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New records of Pseudotachidiidae from South Korea, including a key to species of the Pseudomesochrinae (Copepoda: Harpacticoida)

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Abstract

Two species of the marine harpacticoid family Pseudotachidiidae (Copepoda) are reported from subtidal sediments in the Southern Sea of Korea. *Psammis wellsi* **sp. nov.** (Danielsseniinae) is most closely related to *P. longisetosa* Sars, 1910 but differs from its European congener in the ventral ornamentation of the female genital double-somite, the dorsal ornamentation of the second abdominal somite in the male, the armature of the proximal endite of the maxillary syncoxa, the relative setal lengths and general shape of the female P5, and the relative length of the inner seta of the male P5 endopodal lobe and P6. The female of *Pseudomesochra tatianae* Drzycimski, 1968 is redescribed in detail, constituting the only other record of the species since its discovery at the type locality in western Norway. East Asian records of members of the four subfamilies currently recognized in the Pseudotachidiidae are summarized. Published and other records of the 23 described species in the Pseudomesochrinae are collated and their armature patterns of P1–P5 are tabulated and corrected where necessary. *Pseudomesochra affinis* (Sars, 1920) is removed from its synonymy with *P. longifurcata* T. Scott, 1902 and formally reinstated as a valid species. An updated female-based key to the 19 valid species of *Pseudomesochra* T. Scott, 1902 and four species of *Keraia* Willen & Dittmar, 2009 is presented.

Key words: Copepoda, Danielsseniinae, *Psammis wellsi* **sp. nov.**, Pseudomesochrinae, *Pseudomesochra tatianae*, Southern Sea, subtidal zone, taxonomy

Introduction

The harpacticoid family Pseudotachidiidae currently contains 140 species (including seven of doubtful status) in 32 genera. The long and intricate taxonomic history of the family started with Lang's (1936a) revision of the Thalestridae in which he recognized four subfamilies, including the Pseudotachidiinae which he proposed for the genera *Idomene* Philippi, 1843, *Pseudotachidius* T. Scott, 1898, *Dactylopodella* Sars, 1905 and *Dactylopodopsis* Sars, 191. Subsequently, Willen (1996, 1999, 2000) gradually redefined the taxonomic concept of the Pseudotachidiinae, resulting in its removal from its original position in the Thalestridae, its upgrade to full family status and the recognition of no less than four subfamilies—more than in any other currently recognized harpacticoid family—: Pseudotachidiinae Lang, 1936a, Donsiellinae Lang, 1944, Danielsseniinae Huys & Gee in Huys *et al.*, 1996, and Pseudomesochrinae Willen, 1996. The relationships between these subfamilies are not well understood, partly because the monophyly of the nominotypical subfamily has not been firmly established. Hence, Willen's (2000) classification of the Pseudotachidiidae has not been universally accepted (*i.e.* Boxshall & Halsey 2004). The subfamilial division was accepted by Wells (2007) and is also adopted here pending a rigorous phylogenetic analysis of the family.

The family has a worldwide distribution range, occurring across the entire bathymetric spectrum from the intertidal zone (*e.g.* Mielke 1975, 1997) to the deepest ocean trenches (*e.g.* Itô 1983; Kitahashi *et al.* 2013, 2014). Although many species colonized the continental shelf where they inhabit mostly muddy sediments, pseudotachidiids have achieved their most successful radiation in the deep sea, typically representing one of the most abundant

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harpacticoid families (*e.g.* Willen 2005, 2009; Willen & Schulz 2007; Vasconcelos *et al*. 2008). For example, a recent study in the Angola Basin revealed Pseudotachidiidae to be the most abundant copepod taxon, both quantitatively and in terms of species diversity, with members of the Pseudomesochrinae and Danielsseniinae collectively representing about 90% of the pseudotachidiid species and individuals (Willen 2008). Although the family contains mostly free-living members, at least 15 species in seven genera and two subfamilies are known to be associated with invertebrate hosts, including hermit crabs, isopods and tunicates (Huys 2016).

At least 15 pseudotachidiid genera have previously been recorded in East Asia, representing all four subfamilies (Table 1). Recent and ongoing research revealed a high diversity in Korean waters; however most species have remained undescribed with only seven being named. In an unpublished Ph.D. dissertation Kim (2014a) listed various putative species of *Pseudotachidius*, *Danielssenia* Boeck, 1873, *Pseudomesochra* T. Scott, 1902, *Psammis* Sars, 1910, *Paradanielssenia* Soyer, 1970, *Fladenia* Gee & Huys, 1990 and *Paranannopus* Huys, 2009 in addition to an unknown genus of Pseudotachidiidae. An as yet unidentified species of *Fladenia* was recorded by Kim (2017) off Hansando Island. Previously, Kim & Kim (1997) had described two new donsielliniid species, *Pseudonsiella longicaudata* Kim & Kim, 1977 and *Xylora longiantennulata* Kim & Kim, 1997, from decaying wood infested by limnoriid isopods collected in Namae Port, Kangwondo. Kim *et al*. (2011) described *Sentiropsis coreana* Kim, Lee & Huys, 2011 from sandy sediments collected off Hyeopjae (Jeju Island); this species was subsequently recorded from intertidal localities on Jeju Island (Kim 2017). Kim (2014b) recorded *Xouthous laticaudatus* (Thompson & Scott, 1903) from macroalgal washings in Gyeongnam, and both *Donsiella limnoriae* Stephensen, 1936 and *Donsiella bisetosa* Hicks, 1988 from washings of decaying wood collected in Jeju Island. Since several other records in Kim's (2014b) work have proven to be unreliable (Huys & Lee 2018; Lee & Huys 2019) the authenticity of his pseudotachidiid records remains to be confirmed. The recently reported new species, *Xouthous yeonghooni* Song, Lee, Lee & Khim, 2020, is widely distributed along the coasts of the Korean Peninsula and Jeju Island (Song *et al.* 2020). As part of an ongoing survey of sublittoral substrata in the Southern Sea of Korea here we describe a new species of *Psammis* as well as confirm the first identified record of *Pseudomesochra*, raising the number of named pseudotachidiid species in Korean waters to nine.

Material and methods

Sublittoral sediment samples were taken in the Southern Sea of Korea (Fig. 1) using a Smith-McIntyre grab (0.1 m^2) or Box corer (0.5 m^2). Samples were sieved with a hand net (mesh size 50 μm) and fixed in 10% formalin. Meiofauna was extracted using the centrifugation-flotation technique with Ludox® HS-40 (Burgess 2001). Harpacticoids were sorted under a stereomicroscope (Leica M165 C; Wetzlar, Germany) and the specimens were temporarily mounted in lactic acid on a Higgins-Shirayama (H-S) slide (Shirayama *et al*. 1993) for double-sided microscopic observation. Habitus and appendages were drawn with the aid of a camera lucida mounted on an Olympus BX53 differential interference contrast (DIC) microscope. Pencil drawings were digitally inked and combined into plates using Adobe Illustrator® CC software. After examination, the dissected appendages and urosome were mounted in lactophenol on H-S slides and sealed permanently.

Descriptive terminology follows that of Huys and Boxshall (1991). Abbreviations used in text and figures are: *ae*, aesthetasc; *P1–P6*, first to sixth thoracic legs; *exp(enp)-1(-2,-3)*, the proximal (middle, distal) segment of a ramus.

Type specimens of *Psammis wellsi* **sp. nov.** were deposited in the Marine Biodiversity Institute of Korea (MABIK), Seochun, Korea, and the Korean specimens of *Pseudomesochra tatianae* Drzycimski, 1968 were stored in the National Institute of Biological Resources (NIBR), Incheon, Korea. Additional specimens are kept in the Marine Interstitial fauna Resources Bank (MInRB) in the Korea Institute of Ocean Science & Technology (KIOST), Busan, Korea.

Systematics

Order Harpacticoida Sars, 1903

Family Pseudotachidiidae Lang, 1936a

Subfamily Danielsseniinae Huys & Gee in Huys *et al*., 1996

Genus *Psammis* Sars, 1910

Sars (1910: 339) proposed *Psammis* for its type (by monotypy) and only species *P. longisetosa* Sars, 1910 collected from Farsund in southern Norway. The genus has seen the addition of four species since, *i.e. P. borealis* Klie, 1939 collected north of Iceland, *P. kliei* Smirnov, 1946 from the East Siberian Sea, *P. longifurca* Bodin, 1968 from the Bay of Biscay and *P. longipes* Becker, 1974 from the Peru–Chile (Atacama) Trench (Klie 1939, 1941; Smirnov 1946; Bodin 1968; Becker 1974). Wells (1967) had previously expressed doubts about the validity of the genus, arguing that the only character that separates it from *Danielssenia* is the number of setae on the exopod of P5; however, Gee (1988) pointed out that species of both genera are probably trophically isolated as indicated by differences in mandibular gnathobase morphology and that this—in conjunction with the fused rami of P5—constitutes sufficient evidence for maintaining the genera separate. Huys & Gee (1993) redefined the boundaries of *Psammis* and restricted it to its type species and *P. longipes*. While *P. longifurca* was fixed as the type of the new genus *Bathypsammis* Huys & Gee, 1993, both *P. borealis* and *P. kliei* were tentatively maintained as *species incertae sedis* in the Paranannopidae (= Danielsseniinae; *cf.* Huys 2009) pending further re-examination. In subsequent contributions Gee & Huys (1994) assigned *P. kliei* to the genus *Mucrosenia* Gee & Huys, 1994 as *species incertae sedis* and Huys and Gee (1996) designated *P. borealis* as the type (by original designation) of their new genus *Anapophysia* Huys & Gee, 1996. The original descriptions of both sexes of *P. longisetosa* by Sars (1910: 339–340, plate CCXXV; 1921: 94–95, plate LXV.) were supplemented and largely superseded by a number of subsequent re-examinations including those by Gee (1988: 181–187, Figs. 1–4), Huys and Gee (1993: 72, 75, Figs. 21–22) and Huys *et al*. (1996: 248–249, Figs. 93B, 98, Table 4).

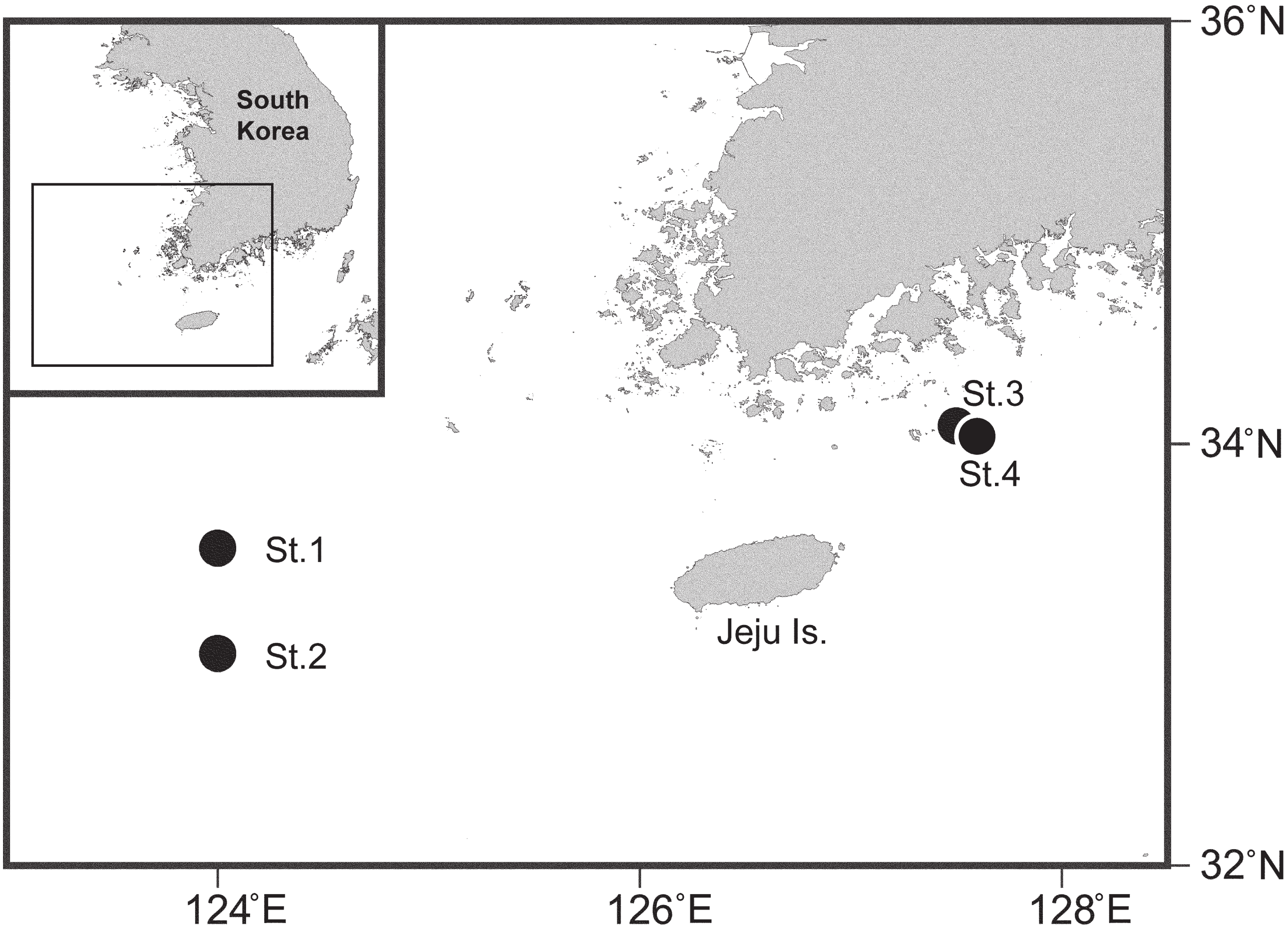

FIGURE 1. Map showing sampling stations in the Southern Sea.

TABLE 1. East Asian records of members of the four subfamilies currently recognized in the Pseudotachidiidae; depth (in m), INT = intertidal.

