setae. Exopod about 5 times as long as wide, ornamented with spinules, and armed with 3 outer, 1 apical and 1 inner seta. Relative length of exopodal setae as depicted.

Male. General body shape as in female, except for genital double-somite (Fig. 27A, B). Total length measured from tip of rostrum to posterior margin of caudal rami ranging from 600 to 660 μm .

Antennule (Fig. 28A), haplocer, 9-segmented (division on distal part of third and fourth segment only visible dorsally); with aesthetasc on fourth and last segment.

Maxilliped (Fig. 28B) sexually dimorphic.

P1 as in female, except for inner element of basis being setiform and naked (arrowed in Fig. 28E).

P2 ENP 1 as in female, except for sexually dimorphic inner spine on second segment (arrowed in Fig. 27C).

P5 (Fig. 28C) with 2 setae on inner baseoendopodal lobe; with some spinules at base of outer seta. Exopod ornamented with outer and inner spinules; about 3 times as long as wide; with 2 outer setae (distalmost smaller), 1 apical and 2 inner elements.

P6 (Figs 27B; 28D) ornamented with spinules at the base of outer seta, and at the base of distal seta and distal spine, the latter strongly bipinnate, hardly reaching posterior margin of third urosomite.

Discussion

The taxonomy and correct identification of specimens of *Tisbe* is not an easy task as one must pay special attention to very subtle details such as ornamentation of outer spines of P1 EXP, ornamentation and general shape of the inner setae of P2-P4 ENP and EXP, armature of mandibular basis, second endopodal segment of maxilliped, female genital field, ornamentation/general shape of the inner setae of P2 ENP 3 which seems to be species-specific, sexual dimorphism, and general shape of somitic frill of urosomites ventrally and dorsally.

In her outstanding revision of *Tisbe*, Volkmann (1979b) defined, among others, the *gracilis* species-group based on the number of segments of A1 in both sexes, armature of the antenna, mandible (basis, exopod and endopod) and maxilliped, general shape and ornamentation of the armature of P1 ENP and EXP, and sexual dimorphism in male maxilliped, basis of P1 and armature of P2 ENP. Volkmann (1979b) also delimited other groups including the *T. bermudensis* group, *T. tenella* group and *T. angusta* group. Other species such as *T. ramphigera* Volkmann, 1979b, *T. celata* Humes, 1954 and *T. finmarchica* (Sars, 1905) could not be included in any of the above species-groups, and each of them could represent distinct species-groups. Since Volkmann's (1979b) revision of the genus *Tisbe* in which 57 valid species were recognized, only 4 new species have been added. Waghorn (1979), probably

Figure 25. *Tisbe monozota* Bowman, 1962. Adult female. **A, B**, EMUCOP-010602-03; **C**, EMUCOP-010602-01. **A**. P1; **B**. P2 (hyaline frills of third exopodal segment arrowed); **C**. P5. Scale bars: **A, C**, 100 μm ; **B**, 200 μm .

Figure 25. *Tisbe monozota* Bowman, 1962. Femelle adulte. **A, B**, EMUCOP-010602-03 ; **C**, EMUCOP-010602-01. **A**. P1 ; **B**. P2 (membranes hyalines du troisième segment de l'exopode indiquées) ; **C**. P5. Echelles : **A, C**, 100 μm ; **B**, 200 μm .

