The *Paracyclops fimbriatus*-complex (Copepoda, Cyclopoida): a revision

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ABSTRACT
The type species of *Paracyclops*, *P. fimbriatus* (Fischer, 1853), is redescribed based on material from the vicinity of St Petersburg in Russia, one of the type localities. The taxonomic status of *P. fimbriatus*, *P. chiltoni* (Thomson, 1882) and *P. imminuta* Kiefer, 1929 are stabilised and a neotype is designated for *P. fimbriatus*. It is revealed that failure to separate *P. imminuta* from the other two species of the complex was the main factor responsible for the taxonomic confusion concerning all three. Characters traditionally used by taxonomists, such as proportional measurements of the caudal rami and the terminal spines of the third endopodal segment of leg 4 are found to vary considerably within populations as well as between populations. Since there is extensive overlap in variability expressed between these three variable species, it is therefore concluded that most early records are unreliable. Previously overlooked characters which can help to differentiate between them are introduced, including the ornamentation of the frontal surface of the coxobasis of antenna, of the posterior surface of leg 1, and of the caudal rami.

KEY WORDS
Copepoda,
P. fimbriatus,
P. imminuta,
P. chiltoni,
taxonomy,
Palaearctic.

RÉSUMÉ
Le complexe Paracyclops fimbriatus *(Copepoda, Cyclopoida) : une révision.* L'espèce-type de *Paracyclops*, *P. fimbriatus* (Fischer, 1853) est redécrite à partir de matériel collecté à St Pétersbourg en Russie, une localité-type. Le statut systématique de *P. fimbriatus*, de *P. chiltoni* (Thomson, 1882) et *P. imminuta* Kiefer, 1929 est redéfini et un néotype est désigné pour *P. fimbriatus*. Il apparaît que la difficulté de séparer *P. imminuta* des deux autres espèces est la raison principale de la confusion systématique régnant dans ce complexe d'espèces. Les caractères utilisés jusqu'à présent, en particulier les mesures relatives des branches furcales et des épines terminales du troisième segment de l'endopodite de P4 présentent des variations considérables pour une population donnée et également entre populations et se recouvrent en partie chez les trois espèces. Cette variabilité extrême ne permet pas de les séparer clairement, les données anciennes paraissant parfois incertaines. D'autres caractères pouvant aider à différencier les trois espèces sont introduits comme l'ornementation de la face frontale du coxobasis de l'antenne, de la face postérieure de P1 (basipodite et coxopodite), des rames furcales et la structure du réceptacle séminal de la femelle.

MOTS CLÉS
Copepoda,
P. fimbriatus,
P. imminuta,
P. chiltoni,
taxonomie,
Paléarctique.

INTRODUCTION

The earliest record assigned to *Paracyclops fimbriatus* (Fischer, 1853) by Dussart & Defaye (1985) is that of the Danish naturalist O. F. Müller who described it under the name *Cyclops crassicornis* Müller, 1785. Müller's (1785) description and illustrations were based on an early copepodid stage and are grossly inadequate, so that it is almost impossible to determine whether he was dealing with a cyclopoid or harpacticoid. The type material of *Cyclops crassicornis* cannot be traced and probably is no longer extant. If *C. crassicornis* is a cyclopoid it can be best considered as *species incertae sedis* in the family Cyclopidae. Unfortunately Sars (1863) identified some of his specimens as *C. crassicornis* although he expressed some reservations about conspecificity with Müller's material. In spite of this uncertainty *C. crassicornis* became established in the literature since other workers (Uljanin 1875; Brady 1878; Herrick 1882) followed Sars and ignored or overlooked Fischer's (1853) important paper on the cyclopids from St Petersburg. It was not until 1892 that Brady (1892) recognized Fischer's (1853) *Cyclops fimbriatus* and discarded Müller's *C. crassicornis* as a valid species of cyclopid. Sars (1913-1918) independently arrived at the same conclusion and regarded it as very questionable that *Cyclops crassicornis* belongs to the genus *Cyclops*.

The origins of the current taxonomic confusion surrounding the genus *Paracyclops* in general, and the so-called *P. fimbriatus* complex in particular, are threefold.

Firstly, Fischer's (1853) original description of the type species *P. fimbriatus*, full and valid by contemporary mid-nineteenth century standards but inadequate by modern standards, has been accepted as the standard reference and consequently has led to problems in later taxonomic work. It is therefore not surprising that the species has been reported from a wide range of freshwater habitats all over the world.

A second factor that has contributed significantly to the taxonomic confusion is the publication of various incompletely described species or forms that are closely related to the type-species and can be considered as forming part of a *P. fimbriatus* species complex: these include *P. chiltoni* (Thomson, 1882), *P. finitimus* Kiefer, 1928, *P. abnobensis* Kiefer, 1929 and *P. fimbriatus* forma *imminuta* Kiefer, 1929.

Finally, in the course of this study it became apparent that the traditional means of differentiating species within the genus *Paracyclops*, such as the morphology of the caudal rami and leg 5, are insufficient and in some cases completely misleading since virtually no account has been taken of intra- or inter-population variation.