DANIELSSENIINAE				
Archisenia sp. 1	Japan	Sagami Bay	1,422–1,460	Shimanaga *et al*. (2004)
Danielssenia typica Boeck, 1873	China	off Yantai (Chefoo), Bohai Sea	30–50	Shen & Bai (1956)
	China	South China Sea	?	Lian & Lin (1994), Chen (2008)
	China	Bohai Sea	18 [1]	Mu *et al*. (2001, 2002)
	China	Jiaozhou Bay, Yellow Sea	3.9–26.2	Ma (2012), Ma & Li (2017)
Danielssenia similis Chislenko, 1978 [2]	Russia	Posyet Bay, Peter the Great Gulf	3–4	Chislenko (1978)
Danielssenia sp.	China	Yellow Sea, between Qingdao and Jeju Island	73–80	Zhang *et al*. (2004, 2005a,b)
	Taiwan	South Bay and Bisha Port, Keelung	?	Lian & Lin (1994), Lian & Huang (2008)
	Russia/Japan	Kuril Trench (bathyal—upper trench slope)	490–2,350	Kitahashi *et al*. (2013)
Danielssenia sp. 1	Korea	South Western Sea, Gwanyang Bay, South Eastern Sea, Jeju-Ieodo area, East Northern Sea	?	Kim (2014a)
Danielssenia sp. 2	Korea	Jeju-Ieodo area	?	Kim (2014a)
Fladenia spp. 1–2	China	Bohai Sea	18 [1]	Mu *et al*. (2001, 2002)
Fladenia sp. 1	Korea	South Eastern Sea, East Southern Sea, East Northern Sea	?	Kim (2014a)
Fladenia sp. nov.	Korea	off Hansando Island, Gyeongsangnam-do	?	Kim (2017)
Paradanielssenia sp. 1	Korea	off Incheon, South Eastern Sea, East Southern Sea	?	Kim (2014a)
Paradanielssenia sp.	Russia/Japan	Kuril Trench (bathyal—trench floor)	490–7,090	Kitahashi *et al*. (2013)
	Japan	Ryukyu Trench (abyssal plain)	4,910–5,710	Kitahashi *et al*. (2014)
Parananopus sp. 1	Korea	South Western Sea	?	Kim (2014a)
Parananopus sp.	Russia/Japan	Kuril Trench (trench floor)	7,000–7,090	Kitahashi *et al*. (2013)
Psammis wellsi **sp. nov.**	Korea	Southern Sea	50.9 –56.7	present account
Psammis sp.	Korea	East Southern Sea, East Northern Sea	?	Kim (2014a)
Sentiropsis coreana Kim, Lee & Huys, 2011	Korea	off Hyeopjae, Jeju Island	2–3	Kim *et al*. (2011)

......*continued on the next page*

TABLE 1. (Continued)

		Jeju City public beach, and Hwasun beach, Seogwipo, Jeju Island	INT	Kim (2017)
Sentiropsis vietnamensis Gómez & Chertoprud, 2009	Vietnam	Mot Island, Nha Trang Bay	5	Gómez & Chertoprud (2009), Chertoprud *et al*. (2009) [3]
DONSIELLINAE [4]				
Donsiella bisetosa Hicks, 1988	Korea	Jeju Island	?	Kim (2014b)
Donsiella limnoriae Stephensen, 1936	Korea	Jeju Island	?	Kim (2014b)
Pseudonsiella longicaudata Kim & Kim, 1997	Korea	Kangwondo, East Sea	?	Kim & Kim (1997)
Xylora longiantennulatata Kim & Kim, 1997	Korea	Kangwondo, East Sea	?	Kim & Kim (1997)
PSEUDOMESOCHRINAE				
Pseudomesochra tatianae Drzycimski, 1968	Korea	Southern Sea	70.8	present account
Pseudomesochra sp. 1	China	continental shelf between Changjiang Estuary and Jeju Island, East China Sea	?	Fleeger *et al*. (1986)
Pseudomesochra sp. 2	China	Taiwan Strait	?	Lian & Wang in Lian *et al*. (2012)
Pseudomesochra sp. 3	China	deep-sea polymetallic nodule mining area in Pacific	?	Lian & Wang in Lian *et al*. (2012)
Pseudomesochra spp. 1–2	Japan	Sagami Bay	1,416–1,460	Shimanaga *et al*. (2004)
Pseudomesochra sp. 1	Korea	Jeju-Ieodo area	?	Kim (2014a)
Pseudomesochra sp.	Russia/Japan	Kuril Trench (bathyal—trench floor)	490–7,090	Kitahashi *et al*. (2013)
	Japan	Ryukyu Trench (bathyal—trench floor)	430–7,150	Kitahashi *et al*. (2014)
PSEUDOTACHIDIINAE				
Dactylopodella flava (Claus, 1866)	China	locality not specified	?	Chen (2008)
	Taiwan	Bisha Port, Keelung	?	Lian & Huang (2008)
Dacylopodella sp.	Taiwan	Bisha Port, Keelung	?	Lian & Huang (2008)

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TABLE 1. (Continued)

	Japan	Ryukyu Trench (abyssal plain)	4,910–5,710	Kitahashi *et al*. (2014)
Pseudotachidius bipartitus pacificus Itô, 1983	Philippines	southeast of Mindanao	5,567	Itô (1983)
Pseudotachidius horikoshii Itô, 1983	Philippines	southeast of Mindanao	5,567	Itô (1983)
Pseudotachidius minutus Itô, 1983	Philippines	southeast of Mindanao	5,567	Itô (1983)
Pseudotachidius sp. 1	Korea	South Eastern Sea	?	Kim (2014a)
Pseudotachidius sp.	Russia/Japan	Kuril Trench (bathyal—upper trench slope)	490–2,350	Kitahashi *et al*. (2013)
Xouthous laticaudatus (Thompson & Scott, 1903) [5, 6]	Korea	Gyeongnam, South Sea	INT	Kim (2014b)
Xouthous purpurocinctus (Norman & Scott, 1905)	Japan	Tosa Bay, Shikoku Island	INT	Saito (2009)
Xouthous yeonghooni Song, Lee, Lee & Khim, 2020	Korea	East, South and Yellow Seas; Jeju Island	1–20	Song *et al.* (2020)
Unknown genus	Korea	South Eastern Sea	?	Kim (2014a)

[1] : average depth in the Bohai Sea

[2] : relegated to *species inquirenda* and regarded as potential synonym of *D. typica* by Huys & Gee (1993) who erroneously attributed the authorship to Chislenko (1971).

[3] : as *Sentiropsis* sp. nov.

[4] : Lian *et al*. (2012) list a record of *Xylora bathyalis* Hicks, 1988 (as *X. calyptogenae* Willen, 2006) from the South China Sea but erroneously cite the original description by Willen (2006) as the source reference. The species was described from Edison Seamount, a hydrothermally active submarine volcano in the New Ireland Fore-Arc system (Papua New Guinea).

[5] : Kim's (2014b: 32–33, Fig. 9) description of P5 shows that he was not dealing with *X. laticaudatus* or any another species of *Xouthous* Thomson, 1883; possibly his material belongs to the genus *Idomenella* T. Scott, 1906 based on his photographs of P1 and P5.

[6] : Lian *et al*. (2012) lists this species (as *Idomene laticaudata* Thompson & Scott, 1903) from the South China Sea but erroneously cite Scott (1909) as the source reference; Scott reported it from the Aru Islands in Maluku, Indonesia, southwest of Papua New Guinea.

Psammis wellsi sp. nov.

(Figs. 2–7)

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Type locality. South Korea, Southern Sea, 33º00'N, 124º00'E, 50.9 m depth (St. 2 in Fig. 1).

Type material. Holotype ♂ (reg. no. MABIK CR00246486) dissected on seven slides, paratype ♀ (reg. no. MABIK CR00246487) dissected on eight slides, and paratype ♂ (reg. no. MABIK CR00246488) dissected on seven slides. All type specimens were collected from the type locality on 25 April 2017.

Additional material. 1 ♀ (reg. no. MInRB-Hr47-S001) dissected on seven slides, 1 ♂ (reg. no. MInRB-Hr47-S002) dissected on six slides, and 1 ♂ (reg. no. MInRB-Hr47-L001) preserved in 80% ethanol, collected from St. 2, 33º00'N 124º00'E, 48.6 m depth, 5 June 2015; 1 ♀ (reg. no. MInRB-Hr47-S003) dissected on seven slides, collected from St. 3, 34º04'N, 127º30'E, 56.7 m depth, 23 April 2017; 1 ♀ (reg. no. MInRB-Hr47-S004) dissected on seven slides, collected from St. 4, 34º03'N, 127º34'E, 59.0 m depth, 27 May 2018. All additional material was deposited in KIOST.

Etymology. The species is named in honour of the late Prof. J.B.J. Wells who made tremendous contributions to the systematics and taxonomy of harpacticoid copepods.

Description of male. Body length from anterior end of rostrum to posterior end of caudal rami about 710 μm (measured in lateral aspect). Body (Fig. 2A–C) semi-cylindrical, slightly tapering towards posterior end of caudal rami; separation between prosome and urosome weakly defined. Cephalothorax (Fig. 2A–B) bell-shaped in dorsal aspect, about 1.1 times longer than maximum width. Pedigerous somites gradually tapering posteriorly; pleurotergites with backwardly produced ventrolateral corners, becoming gradually more developed from second to fourth pedigerous somites. Genital and first abdominal somites (Figs. 2A–C, 3A) separate. Penultimate somite with lobate pseudoperculum, reaching to about halfway length of anal somite and covering anal opening. Anal somite deeply cleft medially, with pair of dorsal sensilla; anal opening triradiate and furnished with denticulate hyaline frill.

Dorsal and lateral surfaces of cephalothorax and body somites ornamented with sensilla and pores as illustrated (Figs. 2A–C, 3A); sensilla absent on penultimate somite and on lateral and ventral surfaces of anal somite. Somites bearing P2–P4 with dorsal transverse spinule row near posterior margin, becoming increasingly wider in successive somites; transverse spinule row on P5-bearing somite interrupted middorsally; P6-bearing somite with a continuous spinule row running dorsally and laterally; first and second abdominal somites with continuous spinule row running all around; third abdominal somite with spinule row midventrally and continuous row running laterally and dorsally; posterior margin of anal somite with minute spinules dorsally and larger ones laterally and ventrally (Figs. 2A–C, 3A). Urosomites with additional transverse rows of minute spinules on dorsal surface. Hyaline frills of cephalothorax and body somites (except P4-bearing and anal somite) minutely denticulate.

Rostrum (Fig. 2A–B) large and broad, bell-shaped and slightly ventrally deflected; with two pairs of sensilla anteriorly and one pore middorsally.

Antennule (Fig. 3C–C') subchirocer, 9-segmented; with geniculation between segments 6 and 7; segment 1 with three rows of spinules along anterior margin; segments 4 and 5 small; segment 6 enlarged and swollen, with aesthetasc; segments 7–9 short and slender, collectively forming claw-like terminal unit; segment 7 with one modified element; segment 9 with small aesthetasc. Armature formula as follows: 1-[1 pinnate], 2-[1 pinnate], 3-[2 + 6 pinnate], 4-[1 + 7 pinnate], 5-[1 pinnate], 6-[1 pinnate + 5 + (1 + ae)], 7-[1 modified], 8-[1 + 1 pinnate], 9-[5 + (1 + ae)]. Each aesthetasc fused basally to adjacent seta.

Antenna (Fig. 4A). Coxa small, unornamented. Allobasis with one long abexopodal seta. Exopod 3-segmented; exp-1–3 with two, one, and three pinnate elements, respectively (distal ones on exp-3 stout and spiniform); exp-2 smallest; exp-3 ornamented with few spinules around bases of apical spines. Free endopod ornamented with two groups of stout spinules and two surface frills; lateral armature comprising two stout pinnate spines and one pinnate seta; distal armature composed of one stout spinulose spine, four geniculate setae, and two small setae, one of which fused basally to adjacent long geniculate seta.

Mandible (Fig. 4B). Coxa with small blunt process medially, long spinules proximally, and two rows of minute surface spinules distally near gnathobasal margin; ganathobase with five multicuspidate spinous processes (gradually descreasing in size towards dorsal corner), six long spinules, and unipinnate seta at dorsal corner. Palp biramous, composed of basis and 1-segmented rami. Basis with four pinnate setae (one of which plumose near its base and with short pinnules along most of its length; others entirely plumose) and three rows of setules. Exopod with plumose seta laterally, and one bare plus one plumose seta apically; with few spinules laterally. Endopod with plumose seta laterally, and one plumose and two bare setae apically.

Maxillule (Fig. 4C). Praecoxal arthrite with two tubular setae on anterior surface and long spinules posteriorly and along inner margin; distal armature composed of nine pinnate or serrate spines and one bare seta. Coxal endite with two stout spinulose spines having long tubular extension distally, and one spine and two tubular elements subdistally. Basal endite with plumose seta along outer margin, and one bare, one spine-like and two plumose setae distally. Exopod broader and longer than endopod, with three plumose setae apically, and ornamented with long setules along inner margin and short spinules around base of distalmost seta. Endopod with one bare and two plumose apical setae; outer margin with long setules.

Maxilla (Fig. 4D). Syncoxa with two rows of pinnules along outer margin, and three endites; each endite with one slender seta bearing tubular extension and two stout spines, outer one of which ornamented with two long spinules halfway up its length and one tubular extension. Allobasis with distal armature comprising stout claw, one small spine with serrate tip and two tubular elements; outer margin with spinules. Endopod small, 1-segmented; with spiniform seta and three tubular elements.

Maxilliped (Fig. 4E) subchelate. Syncoxa with one very long spinulose seta accompanied by very small seta (indicated by arrowhead in Figure 4E) and spinule row at its base; inner margin with row of long setules. Basis with very long spinulose seta on palmar margin near articulation with endopod; ornamentation consisting of small spinules near distal outer margin and on anterior surface and strong spinules near palmar margin. Endopodal represented by claw-like process, with small accessory seta anteriorly near its base.

P1 (Fig. 5A). Intercoxal sclerite broad, with convex distal margin. Coxa large; anterior surface with two rows of stout spinules and several rows of minute spinules. Basis with stout, naked outer seta and spinulose inner spine; anterior surface with row of stout spinules along distal margin, smaller spinules around base of inner spine in addition to two rows of small/minute spinules in proximal half; with integumental pore near insertion site of outer seta. Exopod 3-segmented; all segments with stout spinules along outer and distal margins; exp-1 with additional row of stout spinules on anterior surface; exp-2 about as long as wide, with anterior pore; exp-3 about 1.5 times as long as wide. Endopod 2-segmented, exceeding distal margin of exp-3; both segments with stout spinules along outer and distal margins; enp-1 broad, slightly longer than wide, with anterior pore; enp-2 about 2.6 times as long as greatest width, with anterior pore near distal margin.

P2–P4 (Figs. 5B, 6A–B) with 3-segmented protopods and rami. Intercoxal sclerites with convex distal margin, forming paired pointed processes. Praecoxa small, with row of spinules along distal margin (not shown for P3). Coxae large; with two rows of stout spinules along distal margin in addition to several rows of small spinules and one integumental pore on anterior surface. Bases smaller than coxae, with long, unipinnate outer seta; anterior surface with row of stout spinules near boundary with coxa, minute spinules along distal margin near articulation with endopod and one spinule near base of outer seta. Exopodal segments with stout spinules along outer margin and typically around distal outer corner; exp-1 with stout spinules on anterior surface; outer distal corner of exp-1–2 produced into spinous process; distal margin of exp-1–2 with incised hyaline frill; anterior pores present on P2 exp-3, P3 exp-2 and P4 exp-2–3.

P2 endopod (Fig. 5B) distinctly longer than exopod. Enp-1 shortest; outer margin armed with two rows of stout spinules; outer distal corner forming spinous process with integumental pore on anterior surface; inner margin with short, pinnate spiniform element. Enp-2 without ornamentation along outer margin; outer distal corner drawn out into long spinous apophysis, reaching to insertion site of distal inner seta of enp-3; inner margin with spinule and two fine setae. Enp-3 elongate, forming slightly curved apical process (homologous to outer spine of ♀); outer margin with few spinules; inner margin with two well developed setae (homologous to inner setae of ♀) and two vestigial elements (homologous to distal setae in ♀).

P3 endopod (Fig. 6A) about as long as exopod. Enp-1 shortest; with spinules along outer margin and short, naked spiniform element along inner margin; outer distal corner forming small spinous process with anterior pore. Enp-2 with naked outer margin; outer distal corner produced into acutely recurved process with pore on its anterior surface; inner margin with spinule and short bipinnate element. Enp-3 with few stout spinules along outer margin; inner distal seta extremely reduced.