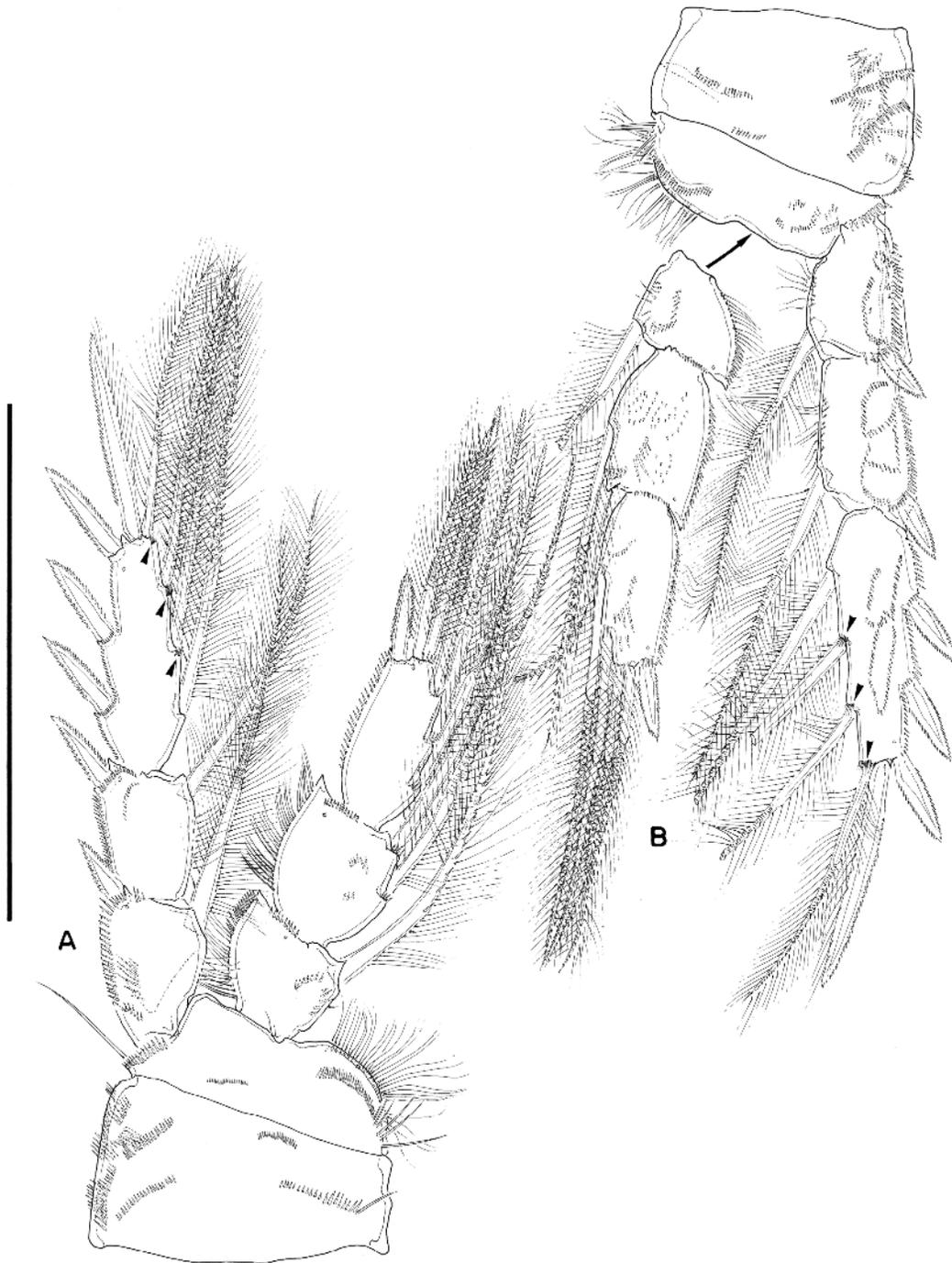


Figure 26. *Tisbe monozota* Bowman, 1962. Adult female. EMUCOP-010602-03. **A.** P3 (hyaline frills of third exopodal segment arrowed); **B.** P4 (hyaline frills of third exopodal segment arrowed). Scale bar: 200 μ m.

Figure 26. *Tisbe monozota* Bowman, 1962. Adult female. EMUCOP-010602-03. **A.** P3 (membranes hyalines du troisième segment de l'exopode indiquées) ; **B.** P4 (membranes hyalines du troisième segment de l'exopode indiquées). Echelle : 200 μ m.

unaware of Volkmann's (1979b) revision, described *T. prolata* from White Island (Antarctica). Waghorn (1979) concluded that *T. prolata* is unique among *Tisbe* species in

respect of its very long caudal rami, and suggested some similarity with *T. remota* (Farran, 1926), whose placement by Lang (1948, 1965) in the genus *Tisbe* was questioned by