Recent progress in copepod systematics has raised the level of taxonomic resolution of these freshwater copepods and it has been demonstrated several times that many cyclopoid species, reported earlier as cosmopolitan in freshwater habitats, have a restricted geographical distribution (Kiefer 1981; Van de Velde 1984; Reid 1998). A similar situation has been demonstrated for the Cladocera (Frey 1980, 1982) and the Rotifera (Dumont 1983).

Prior to this revision, the geographical records and major synonyms of *P. fimbriatus* and *P. chiltoni* were summarized by Dussart & Defaye (1985) and indicated cosmopolitan distributions for both. So, it became vital to describe typical *P. fimbriatus* in detail. Attempts were made to locate the type material but Fischer's material is, in all probability, no longer extant. Unfortunately, Fischer did not designate a single type locality. Fischer's (1853) original paper was entitled "Contribution to the knowledge of Cyclopoids from the area of St Petersburg" and in this paper, it was stated that the *P. fimbriatus* material was collected from Madeira island, the vicinity of Baden-Baden (Germany), Iwanofskoje and Peterhof (around St Petersburg). There was no clear indication on which material his original description was based.

An attempt was made to collect *Paracyclops* material from the vicinity of St Petersburg. No *Paracyclops* material was found in the Peterhof pond but abundant *Paracyclops* material was collected from other localities in the vicinity of St Petersburg. The redescription given here is based on a neotype selected from this material, and supplemented by examination of numerous other collections from the Palaearctic region.

Examination of four unsorted samples from the vicinity of St Petersburg revealed four *Paracyclops* species: *P. fimbriatus*, *P. chiltoni*, *P. imminuta* and *P. poppei*. *Paracyclops poppei* can easily be separated from the other three species, but *P. fimbriatus*, *P. chiltoni* and *P. imminuta* are easily confused. Traditional means of differentiating between these taxa, such as the morphology of the caudal rami, the proportional length of terminal spines of leg 4 and the structure of leg 5 are insufficient and in some cases misleading, therefore most early records are unreliable.

The object of this paper is to redescribe *P. fimbriatus*, *P. imminuta* and *P. chiltoni* in detail, to identify their major synonyms and to introduce previously overlooked characters which are important in differentiating them.

METHODS

Specimens were dissected and mounted in lactophenol. Broken glass-fibres were added to prevent the appendages from being compressed by the coverslip and to facilitate rotation and manipulation which allowed viewing from all sides. All drawings were made with the aid of a camera lucida using an Olympus BH-2 microscope equipped with Nomarski differential interference contrast and all measurements made with an ocular micrometer. Body lengths were measured from the base of the rostrum to the posterior edge of the caudal rami. Body width is given as the widest part of the cephalothorax. In the spine and seta formula of the swimming legs Roman numerals and Arabic numerals are used for spines and setae, respectively. The terminology proposed by Huys & Boxshall (1991) is adopted. The terms "frontal" and "caudal" introduced by Van de Velde (1984) to denote the anterior and posterior surface of the antennary coxobasis are also adopted.

ABBREVIATIONS

NHM — The Natural History Museum, London;
MNHM — Muséum national d'Histoire naturelle, Paris;
ZM — Zoologisk Museum, Oslo;
USNM — United States National Museum, Smithsonian Institution, Washington.

SYSTEMATICS

Paracyclops fimbriatus (Fischer, 1853)
(Figs 1-9)

Original description:
Cyclops fimbriatus Fischer, 1853 [*Bull. Soc. Imp. Nat. Moscou* 26, 1: 94, figs 19-28, 30].

Synonymy:
Cyclops fimbriatus Fischer, 1853: 94, pl. III, figs 19-28, 30.

Cyclops crassicornis O. F. Müller, 1785 *sensu* Brady 1878: 118, 119, pl. 23, figs 1-6.

Cyclops soli Kokubo, 1912: 102, pl. II, figs 24-26.

Platycyclops fimbriatus (Fischer, 1853) – Sars 1913-1918: 81, 82, pl. L.

Cyclops (*Paracyclops*) *fimbriatus* Fischer, 1853 – Pesta 1928: 114-116, figs 96A-D, 97A-C. – Reuter-Schiltz & Hoffmann 1970: 229-231, figs 27-31.

Paracyclops fimbriatus f. *typica* (Fischer, 1853) – Kiefer 1929: 50, Abb. 53.

Paracyclops abnobensis Kiefer, 1929: 51, Abb. 57-59.

Paracyclops vagus Lindberg, 1939: 45-50, figs 1a-l.

TYPE MATERIAL. — A neotype is designated herein and deposited in the collection of the NHM, Reg. No. 1997.1762. It is a female collected at P. Dudergofka, St Petersburg, Russia and dissected on 4 slides.

