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Pleuromamma johnsoni, a new looking-glass copepod from the Pacific Ocean with redescriptions of *P. robusta* (Dahl, 1893), *P. antarctica* Steuer, 1931 new rank, and *P. scutullata* Brodsky, 1950 (Crustacea: Calanoida: Metridinidae)

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Abstract: Males and females of *Pleuromamma johnsoni* are distinguished from all other species of the genus by the presence of a slightly asymmetrical knob on the cephalon dorsal to rostral area; males lack a distal segmental attenuation of the 14th segment of the geniculate antennule (A1), a morphology unique among males of *Pleuromamma*. *P. johnsoni* has been found in samples collected from 11° to 14°N and 97° to 126°W, and appears to be restricted to the eastern tropical Pacific Ocean north of the equator. It is the second species of the genus in which both bilaterally asymmetric morphs are found among females and males (33% of females and 93% of males are left). *P. robusta*, *P. antarctica* but *P. scutullata* are similar in size to *P. johnsoni*; their males also have bilaterally symmetrical attenuations on the proximal endopodal segment of swimming leg 2 and possess a distal attenuation on the 14th segment of the geniculate A1. The latter three species differ from each other in the spinule patterns on abdominal somites, shape of the 14th segment of the geniculate A1, and shape of the medial attenuation of the basis and of the proximal exopodal segment of leg 5 of males. Differences also are found in shape of the genital prominence and the denticle patterns of leg 5 of females.

Key words: *Pleuromamma*, new species, new rank, Copepoda, Pacific Ocean

Introduction

Nine species presently are recognized in the calanoid copepod genus *Pleuromamma*, along with a number of forms among several of the nine species. Most of the species have been known for almost a century; the youngest named species, *P. scutullata*, was described almost fifty years ago (Brodsky 1950). Calanoid copepods belonging to *Pleuromamma* are recognized easily by the presence of a dark organ or "pigment knob" of secretory function (Blades-Eckelbarger & Youngbluth 1988) on the left or right side of the second thoracic somite, although a single specimen of *P. gracilis* has been described with a dark organ on both sides of

the somite (Bytinski-Salz 1933). There also is an extensive set of smaller pores (openings of secretory glands) on the body and appendages of species of *Pleuromamma*. Park & Mauchline (1994) have used the location of these pores on body somites to infer phylogentic relationships among several species; previous hypotheses about species relationships utilized the expression of bilateral asymmetry among selected structures (Dahl 1893) or the expression of dimorphism among all asymmetrical structures (Steuer 1932). Species of *Pleuromamma* are free-swimming and are found in almost all oceanic habitats. A number of species are known to undertake complex, diel vertical migrations (Bennett & Hopkins 1989). Factors selecting for the dimorphism of their bilaterally asymmetrical structures (Ferrari 1984) are unknown.

A new species, *P. johnsoni*, is described here and compared to *P. robusta* (Dahl 1893) from the Atlantic Ocean, *P. antarctica* new rank, a previously described form (Steuer 1931) of *P. robusta* from the Southern Ocean, and *P. scutullata* Brodsky, 1950 from the Gulf of Alaska. Neotypes are assigned for the older two species. *P. johnsoni* is the second species, along with *P. indica*, whose dimorphism for bilaterally asymmetrical structures is expressed in both females and males. This brings to eleven the number of species in the genus.

Materials and Methods

Location and other collecting data for samples from which specimens were removed for morphological analysis are listed in Table 1. Specimens were cleared in 100% lactic acid, stained by adding a solution of chlorazol black E dissolved in 70.0% ethanol/30.0% water, and examined with bright-field optics or with differential interference optics. Drawings were made with a camera lucida.

Table 1. Sampling locations from which specimens were measured; Cr=cruise; St=station; Lat=latitude; Long=longitude; u=unknown or not applicable; depth in meters. Programs are: Deep-Sea E=German Deep-Sea Expedition; DeepDump=survey of Deep Water Dumpsite 106 (off Delaware); Eastropac=survey of the eastern tropical Pacific Ocean by the U.S. National Marine Fisheries Service; IPHC=survey of the Gulf of Alaska by the International Pacific Halibut Commission; Plankton E=Plankton Expedition of the Humboldt Foundation; USARP=U.S. Antarctic Research Program; Volcano 7=study of the oxygen minimum water in the vicinity of Volcano 7 Seamount.

Program	Vessel	Cr	St	Lat	Long	Date	Depth
Deep-Sea E	*VALDIVIA*	u	139	55°01'S	021°34'E	05/xi/1898	0–1500
DeepDump	*ALBATROSS IV*	1	1	38°46'N	072°47'W	11/v/1974	0–750
DeepDump	*OREGON II*	3	2m	37°01'N	074°08'W	20//ii/1975	0–200
Eastropac	*WASHINGTON*	75	15	14°28'N	119°03'W	21/ii/1968	0–221
Eastropac	*WASHINGTON*	75	18	12°24'N	118°57'W	21/ii/1968	0–212
IPHC	u	928	7C	58°55'N	147°22'W	21/i/1928	500–600
Plankton E	*NATIONAL*	u	015	60.3°N	27.0°W	23/vii/1889	0–540
Plankton E	*NATIONAL*	u	042	42.4°N	55.7°W	02/viii/1889	0–750
Plankton E	*NATIONAL*	u	180	01.1°N	16.4°W	06/ix/1889	0–350
Plankton E	*NATIONAL*	u	181	01.1°N	16.4·W	06/ix/1889	375–575
USARP	*ELTANIN*	05	306	60°09'S	070°08'W	02/xi/1962	0–757
USARP	*ELTANIN*	06	383	55°52'S	056°03'W	24/xii/1962	1693–1821
USARP	*ELTANIN*	33	2187	56°59'S	119°54'W	27/iv/1968	0–1829
USARP	*ELTANIN*	34	2239	60°10'S	144°58'E	16/vii/1968	50–100
Volcano 7	*ATLANTIS II*	u	M5N2	13°21.81'N	102°30.03'W	27/xi/1988	295–397
Volcano 7	*ATLANTIS II*	u	M7N3	13°26.05'N	102°31.55'W	27/xi/1988	694–795

Prosome and urosome are Pr and Ur, respectively. Thoracic and abdominal somites (Th and Ab) are numbered according to their appearence during development as interpreted from data of Hulsemann (1991). The first and oldest thoracic somite bears the maxilliped and is fused with the cephalon. The youngest is the seventh; among calanoids it is the only thoracic somite without an appendage. In adult calanoids the seventh is the first somite of the urosome, and in adult females it is fused to the second abdominal somite to form the genital complex. The first and oldest abdominal somite is the most posterior; it bears the caudal rami. The youngest is immediately anterior to the oldest, and the remaining abdominal somites anteriorly increase in age and decrease in numerical designation.

Cephalic appendages are abbreviated A1=antennule; A2=antenna; Mn=mandible; Mx1=maxillule; Mx2=maxilla. Appendages on thoracic somites are Mxp=maxilliped (thoracopod 1); P1–4=swimming legs (thoracopods 2–5); leg 5 (thoracopod 6) is not a swimming leg of *Pleuromamma*. The caudal ramus is CR. Designations of appendage segments generally follow Ferrari (1995); exceptions are the protopod of Mx1 which follows Boxshall (1985) and Mx2 whose four proximal endites associated with the praecoxa and coxa are designated endites 1–4. Ramal segments on thoracopods (Mxp, P1–4 and leg 5) are numbered by their appearence during development and not proximal-to-distal as is the usual case in copepod descriptions. On the Mxp the distal segment is the first endopodal segment, and the second endopodal segment is immediately proximal to the first. Third endopodal segment is immediately distal to the basis. The fourth endopodal segment is immediately distal to the third. The fifth endopodal segment is the middle segment.

The distal segment of a ramus of P1–4 and leg 5 (Figs 1H; 4A–E; 5E, F; 7E, L, K; 8H, I; 9D, I, J) is the first segment. The second segment is immediately distal to the basis and the third segment, the middle one, is immediately proximal to the distal (or first) segment. For a 3-segmented ramus, the proximal segment is the second segment, the middle segment is the third segment, and the distal segment is the first segment. The ramus of leg 5 is interpreted as an exopod based on the presence of medial and lateral setae on its distal segment at CV of *P. xiphias* (see Ferrari 1985). The ramus is 3-segmented in males but appears 2-segmented in females. However, the female distal segment is a complex, homologous to the middle and distal segments of the male. The long seta of female leg 5 is homologous to the medial seta of the middle segment of exopod of P1–4 because it is first present at CV. In males, the middle segment of the leg 5 located on the same side as the gonopore bears a distinct seta on its medial attenuation anteriorly and a complex thumb-like seta with dense setules on posterior face proximally. We have interpreted this latter seta as the medial seta of the segment because that seta in the female is transformed among the arietelloidean families Augaptilidae, Heterorhabdidae, Lucicutiidae, Metridinidae and Phyllopidae. In the text, the number of setae recorded for ramal segments of the thoracopods follows these schemes.

