

New *Tachidiella* (Copepoda, Harpacticoida, Tisbidae) from the Antarctic and Norway including a review of the genus

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ABSTRACT

The genus *Tachidiella* Sars, 1909 is revised on the basis of material from Norway, Helgoland, the Celtic Sea and the Antarctic. The type species *T. minuta* Sars, 1909 is redescribed and compared with previous descriptions of the species. *T. minuta* sensu Pallares (1979) from Tierra del Fuego is attributed distinct specific status as *T. patagonica* n. sp. The Baltic record of *T. minuta* sensu Arlt (1983) is identified as *T. reducta* n. sp. which occurs sympatrically with *T. minuta* in Frierfjord/Langesundfjord, Norway. A new species *T. kimi* is described from Marian Cove in King George Island, South Shetlands and represents the first record of the genus from the Antarctic. *T. kimi* n. sp. differs from *T. reducta* n. sp. by the presence of normally developed setae on the caudal rami, P2-P4 enp-3 and P4 exp-3. A key to species is presented.

KEY WORDS

Copepoda,
Harpacticoida,
Tachidiella,
review,
Antarctic,
Norway.

RÉSUMÉ

Nouveaux Tachidiella (Copepoda, Harpacticoida, Tisbidae) de l'Antarctique et de Norvège, avec une révision du genre.

Le genre *Tachidiella* Sars, 1909 est révisé à partir du matériel récolté en Norvège, à Helgoland, en Mer Celtique et dans l'Antarctique. L'espèce-type *T. minuta* Sars, 1909 est redécrite et comparée aux précédentes descriptions de l'espèce. *T. minuta* sensu Pallares (1979), de la Terre de Feu, se voit attribuer un statut d'espèce distincte sous le nom de *T. patagonica* n. sp. *T. minuta* sensu Arlt (1983), de la Baltique, est identifiée sous le nom de *T. reducta* n. sp., qui cohabite avec *T. minuta* dans les Frierfjord/Langesundfjord en Norvège. Une nouvelle espèce, *T. kimi*, est décrite de l'anse Marian, île du Roi George, dans les Shetlands du Sud, et constitue le premier signalement du genre dans l'Antarctique. *T. kimi* n. sp. se distingue de *T. reducta* n. sp. par la présence de soies normales sur les rames caudales, P2-P4 enp-3 et P4 exp-3. Une clé des espèces est présentée.

MOTS CLÉS

Copepoda,
Harpacticoida,
Tachidiella,
révision,
Antarctique,
Norvège.

INTRODUCTION

Sars (1909) proposed *Tachidiella* to accommodate *T. minuta* which he described from 20 m depth in the Skutesnæs (Skudesnes) area along the southwest coast of Norway. The genus remained monotypic until Lang (1965) described *T. parva* from Monterey Bay in California. Sars (1909) was clearly indecisive about the taxonomic position of *Tachidiella*. He placed the genus in the Tachidiidae since it combined characters of both *Tachidius* Lilljeborg, 1853 and *Pseudotachidius* T. Scott, 1898 (now Thalestridae), however also pointed out the similarity with *Bradya* Boeck, 1873 (Ectinosomatidae) in the structure of the maxilliped and made a cursory remark on the resemblance in general body shape between *Tachidiella* and *Idyæa* Philippi, 1843 (= *Tisbe* Lilljeborg, 1853: Tisbidae). Monard (1927) followed Sars' course of action and retained *Tachidiella* in the Tachidiidae. The close similarity with *Idyella* Sars, 1906 in the female genital field and with *Idyanthe* Sars, 1909 in the male P2 endopod prompted Lang (1944,

1948) to assign the genus to the subfamily Idyanthinae in the Tisbidae.

T. minuta has been recorded from a number of other localities in northwest Europe, the Mediterranean and Argentina. However, examination of some of the illustrated records (Arlt 1983; Pallares 1979) revealed certain morphological discrepancies with Sars' (1909) original description. In addition, some authors (Bodin 1970, 1997; Arlt 1983) have questioned the validity of *T. parva* and considered it a geographical variety of the type species. Finally, re-examination of Norwegian material, initially identified as *T. minuta*, revealed the sympatric occurrence of an as yet undescribed species. A second new species was collected in Antarctica during the ninth winter leg of the Korea Antarctic Research Program (KARP) at King Sejong Station, King George Island.

In this paper we redescribe *T. minuta* on the basis of material from Norway, Helgoland and the southern Celtic Sea, review earlier records of this species and describe two new species from Norway and the Antarctic.

METHODS

Specimens were dissected in lactic acid and the dissected parts were mounted on slides in lactophenol mounting medium. Preparations were sealed with Glyceel® or transparent nail varnish. All drawings have been prepared using a camera lucida on an Olympus BH-2 or a Zeiss Axioskop differential interference contrast microscope.

The descriptive terminology is adopted from Huys *et al.* (1996). Type series are deposited in the collections of the Muséum national d'Histoire naturelle in Paris and The Natural History Museum in London. Scale bars in figures are indicated in μm .

Antarctic specimens were collected in Marian Cove, a glacier-eroded fjord located in front of the King Sejong Station, the Korean Antarctic base (62°13'24.4"S, 58°47'03.4"E) on King George Island, South Shetland Islands (West Antarctica). It is bounded by the Weaver Peninsula on the northwest and by the Barton Peninsula on the southeast, and is bathymetrically separated from Maxwell Bay by a shallow (less than 20 m) submarine sill at the mouth. Small valley glaciers, draining southwest from the cove heads, debauch large amounts of icebergs and turbid melt-water into the cove during the summer months. The intertidal zone consists exclusively of large-sized rocks and gravel which extend into the shallow subtidal zone to about 15-20 m depth. Below this depth the bottom sediment is dominated by very fine mud accounting for over 80% of the upper 90 cm layer in the subtidal zone of Marian Cove (Hong *et al.* 1991).

Sediment samples were taken at about one or two week intervals, from January 22 to October 29, 1996. The water depth of the sampling region ranged between 30-40 m. Bottom sediments were sampled with a free fall corer.

ABBREVIATIONS USED

ae	aesthetasc;
P1-P6	first to sixth thoracopod;
exp(enp)-1(2, 3)	proximal (middle, distal) segment of a ramus;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHM	The Natural History Museum, London.

SYSTEMATICS

Family TISBIDAE Stebbing, 1910
Subfamily IDYANTHINAE Lang, 1944
Genus *Tachidiella* Sars, 1909

TYPE SPECIES. — *Tachidiella minuta* Sars, 1909 [by monotypy].

OTHER SPECIES. — *T. parva* Lang, 1965; *T. kimi* n. sp.; *T. patagonica* n. sp.; *T. reducta* n. sp.

DIAGNOSIS. — Prosome dorsoventrally flattened and distinctly wider than urosome. Posterior margin of cephalothorax and somites bearing P2-P3 with internal crenulate pattern. Original segmentation of ♀ genital double-somite marked by lateral constriction and transverse internal chitinous rib ventrally, laterally and laterodorsally. Copulatory pore moderately large, positioned anteriorly of transverse rib; genital apertures fused medially forming common genital slit. Sexual dimorphism in antennule, P2 endopod, P5, P6 and genital segmentation.

Rostrum large, defined at base. Antennules short, with numerous pinnate setae; 8-segmented in both sexes; in ♀ with aesthetasc on segment 4 and 8 (acrothek); subchirocer in ♂ with geniculation between segments 6 and 7 and aesthetasc on segments 6 (lobate) and 8 (acrothek). Antenna with distinct basis; enp-1 without seta; enp-2 with four lateral and seven distal elements; exopod 2-segmented with armature formula [2,4]. Mandibular palp biramous; basis with four setae; endopod 1-segmented, with three lateral and five distal setae; exopod 2-segmented with setal formula [4,2]. Maxillule with well-developed endopod (six setae) and exopod (three setae); coxa and basis with five and eight elements, respectively. Maxilla with four endites on syncoxa, enditic formula [3,3,3,3]; endopod 3-segmented. Maxilliped highly diagnostic; syncoxa with one short and one very long seta; basis with one spine on palmar margin; endopod indistinctly 2-segmented with setal formula [3,2].

P1-P4 with 3-segmented rami. P1 with six elements on exp-3; endopod not prehensile, enp-2 shortest. P2 enp-1 inner element stout and spiniform. P1-P4 enp-2 with strongly produced outer distal corner; enp-3 outer distal spine remarkably elongate and closely set to two shorter apical setae. P2 enp-3 modified in ♂; represented by asetose, pointed or curved segment. Swimming leg setal formulae:

	Exopod	Endopod
P1	0.1.123	1.1.021
P2	1.1.223	1.2.121 [1.2.0 in ♂]
P3	1.1.323	1.1.[2-3]21
P4	1.1.323	1.1.221

P5 with separate exopod and baseoendopod. Exopod round or ovoid, with four elements. Endopodal lobe well-developed in ♀, trapezoid or subrectangular, with three setae; rudimentary and medially fused in ♂, with two elements.

P6 forming well-developed opercula in ♀, with one vestigial and two well-developed setae; asymmetrical in ♂ (with dextral or sinistral configuration), with two setae and one spine.

Caudal ramus wider than long, with seven setae; seta V frequently swollen in proximal part.

Tachidiella minuta Sars, 1909

TYPE LOCALITY. — Skudesneshavn, SW Norway; depth 20 m.

TYPE MATERIAL. — Zoologisk Museum, Oslo: syntypes, 7 ♀ ♀ in alcohol, reg. No. F 20389.

MATERIAL EXAMINED. — (a) Frierfjord/Langesundfjord, Norway, depth 99 m: 1 ♀ dissected on nine slides (NHM reg. No. 1998.2619); other material (4 ♀ ♀ in alcohol) deposited under NHM reg. Nos 1998.2620-2623; coll. R. Huys, 1985; the identity of this material has been confirmed by one of us (R. H., December 1990) through comparison with Sars' syntypes;

(b) From Dr J.M. Gee: 1 ♀ (NHM reg. No. 1998.2625) dissected on ten slides, and 1 ♂ (NHM reg. No. 1998.2624) dissected on nine slides, respectively; 3 ♀ ♀ and 3 ♂ ♂ in alcohol (NHM reg. No. 1998.2626-2631); collected in southern Celtic Sea; 50°30'N, 7°0'W (IMER station CS2), depth 105 m;

(c) Zoologisches Museum der Universität Kiel, Walter Klie collection: 1 ♀ and 1 ♂ dissected on one slide each (reg. No. Cop 105-106); Helgoland ("Tiefe Rinne"), 04.X.1935, coll. H.W. Schäfer.

REDESCRIPTION

Female

Total body length 388-442 µm (n = 7; \bar{x} = 417 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 147 µm. Urosome narrower than prosome (Fig. 1A).

Cephalothorax with irregularly crenulated internal pattern along posterior margin; pleural areas well-developed, rounded; ornamentation consisting of sensillae and few pores as illustrated in Fig. 1A. Rostrum large (Figs 1A; 2D), 1.2 time as long as basal width, tapering anteriorly; with rounded anterior margin; completely defined at

base; with pair of lateral sensillae near apex, and one middorsal plus two dorsolateral pores in anterior third.

Pedigerous somites bearing P2-P3 with irregularly crenulated internal pattern along posterior margin. All prosomites with smooth hyaline frills (Fig. 1A).

Urosome (Fig. 1A, B) 5-segmented, comprising P5-bearing somite, genital double-somite and three free abdominal somites. All urosomites with surface ornamentation consisting of several rows of spinules dorsally and laterally. Hyaline frills of urosomites minutely denticulate. Ventral hind margin with large spinules (Fig. 1B).

Genital double-somite (Fig. 1B) incompletely fused with transverse internal rib all around except middorsally; original segmentation also marked by lateral constriction. Genital field with midventral copulatory pore (arrowed in Fig. 1B) located in median depression; paired integumental pockets and secretory pores present anterior to copulatory pore; gonopores fused medially forming single genital slit covered on both sides by large opercula derived from sixth legs; P6 bearing one pinnate outer seta and one long pinnate seta apically; small spinule-like process representing vestigial seta present near apical seta.