P4 endopod (Fig. 6B) distinctly shorter than exopod, extending just beyond distal margin of exp-2. Enp-1 without spinular ornamentation along outer margin; outer distal corner forming minute process with anterior surface pore. Enp-2 with few coarse spinules along outer margin; outer distal corner produced into spinous process with anterior pore. Enp-3 longest; outer margin with one stout spinule; inner distal seta extremely reduced.

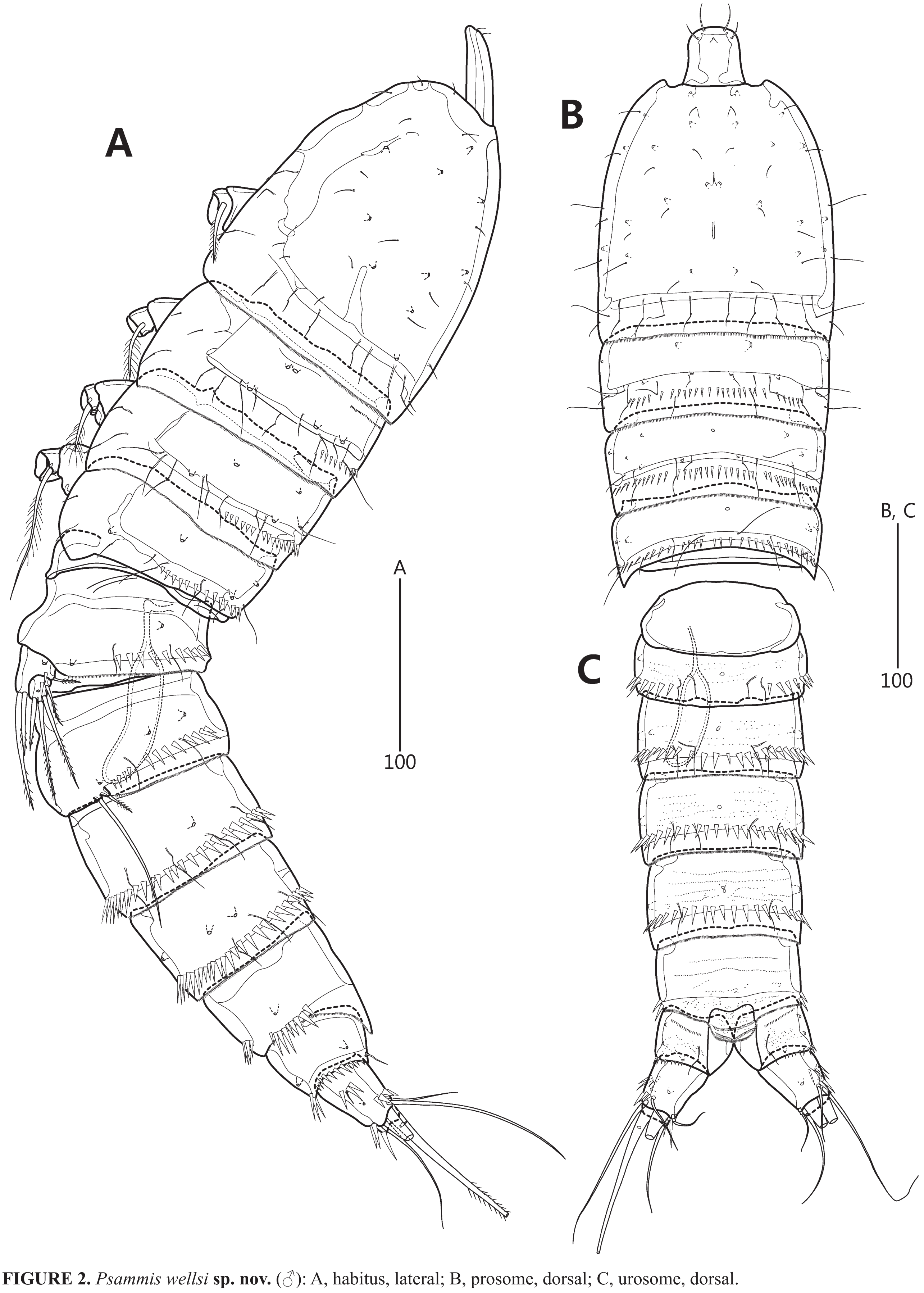

FIGURE 2. *Psammis wellsi* **sp. nov.** (♂): A, habitus, lateral; B, prosome, dorsal; C, urosome, dorsal.

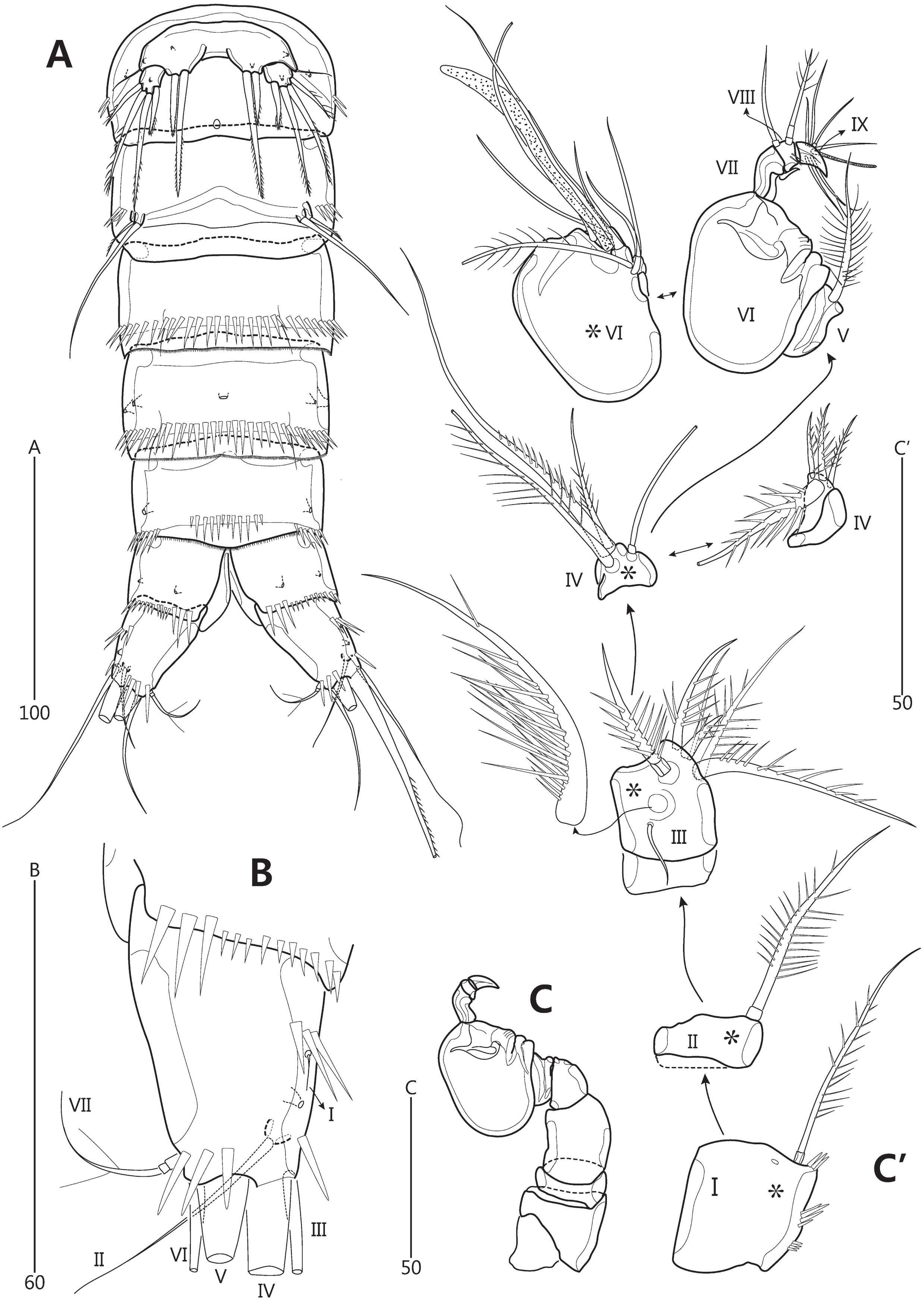

FIGURE 3. *Psammis wellsi* **sp. nov.**, (♂): A, urosome, ventral; B, left caudal ramus, ventral; C, antennule (armature omitted); C', antennule (disarticulated; segments shown in posterior view indicated by asterisks).

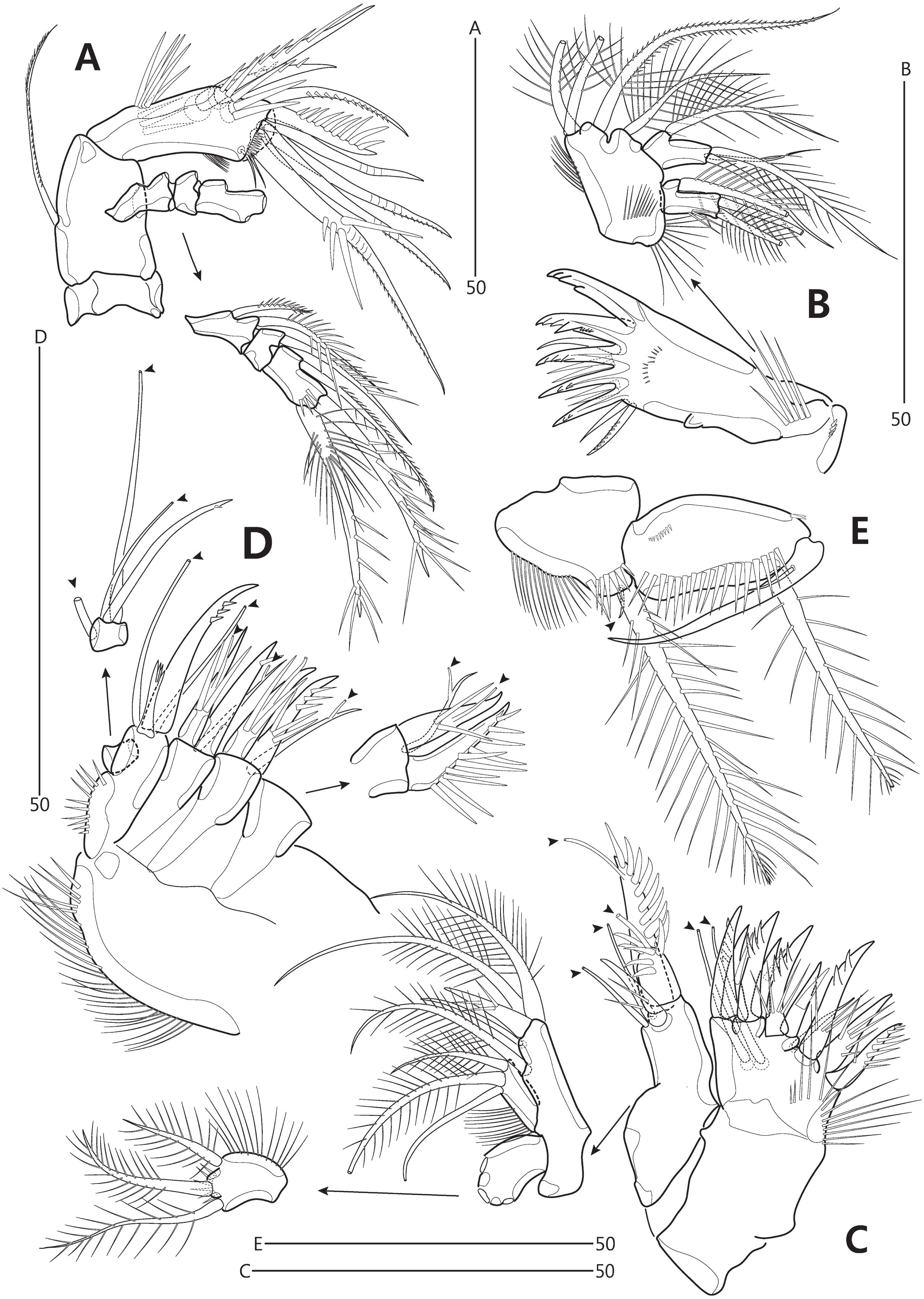

FIGURE 4. *Psammis wellsi* **sp. nov.** (♂): A, antenna (inset showing disarticulated exopod with complete armature); B, mandible with disarticulated palp; C, maxillule with disarticulated palp (exopod shown in separate inset); D, maxilla (praecoxal endite and endopod shown in separate insets); E, maxilliped (minute seta on syncoxa indicated by arrowhead). Arrowheads in C–D indicate tubular setae or extensions.

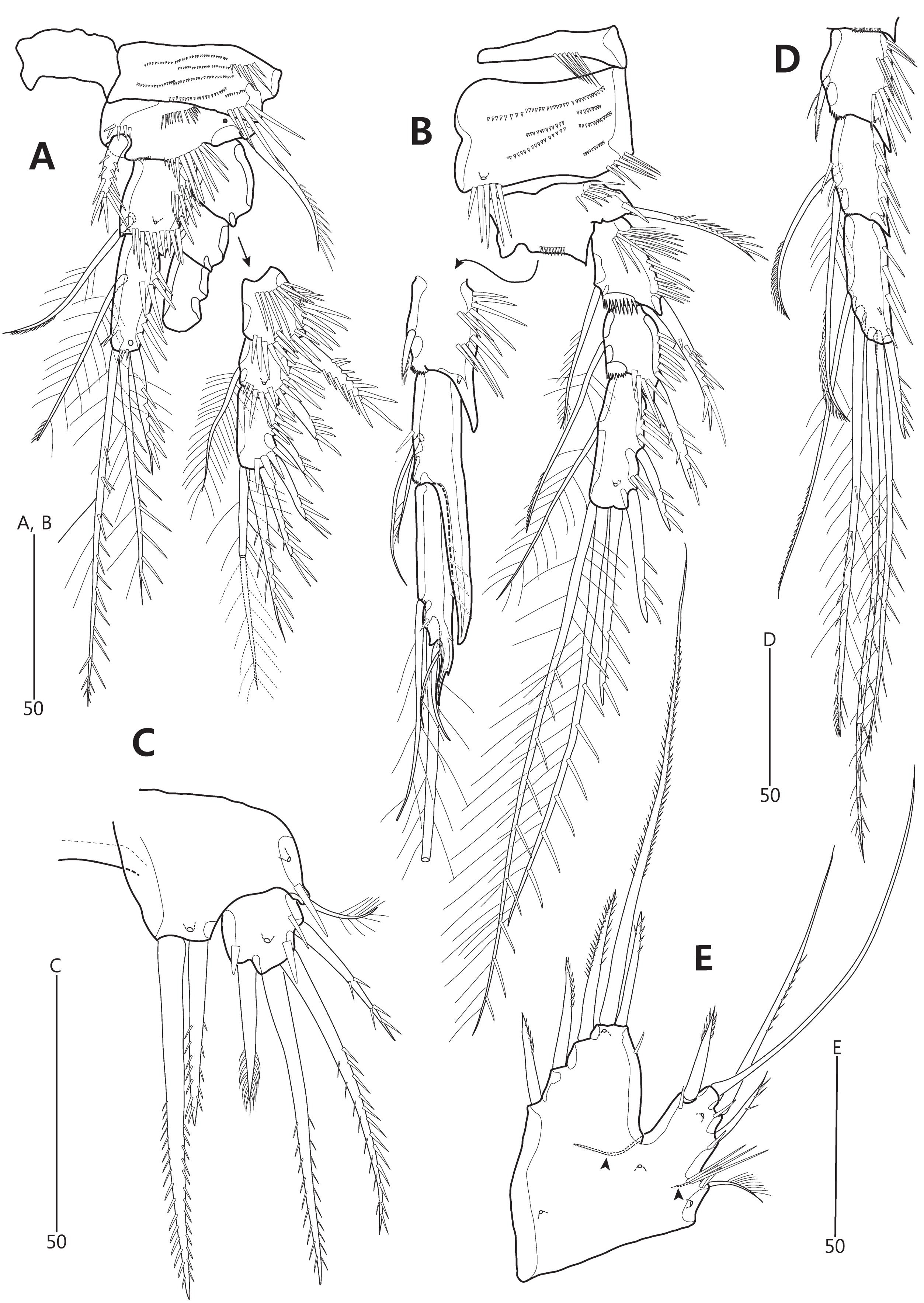

FIGURE 5. *Psammis wellsi* **sp. nov.** (♂: A–C) (♀: D–E): A, P1, anterior (disarticulated exopod shown in inset); B, P2, anterior (disarticulated endopod shown in inset); C, left P5, anterior; D, P2 endopod, anterior; E, right P5, anterior.