Articulating armament elements of appendage segments here are setae regardless of their position or degree of rigidity. Two setae and one aesthetasc on a segment of A1 are designated 2+1. Setules are epicuticular extensions of a seta; denticles are epicuticular extensions of an appendage segment; spinules are epicuticular extensions of a somite. Von Vaupel Klein's organ (Ferrari 1995) on P1 consists of the curved basal seta with setules, and denticles plus any pores on the anterior face of the endopod.

Terms for the female genital field are from Cuoc et al. (1997). There is an extensive set of pores (usually openings of secretory glands) on the body (Park & Mauchline 1994) and appendages of species of *Pleuromamma*. The positions of only a few of these pores are noted in locations close to significant morphological features of a somite or appendage. Species of

Pleuromamma also exhibit a distinctive bilateral asymmetry in a series of primary and secondary sex structures each of whose position, left or right, is linked to the position of all of the others on the body (Ferrari 1984). We locate this linked asymmetry by the position of the dark organ on Th2. The geniculate A1 of the adult male of *Pleuromamma* has a set of apparently rigid elements on segments near the geniculation: one element each on segment 12 (second segment proximal to the geniculation) and segment 13 (segment proximal to the geniculation), and two or three elements on segment 14 (distal to the geniculation). Ferrari & Benforado (1998) identify the first four elements as setae for *P. xiphias*; the fifth, if present on the distal corner of segment 14, is a segment attenuation.

Synonomy listings are restricted to citations of publications presenting original data about morphology.

Metridinidae Sars, 1902

Pleuromamma Giesbrecht, 1898

Giesbrecht proposed this name to replace *Pleuromma* Claus, 1863 in Giesbrecht & Schmeil (1898).

Type species

Diaptomus abdominalis (Lubbock, 1856)

Pleuromamma johnsoni new species

Specimens

Holotype (United States National Museum, USNM #279058) a dissected 3.1 mm left male; allotype (USNM #279059) a dissected 3.5mm left female; remaining paratypes (6 males, 28 females), some partly dissected, from *WASHINGTON* Cr. 75, Stn 15 at 14°28'N, 119°03'W (USNM #279073). Length statistics of specimens in Table 2. Specimens examined for asymmetry are found in Table 3.

CVI female

Pr (Fig. 1A): 5 segments; 1st a complex of 5 cephalic somites plus Th1; Th2–4 simple and articulated; Th5 articulated anteriorly and fused to Th6 posteriorly. Th2 with dark organ on

Table 2. Length data (mm) for *Pleuromamma johnsoni*. *n*=number of specimens; Mpr/ur=mean of ratio of prosome length to urosome length. Other column headings as for Table 1.

Vessel			Female				Male			
			Total length				Total length			
	Cr	St	*n*	mean	(range)	Mpr/ur	*n*	mean	(range)	Mpr/ur
Washington	75	15	10	3.6	(3.4–3.8)	2.9	4	3.0	(3.0–3.1)	2.3
Washington	75	18	5	3.6	(3.3–3.8)	2.7	4	3.1	(2.8–3.5)	2.4
Atlantis II		M5N3	10	3.6	(3.4–3.8)	2.9	10	2.8	(2.6–3.2)	2.4
Atlantis II		M7N3	4	3.8	(3.7–3.9)	2.4	5	3.2	(3.2–3.3)	2.4

Table 3. Numbers of left and right females and males of *Pleuromamma johnsoni* from selected samples. Frl=number of right/left females; Mrl=number of right/left males. Other column headings as for Table 1.

Program	Vessel	Cr	St	Lat	Long	Date	Depth	Frl	Mrl
Eastropac	*ARGO*	11	032	17°54'N	119°00'W	29/i/1967	0–207	41/22	2/9
Eastropac	*ARGO*	11	040	15°10'N	118°53'W	30/i/1967	0–212	54/27	0/27
Eastropac	*ARGO*	11	048	12°36'N	119°00'W	01/ii/1967	0–204	20/5	2/8
Eastropac	*ARGO*	11	060	08°53'N	119°00'W	02/ii/1967	0–204	1/0	0/0
Eastropac	*ARGO*	11	114	02°37'S	119°02'W	07/ii/1967	0–207	1/0	0/0
Eastropac	*ARGO*	11	306	12°04'N	126°00'W	27/ii/1967	0–207	9/4	1/0
Eastropac	*JORDAN*	60	014	16°30'N	118°42'W	22/xii/1967	0–213	12/7	0/12
Eastropac	*JORDAN*	60	022	13°38'N	118°53'W	23/xii/1967	0–211	24/18	2/5
Eastropac	*JORDAN*	60	030	10°53'N	118°50'W	24/xii/1967	0–204	2/0	0/0
Eastropac	*JORDAN*	60	287	11°09'N	097°48'W	27/i/1968	0–204	2/0	0/1
Eastropac	*JORDAN*	60	295	14°22'N	097°51'W	28//i//1968	0–159	11/2	0/2
Eastropac	*WASHINGTON*	75	15	14°28'N	119°03'W	21/ii/1968	0–221	20/8	0/4
Eastropac	*WASHINGTON*	75	18	12°24'N	118°57'W	21/ii/1968	0–212	5/2	0/2
Volcano 7	*ATLANTIS II*		M5N2	13°21.81'N	102°30.03'W	27/xi/1988	295–397	137/74	0/29
Volcano 7	*ATLANTIS II*		M9N3	13°42.35'N	102°27.94'W	28/xi/1988	146–1136	2/2	0/5

right or left side; dark organ (Fig. 2A) anteriorly and posteriorly pointed, dorsally and ventrally rounded. Rostral area (Fig. 1E, F), including 2 paired anterior spinules, set off from rest of head by a groove; rostrum comprises a pair of ventrally-pointing, non-articulating attenuations of the cephalon with spinules. Dorsal to rostral area a large anterior pore bounded by slightly asymmetrical lateral extensions of a dorsal knob; a pair of pores dorsal to the knob and 3 pairs lateral to the rostral area. A large, cuticular ridge separates area of articulation of A1 from remainder of cephalic region. Labrum and paragnaths (Fig. 1G).

Ur (Fig. 1B): 3 segments; anterior segment a genital complex of Th7 and Ab2; genital complex symmetrical, as viewed ventrally (Fig. 1C). Viewed laterally (Fig. 1D), ventral edge of complex projects anteriorly and tapers smoothly posteriorly; copulatory pore located about half the distance between anterior and posterior edge of genital complex. Gonopores ventral and anterior; ventral branch of seminal duct leading to the area of left opening on right females, and to the right opening on left females. Posterior lobes of seminal receptacle extend laterally. Posterior corners of Ab1 attenuate with 3 pores at each corner and column of spinules lateral and ventral to attenuate corner.

A1 (Fig. 2B–E): 23 articulating segments (one poorly expressed arthrodial membrane within the seventh segment) with 7+3, 2+1, 2+1, 2+1, 2+1, 2+1, 6+3, 2+1, 2+1, 2+1, 2+1, 2+1, 2+1, 2+1, 2+1, 2+1, 1, 1, 2, 2+1, 2, 4+3 setae+aesthetascs. Articulating segments 1 and 2 on a few specimens with a small attenuation proximal to last seta+aesthetasc combination

A2 (Fig. 3A): coxa with 1 seta on a well developed lobe; basis with 2 setae. Re 8-segmented with 1, 1, 1, 1, 1, 1, 1, 4 setae. Ri 2-segmented with 2, 16 (7 terminal, 9 subterminal) setae.

Mn (Fig. 3B, C): coxa as illustrated; basis with 4 setae. Re 5-segmented (arthrodial membranes separating segments not developed posteriorly) with 1, 1, 1, 1, 2 setae. Ri 2-segmented with 4, 10 setae.

Mx1 (Fig. 2F): praecoxal endite with 11 apical, 1 anterior and 4 posterior setae. Coxal epipodite with 9 setae and endite with 5 setae. Basal exite with 1 seta; proximal endite with 4