Anal somite (Fig. 1A-C) largely telescoped into penultimate somite; with weakly developed operculum flanked by rows of spinules; ventral hind margin with coarse spinules laterally and fine spinules medially. Pseudoperculum not developed.

Caudal rami (Fig. 1B, C) short, cylindrical, wider than long; each ramus with seven setae; seta I bare, shortest; seta II bare; seta III bare, positioned ventrolaterally; setae IV and V fused basally, well-developed with internal fracture planes, bipinnate; seta V about 1.5 time length of seta IV, somewhat swollen in its proximal region; seta VI bipinnate and well-developed; seta VII tri-articulate at base, positioned at inner distal corner. Ventral posterior margin with row of coarse spinules interrupted by large conical pore.

Antennule (Fig. 2D) short, 8-segmented; segment 2 longest. Armature formula as in *T. kimi* n. sp.

Antennary exopod (Fig. 2E) small, 2-segmented;

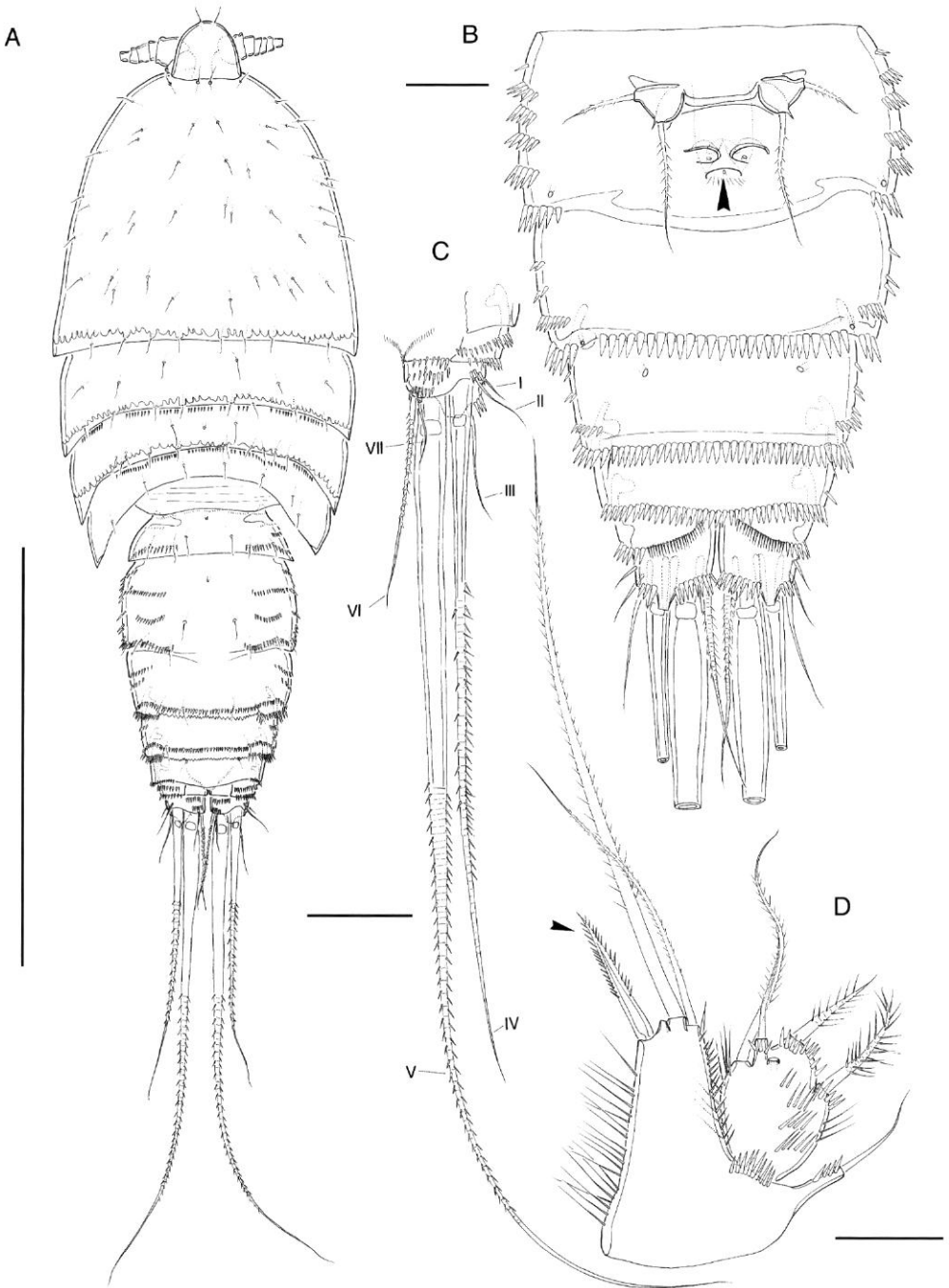


FIG. 1. — *Tachidiella minuta* Sars, 1909 (♀). **A**, habitus, dorsal; **B**, urosome, ventral [excluding P5-bearing somite; copulatory pore arrowed]; **C**, right caudal ramus, dorsal; **D**, P5, anterior [inner spine arrowed]. Scale bars: A, 200 µm; B, D, 20 µm; C, 25 µm.

armature formula [2, 4]; outer distal seta of exp-2 (arrowed in Fig. 2E) strongly reduced, and much smaller than inner distal seta.

Basic structure of mouth parts principally as in Sars' (1909) illustrations; armature as in *T. kimi* n. sp. (see below).

Swimming legs P1-P4 (Figs 2A, B; 3A, B) with wide intercoxal sclerites and well developed praecoxae (not figured). Coxae and bases with anterior and posterior rows of surface spinules as figured. Exopods and endopods 3-segmented.

P1 (Fig. 2A). Basis with one strong, bipinnate spine and long setules along inner margin and with one stout bipinnate spine and few spinules along outer margin. Exp-1 with one stout unipinnate spine; exp-2 with one unipinnate, outer spine and one long, plumose, inner seta; exp-3 with one bipinnate and three unipinnate spines, and two plumose setae. Endopod about twice as long as exopod; enp-1 with one strong, plumose inner seta; enp-2 with spinous outer distal corner and one long plumose inner seta; enp-3 with one short bipinnate spine flanked by plumose inner seta and long unipinnate outer spine.

P2-P4 (Figs 2B; 3A, B). Basis with plumose seta on outer margin. Segment 1 and 2 of both exopod and endopod with anterior coarse frill at inner distal corner. Endopodal segments with coarse spinules along outer margin; enp-2 with spinous outer distal corner, and 5-6 spinules posteriorly near inner distal corner. P2-P3 endopod slightly longer than and P4 endopod shorter than exopod. Exopodal spines typically serrate, that on P4 exp-1 particularly small. Enp-3 outer distal spine elongate, adjoined by two comparatively short setae. P2-P4 armature formula as follows:

	Exopod	Endopod
P2	1.1.223	1.2.121
P3	1.1.323	1.1.321
P4	1.1.323	1.1.221

Fifth pair of legs (Fig. 1D) not fused to supporting somite; rami separate. Baseoendopod forming distinct outer setophore bearing basal seta and row of spinules. Endopodal lobe trapezoid,

extending beyond distal margin of exopod, with one strong, bipinnate inner spine (arrowed in Fig. 1D), one very long, bipinnate apical seta and one bipinnate outer seta; apical and inner elements separated by conical pore; with setules along inner margin and spinules along outer margin and around articulation with exopod. Exopod ovoid with four pinnate elements, inner one longest; anterior surface with rows of spinules and large secretory pore.

Male

More slender than ♀. Body length 323-356 µm (n = 3; \bar{x} = 336 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Urosome narrower than prosome (Fig. 4A).

Posterior margin of cephalothorax and somites bearing P2-P3 with irregularly crenulated internal pattern as in ♀. Urosome (Fig. 4A, C) 6-segmented, comprising P5-bearing somite, genital somite and four abdominal somites. All urosomites with surface ornamentation consisting of several rows of small spinules laterally and dorsally. Hyaline frills of urosomites minutely denticulate. Ventral hind margin with large spinules as in ♀.

Antennule (Fig. 4B) 8-segmented; subchirocer with geniculation between segments 6 and 7. Segment 1 with several rows of spinules along anterior margin; segment 2 represented by small sclerite along anterior margin; segment 5 consisting of two small sclerites; segment 6 largest, swollen; segment 7 forming dorsal spinous process overlying anterior part of triangular segment 8. Segmental homologies: 1-(I), 2-(II) 3-(III-VIII), 4-(IX-XII), 5-XIII, 6-(XIV-XX), 7-(XXI-XXIII), 8-(XXIV-XXVIII). Armature formula as in *T. kimi* n. sp.; aesthetascs on segments 6 and 8 trilobate.

P2 endopod (Fig. 2C) 3-segmented; modified. Enp-1 and -2 as in ♀. Enp-3 represented by small aetose segment produced distally into blunt extension (arrowed in Fig. 2C) and minute spinous process at two thirds the inner margin length; outer margin with spinules.

Fifth pair of legs (Fig. 4D) defined at base and fused medially. Baseoendopod with long setophore bearing outer basal seta; endopodal lobe

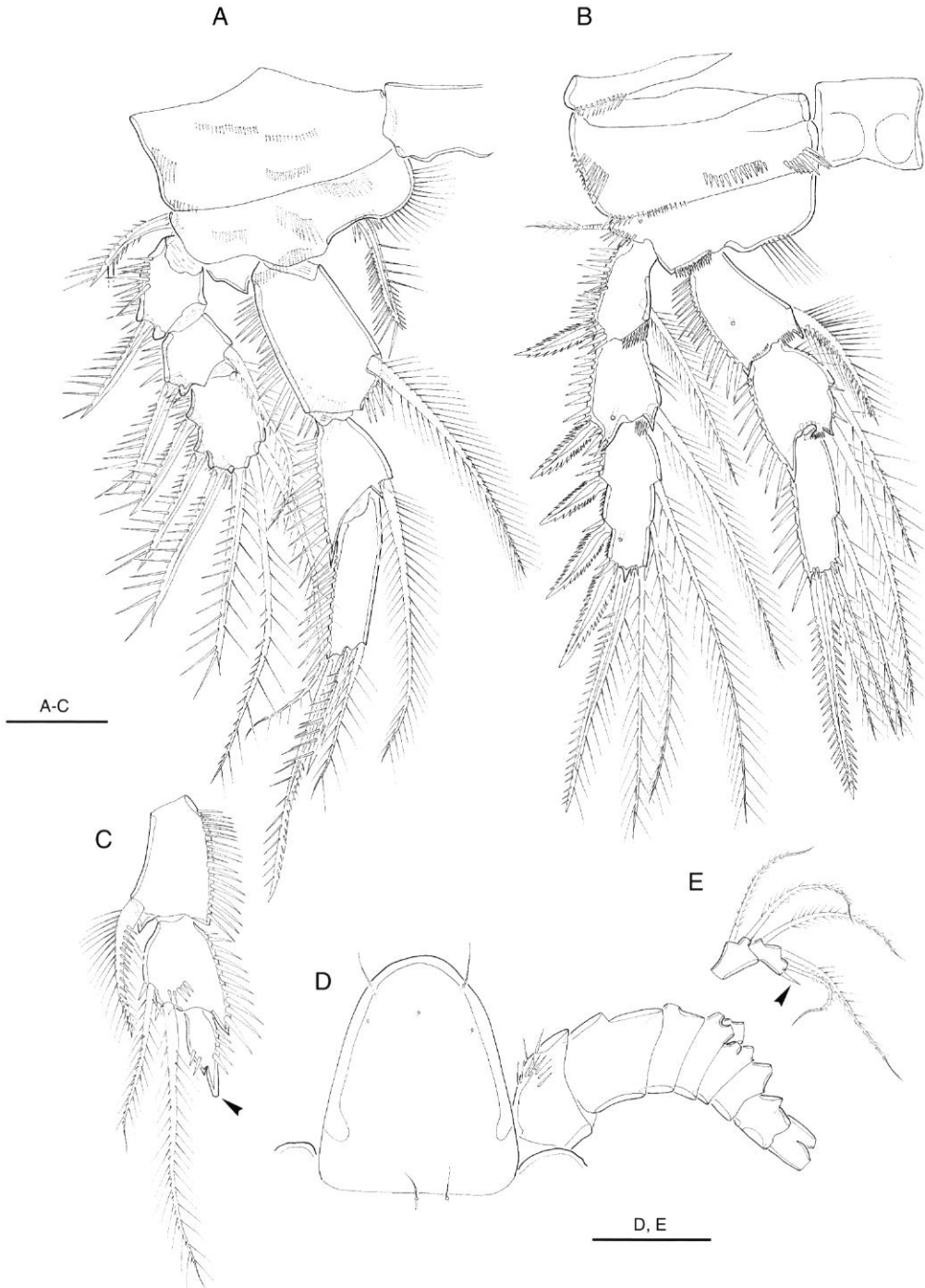


FIG. 2. — *Tachidiella minuta* Sars, 1909. **A**, P1 ♀, posterior; **B**, P2 ♀, anterior; **C**, P2 endopod ♂, posterior [blunt tip of last endopodal segment arrowed]; **D**, rostrum and right antennule ♀ [armature omitted], dorsal; **E**, antennary exopod ♀ [outer distal seta arrowed]. Scale bars: A, C, D, E, 20 µm; B, 25 µm.