OTHER MATERIAL. — **Russia.** River Igora (Neva system), about 10-15 km east of St Petersburg, depth 0.5 m, t 18 °C, 22.VII.1996, coll. V. Alekseev: 14 ♀♀. — P. Dudergofka, St Petersburg, 27.VII.1996, depth 0.5 m, t 18 °C, coll. V. Alekseev: 4 ♀♀. — River Ravan (Ladoya system), about 100 km east of St Petersburg, depth 0.2-0.5 m, t 17 °C, 22.VII.1996, coll. V. Alekseev: 2 ♀♀. — St Petersburg, water supply system, pond JWS, July 1984, coll. V. Alekseev: 1 ♂. — Baikal pulp & paper mill, pond of cleaning system, in the vicinity of Lake Baikal, 9.VII.1984, coll. V. Alekseev: 4 ♀♀, 3 ♂♂.
Turkey. Demirköprü, coll. Ü. Demirhindi: 7 ♀♀ (NHM 1966.3.24.23).
Sweden. Lake Malar, Upland: 4 ♀♀ (Norman Collection, NHM 1911.11.8.40935-939).
Ireland. Locality unspecified: 24 ♀♀, 7 ♂♂ (Norman Collection, 1911.11.8.40915-934; selected from more than 200 specimens in mixed sample, mostly *P. imminuta*). — Rossmore, Co. Monaghan: 1 ♀ (NHM 1911.11.8.40914).
Palestine. 33 ♀♀ (NHM 1938.3.9.83-89 1002a).
Norway. 69 ♀♀, 16 ♂♂ (G. O. Sars Collection ZM, F20478; no locality is given by G. O. Sars on the original label but on a second label is written "Norv" which indicates that the material is probably from Norway. This material contains a mixture of *P. fimbriatus* and *P. imminuta*.)
Mongolia. Lake Orog Nuur, Goby Desert, 11.VII. 1995, coll. V. Alekseev: 1 ♀, 14 ♂♂.
India. Nagarjuna University reservoir fed from River Krishna, 4.VIII.1976, coll. Y. Ranga Reddy: 7 ♀♀, 6 ♂♂. — River Krishna at Vijayawada, 16°31'N - 80°39'E , January 1974: 3 ♀♀.
Finland. Province of South Häme, municipality of Lammi, Lake Pääjärvi, western arm, organic ooze mixed with mineral particles at 3-5 m depth, 61°04'N - 25°08'E, 18.XI.1996, coll. J. Sarvala: 25 ♀♀, 1 ♂.
Germany. Oldenburg, 2.VIII.1996, coll. T. Ishida: 26 ♀♀, 12 ♂♂.
Japan. Tomakomai, Hokkaido, 4.XI.1987: 4 ♀♀, 8 ♂♂. — Same locality, 12.V.1987: 6 ♀♀, 1 ♂. — Ryuku, 12.V.1996, coll. T. Ishida: 1 ♀, 1 ♂ . — Lake Biwa, Honshu, 17-18.III.1986, coll. T. Ishida: 2 ♀♀ dissected on two slides. — Hokkaido University, Sapporo, Hokkaido, 9.VIII.1987, coll. T. Ishida: 6 ♀♀ whole mounts on 1 slide, 2 ♂♂ whole mounts on 1 slide, 2 ♀♀ dissected on slide. — Tokachi, Hokkaido, 5.VIII.1983, coll. T. Ishida: 1 ♀, 1 ♂ whole mounts.
Uzbekistan. Town Muynak near Aral Sea, Kashkadavya Region, Chauvak Reservoir, Tashkent Region, coll. I. M. Mirabdullayev: 6 ♀♀.
Scotland. Loch Ness, 19.VII.1992: 7 ♀♀, 5 ♂♂.

DISTRIBUTION. — Examination of numerous collections of *Paracyclops* from the Palaearctic, Nearctic regions, and from Africa has revealed that *P. fimbriatus* is not as widely distributed as previously believed (Karaytug 1998). Based on examined materials, *P. fimbriatus* is, at present, known to be distributed in Europe and Asia extending eastwards to include Turkey, Palestine, China, Japan and India. *P. fimbriatus* appears to be widely distributed throughout the Palaearctic region.

REDESCRIPTION
Adult female

Body length and width not including caudal setae given in Table 1. Prosome (Fig. 1C) with cephalothorax narrowing anteriorly and three free pedigerous somites decreasing in width from anterior to posterior. Third pedigerous somite with minutely denticulate hyaline frill along the posterior margin. Third and fourth pedigerous somites with patch of spinules at each posterolateral corner. Urosome (Fig. 2A, B)