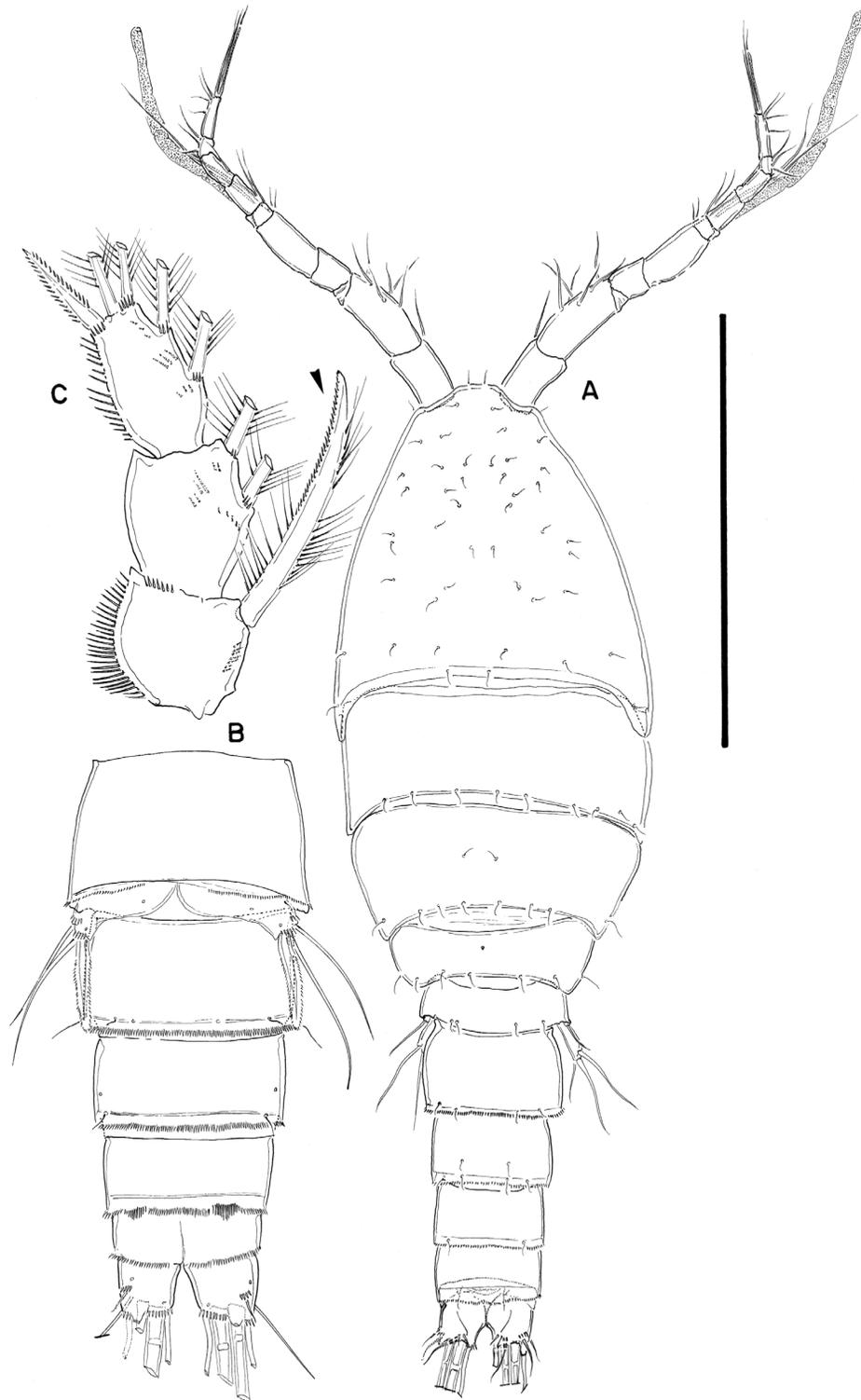


Figure 27. *Tisbe monozota* Bowman, 1962. Adult male. **A**, EMUCOP-010602-06; **B**, **C**, EMUCOP-010602-08. **A**. habitus, dorsal; **B**. urosome, ventral (P5-bearing somite omitted); **C**. endopod of P2 (inner dimorphic element on first segment arrowed). Scale bars: A, 300 μ m; B, 200 μ m; C, 126 μ m.

Figure 27. *Tisbe monozota* Bowman, 1962. Mâle adulte. **A**, EMUCOP-010602-06 ; **B**, **C**, EMUCOP-010602-08. **A**. habitus, vue dorsale ; **B**. urosome, vue ventrale (segment portant P5, omis) ; **C**. endopode du P2 (épine dimorphique interne du premier segment, indiquée). Echelles : A, 300 μ m ; B, 200 μ m ; C, 126 μ m.