Armature formulae of P1–P4 as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	1.1.123	1.2.22*apo [1.2.221 in ♀]
P3	1.1.223	1.1.32**1
P4	1.1.223	1.1.22**1

* both distal elements reduced in size in ♂; ** inner distal element extremely small in both sexes; apo = apophysis.

P5 (Fig. 5C). Baseoendopod broad, with small outer setophore bearing plumose seta and one stout spinule; anterior surface with one pore near outer margin and one pore near distal margin of endopodal lobe; endopodal lobe relatively small, reaching halfway down exopod, and with two pinnate spines (outer one twice as long as inner one). Exopod small with three stout marginal spinules, one serrate spine and three bipinnate setae.

Sixth pair of legs (Fig. 3A) symmetrical and fused to genital somite; each P6 represented by two setae, inner one naked and four times as long as pinnate outer one. Spermatophore elongate-oval (length: 85 µm).

Caudal rami (Figs. 2A, C, 3A–B) distinctly divergent; about 1.25 times as long as maximum width (measured in ventral aspect: Fig. 3B) and tapering posteriorly; inner distal corner with spinules ventrally; with seven setae. Seta I extremely small, ventral; positioned at 1/3 distance of outer margin; concealed by row of spinules. Seta II arising from dorsal surface near posterior margin; surrounded at base with few spinules. Seta III located at outer distal corner; about 2.5 times as long as seta II. Setae IV–V terminal, well developed; pinnate distally. Seta VI located at inner distal corner, slightly longer than caudal ramus length. Seta VII tri-articulated at base; arising from inner margin in distal 1/5 of ramus; sparsely plumose.

Description of female. Body length about 670 µm (measured in lateral aspect). Sexual dimorphism expressed in antennule, P2 endopod, P3 endopod, P5, P6, and in urosomal segmentation.

Urosomites 2–3 (Fig. 7A–B) completely fused forming genital double-somite; original segmentation marked by transverse chitinous ribs ventrally and laterally. Genital field (Fig. 7C) with small copulatory pore posterior to genital slit; copulatory duct short, leading to paired seminal receptacles located at level of genital slit; vestigial P6 with one plumose seta. Paired blind-ending cuticular invaginations discernible posterior to genital field.

Antennule (Fig. 7D–D') short, 4-segmented; segment 1 with two rows of spinules along anterior margin; segment 2 with dorsal pore; segments 3 and 4 each with aesthetasc. Armature as follows: 1-[1 pinnate], 2-[3 + 6 pinnate], 3-[10 + 3 pinnate + (1 + ae)], 4-[7 + 5 pinnate + (1 + ae)]. Each aesthetasc fused at base to adjacent seta.

P2 endopod (Fig. 5D). Outer distal corner of enp-2 produced into small spinous process instead of elongate apophysis in ♂; inner setae much longer than in ♂. Enp-3 relatively shorter than in ♂, about three times as long as wide; with two inner setae, two long apical setae and one outer spine; with pore on anterior surface. Outer margin of all segments with strong spinules.

P3 enp-2 similar to P2 enp-2 (outer distal corner not produced into acutely recurved process).

P5 (Fig. 5E). Exopod and baseoendopod completely fused forming deeply incised bilobate plate; original segmentation marked by two incomplete surface furrows on posterior surface (indicated by arrows in Fig. 5E); anterior surface with three pores in proximal half, one pore near distal margin of endopodal lobe and one pore on exopodal lobe; outer basal setophore small, with short plumose seta surrounded by long spinules at base. Endopodal lobe well developed, tapering distally with stepped inner margin and slightly convex outer margin; distal margin with one short and one long pinnate seta (inner 4.2 times length of outer one); inner margin with three pinnate setae, distal one being 1.35 times length of middle one and 0.3 times length of inner apical seta; distance from inner proximal corner to insertion site of proximalmost inner seta 1.6 times length of inner margin. Exopodal lobe with four setae; outer margin with one short and one long pinnate seta, each with single spinule at base; apical margin forming cylindrical peduncle with one long bare seta; inner margin with one small apically serrate seta; length ratio of apical seta/proximal inner seta 4.5.

Remarks. Huys & Gee (1993) distinguished *P. longisetosa* from *P. longipes* using the following suite of characters: (1) number of setae on the mandibular basis (four in *P. longisetosa vs* three in *P. longipes*); (2) length of anterior seta on maxillipedal syncoxa (distinctly longer in *P. longipes*); (3) ratio of endopod length to exopod length in P1–P3 (considerably higher in *P. longipes*); (4) number of exopodal setae on female P5 (four in *P. longisetosa vs* five in *P. longipes*); and (5) body length of female (± 550 µm in *P. longisetosa vs* ± 890 µm in *P. longipes*). Our

Korean specimens agree well with *P. longisetosa* in characters (1)–(4) but differ in a number of other morphological features justifying their recognition as a distinct species, *P. wellsi* **sp. nov.**: (1) ventral ornamentation of genital double-somite, *i.e.* spinules of posterior row uniform in size in *P. longisetosa* (Huys & Gee 1993: Fig. 22D) but showing distinct size discrepancy between midventral and lateroventral spinules in *P. wellsi* **sp. nov.** (Fig. 7B); (2) dorsal ornamentation of second abdominal somite in ♂, *i.e.* transverse spinule row interrupted middorsally in *P. longisetosa* (Gee 1988: Fig. 1) *vs* continuous in *P. wellsi* **sp. nov.** (Fig. 2C); (3) proximal endite of maxillary syncoxa bearing additional slender seta with tubular extension in *P. wellsi* **sp. nov.**; (4) morphology of ♀ P5, *i.e.* posterior surface with incomplete furrow marking original proximal margin of exopodal lobe (*P. wellsi* **sp. nov.**) or without (*P. longisetosa*), the number of secretory pores on anterior surface are different between *P. wellsi* **sp. nov.** (Fig. 5E) and *P. longisetosa* (Huys & Gee 1993: Fig. 22E), endopodal lobe more elongate in *P. longisetosa* (distance from inner proximal corner of baseoendopod to insertion site of proximalmost inner seta 1.8 times length of inner margin *vs* 1.6 times in *P. wellsi* **sp. nov.**) and with straight (*vs* slightly convex) outer margin; (5) relative lengths of setae of ♀ P5 endopodal lobe, *i.e.* inner apical seta 3.2 times length of outer apical one and 2.4 times that of distal inner seta in *P. longisetosa* (Huys & Gee 1993: Fig. 22E) (*vs* 4.2 and 3.2 times, respectively, in *P. wellsi* **sp. nov.**; Fig. 5E), and distal inner seta 1.7 times (*vs* 1.35) length of middle inner one; (6) length ratio of apical seta/proximal inner seta of ♀ P5 exopodal lobe, *i.e.* 3.0 in *P. longisetosa* (*vs* 4.5 in *P. wellsi* **sp. nov.**); (7) male P5 with well developed spinular row near articulation with exopod (*vs* 1–2 spinules in *P. wellsi*) and inner seta of endopodal lobe about three times as long as outer one in *P. longisetosa* (Huys & Gee 1993: Fig. 22F) (*vs* twice in *P. wellsi* **sp. nov.**; Fig. 5C); and (8) inner seta of ♂ P6 about 1.3 times as long as outer one in *P. longisetosa* (Huys & Gee 1993: Fig. 22G) (*vs* about four times in *P. wellsi* **sp. nov.**; Fig. 3A).

Published body size measurements of *Psammis* species are predominantly based on very few specimens and should therefore be used with caution when applied to species discrimination. *Psammis longipes* appears to be larger than its two congeners; however, the species is known from only two females and the body size (890 µm) given by Becker (1974) is probably based on only one of them. Similarly, the original description of the female of *P. longisetosa* was based on two specimens (550 µm) only (Sars 1910), while the subsequent description of the male (Sars 1921) was based on a single individual (720 µm). Gee (1988) was the first to give size ranges based on numerous specimens (670–700 µm for ♀♀; 580–750 µm for ♂♂) but note that in this case body length was measured from the base of the rostrum to the posterior margin of the anal somite. The single male (710 µm) and both females (670 µm) of *P. wellsi* clearly fall within this range, the sample size, however, being admittedly small.

In addition to its type locality in Farsund (Norway, Vest-Agder county) (Sars 1910, 1921), *P. longisetosa* has also been reported from other sites in Scandinavia including Risør and Bjørnehodet Bay in southern Norway (Gee 1988; Gee *et al*. 1985—as *P. longipes*; Warwick *et al*. 1988), and the Gullmar Fjord, the Koster Islands and the Skagerrak strait off the west coast of Sweden (Lang 1948; Por 1964). The single female recorded by Por (1965) from Raunefjorden near Bergen (Norway) differs significantly in the morphology of P1, P5, last abdominal somite and caudal rami and probably does not belong to *P. longisetosa* (*cf.* Huys & Gee 1993: 72). In the Baltic Sea it was sighted in the Baltic proper (Drzycimski 1997) and in the Słupsk Furrow (Drzycimski 2000). Huys *et al*. (1992) reported it from the deeper waters of the North Sea while further west it has been recorded along the west coast of Scotland in Loch Nevis (Wells 1965) and Loch Creran (Saunders 2000; E. Ólafsson, pers. commn). The southernmost records of *P. longisetosa* are those by Soyer (1970, 1971) who collected it in the Banyuls region (Pyrénées-Orientales) in southern France.

Psammis longipes was originally described from 5,000 m depth in the Peru–Chile (Atacama) Trench (Becker 1974) and has been recorded from other deepwater localities since. Nikolov (2011) reported it from Atwater Valley, a cold seep located at ~ 2200 m depth in the northern Gulf of Mexico. Ritt *et al*. (2012) found the species in the cold-seep benthic communities associated with the Napoli and Amsterdam mud volcanoes located on the Mediterranean Ridge (see also Ritt 2010). Plum *et al*. (2015) reported it from natural hydrocarbon seeps of the upper Louisiana slope in the Gulf of Mexico (Green Canyon) at a depth of 1,408 m but mistakenly stated (p. 428) that the species had previously "… only been reported from shallow-water habitats". Recently, George *et al*. (2018) discovered *P. longipes* on the eastern Mediterranean Anaximenes Seamount where it represented one of the most abundant species of the harpacticoid community. Provided these records are genuine it appears *P. longipes* is widely distributed throughout the world's deep sea basins. Baguley (2004) also recorded "*P.* aff. *longipes*" from the deep sea in the Northern Gulf of Mexico but the authenticity of this record remains unconfirmed. The same applies to the various unidentified *Psammis* records published from the Middle Atlantic Outer Continental Shelf off the coast of New Jersey (Boesch *et al*. 1981), the continental shelf off southwestern Vancouver Island, British Columbia (Brinkhurst

1987), the San Diego Trough (Thistle & Eckman 1990; Eckman & Thistle 1991), the Magellan region (Straits of Magellan and Beagle Channel) (George 1999, 2005), the northeastern Pacific off the western coast of the U.S.A. (Sedlacek 2007), the cold seep sites Green Canyon and Atwater Valley in the Gulf of Mexico (Degen 2010; Degen *et al*. (2012) and the Anaximenes Seamount in the eastern Mediterranean (George *et al*. 2018). It remains to be confirmed whether Kim's (2014a) record of *Psammis* sp. from the East Southern Sea and East Northern Sea of Korea is conspecific with *P. wellsi* **sp. nov.**

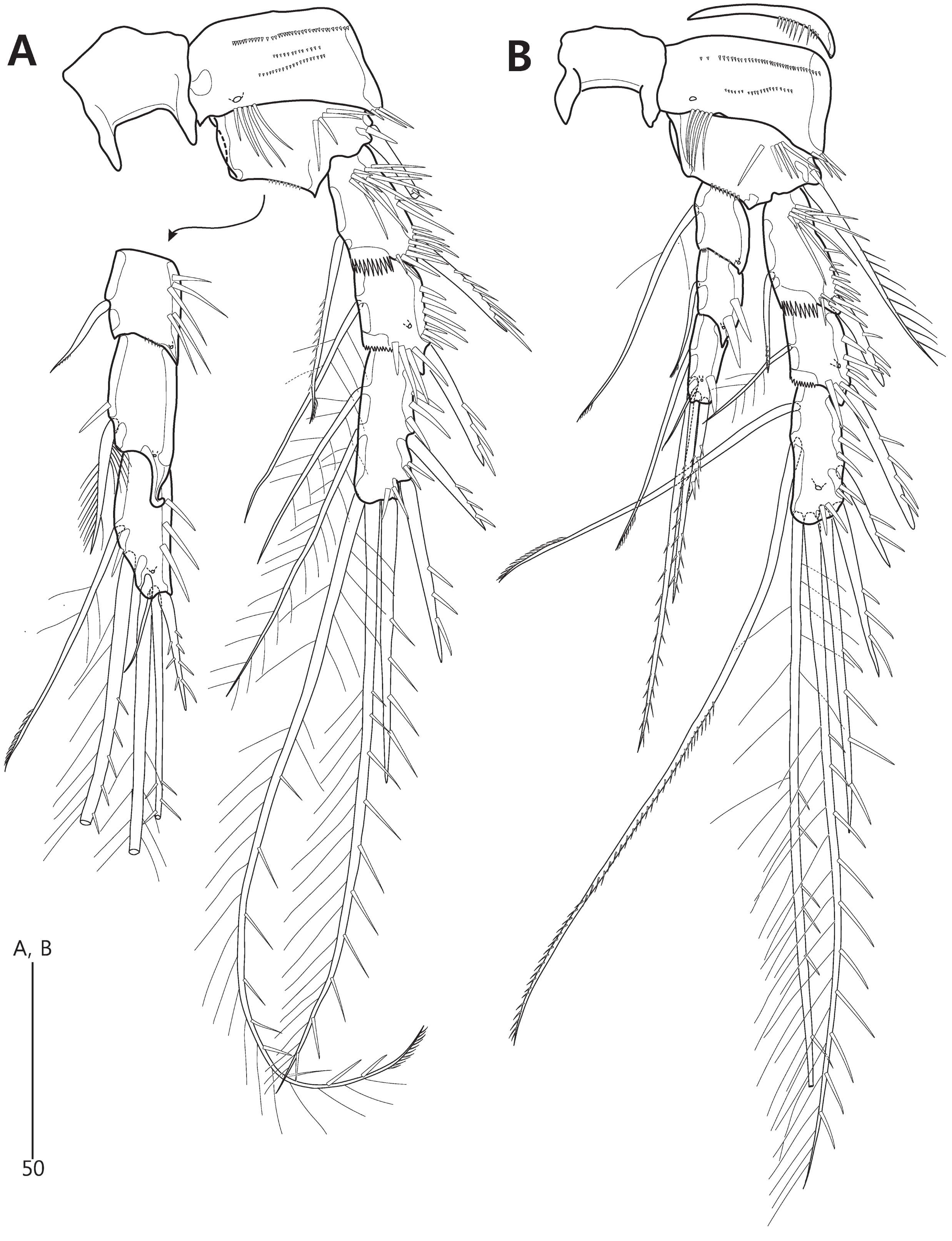

FIGURE 6. *Psammis wellsi* **sp. nov.** (♂): A, P3, anterior (disarticulated endopod shown in inset); B, P4, anterior.