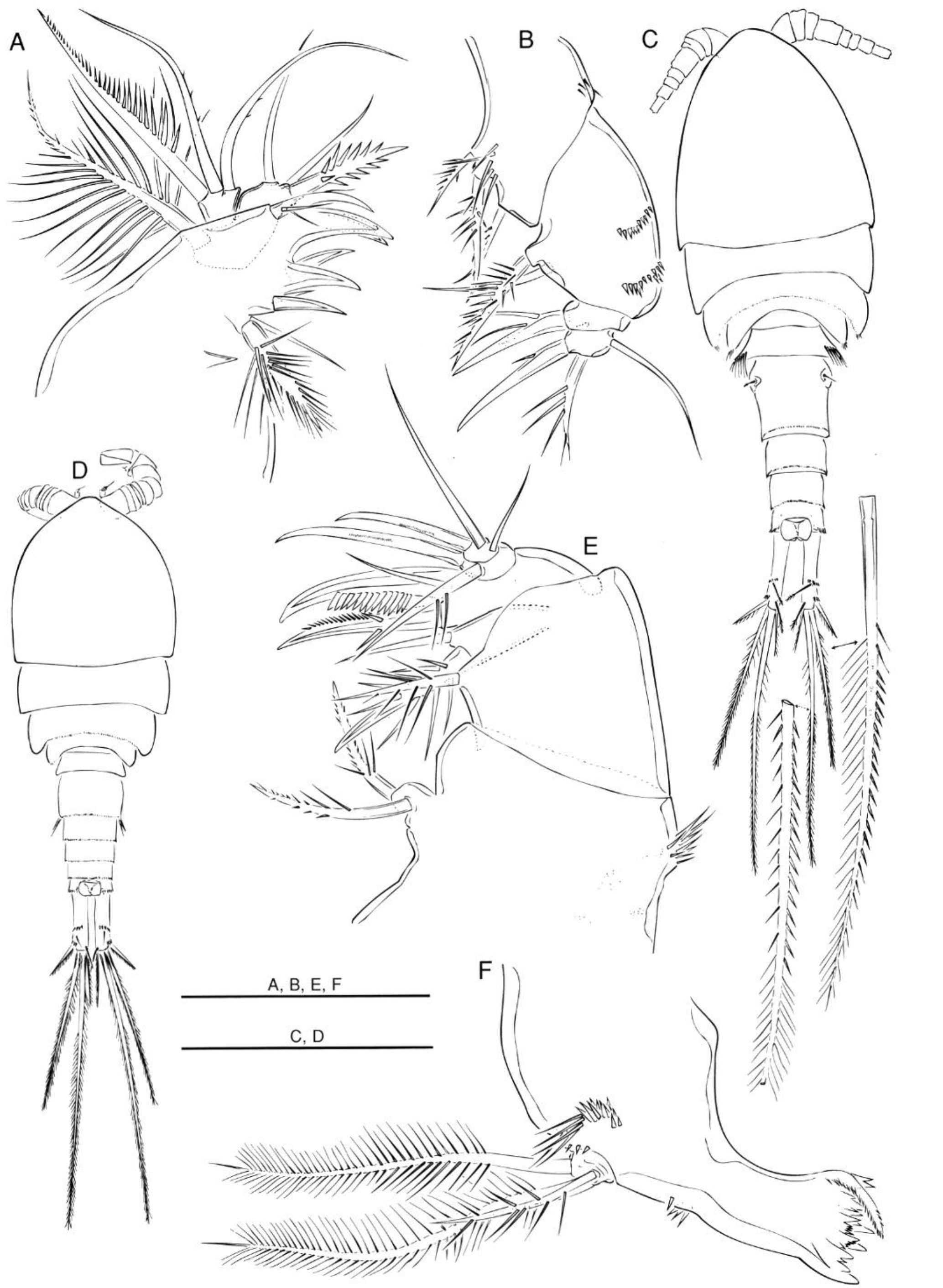

FIG. 1. — *P. fimbriatus*; **A**-**C**, **E**, **F**, neotype, adult ♀; **D**, adult ♂; **A**, maxillule; **B**, maxilliped; **C**, body, dorsal; **D**, body, dorsal; **E**, maxilla; **F**, mandible. Scale bars: A, B, E, F, 50 µm; C, D, 400 µm.