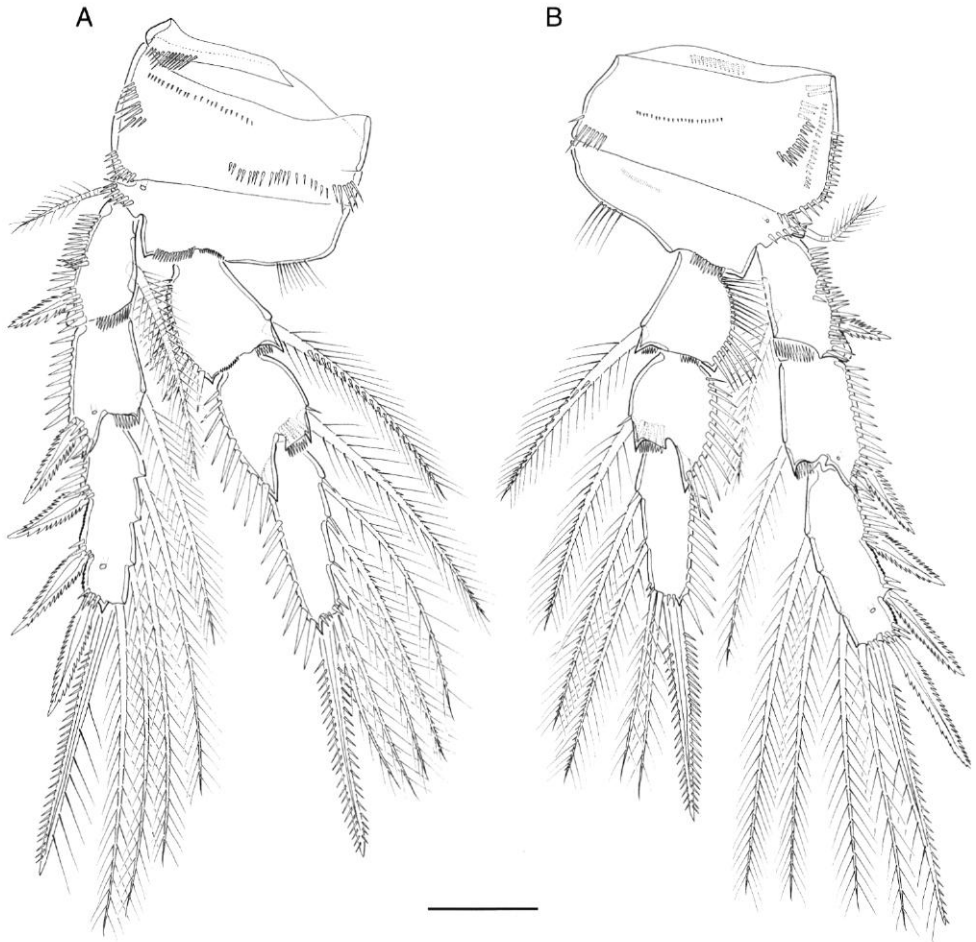


FIG. 3. — *Tachidiella minuta* Sars, 1909 (♀). **A**, P3, anterior; **B**, P4, anterior. Scale bar: 25 µm.

rudimentary, represented by two bare setae, inner one being minute. Exopod ovoid as in ♀, with four bipinnate setae, inner one longest; several rows of marginal spinules as figured.

Sixth pair of legs (Fig. 4C, D) asymmetrical; represented on both sides by well-developed plate (fused to ventral wall of supporting somite along one side; articulating at base and covering gonopore along other side); outer distal corner lobate, bearing one strong bipinnate spine flanked by naked inner and bipinnate outer seta; small spinules present around bases of elements.

REMARKS

Our redescription agrees closely with Sars' (1909) illustrations, except for the following differences which can be attributed to imperfect observation of this small species: (1) the irregularly crenulated hind margin of the cephalothorax and first prosomites was not illustrated; this conspicuous feature was also overlooked by all other authors with the exception of Soyer (1967) who described this margin as "festonnée"; (2) Sars described the rostrum as "not defined behind" although his illustration seems to hint at a basal suture; (3)

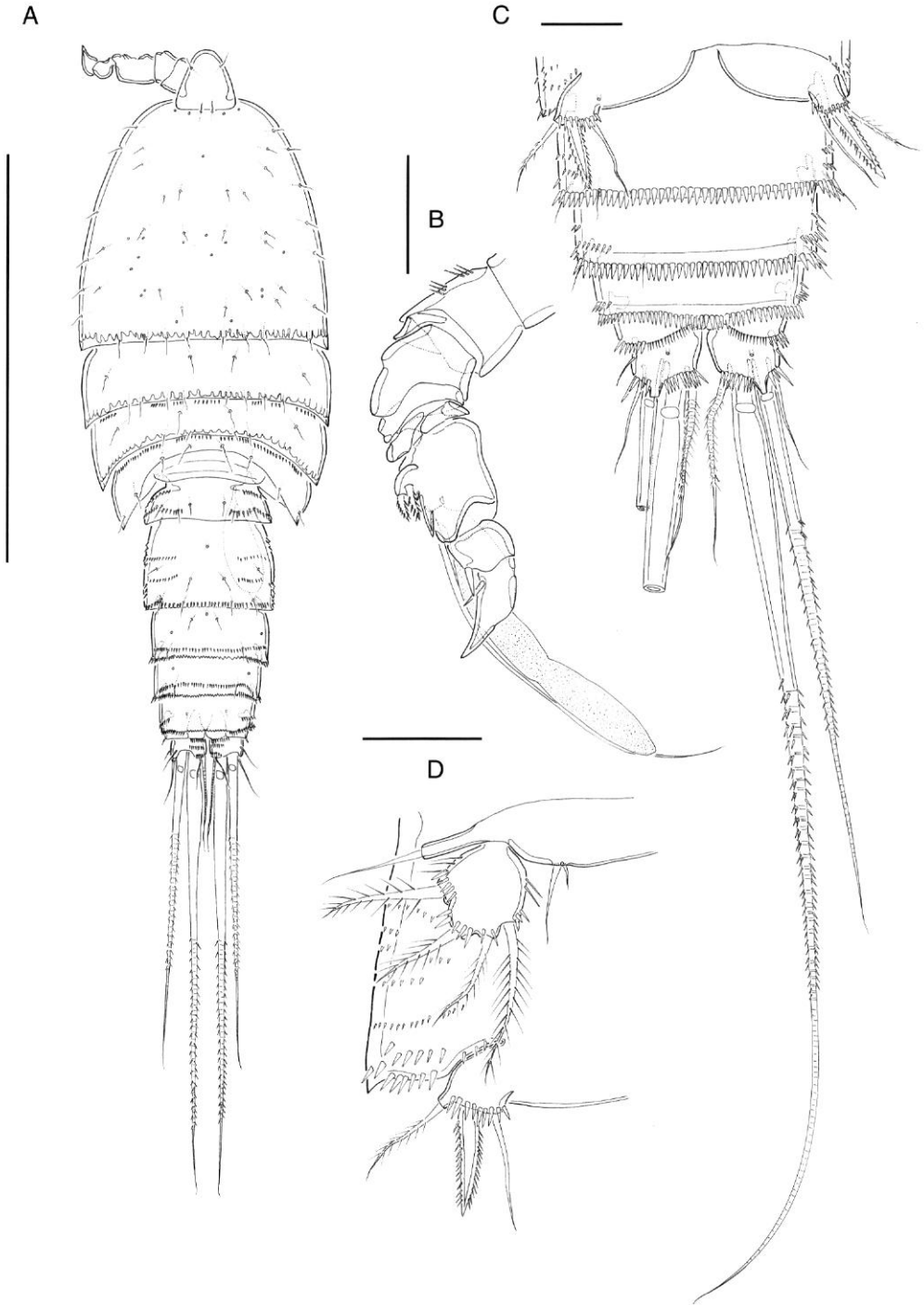


FIG. 4. — *Tachidiella minuta* Sars, 1909 (δ). **A**, habitus, dorsal; **B**, antennule [armature largely omitted]; **C**, urosome [excluding P5-bearing somites], ventral; **D**, P5 and P6, ventral. Scale bars: A, 200 μ m; B, C, D, 20 μ m.

there is some confusion over the precise setal distribution on the antennary exopod since Sars claimed a total of five setae, two on the proximal and three on the distal segment. Lang (1965) pointed out that Sars had figured three setae on both segments whereas our observation of *T. minuta* and all its congeners revealed four setae on the distal segment, suggesting that Sars had figured the correct number of setae but had drawn the segment boundary in the wrong position; (4) the mandibular endopod was described as 1-segmented; (5) the setal counts on the coxa, basis and endopod of the maxillule are incomplete; (6) the large seta on the maxillipedal syncoxa was overlooked and the endopod was described as 1-segmented.

Soyer (1967) remarked that his single female specimen from Banyuls differed slightly from Sars' description in the swimming leg armature formula, notably in the presence of an inner seta on P2-P3 exp-1. In this respect it should be noted that Lang (1948: 360-361, 364) had already pointed out this oversight and had corrected the formula accordingly.

Males of *T. minuta* are particularly scarce. The three illustrated accounts of the male are all based on a single specimen and differ in some significant aspects from each other (Lang 1948; Klie 1949; Bodin 1970). Lang's description is particularly vague with respect to the male P5 ("*nur durch einige Borsten vertreten*") and his illustration of the male P2 endopod is clearly incorrect (Klie 1949). The long seta figured on the distal endopod segment must originate from either another leg or from the middle segment which was illustrated with only one inner seta. Klie (1949) corrected this misinterpretation but was equally unsuccessful in his observation of the male P5. We have re-examined Klie's material from Helgoland and can confirm that he was dealing with *T. minuta*. Our re-examination agrees in all aspects with Bodin's (1970) excellent illustrations based on his single La Rochelle male. *T. minuta* can be differentiated from its known congeners by the following characters: (1) the outer distal seta on the distal antennary exopod segment is very reduced instead of strongly developed; (2) the endopodal lobe of ♀ P5 bears a strong, bipinnate inner spine (arrowed in

Fig. 1D) instead of a short bipinnate seta; (3) exp-3 P2 in ♂ has a blunt tip rather than a sharply pointed one.

T. minuta is largely restricted to north-west Europe with a single outlier in the Mediterranean (Soyer 1967). The latter record from Banyuls-sur-Mer is not accompanied by illustrations which could positively identify the species and therefore requires confirmation. Reliable records of the type species include Norway: Skudesneshavn (Sars 1909), Frierfjord/Langesundfjord (present account); Sweden: Gullmar Fjord (Lang 1948); Germany: Helgoland (Klie 1949); Scotland: Loch Nevis (Wells 1965), Forth Estuary (Moore 1987); Isle of Man (Moore 1979); England: Celtic Sea (present account); France: Roscoff (Monard 1935), La Rochelle (Bodin 1970), Baie de Douarnenez (Bodin 1984). The species from Tierra del Fuego figured in Pallares' (1979) description is not conspecific with *T. minuta* (see below *T. patagonica* n. sp.). Arlt's (1983) record of *T. minuta* from the Kattegat almost certainly refers to *T. reducta* n. sp. (see below).