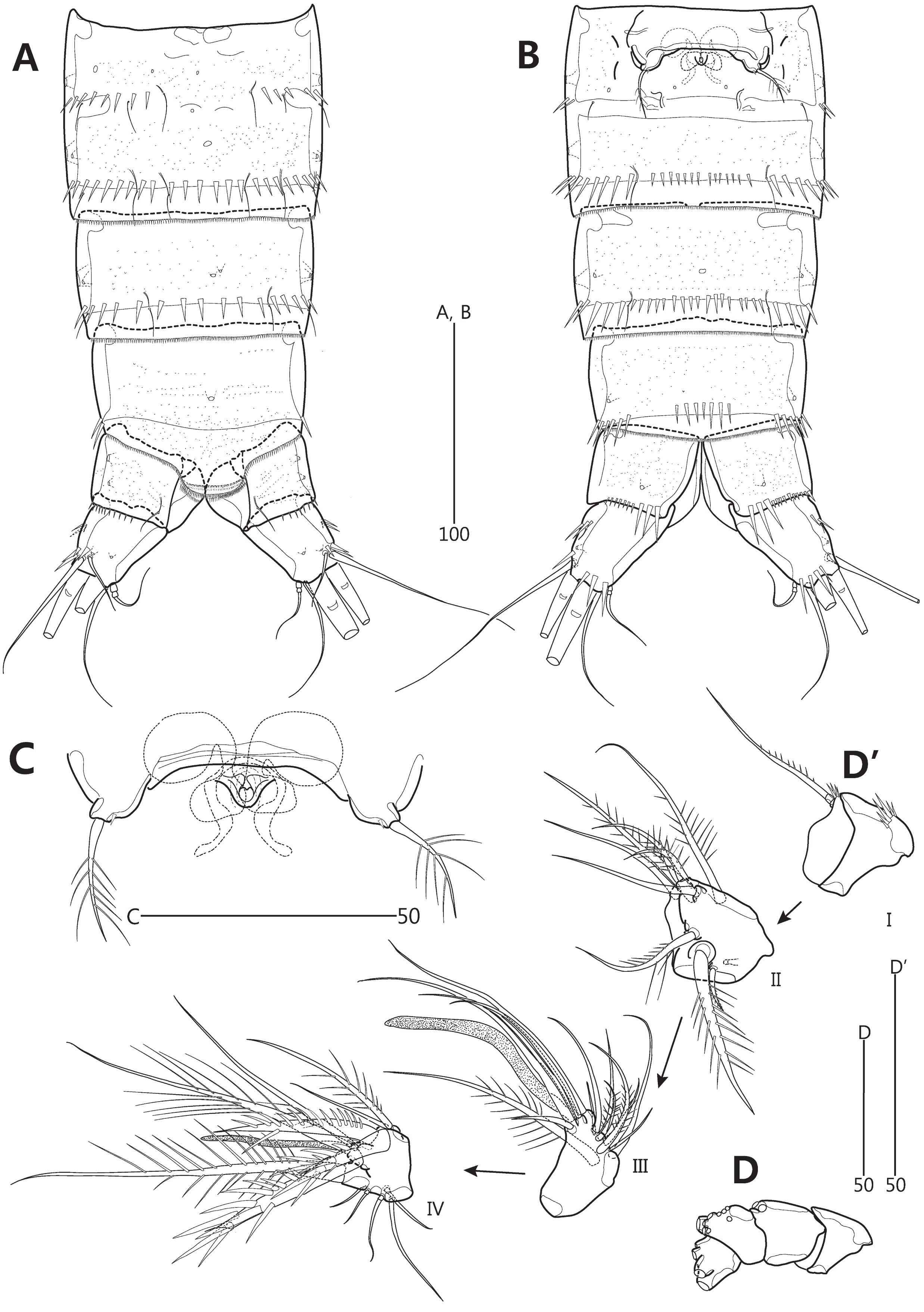

FIGURE 7. *Psammis wellsi* **sp. nov.** (♀): A, urosome, excluding P5-bearing somite, dorsal; B, same, ventral; C, genital field; D, antennule (armature omitted); D’, antennule disarticulated, dorsal.

Subfamily Pseudomeschrinae Willen, 1996

Genus *Pseudomesochra* T. Scott, 1902

The genus—initially believed to be intermediate between *Mesochra* Boeck, 1865 (Canthocamptidae) and *Cletodes* Brady, 1872 (Cletodidae)—was established by Scott (1902: 461) to accommodate the type species *P. longifurcata* T. Scott, 1902 (by monotypy) from Loch Etive on the west coast of Scotland. Unaware of this description Sars (1906: 191) proposed the genus *Stenheliopsis* in the Diosaccidae (= Miraciidae) for its type and only species *S. divaricata* Sars, 1906 from the south and west coasts of Norway, and subsequently added three new species, *S. latifurca* Sars, 1911, *S. media* Sars, 1911 and *S. affinis* Sars, 1920, all from southern Norway (Sars 1911, 1920). Prior to these contributions Scott & Scott (1901: 343) had already described the morphologically similar species, *Jonesiella brucei* Scott & Scott, 1901, from east of Hopen, Svalbard Archipelago. Brady (1880: 31) had placed *Jonesiella* Brady, 1880 (containing the species *J. fusiformis* Brady, 1880 and *J. spinulosa* Brady, 1880) in the subfamily Stenheliinae. Sars (1909: 328, 336) considered *Jonesiella* a junior subjective synonym of *Danielssenia* in the Tachidiidae, with *J. brucei* being treated as a valid member of this genus. Note that as a result of reconsidering the status of *Danielssenia fusiformis* (Brady, 1880) nec Sars (1910) (the type species of *Jonesiella*) *Jonesiella* has now been reinstated as a valid genus in the Danielsseniinae (then Paranannopidae) (Huys & Gee 1993: 62).

Monard (1927: 149, 159, 164) maintained *Stenheliopsis* in the Diosaccidae, placed *Pseudomesochra* in the Canthocamptidae, and considered both *Jonesiella* and *Danielssenia* as valid members (without listed species) of the Tachidiidae. In a later report (Monard 1935: 16) it transpired that the author intended to restrict *Jonesiella* to include only *J. brucei*, a course of action that is in violation with the Code (ICZN Art. 67.2). Gurney (1932: 50) expressed the dissenting view that *Pseudomesochra* should probably be assigned to the Cletodidae. The author (Gurney 1932: 49) also proposed the new replacement name *Nannomesochra* for the junior homonym *Pseudomesochra* Gurney, 1927 which was introduced for a new genus of Canthocamptidae (Gurney 1927: 542).

Having been associated with four different families Lang (1936b: 174; 1936c: 447–448) finally resolved the taxonomic mess surrounding *Pseudomesochra* by relegating *Stenheliopsis* to a junior subjective synonym of the latter and placing the genus in the Diosaccidae (= Miraciidae), therefore endorsing Sars's (1906: 192) earlier opinion that it is most closely related to *Stenhelia* Boeck, 1865. He also considered *Jonesiella brucei* a valid species of *Pseudomesochra*.

The familial assignment of the genus remained unchallenged until Willen (1996) transferred it from the Miraciidae as the type of a new subfamily Pseudomesochrinae in the Paranannopidae. Huys *et al*. (1996: 236), building on the non-availability of the generic name *Paranannopus* Lang, 1936d [*nomen nudum*], introduced the new family name Danielsseniidae to replace Paranannopidae [*nomen nudum*], since family-group names taking their stem from an unavailable (and thus invalid) generic name, also become unavailable (ICZN Arts 11.7.1.1 and 63–64). The family Paranannopidae was relegated to a subfamily of the Pseudotachidiidae by Willen (1999); hence at this rank it should be cited as Danielsseniinae Huys and Gee in Huys *et al*. (1996) (*cf.* Huys 2009: 11). Willen (2000) maintained the Pseudomesochrinae as one of four subfamilies recognized in her new classification of the Pseudotachidiidae. A second genus, *Keraia* Willen & Dittmar, 2009 was added to the Pseudomesochrinae (Willen & Dittmar 2009). The type genus *Pseudomesochra* has seen the addition of many new taxa since its proposal by Scott (1902) and currently includes 19 species (Table 2). Both *P. perplexa* Bodin, 1968 and *P. gemina* Coull, 1973 have been regarded as *species incertae sedis* by some authors (Willen 1996; Wells 2007) but are recognized as valid here.

Pseudomesochra tatianae **Drzycimski, 1968**

(Figs. 8–11)

Type locality. Norway, Norway, Korsfjord, 60º12'24"N, 05º13'06"E; mud at 512 m depth.

Original description. Drzycimski (1968): 18–20, Abb. 2.

Material examined. 1 ♀ (reg. no. NIBRIV0000853917) dissected on seven slides, 1 ♀ dissected on six slides (reg. no. NIBRIV0000853918), and 2 ♀♀ (reg. no. MInRB-Hr48-L001) preserved together in ethanol. Collected in Southern Sea of Korea, 33º30'N, 124º00'E (St. 1 in Fig. 1), 70.8 m depth, 05 June 2015.

TABLE 2. Antennulary segmentation and armature formulae of P1–P5 in members of *Pseudomesochra* T. Scott, 1902 and *Keraia* Willen & Dittmar, 2009. S = spinous projection (in ♂ of *P. perplexa*); ? = unknown.

	A1	P1		P2		P3		P4		P5 ♀		P5 ♂	
	♀	exp	enp	exp	enp	exp	enp	exp	enp	exp	enp	exp	enp
P. brucei (Scott & Scott, 1901) [1]	6	0.0.022	1.121	unknown	unknown	unknown	unknown	0.1.323	1.1.121	2	4	?	?
P. longifurcata T. Scott, 1902 [2]	6	0.0.022	0.121	0.1.123	1.221	0.1.023	1.221	0.1.023	1.221	–	[3]	?	?
P. divaricata (Sars, 1906) [3]	6	0.0.022	0.121	0.1.0??	1.221	0.1.023	1.221	0.1.0??	1.221	2	3	?	?
P. crispata (Brady, 1910) [4]	7	0.0.022	0.121	0.0.022	1.1.121	0.1.023	1.1.121	unknown	unknown	2	4	?	?
P. latifurca (Sars, 1911)	6	0.1.022	0.121	0.1.123	1.1.121	0.1.123	1.1.121	0.1.123	1.1.021	2	3	?	?
P. media (Sars, 1911) [5]	5	0.1.022	1.121	unknown	unknown	unknown	1.1.221	0.1.323	1.1.121	2	3	?	?
P. affinis (Sars, 1920) [6]	6	0.0.022	0.121	0.1.123	1.221	0.1.023	1.221	0.1.023	1.121	2	3	?	?
P. similis Lang, 1936b [7]	7	0.1.022	0.121	0.1.223	1.1.221	0.1.323	1.1.211	0.1.323	1.1.211	2	4	?	?
P. aberrans Bodin, 1968	6	0.1.022	0.121	0.1.222	1.1.221	0.1.322	1.1.221	0.1.322	1.1.121	2	3	?	?
P. perplexa Bodin, 1968	?	0.0.022	1.121	0.1.222	1.1.12S	0.1.322	1.1.120	0.1.222	1.1.120	?	?	2	0
P. tatianae Drzycimski, 1968	7	0.1.022	0.121	0.1.223	1.1.221	0.1.323	1.1.211	0.1.323	1.1.211	2	4	?	?
P. gemina Coull, 1973	7	0.1.022	0.121	0.1.223	1.1.221	0.1.323	1.1.211	0.1.323	1.1.211	2	4	2	0
P. minor Becker, 1974	6	0.0.022	1.121	0.1.223	1.1.221	0.1.223	1.1.221	0.1.123	1.1.221	2	4	?	?
P. abyssalis Becker & Schriever, 1979 [8]	5	0.0.022	1.121	0.1.222	1.1.221	0.1.322	1.1.121	0.1.322	1.1.111	2	3	?	?
P. beckeri Becker & Schriever, 1979 [9]	6	0.0.022	1.121	0.1.222	1.1.221	0.1.322	1.1.211	0.1.322	1.1.111	2	5	?	?
P. scheibeli Schriever, 1982	6	0.1.022	0.121	0.1.222	1.1.221	0.1.322	1.1.221	0.1.322	1.1.121	2	4	?	?
P. gertwilleni Willen, 1996 [10]	6	0.0.022	0.121	0.1.123	1.1.121	0.1.123	1.1.121	0.1.123	1.1.121	2	4	?	?
P. laptevensis Willen, 1996	7	0.1.022	0.121	0.1.223	1.1.221	0.1.323	1.1.211	0.1.323	1.1.211	2	4	?	?
P. meridianensis Willen, 1996	6	0.0.022	1.121	0.1.223	1.1.221	0.1.323	1.1.221	0.1.323	1.1.121	2	4	?	?
K. tamara (Smirnov, 1946) [11]	6	0.1.022	1.121	1.1.223	1.121	1.1.323	1.221	1.1.323	1.221	2	4	?	?
K. longiseta (Vasconcelos, George & Santos, 2008) [12]	5	0.1.022	1.121	1.1.223	1.121	1.1.223	1.221	1.1.223	1.221	?	4	?	?
K. ricardae Willen & Dittmar, 2009 [12]	5	0.1.022	1.121	1.1.223	1.121	1.1.223	1.221	1.1.223	1.221	2	4	?	?
K. longirostrata Apostolov, 2011	5	0.1.022	1.121	1.1.223	1.321	1.1.323	1.221	1.1.323	1.211	2	4	?	?

[1] : According to Lang (1948: 641) the swimming leg armature pattern is as in *P. longifurcata*, however neither Scott & Scott (1901) nor any other author(s) described or illustrated P2–P3.