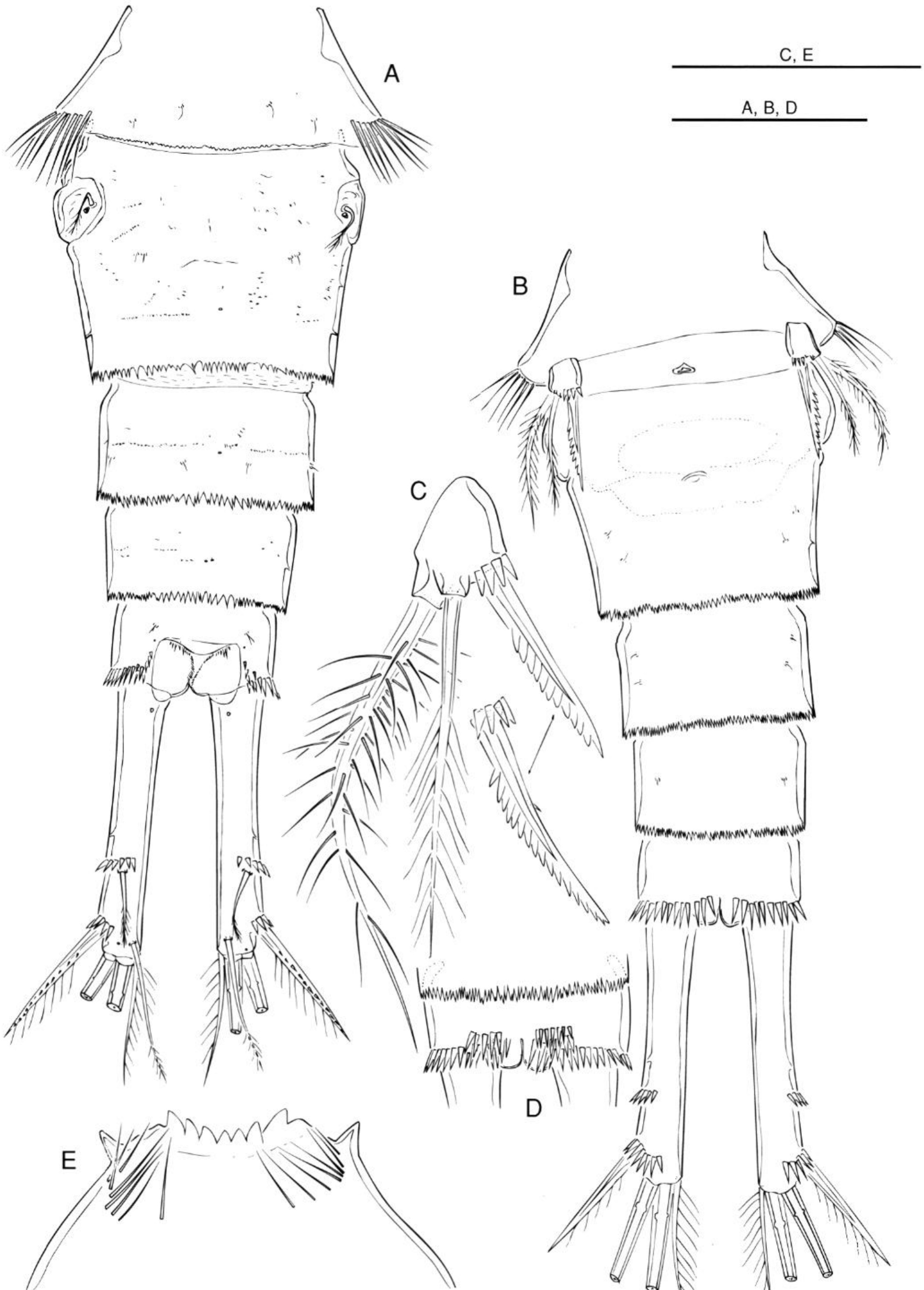

FIG. 2. — *P. fimbriatus*; **A**-**C**, neotype, adult ♀; **D**, non-type ♀; **A**, urosome, dorsal; **B**, urosome, ventral; **C**, leg 5, ventral; **D**, anal somite, ventral (St Petersburg); **E**, labrum. Scale bars: A, B, D, 100 µm; C, E, 50 µm.

FIG. 3. — *P. fimbriatus*; neotype, adult ♀; **A**, antennule with arrow indicating spiniform seta at anterodistal corner on third segment; **B**, antenna, coxobasis and first endopodal segment, frontal; **C**, antenna, caudal. Scale bars: A, 50 µm; B, C, 25 µm.

consisting of fifth pedigerous somite, genital double-somite and three free abdominal somites. Fifth pedigerous somite with fringe-like elongate setules at posterolateral angles. Genital double-somite, second and third abdominal somites ornamented with irregular pattern of fine pits dorsally as figured (Fig. 2A). Seminal receptacle divided into broad anterior and posterior lobes (Fig. 2B). Median copulatory pore located ventrally about halfway along length of genital double-somite. Posterior margin of genital double-somite and following two abdominal somites with finely incised hyaline frill. Anal somite with ventral spinular row extending laterally and dorsally almost to either side of anal operculum. Anal operculum weakly developed, smooth; and opening bordered by spinular row (Fig. 2A).

Caudal rami with slightly convex inner margin; very variable in length and shape (Figs 2A, B, 7A-F); armed with six setae (Fig. 2A); seta (I) absent; anterolateral seta (II) plumose with spinules at base on dorsolateral surface; posterolateral seta (III) unilaterally plumose with spinules along dorsal surface, spinular row at base ventrally extending dorsally; terminal accessory seta (VI) plumose: outer terminal seta (IV) and inner terminal seta (V) well-developed and heterogeneously ornamented (Fig. 1C).

Antennule 8-segmented (Fig. 3A). First segment with ventral spinular rows in proximal half. Segment 3 with partial suture line and spiniform seta near anterodistal corner (arrowed in Fig. 3A). Segment 5 with characteristic short aesthetasc. Segment 7 with aesthetasc located distally on anteroventral margin. Apical segment with aesthetasc fused basally to adjacent seta. Setal formula 8, 12, 6, 5, 2 + 1 aesthetasc, 2, 2 + aesthetasc, 7 + aesthetasc.

Antenna 4-segmented (Fig. 3C), comprising coxobasis and 3-segmented endopod. Coxobasis with complex ornamentation on caudal (Fig. 3C) and frontal (Fig. 3B) surfaces as figured, and armed with two inner spinulose setae plus very long outer spinulose seta representing exopod. First endopodal segment with inner distal spinulose seta and spinules along outer margin. Second endopodal segment with nine setae, of which six along inner margin and three arranged around distal inner corner; ornamented with spinules along outer margin. Third endopodal segment armed with seven setae around apex; outer margin ornamented with short spinules proximally and long spinules distally.

Labrum (Fig. 2E) forming broad posterior outgrowth. Distal margin with strong teeth; anterior surface ornamented with paired groups of long spinules.