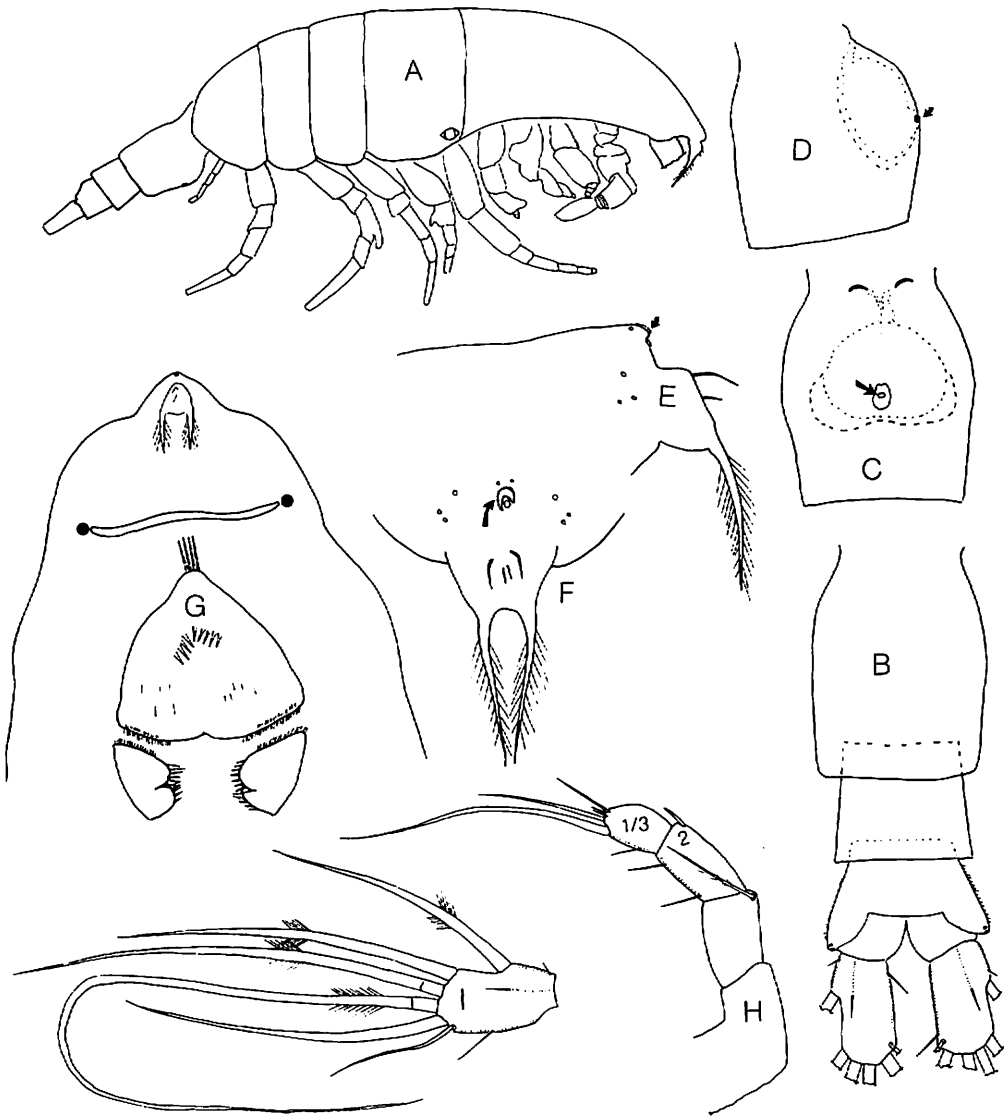


Fig. 1. *Pleuromamma johnsoni*, new species. Female. **A.** Right lateral. **B.** Ur dorsal. **C.** Genital complex ventral (*arrow* to copulatory pore). **D.** Genital complex right lateral (*arrow* to copulatory pore). **E.** Rostral area right lateral (*arrow* to dorsal knob). **F.** Rostral area anterior (*arrow* to dorsal knob). **G.** Labrum with paragnaths (cuticular ridge between *circles*). **H.** Leg 5. **I.** CR. Ramal segments of thoracopods numbered.

setae and distal endite with 5 setae. Ri 1-segmented with sets of 6 and 6 medial, and 5 terminal setae. Re 1-segmented with 11 setae.

Mx2 (Fig. 3D–F): endites 1–4 of praecoxa plus coxa with 10 (5 medial and 5 proximal), 3, 3 and 3 setae; endites of basis with 4 and 4 setae respectively. Re indistinctly segmented with 7 setae.

Mxp (Fig. 2G–H): praecoxa with 3 lobes of 1, 2, 4 setae. Coxal lobe with 4 setae and anterior denticles; coxal epipodite with 1 seta. Basis with 5 setae (2 on a distal medial lobe which is weakly sclerotized where it joins body of segment) and anterior denticles. Ri 5-segmented

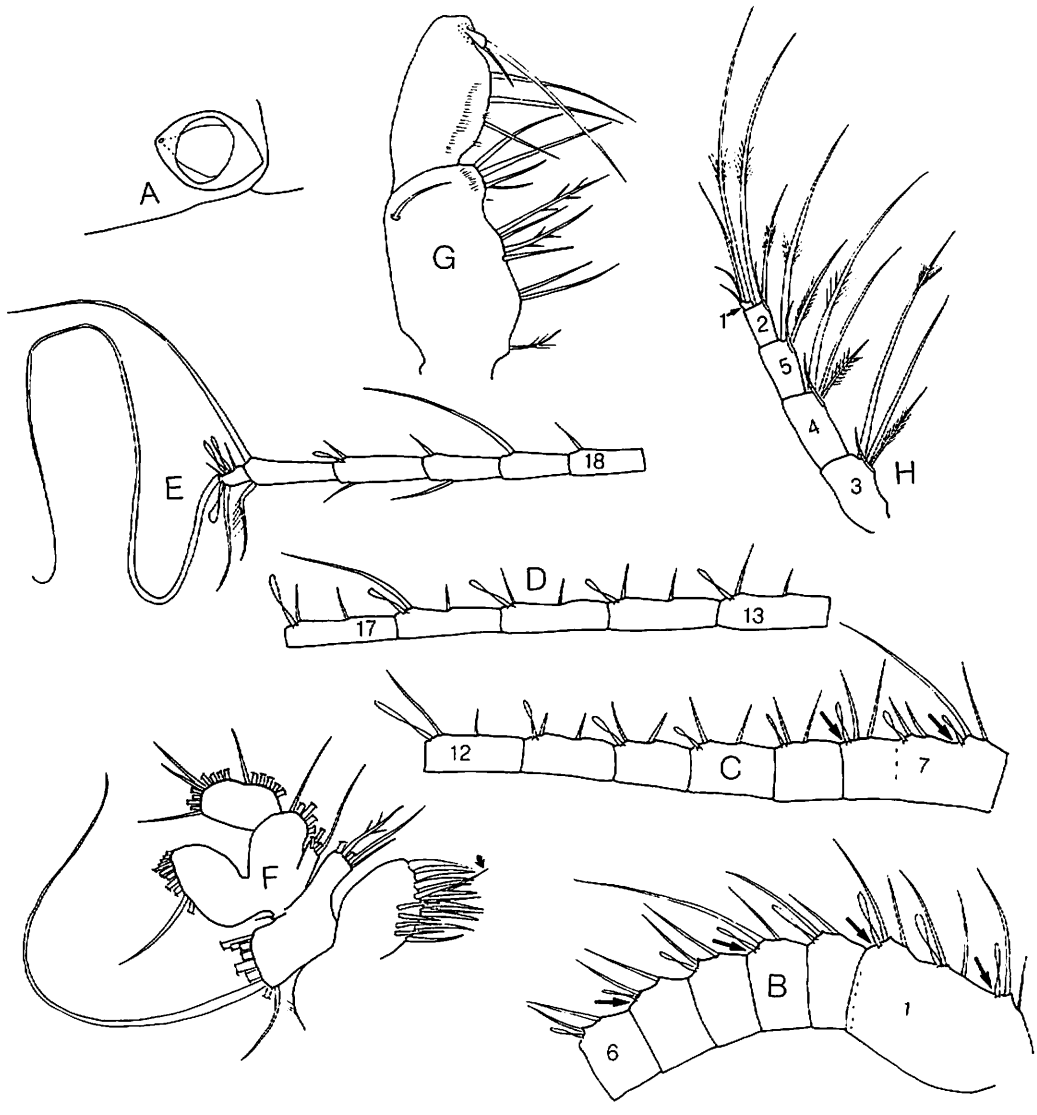


Fig. 2. *Pleuromamma johnsoni*, new species. Female. **A.** Dark organ. **B.** A1 articulating segments 1–6 (*arrows* to location of extra setae on male left A1). **C.** A1 articulating segments 7–12 (*arrows* to location of extra setae on male left A1). **D.** A1 articulating segments 13–17. **E.** A1 articulating segments 18–23. **F.** Mx1 posterior (setules not drawn; *arrow* to anterior seta). **G.** Mxp sycoxa & basis. **H.** Mxp Ri. Ramal segments of thoracopods numbered.

with 4, 3, 4, 4, 3 setae; proximal seta of Ri 2-5 short, slightly curved and pointed anteriorly.

P1 (Fig. 4A, B): coxa with medial seta and medial denticles. Basis with lateral seta, medial seta and medial denticles; lateral region of posterior face drawn out into a distally curved point. Re 3-segmented with 7 (4 medial, 1 terminal, 2 lateral), 2 (medial and lateral), 2 (medial and lateral) setae. Ri 3-segmented with 5 (2 medial, 2 terminal, 1 lateral), 1 (medial) and 2 (medial) setae. Von Vaupel Klein's organ with a row of long, thin denticles near distal anterior edge of Ri2 plus long curved medial seta of the basis.