[2] : Armature pattern of P2–P3 according to Lang (1948), presumably based on observations of material from the Gullmar Fjord. Scott (1902) described the P5 as a "… single lamelliform joint, bearing three long apical setae"; it is conceivable that his statement referred only to the endopodal lobe of P5. Lang (1948) reproduced Sars' (1920) illustration of P5 which was based on *P. affinis*. The species has traditionally been differentiated from *P. divaricata* in identification keys (Lang 1948; Coull 1973; Willen 1996) by the presence of a medial spinular patch near the base of the caudal ramus—in reality a feature characterizing *P. affinis* (Sars 1920: Plate XXXIV; see also [6]) but not *P. longifurcata* (Scott

1902: Plate XXIV, Fig. 35).

[3] : Lang's (1948: 641) statement on the armature of P2 is mistakenly based on Sars' (1906: plate CXXV) illustration of P3; neither P2 nor P4 were figured by Sars but his text description (p. 193) revealed that P2–P4 exp-1 and -3 lack an inner seta and the armature pattern of the endopods is 1.221. Willen's (1996: 103) statement that *P. gertwilleni* shares with *P. divaricata* the presence of an inner seta on P2–P4 exp-3 is therefore wrong. Coull (1973: Table II) and Vasconcelos *et al*. (2008) assumed that the exopodal pattern for P2–P4 was 0.1.023 but this requires confirmation. Unlike other known congeners both members of the female P5 are medially fused in *P. divaricata* (see Sars 1906: plate CXXV).

[4] : As pointed out by Lang (1948) Brady's (1910) illustrations of P2–P3 are probably incorrect and the armature patterns therefore potentially misleading.

[5] : Sars (1911: Supplement Plate 25) shows a P2 with three inner setae (the distal one being smaller than the other two) on exp-3 resulting in a 323 formula. According to Huys & Boxshall (1991: 119) the maximum number of elements on this segment is seven, the presence of only two inner setae being an apomorphy for the Harpacticoida. It is therefore concluded that Sars must have figured P4 instead of P2; this mistake was adopted by Lang (1948), Coull (1973) and Vasconcelos *et al*. (2008).

[6] : Lang (1936b: 174) considered this species a junior subjective synonym of *P. longifurcata*. Characters of both descriptions (Scott 1902; Sars 1920), such as the ornamentation of the caudal ramus, morphology of ♀ P5 and possibly armature of P2–P3, were combined in Lang's (1948) diagnosis of *P. longifurcata* and used unwisely in subsequent identification keys (Coull 1973; Willen 1996) (see also [2]). This course of action also resulted in the unjustified acceptance of a variable armature of P4 enp-2 (Coull 1973: Table II). *Pseudomesochra affinis* exhibits only one (*vs* two in *P. longifurcata*) inner seta(e) on P4 enp-2 and displays (*vs* lacks) a proximal spinular patch along the inner margin of the caudal ramus (Sars 1920: Plate XXXIV). Additional differences are found in the number of mandibular basal setae, the ornamentation and armature of the maxilliped, and in the shape of the caudal ramus (straight *vs* concave outer margin). Based on these differences *P. affinis* is removed from its synonymy with *P. longifurcata* and formally reinstated as a valid species.

[7] : According to Lang (1936b: 176, Abb. 7) P3–P4 enp-3 have only one apical seta, resulting in a 211 armature formula. In his monograph however this formula was changed to 221 (Lang 1948: 593, Table X); it is unclear whether this is a typographical error or the result of new observations. Note that Coull (1973: Table II, 603) and Wells (2007: 689) used the 221 pattern in their keys and so did Vasconcelos *et al*. (2008) in their Table 1 despite Drzycimski (1968: 20) having pointed out the discrepancy.

[8] : Becker & Schriever (1979: 52) erroneously listed the armature formula of P2 exopod as 1.222.

[9] : Becker & Schriever's (1979: 52) description of P3 shows a discrepancy between the text (1.1.221) and the illustration (1.1.211); the latter is adopted here.

[10] : Willen (1996) describes and illustrates the ♀ antennule as 6-segmented but erroneously uses the 7-segmented condition in her identification key (couplet 10).

[11] : According to Willen & Dittmar's (2009) diagnosis of *Keraia* the antennule is 5-segmented; however, it was denoted as 6-segmented by Smirnov (1946) in his text description of *K. tamara* (although only the first four segments were illustrated in full). Smirnov's (1946) armature formulae of the endopods of P2 (1.220) and P3–P4 (1.320) were reinterpreted by Coull (1973) as 1.121 and 1.221, respectively. Smirnov also lists the armature pattern of P4 exopod as 1.1.323 but only illustrates it as 1.1.223. The former is adopted here since it corresponds to the one found in Coull's (1973) specimens from the deep sea off North Carolina. One male was reported by Smirnov (1946)—the only one in the genus *Keraia* so far—but no morphological information was given.

[12] : These species—both described from the Southern Atlantic—are extremely similar and may well be conspecific. They are here provisionally maintained as separate species based on small differences in cephalothoracic length, length ratio of apical setae on the antennary exopod, relative length of P1 endopodal segments and setal arrangement on the ♀ P5 endopodal lobe.

Redescription of female. Total length from anterior margin of rostrum to posterior margin of caudal rami about 615 µm (measured in lateral aspect). Habitus (Fig. 8A–B) slightly pyriform, with distinct separation between prosome and urosome; prosome wider than urosome, greatest width measured at P2-bearing somite. Rostrum (Fig. 8A–C) large, broad, defined at base, with two apical sensilla and two middorsal pores. Cephalothorax bell-shaped, slightly longer than greatest width, and with sensillar pattern and few pores as figured; P2-bearing somite separated from cephalothorax by large arthrodial membrane. Pedigerous somites gradually tapering posteriorly, ornamented with setules; hyaline frills plain; intersomitic membranes of second to fourth somites discernible in dorsal and lateral aspect. Urosome (Figs. 8A, 10A) slightly tapering posteriorly, ornamented with sensilla dorsally and ventrally except for penultimate somite and ventral surface of anal somite. Genital double-somite and abdominal somites 2–3 with multiple transverse rows of fine spinules dorsally. Genital and first abdominal somites completely fused, forming genital double-somite; original segmentation marked externally by slight bilateral constriction and internally by lateral transverse cuticular ribs. Gonopores (Fig. 10C) fused, forming common median genital slit; sixth legs (P6) fused, forming single plate with two bare setae either side. Copulatory pore small, located just posterior to genital slit; connected via short copulatory duct with paired anterior seminal receptacles. Posterior margin of penultimate somite with weakly produced dorsal extension, reaching to proximal fourth of anal somite (Fig. 8A). Anal somite (Fig. 8A) small, cleft medially; with one pair of dorsal sensilla, and minute dorsolateral spinules along posterior margin (not figured); operculum smooth.

Antennule (Fig. 8D–D’) slender, 7-segmented; with aesthetasc on segments 4 and 7; segment 5 shortest; posterior seta on segment 6 enlarged, densely plumose and bi-articulated at base. Setal armature as follows: 1-[1], 2-[7 + 2 pinnate], 3-[5], 4-[2 + (1 + ae)], 5-[2], 6-[5 + 1 pinnate + 1 plumose], 7-[5 + (1 + ae)]. Each aesthetasc fused basally to adjacent seta.

Antenna (Fig. 9A) comprising coxa, allobasis and free endopod. Coxa represented by small, unornamented sclerite. Abexopodal margin of allobasis with spinules in basal half and one bipinnate seta halfway down its length. Exopod 2-segmented; exp-1 shortest, with two closely set setae subdistally; exp-2 about 1.5 times as long as exp-1, with two lateral and two apical setae, and two spinule rows; all exopodal setae bipinnate.

Mandible (Fig. 9B). Coxa with small pointed process medially; gnathobase comprising five bi- or multicuspidate teeth, one bare spine and one pinnate seta, and ornamented with row of minute spinules. Palp comprising basis and 1-segmented rami. Basis broad, arising from coxal peduncle; with two pinnate setae distally. Exopod small; with three inner, one apical and two outer setae; all exopodal setae naked. Endopod twice as long as exopod; with two lateral, one subapical and three apical setae, two of which fused basally; all endopodal setae bare.

Maxillule (Fig. 9C) with well-developed praecoxal arthrite bearing two juxtaposed anterior setae; distal armature consisting of eight spines and one pinnate seta. Coxa with cylindrical endite bearing one unipinnate spine subapically and three naked setae apically. Basal endite with seven naked setae distally. Exopod 1-segmented, with two (sub)apical naked setae. Endopod 1-segmented, longer than exopod, with three apical naked setae.

Maxilla (Fig. 9D). Syncoxa armed with few minute spinules along distal outer margin; proximal endite broad, with two plumose setae; middle endite with one plumose and one bare setae apically; distal endite with one bare and two plumose setae. Allobasis drawn out into acutely recurved claw bearing three accessory setae. Endopod 1-segmented, with four setae.

Maxilliped (Fig. 9E). Syncoxae arising from common bilobate median pedestal; elongate, with spinules at inner distal corner. Basis expanded in distal half, forming lobate expansion along outer margin; with five rows of minute spinules and one long bare seta near distal inner corner. Endopod not expressed.

P1 (Fig. 10D) with wide intercoxal arthrite. Praecoxa small, unornamented. Coxa large, with lobate expansion along outer margin; anterior surface with five rows of minute spinules. Basis smaller than coxa, with bipinnate outer seta and stout, pinnate inner spine; anterior surface with pore and spinules near articulation with endopod and at base of inner spine. Exopod 3-segmented, each segment with spinules along outer margin and outer distal corner; exp-1 longest, with few setules along inner margin; exp-2 about as long as wide; exp-3 slightly longer than exp-2; spines of exp-2 and -3 with spinules along outer margin only. Endopod extending beyond distal margin of exopod, 2-segmented; each segment with spinules along outer and distal margins; enp-1 elongate, not reaching to distal margin of exp-2, unarmed; enp-2 as long as enp-1 but slightly more slender.

P2–P4 (Fig. 11A–C). Intercoxal sclerite large, with convex distal margin. Coxa large; anterior surface naked in P3–P4 but with four rows of minute spinules in P2. Basis smaller than coxa, with minutely pinnate (P2) or plumose (P3–P4) outer seta and spinules near articulation with endopod. Exopod 3-segmented, each segment with spinules along outer margin and distal outer corner; exp-1 typically longest, with setules along inner margin; exp-2 about as long wide, with pore on anterior surface; exp-3 longer than exp-2. Endopod 3-segmented; longer than exopod in P2, about as long as in P3, and shorter than in P4; each segment armed with spinules along outer margin; segments of each ramus progressively narrower from exp-1 to -3; enp-3 gradually reducing in size from P2 to P4, with pore on anterior surface. Armature formulae of P1–P4 as follows:

	Exopod	Endopod
P1	0.1.022	1.121
P2	0.1.223	1.1.221
P3	0.1.323	1.1.211
P4	0.1.323	1.1.211

P5 (Fig. 10E). Intercoxal sclerite minute. Both rami fused, forming single bilobate plate with deep V-shaped notch between exopodal and endopodal lobes. Endopodal lobe broad and rounded, with four long, evenly spaced, naked setae along distal margin; anterior surface with pore between bases of two outermost setae. Exopodal lobe distinctly smaller and subtriangular; with short outer and long apical seta. Outer basal seta naked with its setophore completely absorbed in outer margin of plate.

Caudal rami (Figs. 8A–B, 10A–B) divergent, about twice as long as wide; ventral surface with pore near base of seta II and row of fine spinules along posterior margin; with seven setae: seta I very small, arising halfway down length of outer margin; seta II twice as long as caudal ramus, arising from distal fifth of ramus; setae III and VI long and naked; distal setae IV–V well-developed, pinnate and flexible distally (rat-tail setae *sensu* Willen (1996)); seta IV shorter than seta V; seta VII plumose, as long as caudal ramus, situated halfway down the ramus near the inner margin.

Male. Unknown.

Remarks. Our Korean specimens agree in virtually every morphological aspect with *Pseudomesochra tatianae*, originally described from two fjords along the Norwegian west coast (Drzycimski 1968). The species can readily be identified by the following combination of characters: (1) antennule ♀ with 7-segmented; (2) antennary exopod 2-segmented; (3) extremely reduced maxilliped, lacking expression of the endopod; (4) P1 exp-1 with and enp-1 without an inner seta; (5) P2–P4 exp-3 with three outer spines; and (6) P3–P4 exp-3 with three inner setae. Our Korean female specimens deviate in some minor differences from the original description of *P. tatianae* such as the presence of caudal ramus seta I, the plumose ornamentation of caudal ramus seta VII, and the spinular ornamentation of the maxillipedal basis and P2 coxa. Such discrepancies are undoubtedly based on erroneous observations of morphological minutiae and are insignificant at the taxonomic level.

Pseudomesochra tatianae belongs to a group of species that share the following character states: antennule ♀ 7-segmented, P1 enp-1 as long as or longer than enp-2, P2–P4 exp-3 with three outer spines, and two, three, three inner setae, respectively, P2–P3 enp-3 with two inner setae; P4 enp-3 with four elements, P5 ♀ inner exopodal seta as long as or longer than endopodal setae, and caudal ramus about twice as long as wide. This species group includes *P. similis* Lang, 1936b, *P. laptevensis* Willen, 1996 and *P. tatianae*. The latter differs in the morphology of the maxilliped (reduced and endopod not expressed *vs* endopod represented by small segment bearing seta or short claw) and the length of the inner exopodal seta of P5 ♀ (about as long as outer endopodal seta *vs* distinctly longer in *P. similis* and *P. laptevensis*). *Pseudomesochra tatianae* is also readily distinguished from *P. laptevensis* by the setal armature of P3–P4 enp-3 (two inner setae in *P. tatianae vs* only a single seta in *P. laptevensis*). The species had not been recorded again since its original description although Easton & Thistle (2016) recently reported six individuals from two deep-sea localities (2,698–3,247 m) off the western coast of the U.S.A. which they attributed to *P.* cf. *tatianae*.