Mandible (Fig. 1F) consisting of well-developed coxal gnathobase and reduced palp. Gnathobasis blades pointed, mostly simple, dorsal seta with spinules along inner rim. Palp represented by minute segment, bearing three spinulose setae, two of which very long and one short. Coxa with spinular row along outer margin between palp and gnathobase, and with lateral group of spinules near insertion of palp.

Maxillule (Fig. 1A) consisting of powerful praecoxa and reduced 2-segmented palp. Praecoxal arthrite armed with six setae articulating at base and five spines fused to segment; proximalmost articulating spine spinulose, other spines naked. Proximal segment of palp representing fused coxa and basis, bearing one strong spine and two naked setae apically, plus outer spinulose seta representing exopod. Distal segment of palp, representing endopod, armed with three setae, outermost seta spinulose.

Maxilla 5-segmented (Fig. 1E) comprising praecoxa, coxa, basis and 2-segmented endopod. Praecoxa with spinular rows on outer margin and dorsally. Praecoxal endite with two spinulose setae. Coxa with proximal endite represented by single spinulose seta; distal endite cylindrical, with strong spinulose spine and naked seta apically. Basis drawn out into powerful curved claw bearing coarse spinules along middle part of inner margin; accessory armature consisting of strong spine; with spinular row along convex margin and naked seta. First endopodal segment carrying two setae, second with three setae.

Maxilliped 4-segmented (Fig. 1B) comprising syncoxa, basis, and 2-segmented endopod. Syncoxa armed with three spinulose setae representing endites, few long spinules arranged near base of setae; ornamented with spinular row near outer distal angle. Basis armed with one spinulose and one naked seta; ornamented with