P2 (Fig. 4C): coxa with medial seta. Basis unarmed. Re 3-segmented with 8 (5 medial, 1 terminal, 3 lateral), 2 (medial and lateral), 2 (medial and lateral) setae; anterior face of Re2

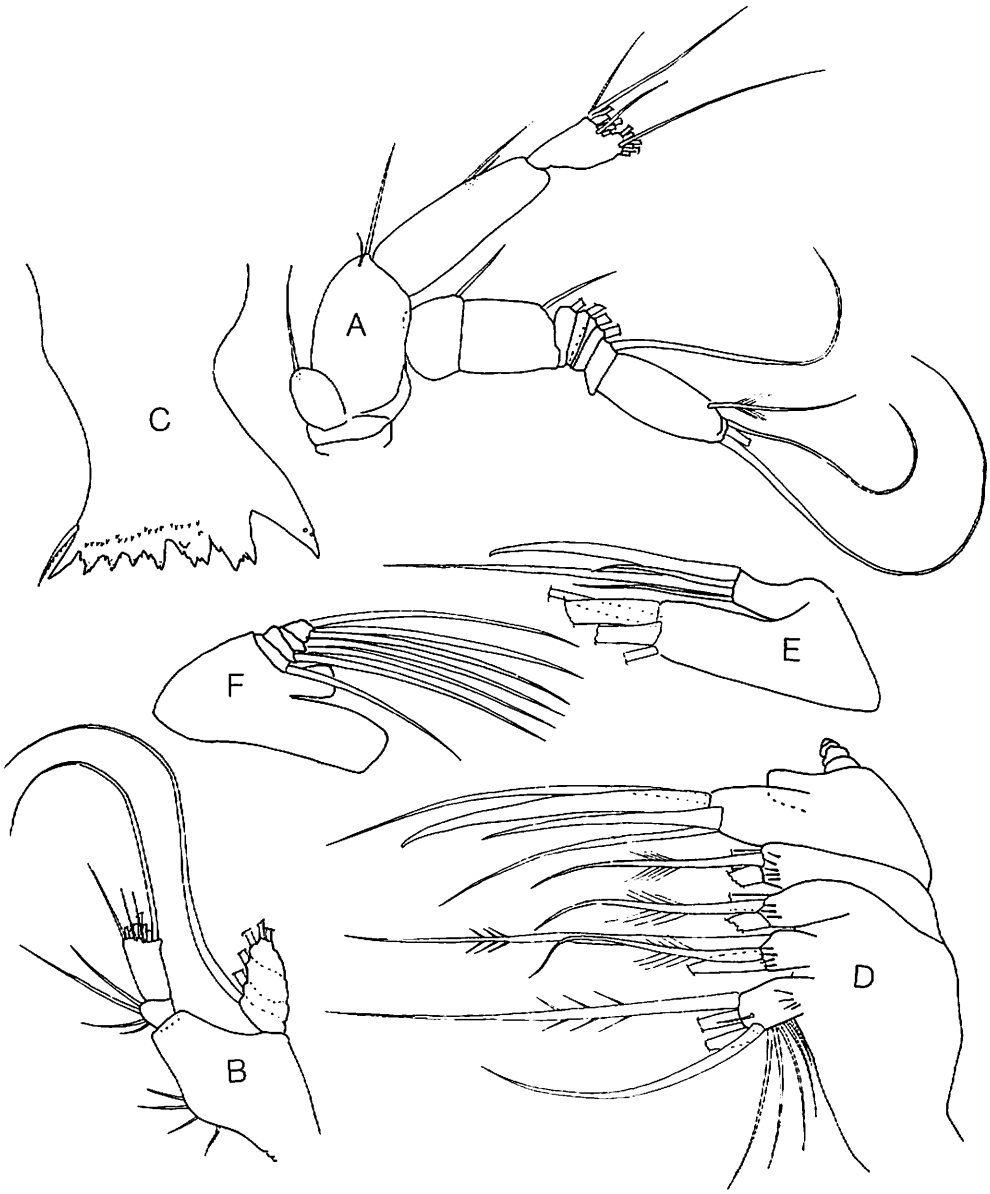


Fig. 3. *Pleuromamma johnsoni*, new species. Female. **A.** A2. **B.** Mn palp. **C.** Mn gnathobase. **D.** Mx 2 first five endites posterior (including proximal basal endite). **E.** Mx 2 basal endites posterior. **F.** Mx 2 distal basal endite+Re anterior.

near proximal/medial edge with a column of epicuticular bumps. Ri 3-segmented with 8 (4 medial, 2 terminal, 2 lateral), 0, 2 (medial) setae; anterior face of Ri2 with a large attenuation facing paired small attenuations proximally and 2 distal-medial attenuations (large distal-medial attenuation marks base of medial seta present in early copepodids).

P3 (Fig. 4D): coxa with medial seta. Basis unarmed. Re 3-segmented with 9 (5 medial, 1 terminal, 3 lateral), 2 (medial and lateral), 2 (medial and lateral) setae; lateral seta of Re2 on a thumb-like projection of the segment. Ri 3-segmented with 8 (4 medial, 2 terminal, 2 lateral), 1 (medial), 2 (medial) setae.

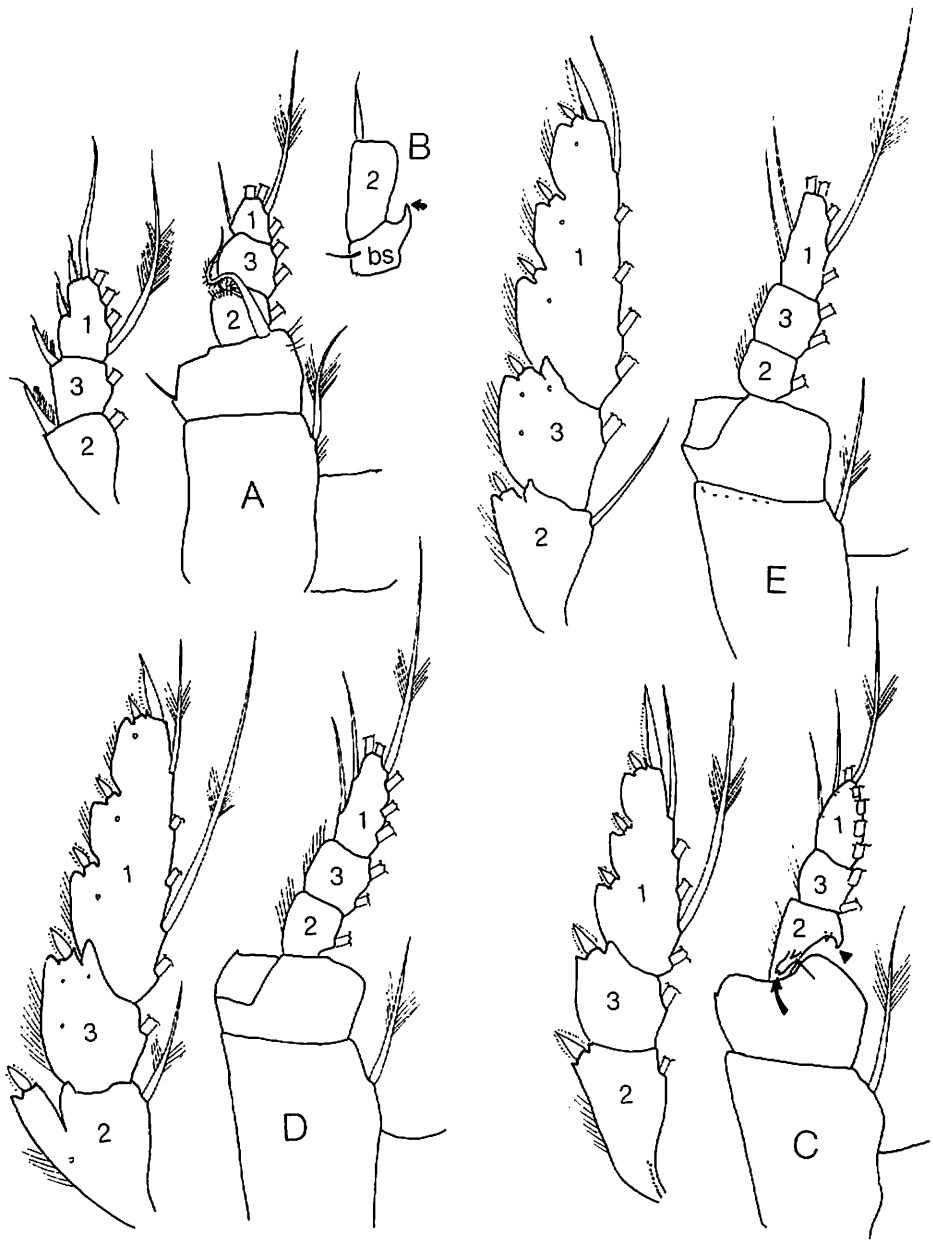


Fig. 4. *Pleuromamma johnsoni*, new species. Female. **A.** P1 anterior; exopod detached to left. **B.** P1 basis+Re2 lateral (*arrow* to posterior attenuation of basis). **C.** P2 anterior; exopod detached to left (*curved arrow* to proximal paired small attenuations; *long arrow* to proximal large attenuation; *arrowhead* to medial attenuation bearing setae at CII). **D.** P3 posterior; exopod detached to left. **E.** P4 posterior; exopod detached to left. Ramal segments of thoracopods numbered.

P4 (Fig. 4E): coxa with medial seta. Basis unarmed. Re 3-segmented with 9 (5 medial, 1 terminal, 3 lateral), 2 (medial and lateral), 2 (medial and lateral) setae. Ri 3-segmented with 7 (3 medial, 2 terminal, 2 lateral), 1 (medial), 2 (medial) setae.