Tachidiella kimi n. sp.

TYPE LOCALITY. — Marian Cove, King George Island, South Shetland Islands, Antarctica.

TYPE MATERIAL. — Holotype ♀ dissected on eleven slides (MNHN-Cp1690); 30.IX.1996. Paratypes are: 1 ♀ dissected on nine slides (NHM reg. No. 1998.2613), 17.IX.1996; 2 ♂ ♂ (MNHN-Cp1691-1692), dissected on six and eight slides, respectively, 5.IX.1996; 1 ♀ (26.I.1996), and 2 ♂ ♂ (5.IX.1996) in alcohol (NHM reg. No. 1998.2614-2616). All specimens are from Marian Cove, King George Island (62°13'24.4"S, 58°47'03.4"E); depth 30-40 m; coll. W. Lee.

ETYMOLOGY. — The species is named after Dr Yeadong Kim who was officer in charge during the 9th winter leg of the KARP.

DESCRIPTION

Female

Total body length 488-498 µm (n = 2; \bar{x} = 493 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 176 µm. Urosome distinctly narrower

than prosome (Fig. 1A). Body somewhat more robust than in *T. minuta*.

Cephalothorax and pedigerous somites bearing P2-P3 with irregularly crenulated internal pattern along posterior margin as in *T. minuta*; pleural areas well developed, rounded; ornamentation consisting of sensillae and few pores as illustrated in Fig. 5A, B. Rostrum large (Fig. 8C), about as long as basal width; with rounded anterior margin; completely defined at base; with pair of tiny sensillae and a middorsal tube-pore near apex (Fig. 8C).

Urosomites (Figs 5A, B; 6A, B) with surface ornamentation consisting of several rows of small spinules laterally and dorsally. Hyaline frills of abdominal somites minutely denticulate. Ventral hind margin with large spinules (longer than in *T. minuta*).

Genital double-somite (Fig. 6A) with original segmentation marked by entire transverse internal rib except middorsally and by lateral constriction. Genital field (Fig. 6A) as in *T. minuta* but copulatory pore larger and positioned more posteriorly (arrowed in Fig. 6A), and paired integumental pockets absent.

Anal somite (Fig. 6A, B) largely telescoped into penultimate somite; with weakly developed operculum flanked by rows of spinules; ventral hind margin with coarse spinules laterally and fine spinules medially. Pseudoperculum not developed.

Caudal rami (Fig. 6A, B) short, cylindrical, wider than long; each ramus with seven setae: setae I-II distinctly longer than in *T. minuta*; seta III bare, positioned ventrolaterally; setae IV and V fused basally, well-developed with internal fracture planes; seta V broken in all specimens examined but presumably longest, not swollen in proximal part and pinnate as in seta IV (cf. ♂ condition); seta VI bipinnate and well developed; seta VII tri-articulate at base, positioned at inner distal corner. Ventral posterior margin with row of coarse spinules interrupted by large conical pore.

Antennule (Fig. 6D, E) short, 8-segmented; with well-developed sclerite around base of segment 1. Segment 1 with spinular rows around anterior margin. Segment 2 longest. Armature formula: 1-[1 pinnate], 2-[11 pinnate], 3-[8 pinnate], 4-[3 pinnate + (1 pinnate + ae)], 5-[2 pinnate], 6-[3 pinnate], 7-[2 bare + 2 pinnate], 8-[4 bare +

2 pinnate + acrothek]. Apical acrothek consisting of small aesthetasc fused basally to one pinnate seta.

Antenna (Fig. 7D, d) 4-segmented, comprising coxa, basis and 2-segmented endopod. Coxa small, without ornamentation. Basis shorter than proximal endopod segment not forming allobasis; with pinnate abexopodal seta distally. Exopod 2-segmented; both segments with one row of spinules apically; armature formula [2, 4]; outer distal seta of exp-2 (arrowed in Fig. 7D) strongly developed, and much longer than inner distal seta. Proximal endopod segment unarmed. Distal endopod segment subequal to proximal one; lateral armature consisting of one minute naked seta (arrowed in Fig. 7D), one geniculate and two pinnate spines; apical armature consisting of one bipinnate spine, one simple and five geniculate setae (simple seta fused basally to geniculate one; Fig. 7E); with one row of spinules on proximal inner margin and two transverse hyaline frills subapically.

Labrum with elaborate spinular ornamentation as in Fig. 9E.

Mandible (Fig. 8D) with well-developed gnathobase bearing several multicuspidate teeth around distal margin and one large pinnate spine at dorsal corner. Palp well-developed, biramous. Basis with four pinnate setae; with long spinules on anterior surface. Exopod 2-segmented, longer than endopod; armature formula [4, 2]; exp-1 with two rows of spinules on anterior surface, proximal seta medially displaced; exp-2 very small. Endopod 1-segmented, with three pinnate lateral setae, and one pinnate plus four bare setae distally.

Paragnaths well-developed lobes; with ornamentation pattern as in Fig. 9F.

Maxillule (Fig. 10C, D). Praecoxal arthrite strongly developed, with two naked setae on anterior surface, ten spines/setae around distal margin, and transverse row of spinules on posterior surface. Coxal endite with one naked seta, four pinnate spines/setae and transverse row of spinules anteriorly. Basis with one strong pinnate spine and seven pinnate setae and two transverse rows of spinules anteriorly. Endopod 1-segmented with six pinnate setae and anterior row of spinules. Exopod 1-segmented, with three plumose

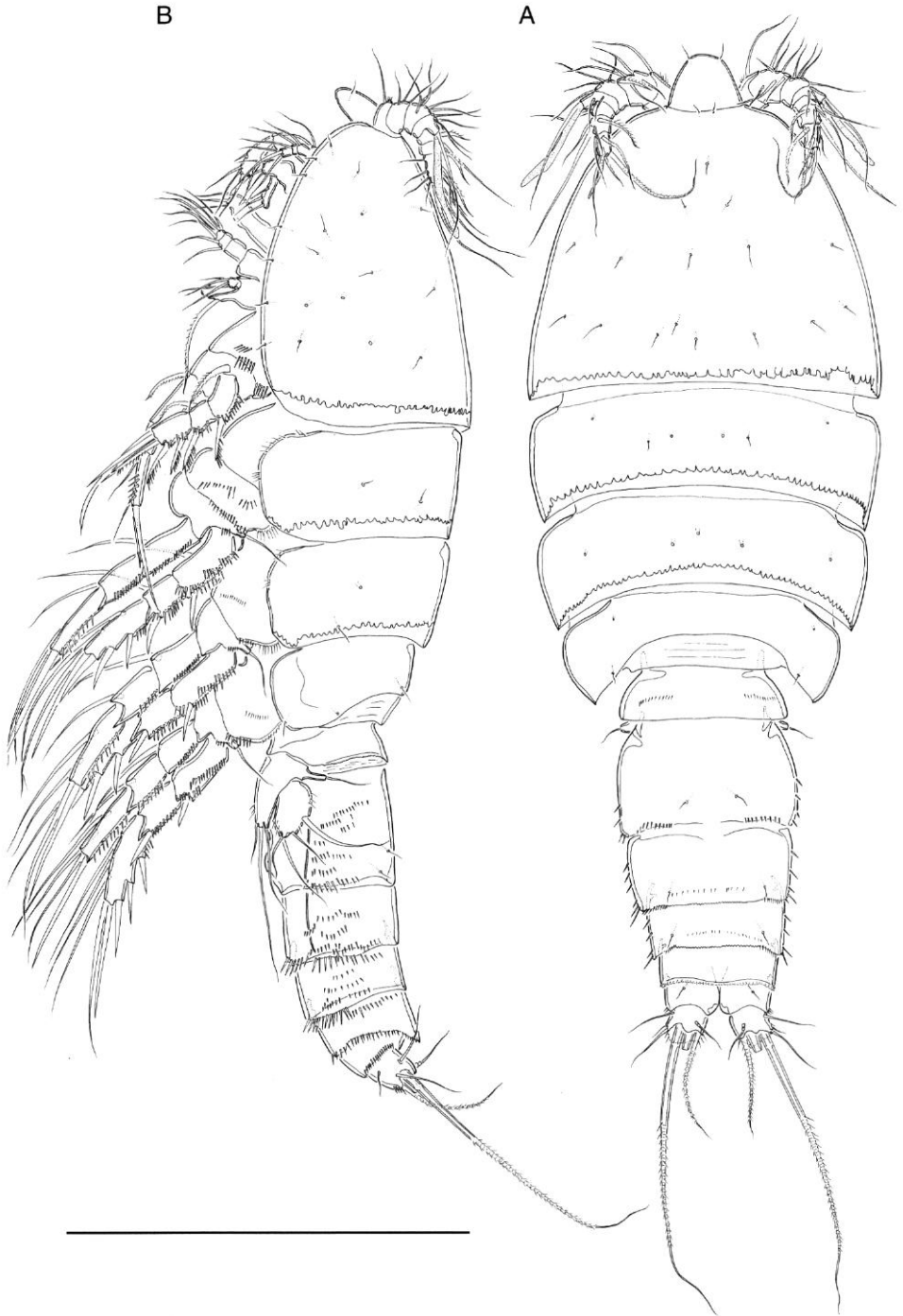


FIG. 5. — *Tachidiella kimi* n. sp. (♀). **A**, habitus, dorsal; **B**, habitus, lateral. Scale bar: 200 μ m.

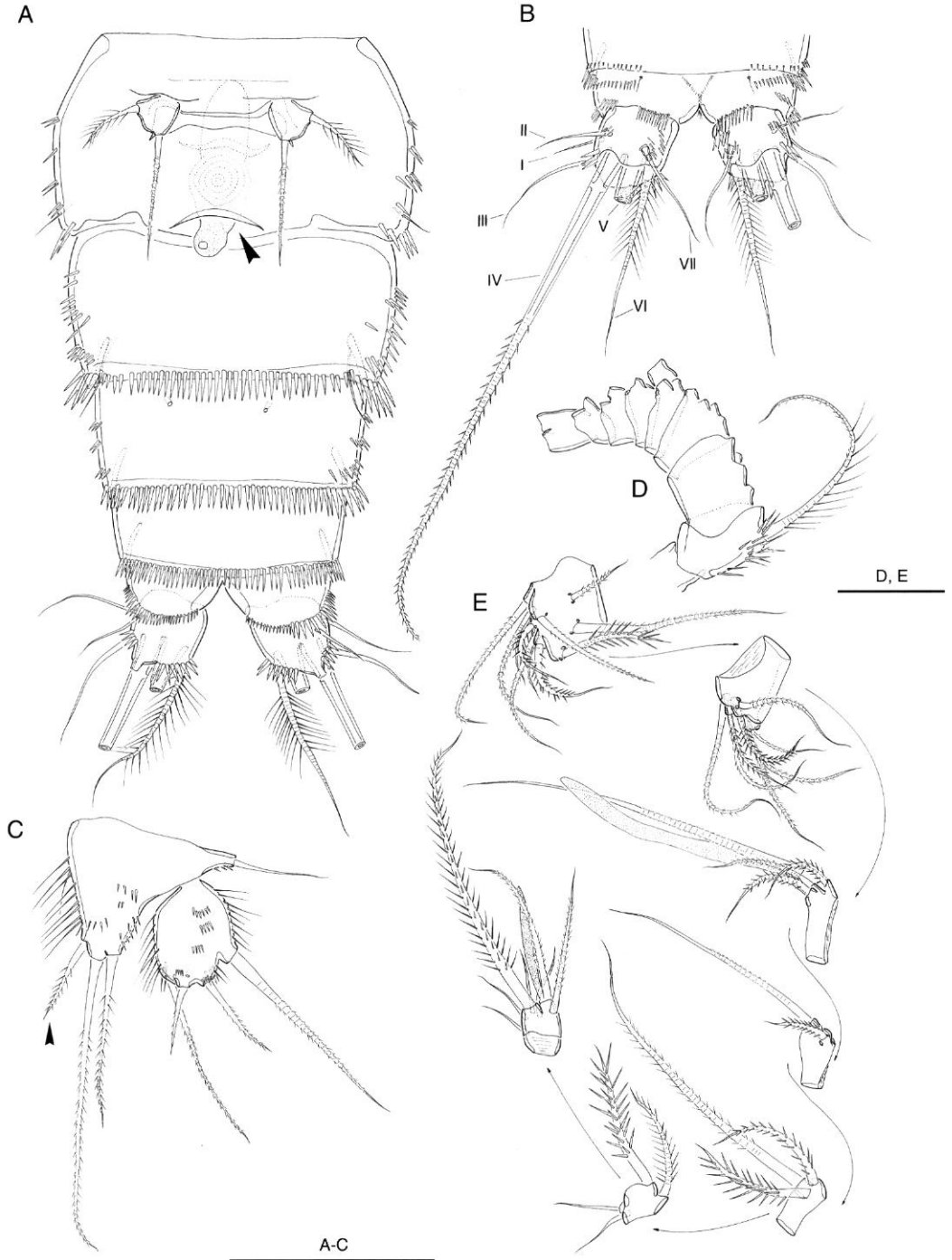


FIG. 6. — *Tachidiella kimi* n. sp. (♀). **A**, urosome [excluding P5-bearing somite; copulatory pore arrowed], ventral; **B**, anal somite and caudal rami, dorsal; **C**, P5, posterior [inner seta arrowed]; **D**, antennule [armature of segments 2-8 omitted]; **E**, antennular segments 2-8. Scale bars: A, B, C, 50 µm; D, E, 20 µm.