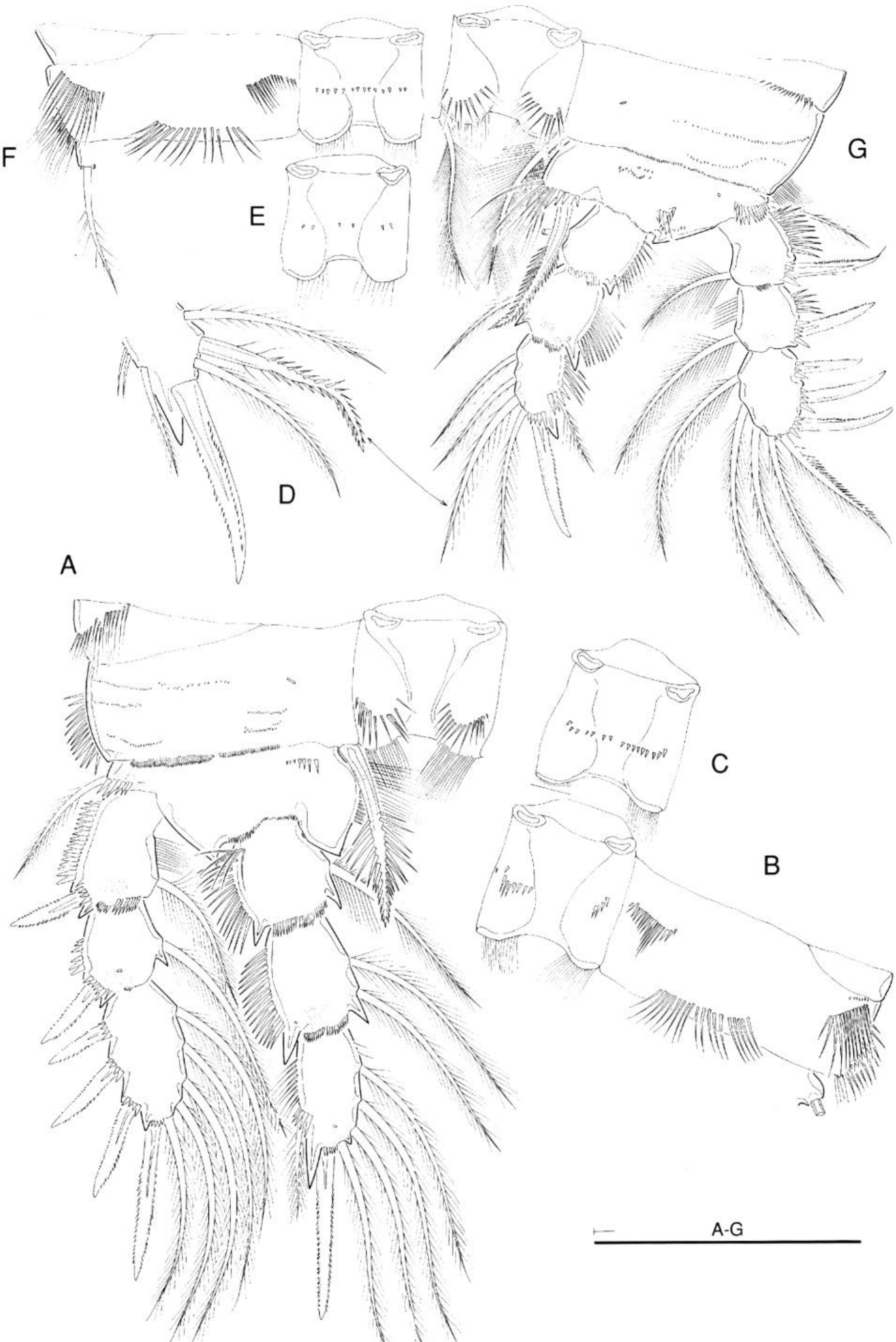

FIG. 4. — *P. fimbriatus*; **A**, **B**, **E**, **G**, neotype, adult ♀; **C**, non-type adult ♀; **D**, adult ♂; **F**, non-type ♀; **A**, leg 2, anterior; **B**, **C**, intercoxal sclerite and coxa of leg 2, posterior; **D**, terminal endopodal segment of leg 1; **E**, **F**, intercoxal sclerite and coxa of leg 1, posterior; **G**, leg 1, anterior view. Scale bar: 100 µm.

two transverse rows of spinules near outer margin. First endopodal segment bearing claw-like seta with spinules at midlength. Second endopodal segment with three setae, one of which naked; other spinulose.

Legs 1 to 4 with 3-segmented protopod (Figs 4A, G, 5A, F). Praecoxa represented by triangular sclerite at outer proximal angle; each protopodal segment with spinular row on outer corner of margin. Coxa with complex ornamentation on both anterior and posterior surfaces as figured. Basis with plumose outer seta. Endopodal segments with long spinules along outer margins. All spines on segments of both rami with spinules at their bases. Exopodal segments 1 and 2 with short spinules along outer margins. Legs 2 to 4 each with spinular rows on anterior surface of endopodal segments 1 and 2 and exopodal segment 1 and posteriorly on exopodal segments 1 and 2. Legs 2 and 3 with posterior spinular rows on endopodal segment 2.

Leg 1 (Fig. 4G): coxa with inner plumose seta. Basis with spinulose spine on inner margin bearing two groups of spinular rows at base, one of which long and fringe-like; also ornamented with spinular rows anteriorly near base of endopod. Intercoxal sclerite ornamented with spinular rows anteriorly (Fig. 4G) and posteriorly (Fig. 4E, F). Exopodal segments 1 and 2 and endopodal segment 2 with spinular rows posteriorly. Spine of exopodal segment 1 with flagellate apex. Seta next to outermost spine of terminal exopodal segment semispinulose (Fig. 4G).

Leg 2 (Fig. 4A): intercoxal sclerite with spinular rows anteriorly and posteriorly (Fig. 4A-C). Coxa with inner spinulose spine.

Leg 3 (Fig. 5F): intercoxal sclerite with (Fig. 5G) or without (Fig. 5F) spinular row anteriorly, with two spinular rows posteriorly (Fig. 5H). Coxa with inner spinulose spine.

Leg 4 (Fig. 5A): intercoxal sclerite with patch of spinules on anterior surface (Fig. 5A) and with three spinular rows posteriorly (Fig. 5B, C). Inner coxal spine with group of setules mainly originating posteriorly (Fig. 5C). Basis with spinular row near inner margin posteriorly (Fig. 5B, C). Endopodal segment 2 without spinular row posteriorly.

Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-I	I-1; I-1; III, 5	0-1; 0-1; 1, I, 4
Leg 2	0-I	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 4
Leg 3	0-I	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 4
Leg 4	0-I	1-0	I-1; I-1; II, I, 5	0-1; 0-2; 1, II, 2

Leg 5 (Fig. 2C) comprising single free segment, armed with one long (almost twice as long as inner spine) multispinulose outer seta, one strong inner spine with 3-4 spinules around base, and one plumose seta in middle. Leg 6 (Fig. 2A) represented by one plumose seta and one tiny spinule dorsolaterally.

Adult male

Body length 716 µm and width 260 µm (St Petersburg), the body length and width measurements of the males from other localities are given in Table 1. Body (Fig. 1D) differing from adult female as follows: urosome 6-segmented (Fig. 8A, C), comprising fifth pedigerous, genital and four free abdominal somites; genital, third, fourth and fifth urosomites ornamented with cuticular pits dorsally (also present ventrally on fourth urosomite). Caudal rami shorter than female.

Antennule digeniculate (Fig. 9A, C, D), indistinctly 15-segmented. Segment 1 armed with eight setae; one seta (seta A) large and modified by ornamentation of strong spinules in proximal and mid sections, tapering to fine point distally (see inset in Fig. 9D); ornamented with row of spinules ventrally (Fig. 9E). Segment 2 with four setae. Segment 3 with two setae. Segment 4 with two setae plus aesthetasc. Segments 5 and six each with two setae. Segments 7 and 8 separated from each other by extensive arthrodial membrane (Fig. 9D): segment 7 with two setae, segment 8 with two setae. Segment 9 with two setae plus a short aesthetasc, fused to segment 8. Segment 10 (= ancestral segment XV) produced on one side into sheath enclosing segment 11 ventrally; armed with two setae, one ornamented with long setules unilaterally, other longer and naked. Segment 11 bearing curved seta ornamented with