Leg 5 (Fig. 1H): coxa unarmed. Basis with thin, lateral seta reaching to distal edge of Re2. Re with 2 articulating segments; proximal segment (homologous to segment 2 of male) with

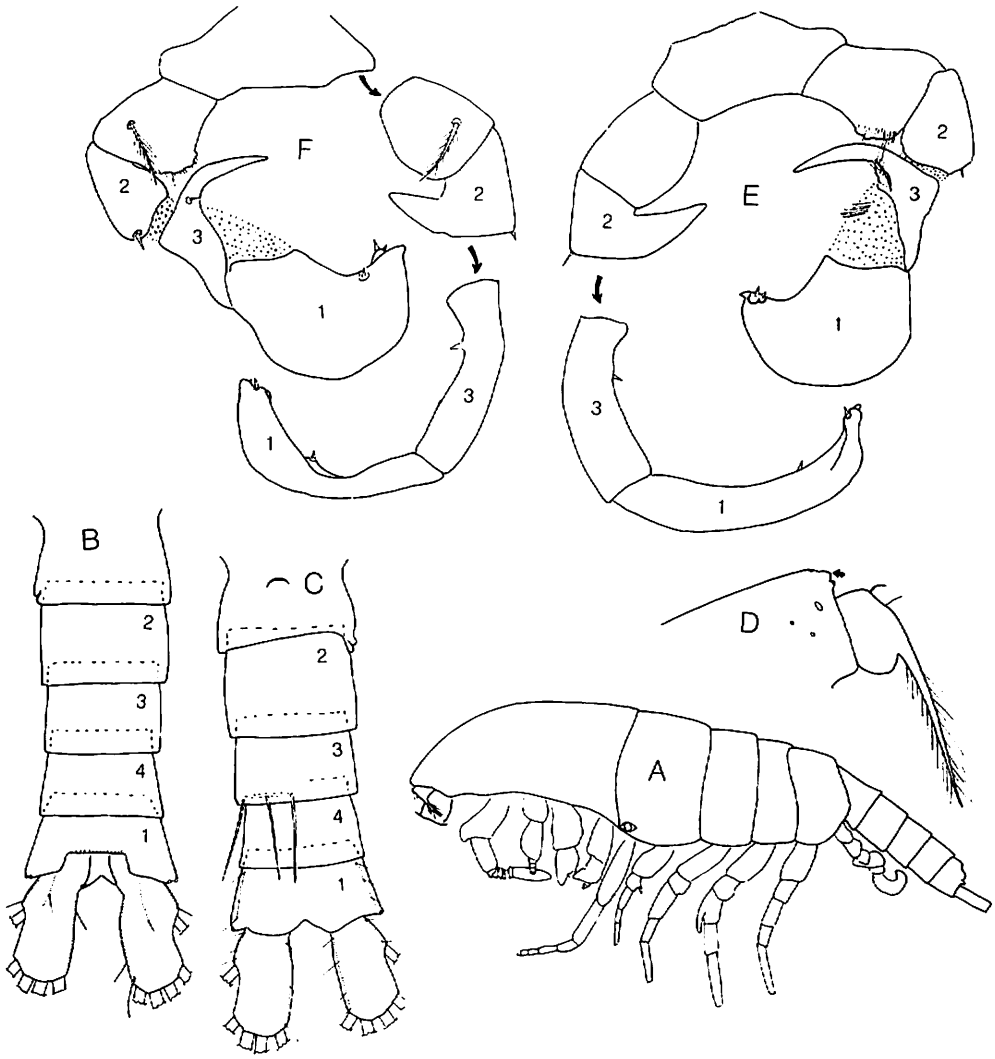


Fig. 5. *Pleuromamma johnsoni*, new species. Male. **A.** Left lateral. **B.** Ur dorsal. **C.** Ur ventral. **D.** Rostral area (arrow to dorsal knob). **E.** Leg 5 anterior (*arrow* connects right coxa to basis and Re2 to Re3). **F.** Leg 5 posterior (*arrows* connect right Re2 to Re3). Abdominal somites and ramal segments of thoracopods numbered.

lateral seta and medial denticles; distal segment a complex of segments 1 and 3 with the elongate seta of segment 3 plus 4 setae of segment 1 and medial denticles; terminal pore near 2 terminal setae.

CR (Fig. 1I): 1 lateral and 4 apical setae thick; dorsal seta thin; denticle row on medial edge of ramus; a second denticle row toward lateral edge, proximal to the lateral seta; a third row on dorsal surface.

CVI male

Differs from CVI female as follows:

Pr (Fig. 5A): rostral area (Fig. 5D) articulating with rest of cephalon; a single pore dorsal to the dorsal knob. The following description applies to males with the dark organ on left side

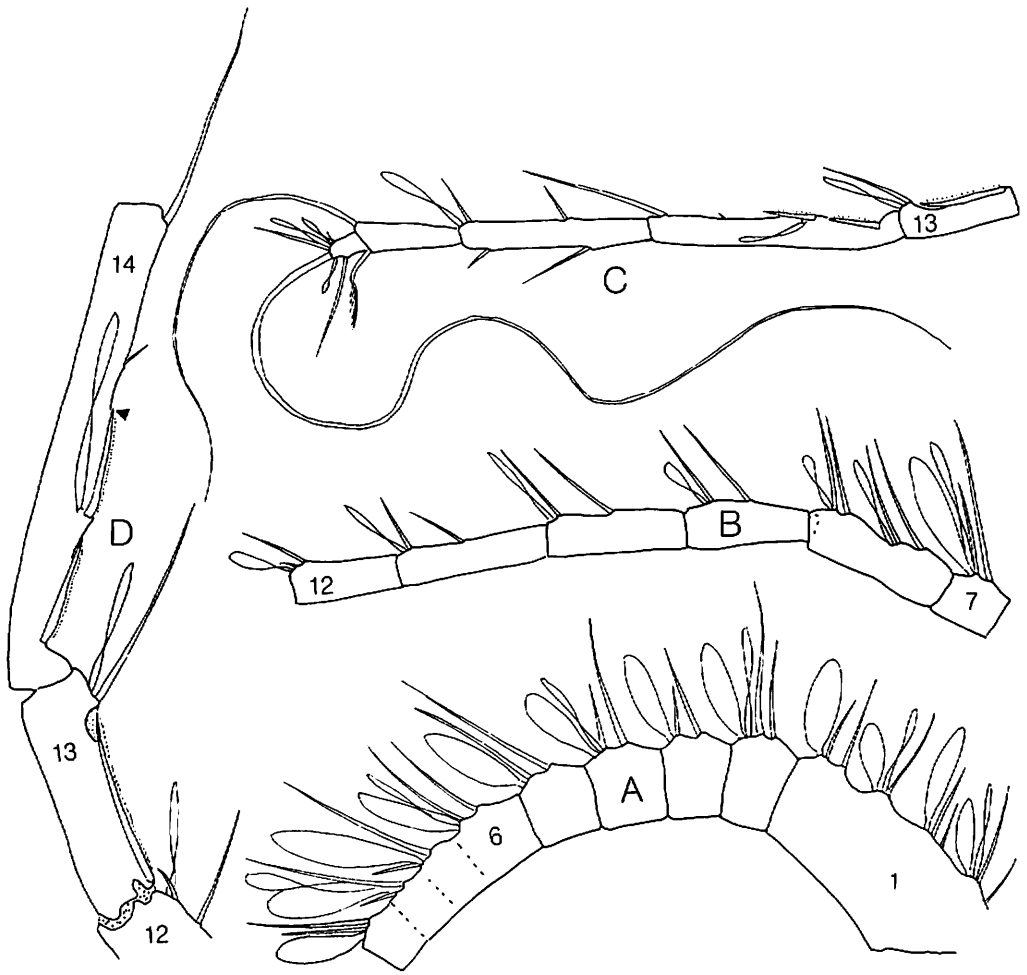


Fig. 6. *Pleuromamma johnsoni*, new species. Male. **A.** Right A1 articulating segments 1–6. **B.** Right A1 articulating segments 7–12. **C.** Right A1 articulating segments 13–17. **D.** Right A1 articulating segments 13–14 (*arrowhead* to tip of distal rigid seta).

only; this morph is the most common.

Ur (Fig. 5B, C): 5 somites; Th7 with left lateral gonopore. Ab3 with row of spinules ventral and posterior on the right side.

Left A1: with 2 extra aesthetascs on the 1st articulating segment, 1 on the 3rd, 1 on 5th, and 2 on 7th (location indicated on Fig. 2B of female).

Right (Fig. 6A–D) 17 articulated segments (4 poorly expressed arthrodial membranes within the sixth segment) with: 7+6, 2+2, 2+1, 2+2, 2+1, 8+6, 2+2, 4+2, 2+1, 2+1, 2+1, 2+1, 2+1, 4+1, 4+1, 2, 4+3 setae+aesthetascs; geniculation between 13th and 14th articulated segments; rigid seta on segment 12 short thick and slightly curved; no distal attenuation of 14th segment.