Figure 28. *Tisbe monozota* Bowman, 1962. Adult male. **A, B**, EMUCOP-010602-07; **C, D**, EMUCOP-010602-08; **E**, EMUCOP-010602-06. **A**. antennule, dorsal; **B**. maxilliped; **C**. P5; **D**. P6; **E**. basis of P1. Scale bars: A, 200 μ m; B, C, D, 100 μ m; E, 167 μ m.

Figure 28. *Tisbe monozota* Bowman, 1962. Mâle adulte. **A, B**, EMUCOP-010602-07 ; **C, D**, EMUCOP-010602-08 ; **E**, EMUCOP-010602-06. **A**. antennule, vue dorsale ; **B**. maxillipède ; **C**. P5 ; **D**. P6 ; **E**. basis du P1. Echelles : A, 200 μ m ; B, C, D, 100 μ m ; E, 167.

Volkman (1979b) who reestablished the genus *Bathyidia* Farran, 1926 with *B. remota* as its type species. *Tisbe japonica* Ho, 1982 which was found associated with *Asterina pectinifera* (Müller & Troschell, 1842) (Asteroidea) in the Sea of Japan, was shown to belong to the *gracilis* species-group (Ho, 1982). Bradford & Wells (1983) showed that *T. spinulosa* Bradford & Wells, 1983 clearly belongs to Volkman's (1979b) species of *Tisbe* with "a P1 setation which is different from the normal type". It but could not be identified with any other known species-group since this species bears some resemblance with both the *gracilis* group and with *T. finmarchica*. Bradford & Wells (1983) suggested also the possibility that *T. spinulosa* should not be placed within *Tisbe* based on the spinulose ornamentation of the body. Unfortunately, most descriptions of *Tisbe* species don't give enough information regarding the surface ornamentation of body somites, probably due to the fact that such ornamentation is sometimes difficult to see and therefore should not be taken into account for species separation within the genus until the presence/absence of such ornamentation is fully documented for all the valid species of *Tisbe*. *Tisbe caymanensis* Yeatman, 1984 from Grand Cayman is unique within *Tisbe* and could represent another species-group based on the armature formula of P1 ENP 3 (with one grooved sword-like spine and a small, slender seta) and P2 EXP 3 (with a dwarfed outer proximal spine).

Tisbe antennulodenticulata sp. nov. cannot be assigned to any of Volkman's (1979b) species-groups due to the combination of the following characters: 7-segmented antennule, small and naked seta on A2 basis, lack of armature on mandibular basis, mandibular exopod with 2 setae only, relative length of spines of P1 ENP 3 (unequal in size), male antennule subchirocer and 7-segmented, and lack of sexual dimorphism in male maxilliped and inner seta of basis of P1. Even though *T. antennulodenticulata* sp. nov. is similar to *T. gracilis* in the ornamentation of outer spines of P1 EXP, P1 ENP 2 and relative size of setae of caudal rami, it is unique within the genus and can be unequivocally separated by the presence of a distal outer extension on the caudal rami where seta III arises, and by the presence of an acute projection on the fifth segment of the male antennule. Following Volkman's (1979b) revision, one of the most reliable species-specific characters is the female genital field. The genital field of *T. antennulodenticulata* sp. nov., as shown in Fig. 2 is unique within the species-group by the presence of only 2 setae representing P6, instead of the most common condition of three setae as shown by Volkman (1979b: 248-249, Fig. 19). Another character that has not been given the attention it deserves is the ornamentation and general shape of the proximal inner seta of female P2 ENP 3, which as shown below for other species herein described, seems to be species-specific and could be of taxonomic value.