The genus *Pseudomesochra* assumes a worldwide distribution as demonstrated by the numerous unidentified species that have been reported, including records from the northeastern Pacific off the western coast of the U.S.A. (Sedlacek 2007; Easton & Thistle 2016), the San Diego Trough (Eckman & Thistle 1988, 1991), the Clarion Clipperton Fracture zone in the north-east Pacific (Radziejewska 2014; Radziejewska & Kotliński 2002), the Kuril Trench in the north-west Pacific Ocean (Kitahashi *et al*. 2013), the Ryukyu Trench (Kitahashi *et al*. 2014), South Andaman (Jayabarathi 2016), the equatorial North Pacific (Mullineaux 1987), the Peru Basin (Willen 1996, 2000), the Magellan Region (Straits of Magellan and Beagle Channel) (George 1999, 2005), New Zealand (Webber *et al*. 2010), the Weddell Sea (Willen 1996), the deep sea off North Carolina (Coull 1973), the Gulf of Mexico (Baguley

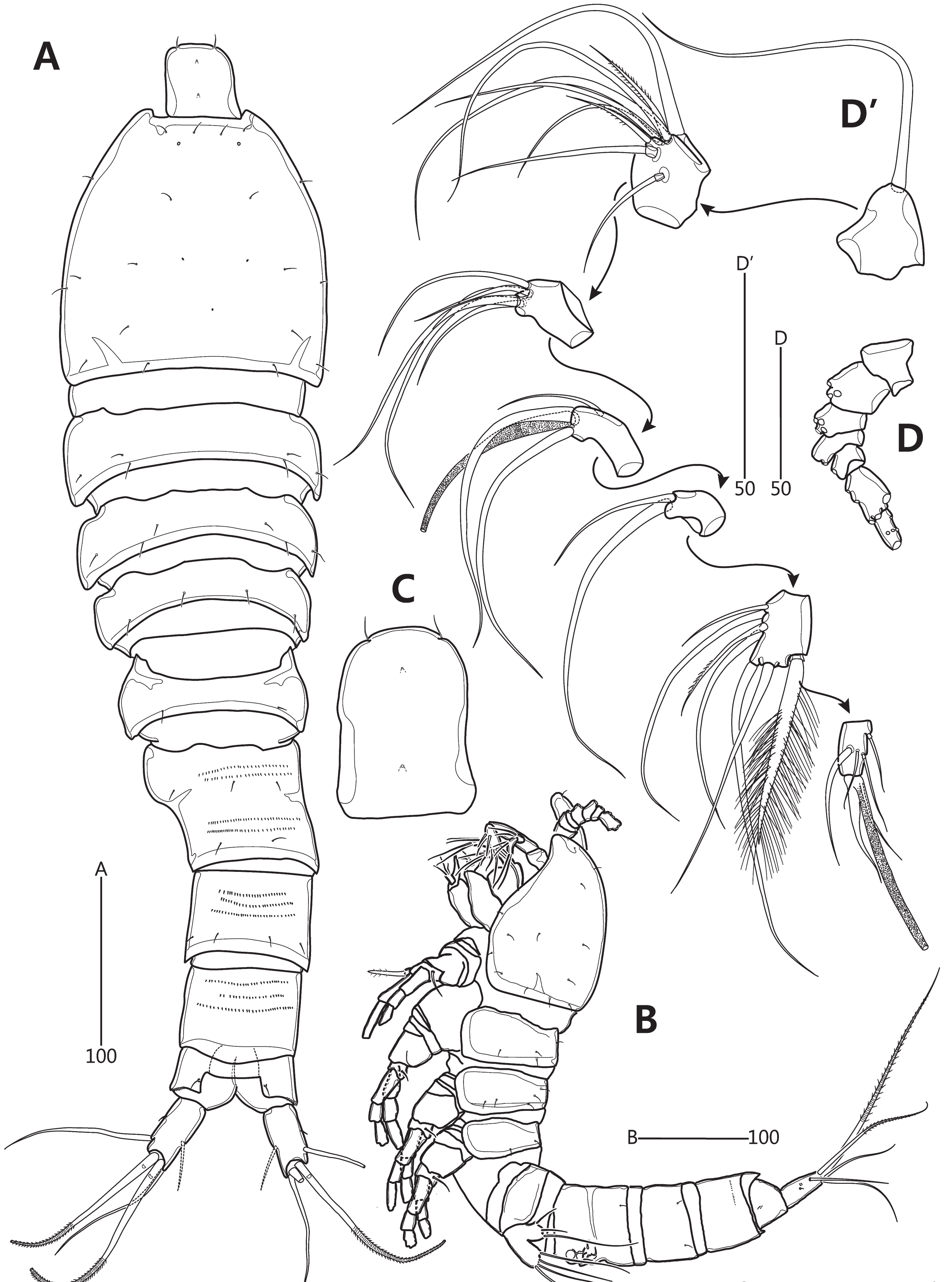

FIGURE 8. *Pseudomesochra tatianae* Drzycimski, 1968 (♀): A, habitus, dorsal; B, habitus, lateral; C, rostrum, dorsal; D, antennule (armature omitted); D’, antennule disarticulated, dorsal.

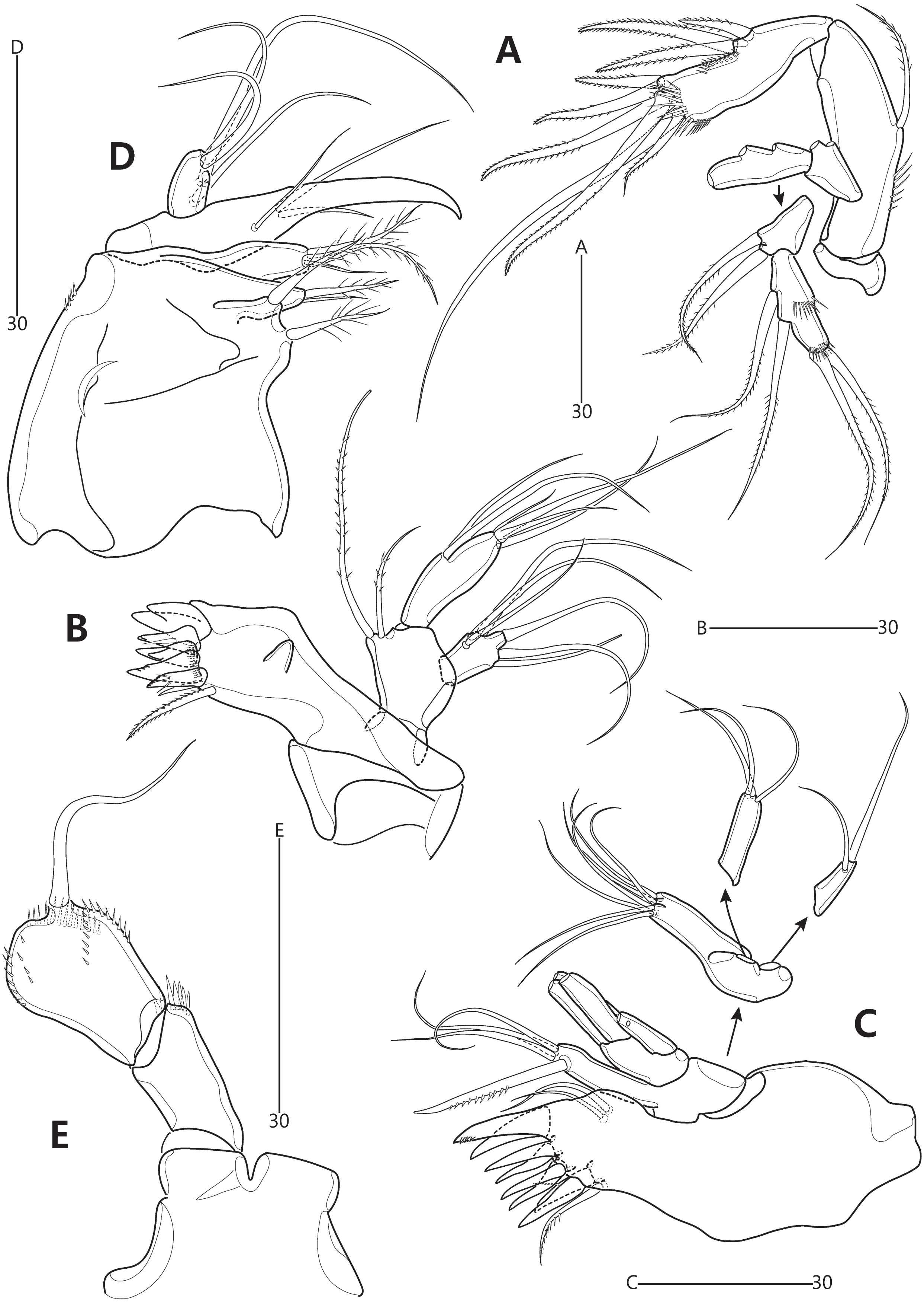

FIGURE 9. *Pseudomesochra tatianae* Drzycimski, 1968 (♀): A, antenna (exopod with complete armature shown in separate inset); B, mandible; C, maxillule (with disarticulated basis and rami); D, maxilla; E, maxilliped.

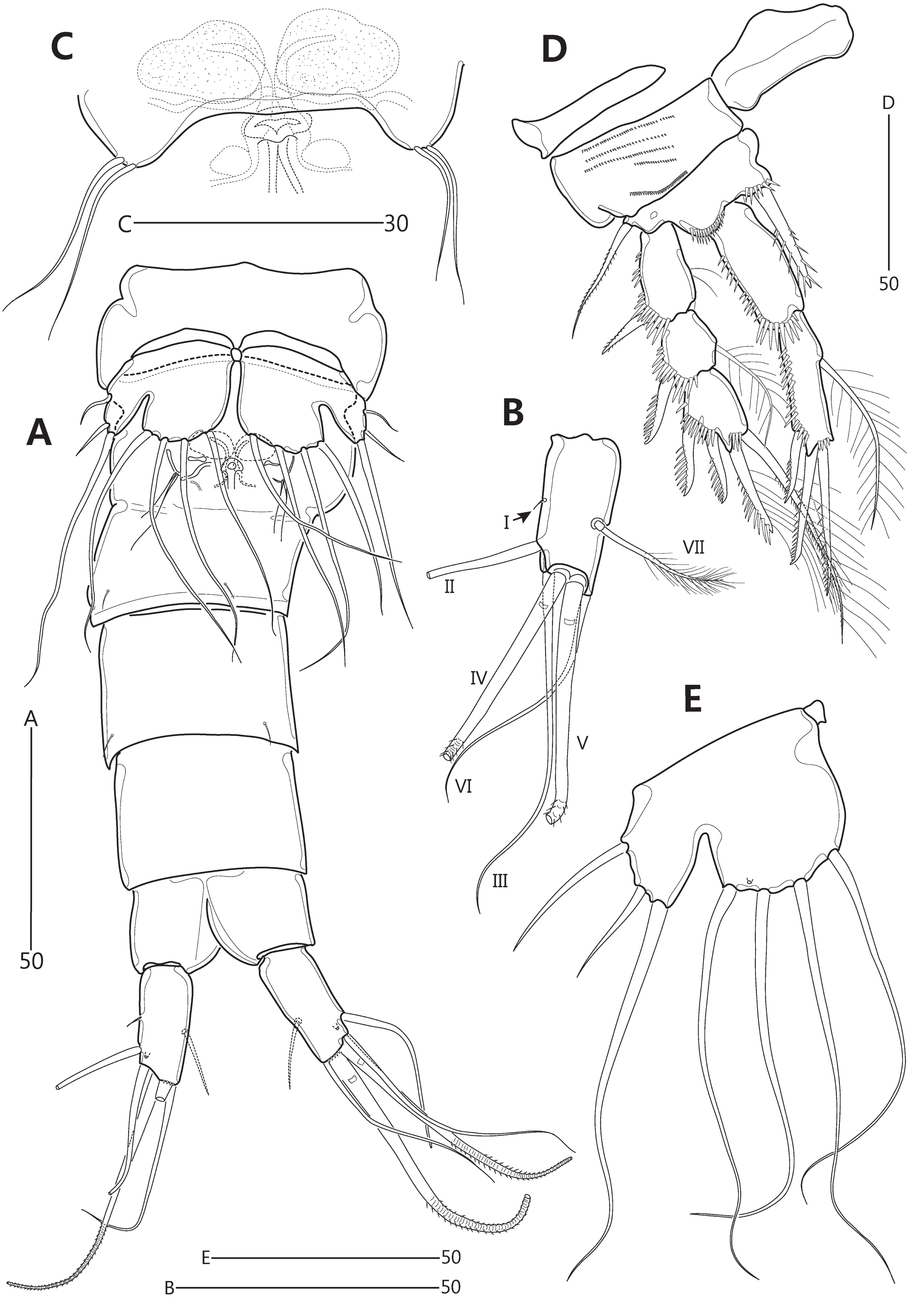

FIGURE 10. *Pseudomesochra tatianae* Drzycimski, 1968 (♀): A, urosome, ventral; B, left caudal ramus, dorsal; C, genital field; D, P1, anterior; E, right P5, anterior.

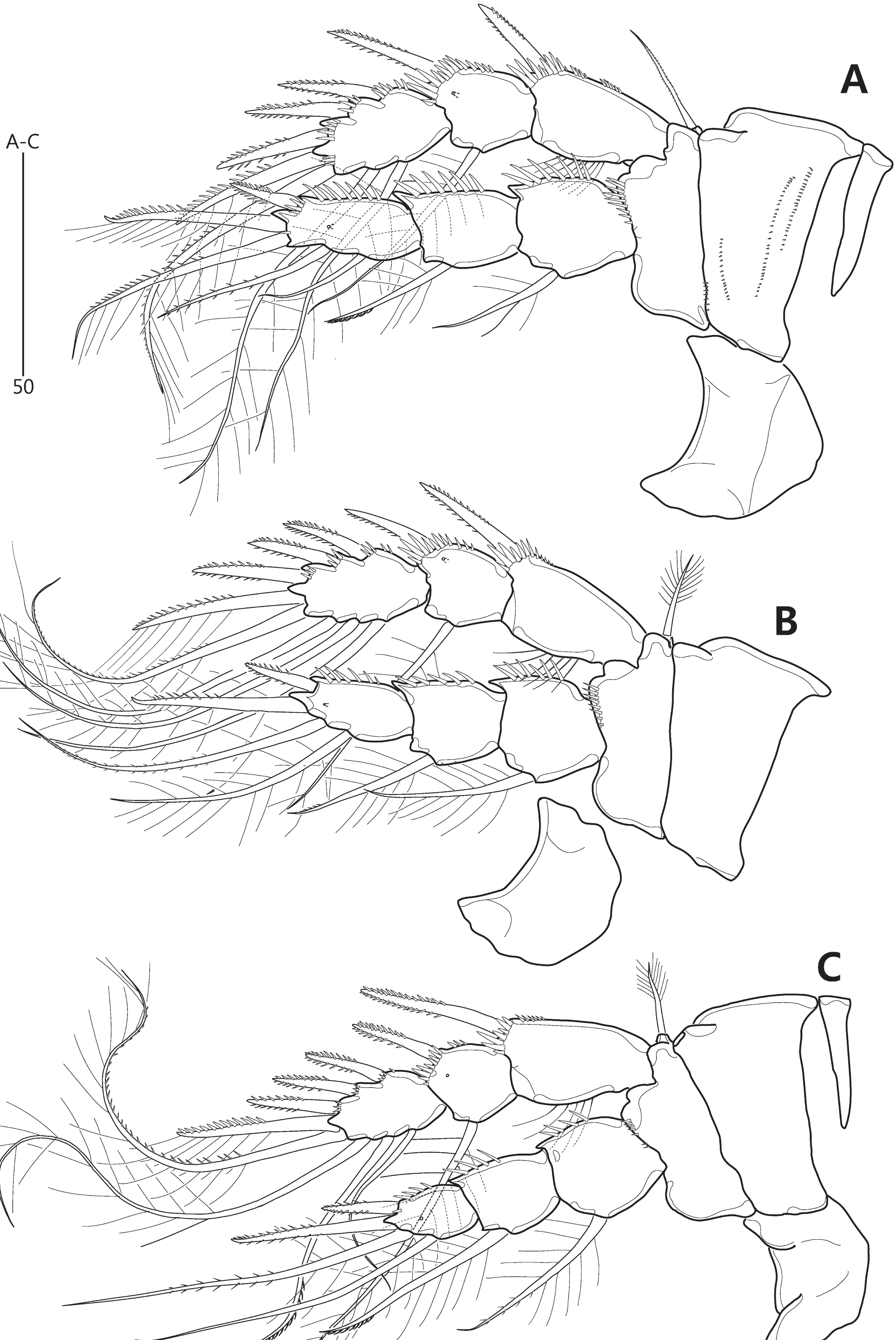

FIGURE 11. *Pseudomesochra tatianae* Drzycimski, 1968 (♀): A, P2, anterior; B, P3, anterior (intercoxal sclerite shown in inset); C, P4, anterior.