Leg 5 (Fig. 5E, F): left coxa unarmed and fused with coupler. Basis with lateral seta and an area of numerous denticles on the medial distal corner. Re 3-segmented with 3, 1, 2 setae; Re2 (proximal segment) relatively simple; Re3 (middle segment) with a long, pointed, medial attenuation, smoothly curved and directed distally; Re1 (distal segment) helmet-shaped with a

small knob distally near 3 terminal setae. Arthrodial membrane medially between distal and middle segment extensively developed with columns of denticles distal to the medial seta. Right coxa unarmed; fused with coupler. Basis with a seta. Re 3-segmented with 3, 1, 1 setae. Re2 (proximal) with a medial triangular attenuation; Re3 (middle) and Re1 (distal) spatulate and curved; Re1 with a small knob distally in area of 3 setae.

Etymology

The name recognizes the many contributions of Martin Wiggo Johnson to systematics and biogeography of Pacific Ocean copepods.

Remarks

In both sexes of *P. johnsoni*, (1) there is an asymmetrical knob dorsal to rostral area which is absent in *P. robusta*, *P. antarctica* and *P. scutullata*, (2) the dark organ is pointed anteriorly and posteriorly (these edges are rounded in the other three species), and (3) the ratio of prosome to urosome is slightly greater than the other species (females: 2.3–2.4 vs 1.8–2.0 for *P. robusta*, *P. antarctica* and *P. scutullata*; males 2.4–2.9 vs 2.0–2.3 for *P. robusta* and 1.6–2.2 for *P. antarctica* and *P. scutullata*). Females of *P. johnsoni* differ from *P. robusta* and *P. antarctica*: (1) in the position of the copulatory pore which is located about half the distance between anterior and posterior edge of genital complex (at the anterior third in the two older species); (2) the presence of medial and lateral denticles in the distal segment complex of leg 5; (3) the absence of asymmetrical spinules on Ab1; and (4) symmetrical denticulation on CR. Males of *P. johnsoni*: (1) lack a distal attenuation on the 14th segment of the geniculate A1 (a unique feature for males of *Pleuromamma*); (2) lack an indentation on the medial attenuation of the middle exopodal segment of left leg 5 (both of these structures are present on the homologous appendages of *P. robusta* and *P. antarctica*); and (3) have a unique pattern of spinulation restricted to the ventral face of Ab3 (compare Fig. 5C with Figs 7G, 8F, 9F).

Males and females from the Volcano 7 area have poorly developed musculature when compared to specimens from other localities. This is most easily described by comparing the promotor and remotor muscles of the distal exopodal segment of the left leg 5 of males (the promotor is broader than the remotor). In Eastropac specimens these two muscles together fill the entire distal segment proximal to the area of the terminal setae. In Volcano 7 specimens, these muscles are thin straps which are easily seen within the segment. The exoskeleton of specimens from Volcano 7 also appears thinner; spinules on the abdominal segments and denticles on the caudal ramus usually are broken and the scars which mark their origin are difficult to see.

The ecology of *P. johnsoni* in the vicinity of Volcano 7 was discussed (as *P. robusta*) by Saltzman & Wishner (1997). Its geographical distribution is sketchily known; usually it is found in samples from 11° to 14°N and 97° to 126°W. In Eastropac samples taken at night between 2100 and 0300 h to about 200 m from 17°54′N to 20°00′S along 119°00′W, *P. johnsoni* is present in three stations north of 12°36′N (in Table 3, *ARGO* Cr. 11, Stns 32–48) and absent from eleven stations south of 06°05′N. Along 126°00′W it was present only at 12°04′N, and absent from two stations to the north and eight others to the south. Samples taken by the *WASHINGTON* and *JORDAN* with the same protocol, and *ATLANTIS II* suggests a distribution between 11° and 14°N east to 97°48′W. *P. johnsoni* was not present in five samples farther north off the southern California basin system (about 33°N, 118°W) or in eight oceanic samples from the Gulf of Alaska. Farther west, it was absent from 31 trawl samples south of Hawaii from 21°N to 14°S between 150° and 160°W.

Table 4. Length data (mm) for *Pleuromamma robusta*. Column headings as for Table 2.

Vessel	Cr	St	Female				Male			
			Total length				Total length			
			n	mean	(range)	Mpr/ur	*n*	mean	(range)	Mpr/ur
Albatross IV	1	1	3	4.1	(4.0–4.1)	2.2	15	3.6	(3.4–3.8)	1.9
Oregon II	3	2m	10	3.6	(3.5–3.7)	2.3	9	3.0	(2.9–3.1)	1.9
National		15	10	3.9	(3.7–4.0)	2.2	5	3.5	(3.4–3.7)	1.8
National		42	8	4.0	(3.7–4.1)	2.1	8	3.4	(3.2–3.6)	1.8
National		180	10	3.2	(3.0–3.5)	2.0	1	3.4		1.8
National		181	2	3.0	(2.7–3.0)	2.0	4	2.9	(2.8–3.0)	1.8

Two asymmetric morphs are found among both females and males of *P. johnsoni*. Among 507 females listed in Table 3, 33% were left, a percentage comparable to *P. xiphias* (Ferrari 1985; Ferrari & Hayek 1990) and presumed for *P. abdominalis* (based on data of Ferrari 1984). Among 105 males listed in Table 3, only 7% were right, although these seven right males comprised 24% of the 29 males from three samples in which right males were found. While the percentage of right males is low, it probably is the result of selection rather than recurrent mutation or a recurrent recombination of rare alleles. Occurrences of one right male for every 500–1000 left males of *P. xiphias*, a species which exhibits a female sex-limited dimorphism in effect, may be the result of a recurrent rate of mutation to the genetic system controlling asymmetry or of a recombination of rare alleles to the same effect, but not of selection. *P. indica* is the only other species of the genus expressing dimorphic asymmetry in both sexes; in the Red Sea about 48% of the adults are right for both sexes, but this percentage drops precipitously to 8% right in the Gulf of Aden and northern Arabian Sea (unpublished observations of Beckmann et al. in Monoculus no. 29: p. 6–8). *P. robusta*, *P. antarctica* and *P. scutullata* do not express a dimorphism in asymmetry; both sexes of these species are right animals.

Pleuromamma robusta (Dahl, 1893)

Pleuromma robustum Dahl, 1893, p. 105–106.

Pleuromamma robusta Sars, 1902, p. 115, pls. 78, 79.

Pleuromamma robusta forma *typica* Steuer,1931, p. 7–8, Fig. 2a.—Steuer, 1932, p. 20–24, Textfigs 69–79, 81–87.

? *Pleuromamma robusta* Wolfenden, 1905, p. 1011, Pl. 96, Figs 34, 35, 36.—Wilson, 1932, p. 26, Fig. 84.—Mori, 1937, p. 70, Pl. 35, Figs 8–10.—Bradford, 1972, p. 44–46, Figs. 4–7.—Björnberg, 1981, p. 642, Figs. 214–219.

Specimens

Neotype (Zoologisches Museum Berlin, ZMB #27238) a 3.4 mm right male, *NATIONAL* St 42. Measurements of other specimens are found in Table 4.

CVI female

Differs from CVI female of *P. johnsoni* as follows:

Pr: without knob dorsal to rostral area. Th2 with dark organ on right side; dark organ (Fig.

Fig. 7. *Pleuromamma robusta* (Dahl, 1893). Female. **A.** Genital complex ventral. **B.** Genital complex right lateral. **C.** Dark organ. **D.** A1 articulating segments 1–2 (*arrows* to segmental attenuations). **E.** Leg 5. Male. **F.** Rostral area. **G.** Ab1–3+CR ventral. **H.** Ab2–3 dorsal. **I.** Ab1 dorsal (*arrow* to set of spinules to left of anal flap). **J.** Left A1 articulating segments 13–14 (*arrowhead* to tip of distal rigid seta; *arrow* to axial angle of segment attenuation). **K.** Leg 5 anterior (*open arrow* connects left coxa and basis; arthrodial membranes and poorly sclerotized areas stippled; *curved arrow* to angled proximal face of attenuation of left Re3; *straight arrow* to twisted attenuation of right Re2). **L.** Leg 5 posterior (arthrodial membranes and poorly sclerotized areas stippled). Abdominal somites and ramal segments of thoracopods numbered.

7C) rounded anteriorly and posteriorly.

Ur: viewed laterally, projection of ventral edge of genital complex (Fig. 7B) more pronounced anteriorly; copulatory pore located at anterior third of the distance between anterior and posterior edge of complex. Ab1 with area of spinules slightly left and anterior of anal flap (as for Fig. 7I of male).

A1: articulating segments 1 and 2 (Fig. 7D) often with a small attenuation proximal to last seta+aesthetasc combination.

Leg 5 (Fig. 7E): Re2 (proximal) with a thick lateral seta, and medial and lateral denticles; Re 1+3 (distal complex) with medial and lateral denticles.

CR: denticle row missing from dorsal surface of right ramus (as for Fig. 7I of male).

CVI male

Differs from CVI male of *P. johnsoni* as follows:

Pr: without knob dorsal to rostral area (Fig. 7F). Th2 with dark organ on right side; dark organ rounded anteriorly and posteriorly.