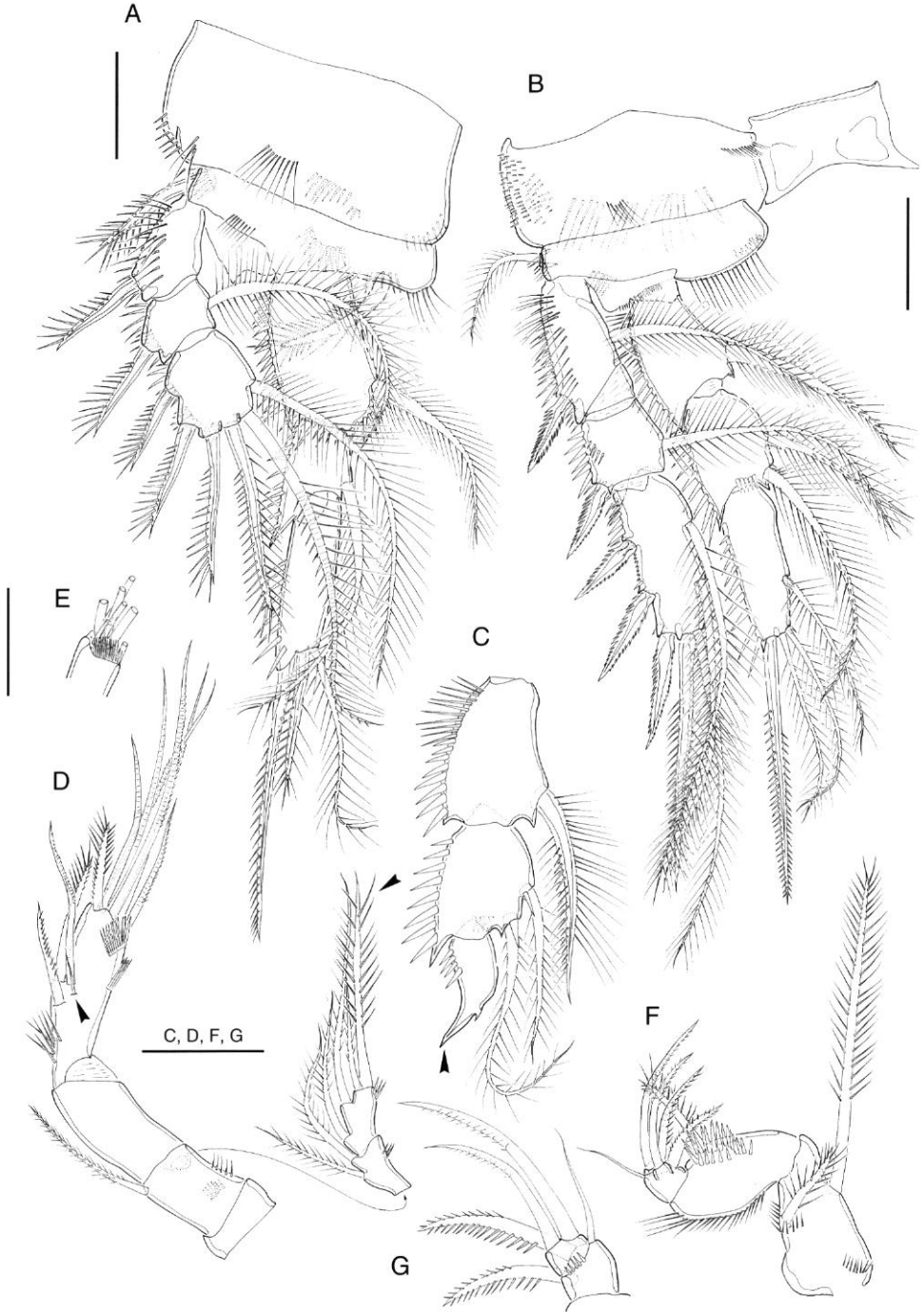


FIG. 7. — *Tachidiella kimi* n. sp. **A**, P1 ♀, posterior; **B**, P2 ♀, posterior; **C**, P2 endopod ♂, anterior [tip of last segment arrowed]; **D**, antenna ♀ [with exopod disarticulated; small lateral element on endopod and outer distal seta on exp-2 arrowed]; **E**, distal part of antennary endopod; **F**, maxilliped ♀; **G**, maxillipedal endopod ♀. Scale bars: 20 µm.

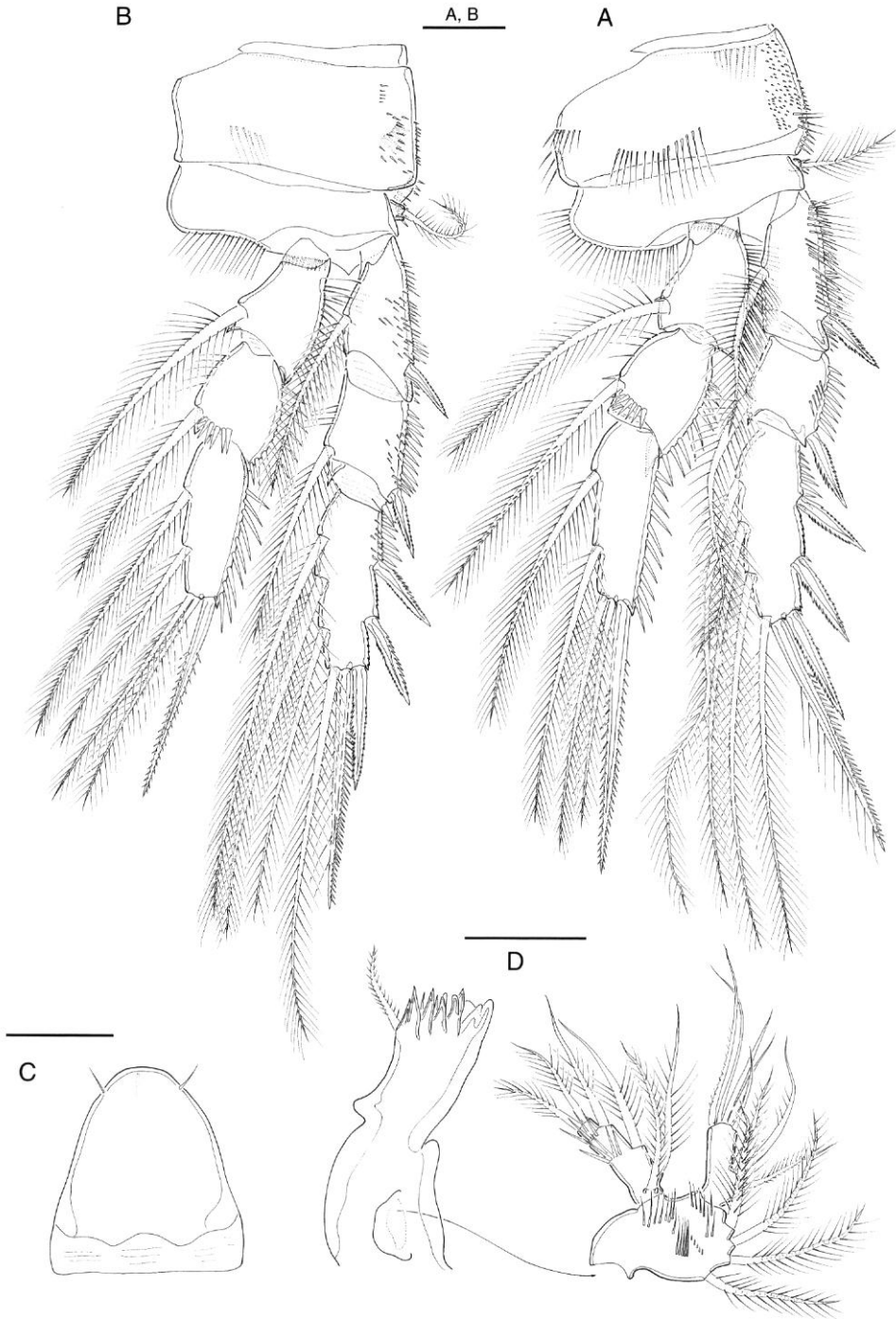


FIG. 8. — *Tachidiella kimi* n. sp. (♀). **A**, P3, posterior; **B**, P4, posterior; **C**, rostrum, ventral; **D**, mandible [with palp disarticulated]. Scale bar: 20 μ m.

setae and row of setules on inner lateral margin. Maxilla (Fig. 10E, F). Syncoxa with four endites (two praecoxal, two coxal); outer margin with rows of spinules; all endites with anterior transverse row of spinules. Praecoxal endites fused basally; proximal endite with two setae and one pinnate spine; distal endite with one seta and two pinnate spines. Proximal coxal endite with one pinnate seta and two pinnate spines; distal coxal endite with one naked seta and two pinnate elements. Allobasis drawn out into strong, slightly curved claw; with small spinules on anterior surface; accessory armature consisting of one pinnate small claw and one bare seta on anterior surface, one naked seta on posterior surface, and two bare setae near insertion of endopod. Endopod 3-segmented; enp-1 and -2 with two geniculate setae; enp-3 with one geniculate, one naked and two plumose setae.

Maxilliped (Fig. 7F, G). Syncoxa with one short pinnate spine on outer distal margin and one very long bipinnate spine on inner margin; with small rows of spinules on anterior surface. Basis with one coarse pinnate spine on distal palmar margin; with one row of setules along outer margin, and two longitudinal spinular rows along palmar margin. Endopod 2-segmented; enp-1 with one naked outer seta and two bipinnate spines, enp-2 with two geniculate apical setae. Swimming legs P1-P4 (Figs 7A, B; 8A, B) with wide intercoxal sclerites and well-developed praecoxae (not figured). Coxae and bases with anterior and posterior rows of surface spinules as figured. Exopods and endopods 3-segmented.

P1 (Fig. 7A) as in *T. minuta* except for inner seta of enp-1 which is distinctly longer.

P2-P4 (Figs 7B; 8A, B) with armature formula as follows:

	Exopod	Endopod
P2	1.1.223	1.2.121
P3	1.1.323	1.1.221
P4	1.1.323	1.1.221

P5 (Fig. 6C) baseopod with short, outer setophore bearing basal seta and row of spinules. Endopodal lobe trapezoid, not extending beyond

distal margin of exopod; with one small, bipinnate inner seta (arrowed in Fig. 6C), one bipinnate apical seta (longest) and one bipinnate outer seta; with rows of short spinules on anterior surface and along outer margin, and long setules along inner margin. Exopod ovoid with one bipinnate outer seta (longest), two short bipinnate setae apically, and one long, bipinnate inner seta; outer seta and apical setae arising from small cylindrical processes; one secretory pore on anterior surface; several rows of small spinules on anterior surface, and dense long setules along inner and outer margins.