2004; Brooks *et al*. 2009; Degen 2010; Degen *et al*. 2012; Plum *et al*. 2015), the Sedlo and Seine Seamounts in the North Atlantic (Büntzow 2011; George 2013), the Porcupine Seabight (Gheerardyn 2007), the Svalbard Archipelago (Kotwicki 2002), the Laptev Sea (Willen 1996), the Anaximenes Seamount in the eastern Mediterranean Sea (George *et al*. 2018) and a marine cave near Marseille (Janssen *et al*. 2013). Buhl-Mortensen *et al*. (2010) found that members of *Pseudomesochra* represented over 30% of the harpacticoid community found on glass sponge skeletons in the cold-water coral degradation zone. This study was partly based on research by Gheerardyn (2007) (see also Gheerardyn *et al*. 2009, 2010) who found seven new species in the Porcupine Seabight in the northeast Atlantic, rendering *Pseudomesochra* one of the most speciose genera in the study area. George *et al*. (2018) reported ten unnamed species of *Pseudomesochra* from the Anaximenes Seamount in the eastern Mediterranean Sea. On the lower trench slope of the Kuril Trench (Kitahashi *et al*. 2013) and on the abyssal seafloor of the Clarion Clipperton Fracture zone (Radziejewska & Kotliński 2002) it is the second most abundant genus accounting for over 10% of total harpacticoid density while in the Ryukyu Trench it is the third most abundant genus across the entire bathymetric range (Kitahashi *et al*. 2014). Sedlacek (2007) identified six species on the continental slope off central California while Baguley (2004) recorded no less than 23 unidentified species from the deep sea in the Northern Gulf of Mexico. Despite this as yet unexplored species diversity in many deepwater areas of the world's oceans it is remarkable that a great proportion of the species described so far are only known from the type locality (Table 3).

Key to species of Pseudomesochrinae

Existing identification keys (Lang 1948; Coull 1973; Willen 1996; Wells 2007) are either out of date or unsound due to misinterpretations or observational errors (see footnotes in Table 2). A new key is presented below which, in the absence of male information for most species, is inevitably based on female characters only. Single male specimens have so far been reported on only four occasions: *Pseudomesochra gemina* (Coull 1973; Willen 1996), *P. perplexa* (Bodin 1968), and *Keraia tamara* (Smirnov, 1946) (Smirnov 1946).

1. Antennule ♀ with conspicuous projection on posterior distal corner of segment 1; antennary exopod enlarged, exp-2 with at least one very long element at its tip; P1 exp-1 elongate, longer than exp-2 and -3 combined; outer elements of P1 exp-1 and -2 setiform; P2–P4 exp-1 with inner seta . . . . *Keraia* Willen & Dittmar, 2009 2

\- Antennule ♀ without conspicuous projection on posterior distal corner of segment 1; antennary exopod not enlarged, with apical setae of distal segment not excessively long; P1 exp-1 not elongate, shorter than exp-2 and -3 combined; outer elements of P1 exp-1 and -2 spiniform; P2–P4 exp-1 without inner seta . . . . *Pseudomesochra* T. Scott, 1902 5

2\. P2 enp-2 with one or two inner setae 3

\- P2 enp-2 with three inner setae . . . . *K. longirostrata* Apostolov, 2011

3\. Antennule ♀ 5-segmented; P3–P4 exp-3 with two inner setae 4

\- Antennule ♀ 6-segmented; P3–P4 exp-3 with three inner setae . . . . *K. tamara* (Smirnov, 1946)

4 Cephalothorax about 1.3 times as long as maximum width; apical segment of antennary exopod with shorter seta about half the size of longest one; P5 endopodal lobe ♀ with one lateral and three apical setae . . . . *K. longiseta* (Vasconcelos, George & Santos, 2008)

\- Cephalothorax about 1.1 times as long as maximum width; apical segment of antennary exopod with longest seta only slightly larger than shorter one; P5 endopodal lobe ♀ with all four setae arranged around apical margin. . . . . *K. ricardae* Willen & Dittmar, 2009

5 P2–P4 endopods 2-segmented 6

\- P2–P4 endopods 3-segmented 8

6 P4 enp-2 with one inner seta; inner margin of caudal ramus with spinular patch near base . . . . *P. affinis* (Sars, 1920)*

\- P4 enp-2 with two inner setae; inner margin of caudal ramus without spinular patch near base. 7

7 P2 exp-3 with inner seta; caudal ramus slightly expanded proximally and with concave outer margin; P5 endopodal lobe ♀ with three very long setae. . . . . *P. longifurcata* T. Scott, 1902

\- P2 exp-3 without inner seta; caudal ramus not expanded at base and with straight inner and outer margins; P5 endopodal lobe ♀ with long middle seta flanked by two shorter ones, all of which markedly shorter than in preceding species . . . . *P. divaricata* (Sars, 1906)

8 P1 exp-2 with inner seta 9

\- P1 exp-2 without inner seta 16

9 Antennule ♀ 5-segmented; P1 enp-1 with inner seta. . . . . *P. media* (Sars, 1911)

\- Antennule ♀ 6- or 7-segmented; P1 enp-1 without inner seta 10

10 P2–P4 exp-3 with one inner seta; P2–P3 enp-3 with one inner seta; P4 enp-3 with three elements . . . . *P. latifurca* (Sars, 1911)

\- P2–P4 exp-3 with two, three, three setae, respectively; P2–P3 enp-3 with two inner setae; P4 enp-3 with four elements. . . . 11

11 Antennule ♀ 6-segmented; P2–P4 exp-3 with two outer spines 12

- Antennule ♀ 7-segmented; P2–P4 exp-3 with three outer spines 13

12 P2–P4 exp-3 subcircular, about as long as wide; P5 endopodal lobe ♀ with three setae; caudal ramus about three times as long as wide . . . . *P. aberrans* Bodin, 1968

- P2–P4 exp-3 subrectangular, distinctly longer than wide; P5 endopodal lobe ♀ with four setae; caudal ramus about four times as long as wide . . . . *P. scheibeli* Schriever, 1982

13 P5 ♀ inner exopodal seta distinctly shorter than endopodal setae; caudal ramus about 1.7 times as long as wide . . . . *P. gemina* Coull, 1973

- P5 ♀ inner exopodal seta as long as or longer than endopodal setae; caudal ramus about twice as long as wide 14

14 Maxillipedal endopod absent; inner exopodal seta of P5 ♀ about as long as outer endopodal seta . . . . *P. tatianae* Drzycimski, 1968

- Maxillipedal endopod represented by small segment with seta or short claw; inner exopodal seta of P5 ♀ distinctly longer than outer endopodal seta 15

15 Antennary exopod with four setae on distal segment; maxilliped with two setae on syncoxa and unarmed basis; P5 endopodal lobe ♀ reaching far beyond distal margin of exopodal lobe . . . . *P. similis* Lang, 1936b

- Antennary exopod with three setae on distal segment; maxilliped with unarmed syncoxa and one seta on basis; P5 endopodal lobe ♀ not reaching beyond distal margin of exopodal lobe . . . . *P. laptevensis* Willen, 1996

16 P1 enp-1 without inner seta; P2–P3 exp-3 with one or no setae 17

- P1 enp-1 with inner seta; P2–P3 exp-3 with two inner setae 18

17 Antennule ♀ 6-segmented; P2–P3 exp-3 with six setae/spines; outer exopodal seta of P5 ♀ very short, about as long as outer basal seta; caudal ramus about eight times as long as wide . . . . *P. gertwilleni* Willen, 1996

- Antennule ♀ 7-segmented; P2–P3 exp-3 with four and five setae/spines, respectively; outer exopodal seta of P5 ♀ well developed, markedly longer than outer basal seta; caudal ramus about 2–3 times as long as wide . . . . . . *P. crispata* (Brady, 1910)**

18 P4 exp-3 with two outer spines 19

- P4 exp-3 with three outer spines 21

19 P4 exp-3 with two inner setae; P4 endopod consisting of three equally narrow, rectangular segments and reaching only narrowly beyond distal margin of exp-2 . . . . *P. perplexa* Bodin, 1968

- P4 exp-3 with three inner setae; P4 endopod extending to about middle of exp-3, with enp-1 and -2 being markedly broader and larger than enp-3 20

20 Antennule ♀ 5-segmented; antennary exopod 2-segmented; P5 endopodal lobe ♀ with three setae; caudal ramus conical in dorsal aspect . . . . *P. abyssalis* Becker & Schriever, 1979

- Antennule ♀ 6-segmented; antennary exopod 3-segmented; P5 endopodal lobe ♀ with five setae, outermost being minute; caudal ramus rectangular in dorsal aspect . . . . *P. beckeri* Becker & Schriever, 1979

21 Maxilliped with one pinnate spine and one naked seta on syncoxa, and long spinules along distal half of endopodal claw; P4 exp-3 with one inner seta; P4 enp-3 with two inner setae . . . . *P. minor* Becker, 1974

- Maxilliped with one pinnate seta on syncoxa, and endopodal claw without spinular ornamentation; P4 exp-3 with three inner setae; P4 enp-3 with one inner seta 22

22 Antennary exopod 2-segmented; caudal rami divergent, equally wide along their entire length and without spinules along inner margin . . . . *P. meridianensis* Willen, 1996

- Antennary exopod 3-segmented; caudal rami juxtaposed with basal portion widest and inner margin bearing fine spinules . . . . *P. brucei* (Scott & Scott, 1901)

* Reinstated species (removed from its synonymy with *P. longifurcata*; *cf*. Table 2).

** Brady's (1910) illustrations of P2–P3 probably contain observational errors and the armature patterns should therefore be treated with caution.

Acknowledgements

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TABLE 3. Published and other records of Pseudomesochrinae (*P.* = *Pseudomesochra*; *K.* = *Keraia*; * = type locality)

Species	Locality	Depth (m)	Reference
P. brucei (Scott & Scott, 1901)	east of Hopen, Svalbard Archipelago*	183–201	Scott & Scott (1901) [1]
	western Laptev Sea (Arctic)	?	Chertoprud *et al*. (2018) [2]
P. longifurcata T. Scott, 1902	Gullmar Fjord (Sweden)	60–120	Lang (1948) [3]
	Upper Loch Etive (Scotland)*	> 110	Scott (1902)
	Firth of Clyde (Scotland)	192	C.G. Moore (pers. commn)
	North Sea	?	Huys *et al*. (1992)
	Magellan Region	219	George (1999, 2005)
P. divaricata (Sars, 1906)	Bukken and Farsund (western and southern Norway)	91.5	Sars (1906) [4]
	Fierfjord/Langesundfjord (southern Norway)	99–107	Heip *et al*. (1988)
	Gullmar Fjord (Sweden)	~100	Lang (1948)
	Skagerak (Sweden)	150–200	Por (1964)
	Loch Nevis (Scotland)	101	Wells (1965)
P. crispata (Brady, 1910)	Gauss Station, south of Kerguelen (Antarctic)*	350–385	Brady (1910)
P. latifurca (Sars, 1911)	Lyngenfjord (northern Norway)*	110	Sars (1911)
	Irish Sea	73–107	Moore (1979; pers. commn)
	Southern Celtic Sea	106	J.M. Gee (pers. commn)
	Thames estuary (England)	?	Attrill (1998) [5]
	Banyuls-sur-Mer (France)	50–75	Soyer (1971)
P. media (Sars, 1911)	Farsund (southern Norway)*	36.5	Sars (1911)
	Gullmar Fjord (Sweden)	20	Lang (1948)
	Loch Nevis (Scotland)	101	Wells (1965)
	Loch Creran (Scotland)	11	E. Ólafsson (pers. commn)
	Southern Celtic Sea	106	J.M. Gee (pers. commn)
	Banyuls-sur-Mer (France)	?	Soyer (1971)
	off North Carolina (U.S.A.)	180–5,250	Coull (1973)
P. affinis (Sars, 1920)	Risør (southern Norway)*	55–73	Sars (1920)
P. similis Lang, 1936b	Väderöarna, Bohuslän (Sweden)*	290–300	Lang (1936b)
	Banyuls-sur-Mer (France)	50–75	Soyer (1971)
	off North Carolina (U.S.A.)	1,050–3,940	Coull (1973)

......continued on the next page

TABLE 3. (Continued)

Species	Locality	Depth (m)	Reference
	Marseille (France)	marine cave	Janssen *et al*. (2013)
P. aberrans Bodin, 1968	Bay of Biscay*	3,950	Bodin (1968)
P. perplexa Bodin, 1968	Bay of Biscay*	3,950	Bodin (1968)
P. tatianae Drzycimski, 1968	Korsfjord (Norway)*	512–680	Drzycimski (1968)
	Husnesfjord (Norway)	520	Drzycimski (1968)
	Southern Sea (South Korea)	70.8	present study
P. gemina Coull, 1973	off North Carolina (U.S.A.)*	2,300	Coull (1973)
	Laptev Sea (Arctic)	?	Willen (1996)
P. minor Becker, 1974	Peru-Chile (Atacama) Trench (Eastern Pacific)*	920	Becker (1974)
P. abyssalis Becker & Schriever, 1979	Iberian deep sea*	3,810	Becker & Schriever (1979)
P. beckeri Becker & Schriever, 1979	Iberian deep sea*	3,920	Becker & Schriever (1979)
P. scheibeli Schriever, 1982	Greenland–Iceland–Faroe Ridge*	500	Schriever (1982)
P. gertwilleni Willen, 1996	Weddell Sea (Antarctic)*	323	Willen (1996)
P. laptevensis Willen, 1996	Laptev Sea (Arctic)*	280	Willen (1996)
P. meridianensis Willen, 1996	Weddell Sea (Antarctic)*	470	Willen (1996)
K. tamara (Smirnov, 1946)	Laptev Sea (Arctic)	869	Smirnov (1946) [6]
	SE of Henrietta Island, East Siberian Sea (Arctic)	60	Smirnov (1946) [6]
	off North Carolina (U.S.A.)	1,050–3,940	Coull (1973)
K. longiseta (Vasconcelos, George & Santos, 2008)	slope of Sergipe (northeastern Brazil)*	492	Vasconcelos *et al*. (2008)
K. ricardae Willen & Dittmar, 2009	Guinea Basin (Eastern Atlantic)*	5,063	Willen & Dittmar (2009)
	Angola Basin (Eastern Atlantic)	5,388–5,432	Willen & Dittmar (2009)
	Cape Basin (Eastern Atlantic)	5,035	Willen & Dittmar (2009)
K. longirostrata	northwest off Iceland	719–720	Apostolov (2011)

[1] : The type locality was cited incorrectly as the coast of Novaya Zemlya, Russia by Sars (1909: 336) or Ireland by Monard (1927: 149).

[2] : As *P.* cf. *brucei*.

[3] : Not certain if the author was dealing with *P. affinis* instead.

[4] : Sars (1906) did not specify the type locality.

[5] : Record to be confirmed.

[6] : Smirnov (1946) did not specify the type locality.

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