Ur: Th7 with right lateral gonopore. Ab1 (Fig. 7I) with area of spinules slightly left and anterior of anal flap. Ab2 (Fig. 7H) dorsally with a column of spinules along the posterior half of the middle of the somite. Ab3 (Fig. 7G, H) ventrally with a large area of spinules posteriorly on right side and a column of spinules posteriorly on left side; dorsally a column of spinules along the posterior half of the middle of the somite.

Left A1: homologous to right A1 of *P. johnsoni*: rigid seta on segment 12 short, thin and straight; tip of distal rigid seta of segment 14 (originating toward the middle of the segment) reaches the axial angle of distal attenuation of the segment (Fig. 7J). Unlike female, there are no attenuations on the first or second articulating segments which are fused on this A1, but which retain an arthrodial membrane between the two segments on the right A1.

Leg 5 (Fig. 7K, L): left (homologous to right of *P. johnsoni*) Re2 (proximal) with medial triangular attenuation twisted at its tip. Right (homologous to left of *P. johnsoni*) basis with lateral row of long denticles on posterior face beginning proximal to the seta. Re3 (middle) medial attenuation distinctly angular on proximal surface; tip of attenuation not reaching middle of distal segment; Re1 (distal) with well sclerotized area anterior and proximal to 3 setae.

CR: denticle row missing from dorsal surface of right ramus.

Remarks

The distribution of *P. robusta* in the Atlantic Ocean based on Plankton Expedition samples was discussed by Dahl (1893) and Pisek (1923), and expanded by Steuer (1932) who included information from *VALDIVIA* samples. Based on our re-examination of specimens from the Plankton Expedition, we confirm its distribution throughout the North Atlantic; it seldom is found above 500m in tropical regions but may occur to the upper 100m in boreal areas. We have not examined specimens attributed to *P. robusta* from other localities.

***Pleuromamma antarctica* Steuer, 1931 new rank**

Pleuromamma robusta forma *antarctica* Steuer, 1931, p. 8, Fig. 2b.—Steuer, 1932, p. 24–25, Textfigs 80, 88, 89.—Vervoort, 1951, p. 123–126, Figs 68, 69.

Specimens

Neotype (Zoologisches Museum Berlin, ZMB #27239) a 3.3 mm right male, *VALDIVIA* Stn

Table 5. Length data (mm) for *Pleuromamma antarctica*. Column headings as for Table 2.

Vessel			Female				Male			
			Total length				Total length			
	Cr	St	*n*	mean	(range)	Mpr/ur	*n*	mean	(range)	Mpr/ur
Valdivia		139	17	4.3	(3.9–4.5)	2.0	12	3.4	(3.2–3.6)	1.7
Eltanin	5	306	9	4.0	(3.9–4.2)	2.2	10	3.2	(3.1–3.3)	1.8
Eltanin	6	383	10	4.0	(3.9–4.1)	2.2	6	3.0	(2.9–3.1)	1.9
Eltanin	33	2187	10	4.2	(4.0–4.4)	2.2	8	3.4	(3.3–3.6)	1.9
Eltanin	34	2239	7	4.1	(3.9–4.2)	2.2	4	3.4	(3.3–3.5)	1.9

139. Measurements of other specimens are found in Table 5.

CVI female

Differs from CVI female of *P. robusta* as follows:

Ur: viewed laterally, distinct projection of ventral edge of genital complex posteriorly (Fig. 8A) not as pronounced as anterior projection.

A1: without small attenuate points on articulating segments 1 and 2.

CVI male

Differs from CVI male of *P. robusta* as follows:

Pr (Fig. 8D): cephalon less vaulted dorsal to rostral area.

Ur: Ab2 ventrally (Fig. 8F) with small areas of spinules posteriorly on left and right side. Ab3 dorsally (Fig. 8E) an area of spinules along the posterior half of the middle of the somite; ventrally (Fig. 8F) with small areas of spinules posterior on right side and left side.

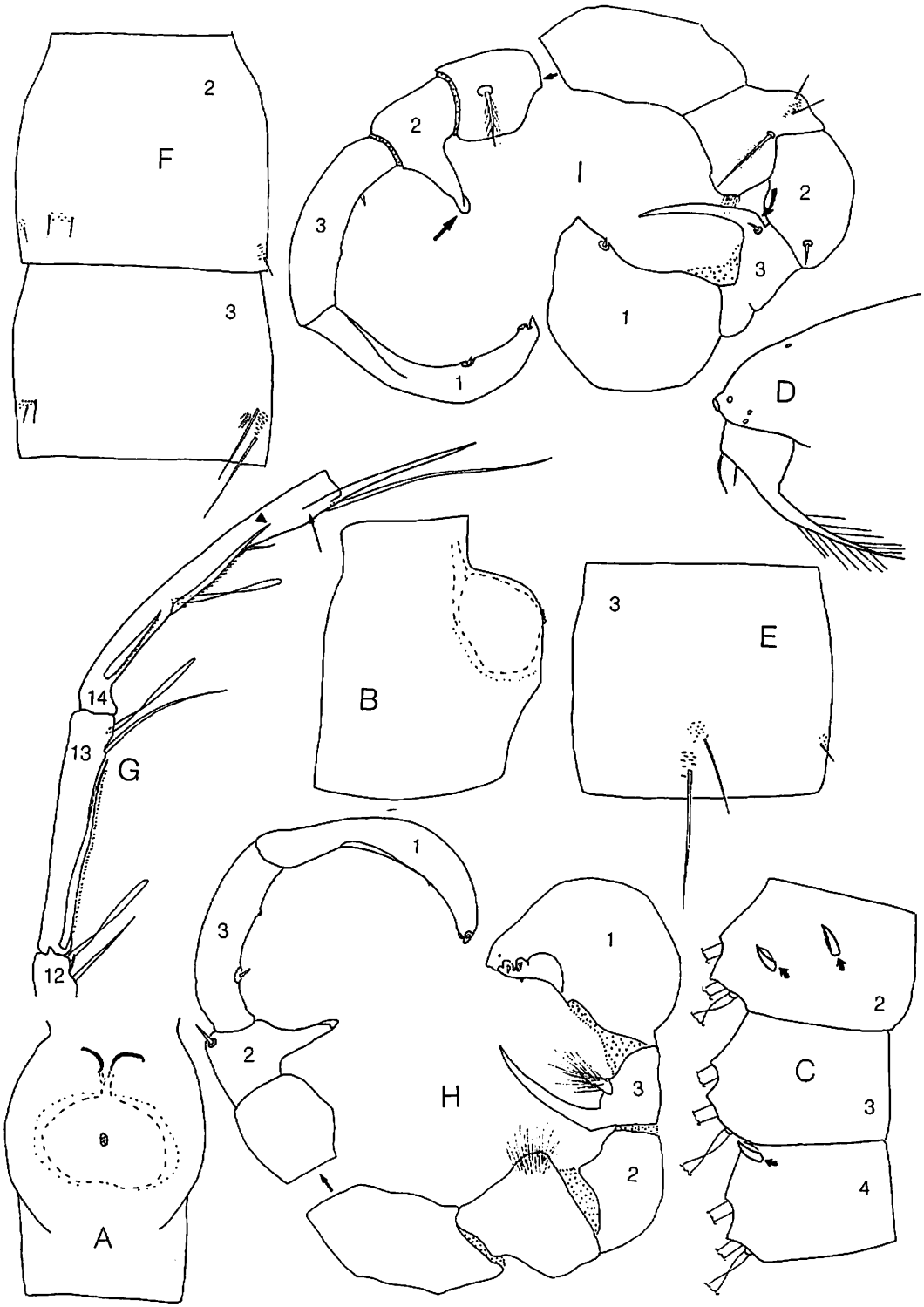
Left A1 (Fig. 8G): tip of distal rigid seta of segment 14 does not reach to axial angle of distal attenuation of the segment.

Leg 5 (Fig. 8H, I): right basis with lateral area of long denticles on posterior face beginning lateral to seta. Re3 (middle) tip of medial attenuation reaches beyond middle of distal segment.

Remarks

Steuer (1931, 1932) initially distinguished a Southern Ocean form of *P. robusta* from the typical form based on larger size, reduction in the degree of spinulation on abdominal somites and absence of small attenuate points on articulating segments 1 and 2 of A1 of females from the Southern Ocean. We have not found female size or degree of spinulation on abdominal somites informative. Females of *P. antarctica* differ from *P. robusta* in the distinct projection

Fig. 8. *Pleuromamma antarctica* Steuer, 1931 new rank. **A.** Genital complex ventral. **B.** Genital complex right lateral. **C.** A1 articulating segments 2–4 (*arrows* to recurved hooks). Male. **D.** Rostral area left lateral. **E.** Ab3 dorsal. **F.** Ab2–3 ventral. **G.** Left A1 articulating segments 13–14 (*arrowhead* to tip of distal rigid seta; arrow to axial angle of segment attenuation). **H.** Leg 5 anterior (*short arrow* connects left coxa and basis; arthrodial membranes and poorly sclerotized areas stippled; *curved arrow* to angled proximal face of attenuation of left Re3; *straight arrow* to twisted attenuation of right Re1). **I.** Leg 5 posterior (*short arrow* connects left coxa and basis). Abdominal somites and thoracopod ramal segments numbered.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posteriorly of the ventral edge of the genital complex; in *P. robusta* the ventral edge posteriorly tapers smoothly. Males of *P. antarctica* differ from those of *P. robusta* as follows: (1) cephalon of *P. antarctica* dorsal to the rostal area not as vaulted as *P. robusta*; (2) the tip of the 2nd rigid setae on segment 14 of left A1 does not reach to the base of the axial angle of the distal attenuation of the segment (but reaches to the base of *P. robusta*); (3) tip of medial attenuation of Re3 of right leg 5 reaches beyond middle of distal segment (but does not reach to the middle of distal segment of *P. robusta*); (4) the more lateral location of the long denticles on right basis of leg 5; (5) unique pattern of spinulation on Ab1, 2, and 3 (compare Fig. 7G, H with Fig. 8E, F).