Male

More slender than ♀. Body length 416-472 µm (n = 3; \bar{x} = 440 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 121 µm. Urosome narrower than prosome (Fig. 9A). Posterior margin of cephalothorax and somites bearing P2-P3 with irregularly crenulated internal pattern as in ♀.

Urosome (Fig. 9A, C) 6-segmented, comprising P5-bearing somite, genital somite and four abdominal somites. All urosomites with surface ornamentation consisting of several rows of small spinules laterally and dorsally. Hyaline frills of urosomites minutely denticulate. Ventral hind margin with large spinules as in ♀. Caudal rami as in ♀ (Fig. 9B); caudal seta V longer than total urosome length, proximal part not swollen.

Antennule (Fig. 10A, B) 8-segmented; subchirocer with geniculation between segments 6 and 7. Segment 1 with several rows of spinules along anterior margin. Segment 2 represented by small sclerite along anterior margin. Segment 5 consisting of two small sclerites. Segment 6 largest; swollen. Segment 7 forming dorsal spinous process overlying anterior part of triangular segment 8. Segmental homologies: 1-I, 2-(II) 3-(III-VIII), 4-(IX-XII), 5-XIII, 6-(XIV-XX), 7-(XXI-XXIII), 8-(XXIV-XXVIII). Armature formula: 1-[1 pinnate], 2-[1 pinnate], 3-[4 + 6 pinnate], 4-[3 + 5 pinnate], 5-[2 pinnate], 6-[1 striated + 9 pinnate + 3 spinous processes + (1 + ae)], 7-[1 striated + 3 spinous processes], 8-[9 + 1 spinous process + acrothek]. Aesthetasc on segment 6 very large, bilobate. Apical acrothek consisting of

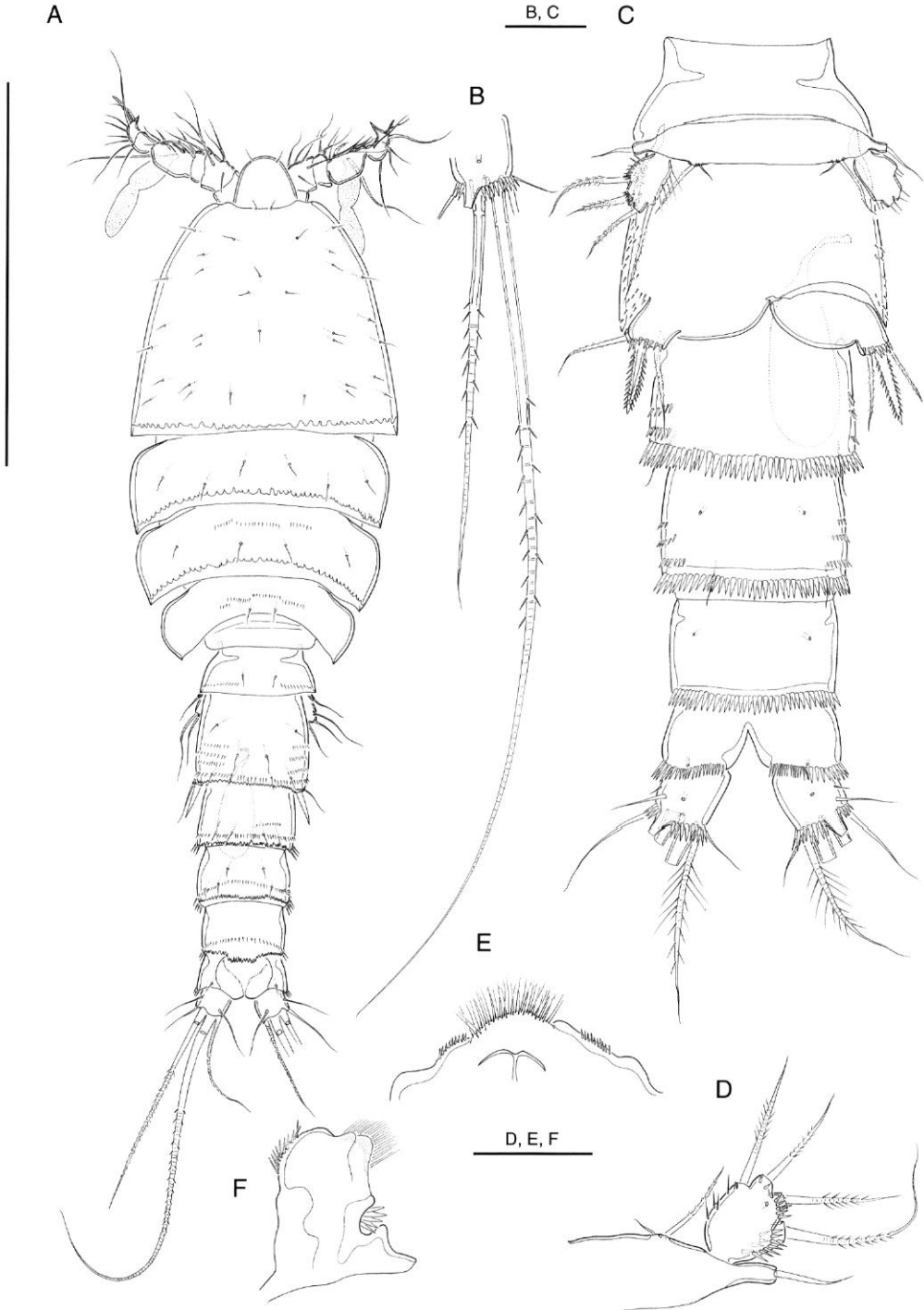


FIG. 9. — *Tachidiella kimi* n. sp. **A**, habitus ♂, dorsal; **B**, left caudal ramus ♂, ventral; **C**, urosome ♂, ventral; **D**, P5 ♂, anterior; **E**, labrum ♀; **F**, paragnath ♀. Scale bars: A, 200 µm; B-F, 20 µm.

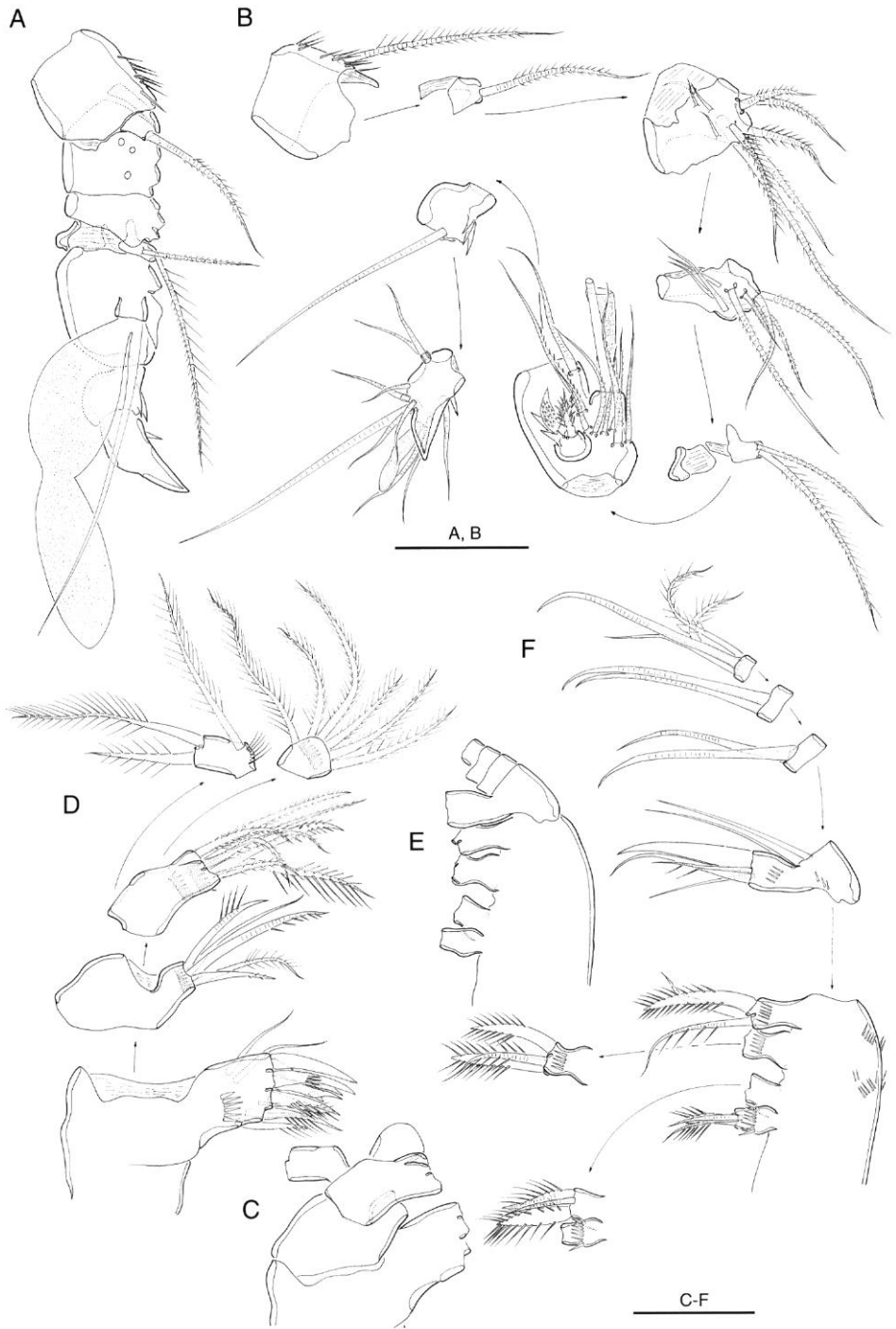


FIG. 10. — *Tachidiella kimi* n. sp. **A**, antennule ♂ [armature largely omitted]; **B**, antennular segments 1-8; **C**, contours of maxillule ♀; **D**, maxillule ♀ [disarticulated]; **E**, contours of maxilla ♀; **F**, maxilla ♀ [disarticulated]. Scale bars: 20 µm.

short bilobate aesthetasc and one striated seta. Spinous processes on segments 6, 7 and 8 representing modified elements.

P2 endopod (Fig. 7C) 3-segmented; modified. Enp-1 and -2 as in ♀; enp-3 represented by small, outwardly curved segment with pointed extension (arrowed in Fig. 7C) and minute sharp process at two thirds the inner margin length; with several spinules along proximal outer margin.

P5 (Fig. 9C, D) baseoendopod with distinct setophore bearing outer basal seta; endopodal lobe rudimentary, represented by one minute, naked inner seta and one pinnate outer seta. Exopod ovoid as in ♀, with four bipinnate setae, outer one longest; several rows of marginal spinules as figured.

Sixth pair of legs (Fig. 9C) as in *T. minuta*.

REMARKS

T. kimi n. sp. is most closely related to *T. reducta* n. sp. from Norway (see below). Both species have only two inner setae on P3 enp-3 and share the short endopodal lobe on the ♀ P5. *T. kimi* n. sp. can be distinguished from its Norwegian congener by the form of the caudal seta V which is not dilated in the proximal part, the large copulatory pore and the normally developed inner setae on P2-P4 enp-3 and P4 exp-3. The pointed, cutely recurved distal segment of the male P2 endopod is a noteworthy feature in this species.

Tachidiella reducta n. sp.

TYPE LOCALITY. — Frierfjord/Langesundfjord, Norway; depth 99 m; muddy substrate.

TYPE MATERIAL. — Holotype ♀ dissected on nine slides (MNHN-Cp1693); paratypes are 1 ♀ (MNHN-Cp1694) and 2 ♀ ♀ (NHM reg. No. 1998.2617-2618) in alcohol; coll. R. Huys, 1985.

ETYMOLOGY. — The species name refers to the reduction in length of some inner setae on P2-P4.

DESCRIPTION

Female

Total body length 326-363 µm (n = 4; \bar{x} = 345 µm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest

width measured at posterior margin of cephalic shield: 129 µm. Urosome narrower than prosome (Fig. 11A).

Cephalothorax and pedigerous somites bearing P2-P3 with irregularly crenulated posterior margin as in *T. minuta*; pleural areas well-developed, rounded; ornamentation consisting of sensillae and few pores as illustrated in Fig. 11A. Rostrum large (Fig. 12A), about as long as basal width; with rounded anterior margin; completely defined at base; with pair of tiny sensillae and a mid-dorsal tube-pore near apex (Fig. 12A).