Gurney (1927) presented a rather brief and incomplete description of *T. longisetosa* Gurney, 1927 from Egypt. Later, Volkman (1979a) described *T. variana* Volkman, 1979 from Bermuda, North Carolina (U. S. A.) and Panama. Following Volkman (1979a), *T. variana* turned out to be related to *T. longisetosa* and *T. bocqueti* Volkman-Rocco, 1972. From her description of *T. variana*, it is clear that Volkman (1979a: 8-9) had the opportunity to check Gurney's material of *T. longisetosa* and announced the redescription of the species. To the best of my knowledge the species has not been redescribed yet. Due to this and the fact that Gurney's (1927) original description lacks the necessary detail, *T. longisetosa* is considered here as species inquirenda within *Tisbe* until its full redescription is available. *Tisbe brigittevolkmannae* sp. nov. falls within the species defined by Volkman (1979b) as possessing the normal armature of P1 ("endopod segment 3 with two spines, subequal in length, the shorter usually of clawlike shape, the other always distinctly penicillate at tip; exopod segment 2 with one outer spine and segment 3 with four spines bearing a tuftlike comb of numerous setules at apex") and is similar to *T. variana*. These two species are identical in almost all of their appendages and armature formulae, and shape and size of armature, but can be separated by the relative length of the inner seta of baseopod and innermost seta of exopod of male P5. Volkman (1979a) observed three accompanying setae on the second endopodal segment of maxilliped in *T. variana*. Only 2 accompanying setae were found in the same maxillipedal segment of *T. brigittevolkmannae* sp. nov. Also, some sexual dimorphism in the male maxilliped was observed for *T. brigittevolkmannae* sp. nov. On this regard, nothing was mentioned in Volkman's (1979a) description of *T. variana*. Of course, the sexual dimorphism observed in the male maxilliped of *T. brigittevolkmannae* sp. nov. is very subtle and consists only of some swelling of the basis and comparatively stronger spinules on the inner margin of the same segment, and could have been overlooked by Volkman (1979a).

Tisbe puelloi sp. nov. is another species with a normal P1. This species seems to be unique within *Tisbe* by the combination of a reduced proximal seta on first exopodal segment of A2, and a well developed seta of mandibular basis. Unfortunately, descriptions of *Tisbe* species rarely include the detailed description of mouth parts since it is believed that they are rather conservative and that armature of P1 and P5 are the most important features for assessing relationships within *Tisbe*. Contrary to this, we believe that a combination of several character states including P1 armature (general shape and ornamentation), relative size of the exopodal setae and inner seta of first and second endopodal segment of A2, relative size of the inner seta of basis of mandible and sexual dimorphism either in

maxilliped, basis of P1 and armature of P2 ENP, could provide better insights into the relationships within *Tisbe*.

During the early 1960s, Bowman (1962) described *T. monozota* Bowman, 1962 from a salt water aquarium in the Smithsonian Institution. The water contained in that aquarium was collected in Bear Cut, between Virginia Key and Biscayne Key, Florida, and was assumed to be the type locality for the species. Volkmann (1974) decided not to include *T. monozota* in her *gracilis* species-group. However, Volkmann (1979b) changed her mind "since there is only one major difference: armature of some of the P1 spines, while most of the other characteristics correspond perfectly", and suggested some phylogenetic relationships between *T. monozota*, and *T. gracilis*, *T. gigantea* Volkmann, 1979, *T. cucumariae* Humes, 1957 and *T. pori* Betouhim-El & Kahan, 1972 even though *T. monozota* "holds a special position". Bowman's (1962) original description is one of the few contributions that describe all of the appendages, but due to some minor flaws and omissions (i. e. armature of male P5, female genital field, shape of caudal rami, basis of male P1, dimorphic spine on male P2 ENP 1), Volkmann (1979b) decided to include a redescription of the species based not on the type material deposited in the USNM by Bowman himself, but on some other specimens probably deposited in the personal collection of Dr. T. E. Bowman which were given the rank of paratype in Volkmann (1979b: 186). On this regard, it has to be noted that the only type material of the species has been deposited by Bowman (1962: 130) in the collection of the USNM. The catalogue number for the paratypes deposited by Bowman (1962) did not appear in the original description, but was found to be USNM107154. The material upon which Volkmann (1979b) based her redescription constitute topotypes and not paratypes as stated by Volkmann (1979b).

This is the first report of *Tisbe monozota* from the Tropical Eastern Pacific, and we considered useful to include a full redescription of the species. As before, *T. monozota* was found inhabiting experimental salt water tanks used for culturing of bullseye puffer (*Sphoeroides annulatus*). *Tisbe monozota* has been collected also near the place where marine water enters the culture system. The fact that this species (and probably some other *Tisbe* species) can be found in experimental tanks gives some hints about the tolerance of the genus to a wide range of temperature and salinity variation.

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