Proximal segments of A1 of males and females occassionally bear recurved hooks on the dorsal surface (Fig. 8C). The hooks, curved teeth of Steuer (1932), seldom occur on both A1, nor were they found consistently on one or more of the segments; their number and location on a segment also were variable. The dorsal position of the hooks does not correspond to the location of attachment points of setae, and the hooks do not appear to be segmental attenuations. Because the animals bearing the hooks were infested with several ciliophoran parasites, these hooks may be an indirect effect of the parasitism.

The distribution of *P. antarctica* is not well known. We have confirmed the identity of specimens from the western part of the Indian sector, the western part of the Atlantic sector and through most of the Pacific sector.

Pleuromamma scutullata Brodsky, 1950

Pleuromamma scutullata Brodsky, 1950, p. 312, Fig. 217 (in Brodskii 1950).—Vaupel Klein, 1970, p. 37, Fig. 14d.

Specimens

From IPHC cruise 928, station 7C: 6 females with mean length of 3.8 mm (range 3.7–3.9 mm) and mean ratio of prosome to urosome of 2.0; 10 males with mean length of 3.2 mm (range 3.0–3.3 mm) and mean ratio of prosome to urosome of 1.9.

CVI female

Differs from CVI female of *P. robusta* as follows:

Pr: posterior edge of Th1, laterally, thickened and rounded.

Ur: viewed laterally, anterior edge of genital complex (Fig. 9B) not as vaulted, with a low hump on ventral edge posteriorly; copulatory pore located about half the distance between anterior and posterior edge of genital complex.

A1: with pronounced attenuate points on articulating segments 1 and 2 (Fig. 9C).

Leg 5 (Fig. 9D): Re 1+3 (distal complex) without lateral denticles.

CVI male

Differs from CVI male of *P. robusta* as follows:

Ur: Ab2 (Fig. 9E–G) ventrally with a small area of spinules posteriorly on left side and laterally a small area on the right side. Ab3 (Fig. 9E–G) ventrally with small areas of spinules posteriorly on left side and laterally areas of denticles on right side.

Left A1: tip of distal rigid seta of segment 14 (Fig. 9H) does not reach to the base of a distal attenuation of the segment; distal attenuation bent at middle. Distinct attenuations on the first and second articulating segments which are fused on this A1, but which retain an arthro-

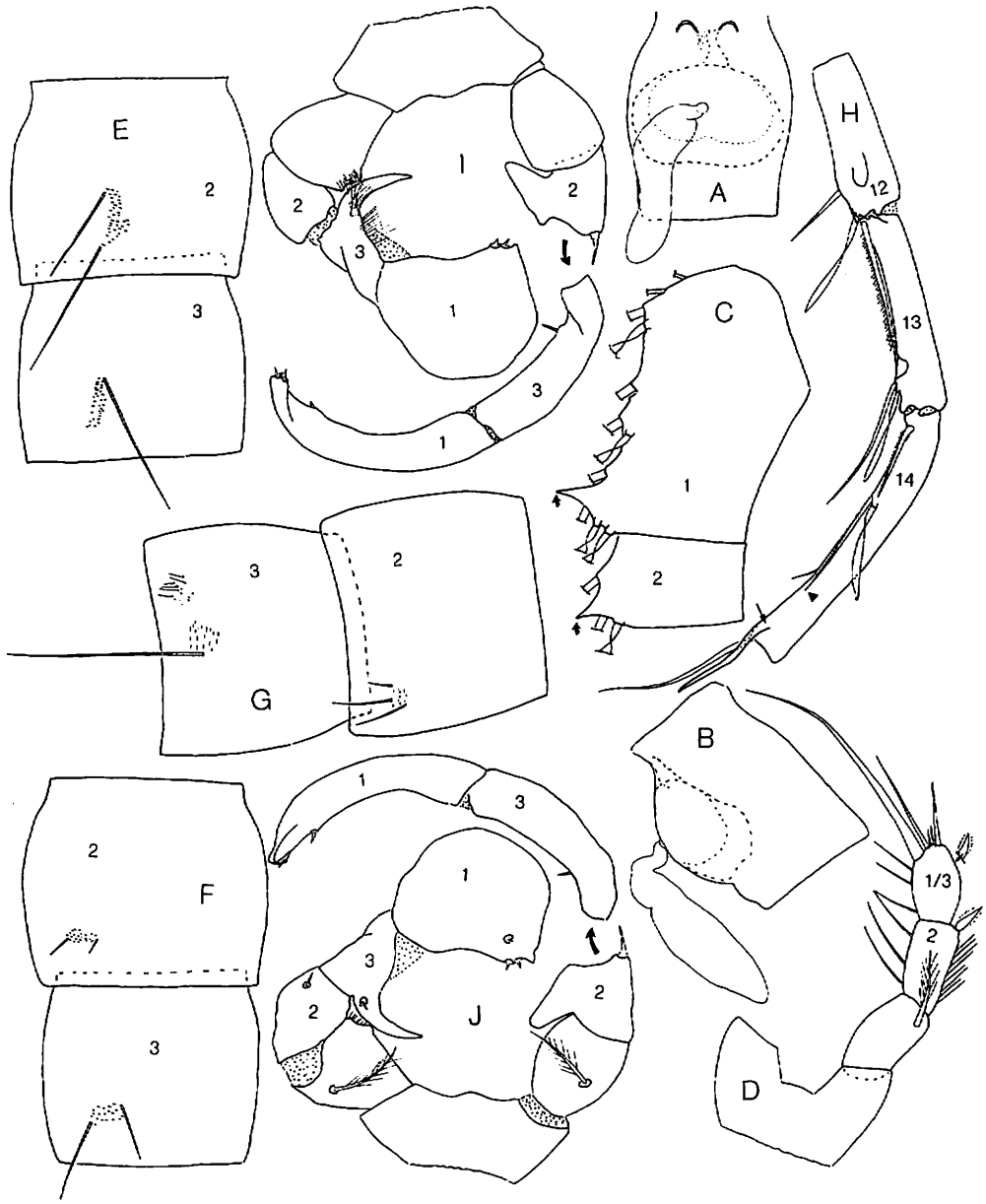

Fig. 9. *Pleuromamma scutullata* Brodsky, 1950. Female. **A.** Genital complex with spermatophore ventral. **B.** Genital complex with spermatophore right lateral. **C.** A1 articulating segments 1–2 (*arrows* to segmental attenuations). **D.** Leg 5 (*arrow* to extra seta and its location). Male. **E.** Ab2–3 dorsal. **F.** Ab2–3 ventral. **G.** Ab2–3 right lateral. **H.** Left A1 articulating segments 13–14 (*arrowhead* to tip of distal rigid seta; *arrow* to axial angle of segment attenuation). **I.** Leg 5 anterior (*arrow* connects left Re2 and Re3; arthrodial membranes and poorly sclerotized areas stippled). **J.** Leg 5 posterior (*arrow* connects left Re2 and Re3; arthrodial membranes and poorly sclerotized areas stippled). Abdominal somites and thoracopod ramal segments numbered.

dial membrane between the two segments on the right A1.

Leg 5 (Fig. 9I, J): left Re2 (proximal) medial triangular attenuation not twisted. Right basis without denticles; Re3 (middle) medial attenuation smoothly curved.

Remarks

On one female, both Re 1+3 (complex) of leg 5 have an extra lateral seta (Fig. 9D). Females are easily distinguished from *P. johnsoni*, *P. robusta* and *P. antarctica* by the laterally thickened and rounded posterior edge of Th1. They share a more posterior location of the copulatory pore with *P. johnsoni* but differ from that species by the anteriorly and posteriorly rounded dark organ, and a less vaulted anterior edge on the genital complex. Males of *P. scutullata* differ from *P. johnsoni* by their anteriorly and posteriorly rounded dark organ, pattern of spinulation on abdominal somites, and attenuation of the 14th articulating segment of A1. Males of *P. robusta* and *P. antarctica* have a left Re2 (proximal segment) of leg 5 with the medial triangular attenuation twisted at its tip and the medial attenuation of the right Re 3 (middle segment) is indented; these attributes are absent on *P. scutullata*. *P. scutullata* originally was reported from the northwestern Pacific Ocean, the Bering Sea and the southern area of Sea of Okhotsk (Brodsky 1950), and later from the Gulf of Alaska (Vaupel Klein 1970).

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