Urosomites (Fig. 11A, B) with surface ornamentation consisting of several rows of small spinules laterally and dorsally. Hyaline frills of abdominal somites minutely denticulate. Ventral hind margin with long spinules (longer than in *T. minuta*).

Genital double-somite (Fig. 11B) with original segmentation marked by entire transverse internal rib except middorsally and by lateral constriction. Genital field (Fig. 11B) as in *T. minuta* but copulatory pore positioned more posteriorly (arrowed in Fig. 11B) at level of transverse rib; paired integumental pockets present.

Anal somite (Fig. 11A, B) largely telescoped into penultimate somite; with weakly developed operculum; ventral hind margin with coarse spinules laterally and fine spinules medially.

Caudal rami (Fig. 11A, B) short, cylindrical, wider than long; each ramus with seven setae: setae I-II distinctly longer than in *T. minuta*; seta III bare, positioned ventrolaterally; setae IV and V fused basally, well-developed with internal fracture planes, bipinnate; seta V longest, swollen in proximal part; seta VI bipinnate and well-developed; seta VII tri-articulate at base, positioned at inner distal corner. Ventral posterior margin with row of coarse spinules interrupted by large conical pore.

Antennule (Fig. 12B) 8-segmented; with well-developed sclerite around base of segment 1. Segment 2 longest. Armature formula as in *T. kimi* n. sp.

Antennary exopod (Fig. 12C) small, 2-segmented; distal segment with one row of spinules apically; armature formula [2, 4]; segment 2 with outer distal seta strongly developed (arrowed in Fig. 12C), and much longer than inner distal seta; inner distal seta short and reduced

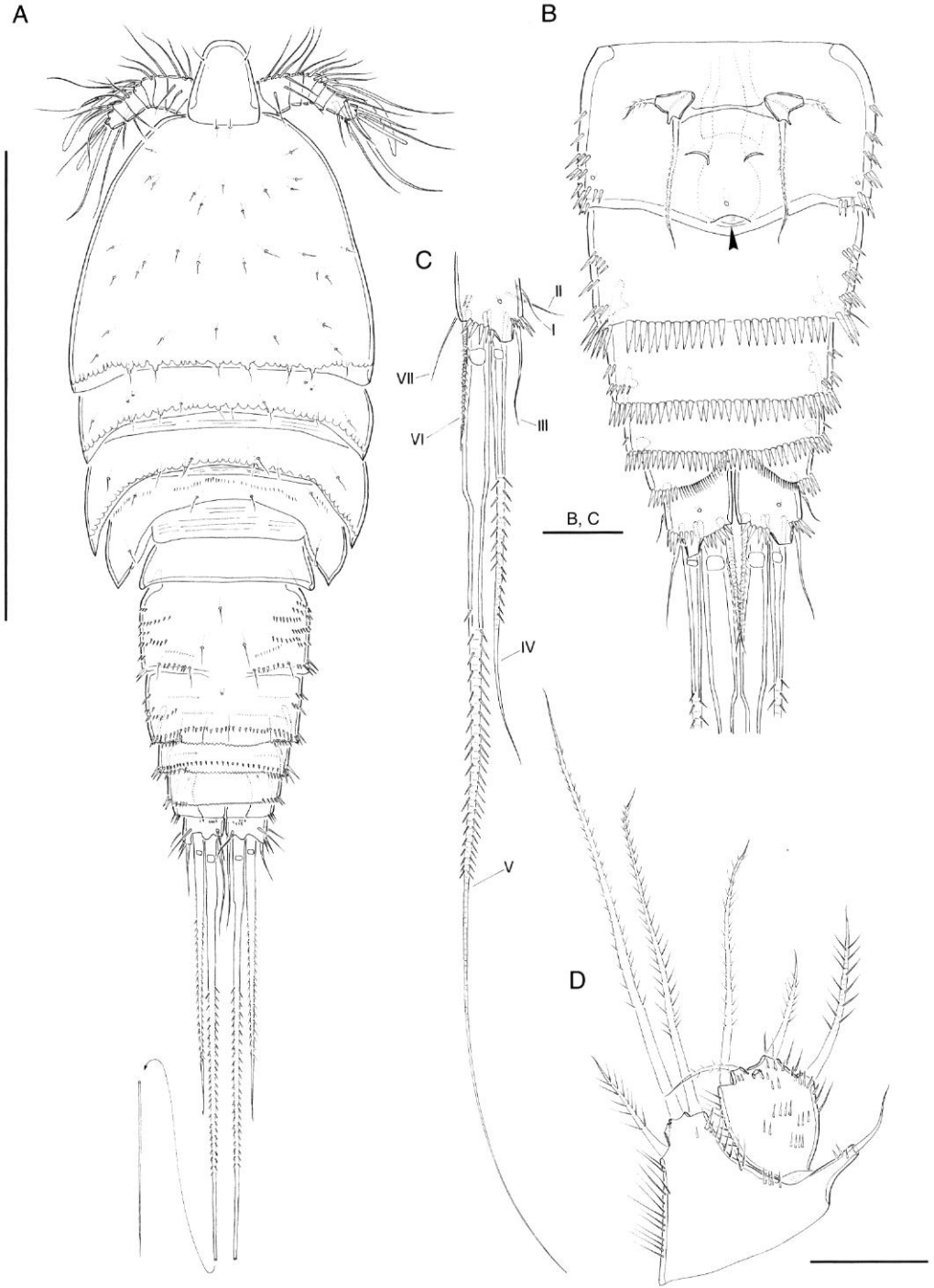


FIG. 11. — *Tachidiella reducta* n. sp. (♀). **A**, habitus, dorsal; **B**, urosome, ventral [excluding P5-bearing somite; copulatory pore arrowed]; **C**, left caudal ramus, ventral; **D**, P5, anterior. Scale bars: A, 200 μ m; B-D, 20 μ m.

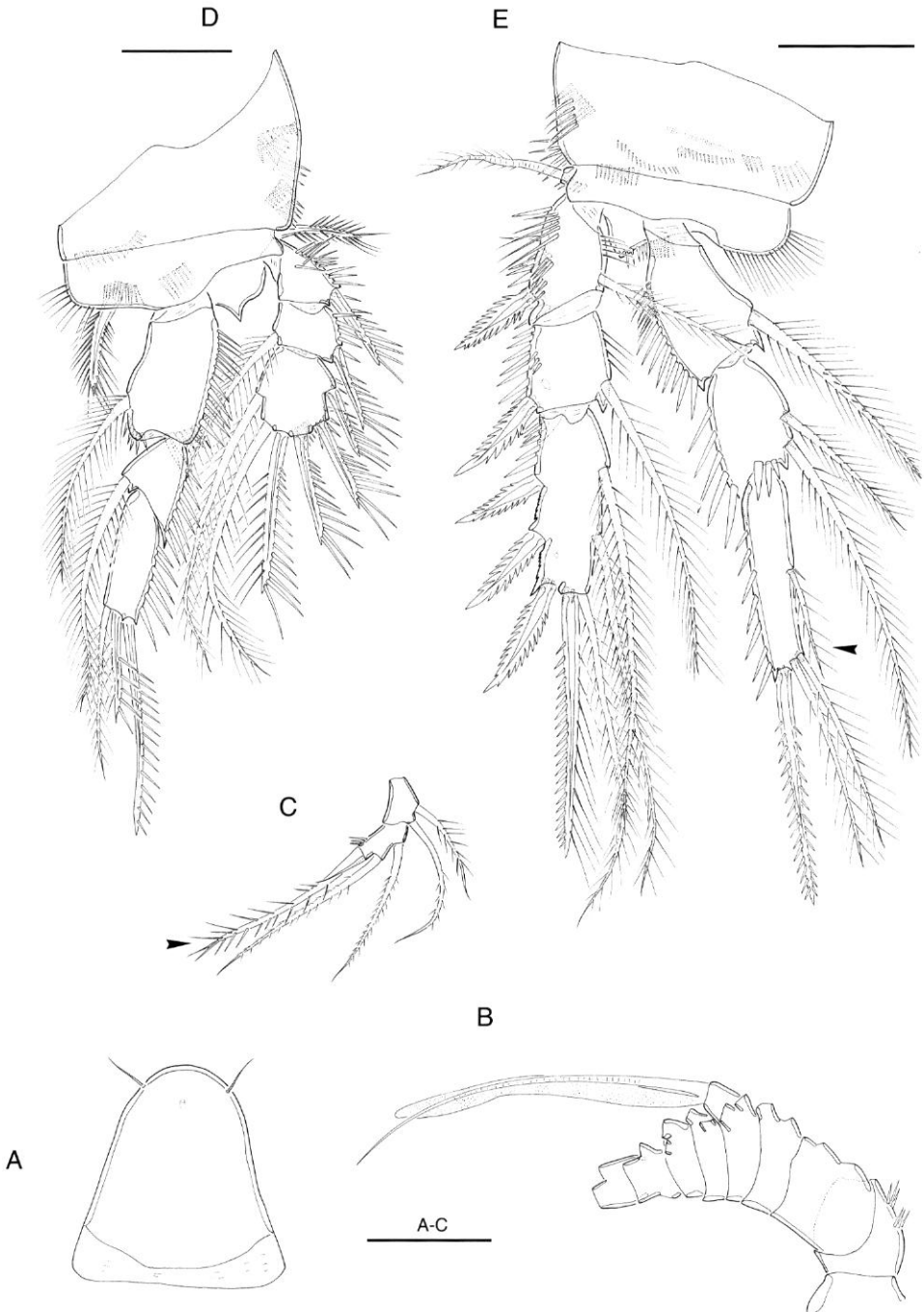


FIG. 12. — *Tachidiella reducta* n. sp. (♀). **A**, rostrum, dorsal; **B**, antennule [armature omitted]; **C**, antennary exopod [outer distal seta on exp-2 arrowed]; **D**, P1, posterior; **E**, P2, posterior [inner seta on exp-3 arrowed]. Scale bars: A, B, C, D, 20 µm; E, 25 µm.

Swimming legs P1-P4 (Figs 12D, E; 13A, B) with wide intercoxal sclerites and well-developed praecoxae. Intercoxal sclerites with row of small spinules on anterior distal margin. Coxae and bases with anterior and posterior rows of surface spinules as figured.

P1 (Fig. 12D) as in *T. minuta*.

P2-P4 (Figs 12E; 13A, B). Outer exopodal spines of P2-P4 coarsely pectinate. P2 endopod (and particularly enp-3) much longer than in *T. minuta*; inner seta of enp-1 distinctly longer than in *T. minuta*, that of enp-3 (arrowed in Fig. 12E) markedly reduced in length. P3 endopod slightly longer than exopod; distal inner seta of enp-3 (arrowed in Fig. 13A) reduced in length. P4 endopod subequal to exopod; distal inner seta of enp-3 and exp-3 (arrowed in Fig. 13B) reduced in length. Armature formula as follows:

	Exopod	Endopod
P2	1.1.223	1.2.121
P3	1.1.323	1.1.221
P4	1.1.323	1.1.221

P5 (Fig. 11D) baseopod with distinct, outer setophore bearing short basal seta and row of spinules. Endopodal lobe trapezoid, not extending to distal margin of exopod, with one bipinnate outer seta and one bipinnate seta apically (longest), and one small bipinnate inner seta; spinules along inner and outer margins. Exopod ovoid with one bipinnate outer seta, two short bipinnate setae apically, and one long bipinnate inner seta (longest); one secretory pore on anterior surface; several rows of small spinules on anterior surface, and long setules along inner and outer margins.

Male

Unknown.

REMARKS

The relationship of this species to *T. kimi* has already been discussed (see above). The most striking character of *T. reducta* n. sp. is the reduction in length of the distal inner seta on P2-P4 enp-3 and P4 exp-3. Both *T. minuta* and

T. reducta display a reduced and a well-developed seta on the apex of the distal antennary exopod segment, however in the latter it is the inner distal seta that has undergone reduction (compare Figs 2E and 12C). The row of small spinules on the intercoxal sclerite of the swimming legs is a unique characteristic for this species.

Arlt (1983) figured the female P5 of a *Tachidiella* specimen which he identified as *T. minuta* on the basis of the number of setae on the exopod. This specimen which was collected in the Kattegat (Baltic) also resembled *T. parva* in the relative proportion of the endopodal lobe which led Arlt to believe that the latter was only a geographical variety of *T. minuta*. From the shape of the endopodal lobe and relative length of the setae there is little doubt, however, that the author was dealing with *T. reducta*.

Tachidiella parva Lang, 1965

TYPE LOCALITY. — Monterey Bay, off Hopkins Marine Station, California, U.S.A.; sand with detritus, depth 26 m.

TYPE MATERIAL. — Naturhistoriska Museet, Stockholm: syntypes (3 ♀ ♀ in alcohol), reg. No. 501.

REMARKS

Lang's (1965) description, which was based on females only, contains some significant deficiencies or misinterpretations. His statement that the rostrum is not defined at base and "without sensory setae" is doubtful since in all other congeners the rostrum is clearly articulating and provided with sensillae. Such marked variation is unlikely to be found within a single genus. The armature formula [3, 3] of the antennary exopod which according to Lang (1965: 150) is also found in the type species *T. minuta* is similarly doubtful. We suspect that the distal seta on the proximal exopodal segment in Lang's fig. 80a really belongs to the distal segment, implying a [2, 4] formula as in all other species of the genus. The presence of only three setae on the mandibular basis also requires confirmation since in other *Tachidiella* species a total of four setae is recorded. Bodin (1970) pointed out the internal inconsistency between the description of

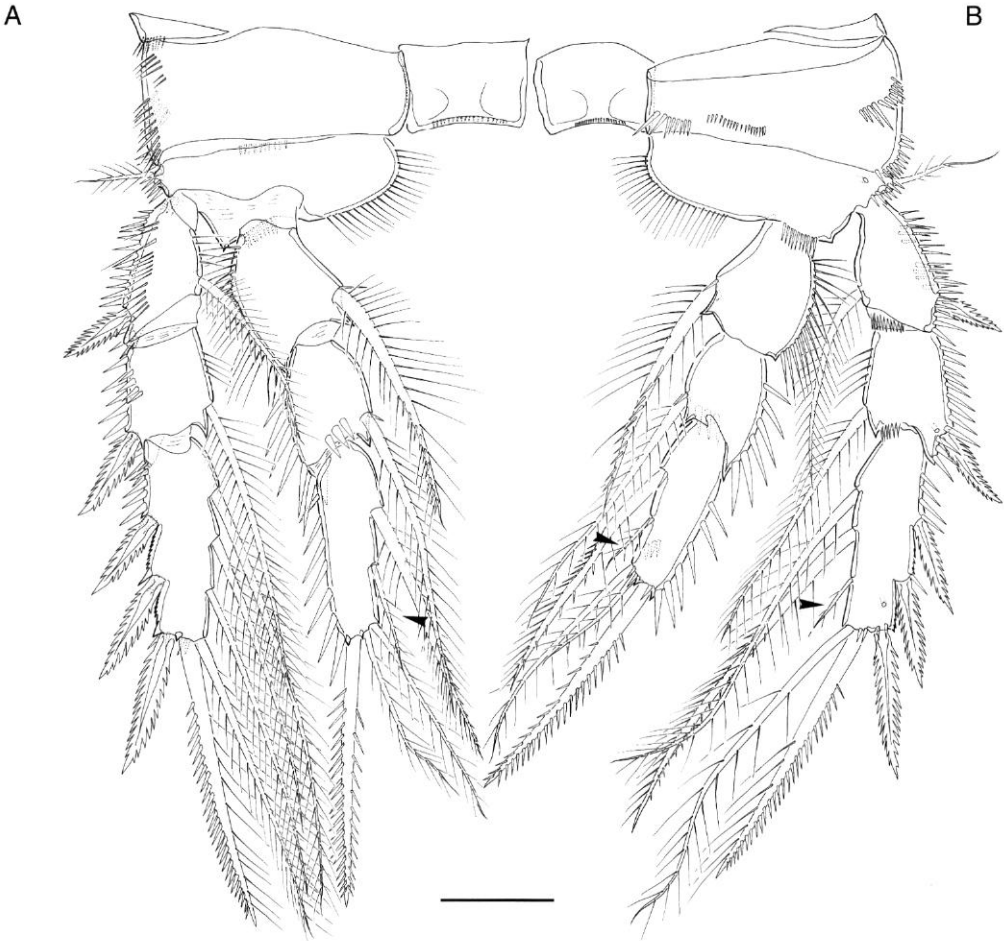


FIG. 13. — *Tachidiella reducta* n. sp. (♀). **A**, P3, posterior [short inner seta on exp-3 arrowed]; **B**, P4, anterior [short inner setae on exp-3 and enp-3 arrowed]. Scale bar: 20 μ m.

T. parva and the accompanying species key. The latter, which is based solely on P5 characters, implies five exopodal setae for *T. parva* which is in contradiction with Lang's text and fig. 81c, illustrating only four setae on the exopod.

Lang (1965) differentiated *T. parva* from *T. minuta* on the basis of the long setae and spines on P1 exp-3, the caudal rami and the P5. Bodin (1970) remarked that there was no distinct difference in the length of the setae and spines of P1 exp-3 between Lang's *T. parva* and his own material of *T. minuta* from La Rochelle, an observation which was confirmed by the pre-

sent redescription. Pending the discovery of the male of *T. parva*, Bodin (1970) suggested to consider this species as a junior synonym or at most a geographical variety of *T. typica*. In his catalogue (1997 and earlier editions) *T. parva* was subsequently ranked as a "species incerta". Arlt (1983) also believed that *T. parva* was probably only a variety of *T. minuta*, however, it is now clear that his conviction arose from observations of *T. reducta*, a species which, at least in terms of P5 morphology, holds an intermediate position between *T. parva* and the type species. *T. parva* has the same swimming leg armature

fomula as in *T. minuta* but can be readily distinguished by (1) the narrower and longer rostrum; (2) the form of caudal seta V which is not swollen in the proximal part; (3) the length and shape of the outer apical seta of the antennary exopod; (4) the longer outer exopodal spines of P2-P4 exp-1 and -2; (5) the short endopodal lobe of ♀ P5 not extending beyond distal margin of exopod; (6) the ventral ornamentation on the urosomites. *T. parva* has not been recorded since its original description.

Tachidiella patagonica n. sp.

Tachidiella minuta Sars, 1909 *sensu* Pallares (1979)

TYPE LOCALITY. — Isla de los Estados, Tierra del Fuego (Argentina), primarily in washings of *Macrocystis pyrifera* holdfasts. Pallares (1979) collected material in both Bahía Cook and Bahía Vancouver.

MATERIAL EXAMINED. — None. Pallares' (1979) original material consisting of an unspecified number of specimens is almost certainly lost (F. Cremonte, pers. comm.). Hence, *P. patagonica* is necessarily based only on the description and illustrations given by Pallares (1979: pp. 2-3, L à m. I, figs 1-13). Holotype designation is impossible due to the lack of evidence indicating that either of the illustrated descriptions (female or male) were based on a single specimen. All specimens which formed the basis of Pallares' description are therefore regarded here as syntypes [ICZN Art 73(b)(i)]. Since the syntypes originated from two localities, the type locality is all of the places of origin pending lectotype or neotype designation [ICZN Arts 73(b)(iii), 74(a)(iii) and 75(f)].

ETYMOLOGY. — The species name refers to Patagonia in South America, which includes the type locality.

REMARKS

Pallares (1979) gave a brief redescription of *T. minuta* from *Macrocystis* washings and plankton samples taken in the vicinity of these algae in both Cook and Vancouver Bays off the Isla de los Estados, Tierra del Fuego. Although we suspect that some of the setae and spines might not have been drawn at their real length (e.g. P5 baseo-endopod ♀; P2 enp-1 ♂), we consider the Argentinean specimens sufficiently different from the NW European population in order to attribute them distinct species status. Discrepancies are found in (1) the antennary exopod which has two well-developed apical setae on exp-2 (outer apical seta vestigial in *T. minuta*); Pallares (1979) shows a supernumerary short seta on the apex but mentions only a total of four (including the two lateral ones) in the text; (2) the distal half of the P5 exopod in both sexes is more elongate than in *T. minuta* (as evidenced by the relatively more proximal position of the outer seta); (3) the endopodal lobe of ♀ P5 is rectangular (instead of trapezoid) and does not extend beyond the distal margin of the exopod as in *T. minuta*; (4) P2 enp-3 of ♂ is narrower and more attenuate than in *T. minuta*; (5) caudal seta IV is swollen in its proximal region as in seta V; (6) body length: 533-543 µm (♀), 350-433 µm (♂). Pallares (1979) shows only two outer spines on P4 exp-3 (her Lám. I-12) but from the setal formula given in the text the real number seems to be three as in other members of the genus.

T. patagonica n. sp. is geographically closest to *T. kimi* from the South Shetlands but differs from this species in the P3 endopod setal formula, form and shape of P5 in both sexes and detailed structure of the ♂ P2 endopod.

KEY TO THE SPECIES

- | | | |
|----|------------------------------------------------------------------------------------------------------------------|-----------------------|
| 1. | P3 enp-3 with two inner setae | 2 |
| — | P3 enp-3 with three inner setae | 3 |
| 2. | Proximal region of caudal seta V swollen; distal inner seta of P2-P4 enp-3 and P4 exp-3 reduced | <i>reducta</i> n. sp. |
| — | Proximal region of caudal seta V not swollen; distal inner seta of P2-P4 enp-3 and P4 exp-3 well-developed | <i>kimi</i> n. sp. |

3. P5 ♀ endopodal lobe extending beyond distal margin of exopod; outer distal seta of antennary exopod strongly reduced *minuta* Sars, 1909
 — P5 ♀ endopodal lobe not extending beyond distal margin of exopod; antennary exopod with two well developed apical setae 4
4. P5 ♀ endopodal lobe trapezoid; outer seta of P5 ♀ exopod arising from distal half of outer margin; proximal region of caudal setae V and IV not swollen *parva* Lang, 1965
 — P5 ♀ endopodal lobe subrectangular; outer seta of P5 ♀ exopod arising from proximal half of outer margin; proximal region of caudal setae V and IV swollen *patagonica* n. sp.

ADDITIONAL REMARKS

Species differentiation within the genus *Tachidiella* is usually tedious due to the small size of most species (0.4-0.5 mm). Identification is primarily based on differences in the antennary exopod, P3 endopodal setation and the shape of the fifth legs and caudal ramus setae. The mouth-parts and remaining swimming legs are remarkably conservative and the usefulness of the swimming leg sexual dimorphism in the male is limited as a species discriminant. The latter is restricted to the P2 endopod, however, the homology of the modified distal segment in the male is not well understood. In the female this segment bears one inner and three apical elements, none of which is retained in the male. In some species such as *T. kimi* there is a trace of a minute spinous process along the inner margin (Fig. 7C) which might represent the positional homologue of a seta in the female. Lang (1948) illustrated a long seta in this position which is reminiscent of the condition found in *Zosime* Boeck, 1873. It might well be possible that Lang had accidentally figured a male *Zosime* since representatives of this genus are equally minute and often co-occur with *Tachidiella* species. Fiers' (1991) recent study on the copepodid development of *Z. pacifica* Fiers, 1991 revealed that the modification of the male P2 endopod is not expressed until the final moult.

Additional differences between species can also be found in the detailed structure of the genital field, i.e. in the size and location of the copulatory pore, and the presence or absence of paired integumental pockets anterior to the copulatory pore. Similar cuticle-lined invaginations have also been reported for the genital field of most

Paranannopidae (Gee & Huys 1990, 1991, 1994; Huys & Gee 1992, 1993, 1996) but in this family they are usually sited posterior to the copulatory pore. The function of these pockets is unknown. Finally, the shape of aesthetascs on the male antennule was found to differ between *T. minuta* (trilobate: Fig. 4B) and *T. kimi* n. sp. (bilobate: Fig. 10A), however, this would require confirmation by additional observation of a larger number of specimens.

Acknowledgements

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