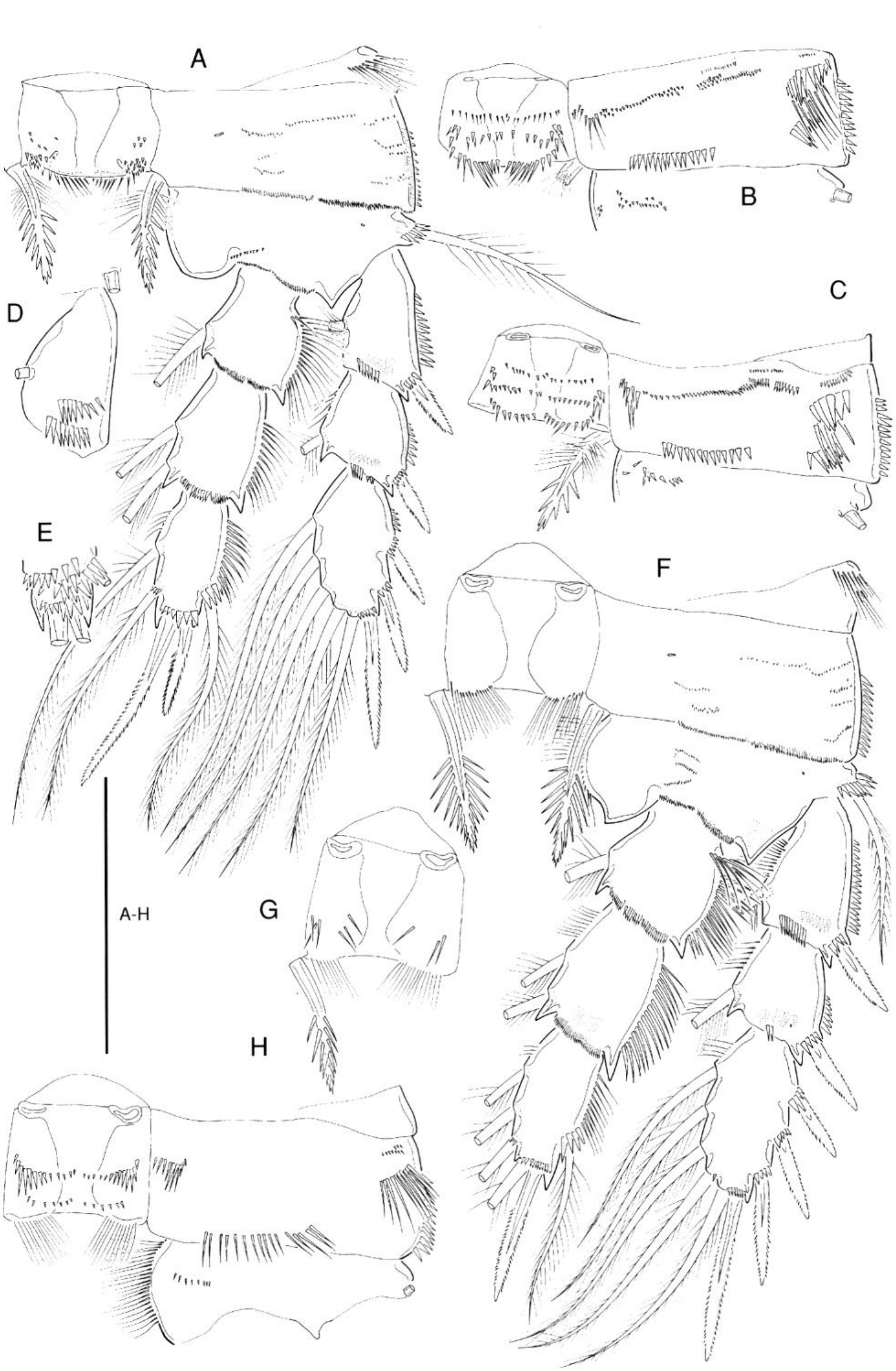

FIG. 5. — *P. fimbriatus*; **A**, **B**, **F**, neotype, adult ♀; **C**, **D**, **E**, non-type ♀; **A**, leg 4, anterior; **B**, **C**, intercoxal sclerite and coxa of leg 4, posterior; **D**, first exopodal segment of leg 4, posterior (Finland); **E**, terminal endopodal segment of leg 4, anterior; **F**, leg 3, anterior; **G**, intercoxal sclerite of leg 3, anterior; **H**, intercoxal sclerite and coxa of leg 3, posterior. Scale bar: 100 µm.

TABLE 1. — Body length (BL) and width (BW) measurements (in µm) of adult *Paracyclops fimbriatus* from various localities (N, number of specimens measured).

LOCALITY	SEX	BL (mean ± SD)	RANGE	BW (mean ± SD)	RANGE	N
St Petersburg (River Igora)	♀	885 ± 92.5	684-1017	309 ± 12.6	289-333	14
St Petersburg (P. Dudergofka)	♀	916 ± 91.5	815-993	370 ± 12.5	358-383	3
Russia (Vicinity of Lake Baikal)	♀	862 ± 52	802-894	314 ± 7.5	306-321	3
	♂	754 ± 16	738-770	254 ± 5	249-259	3
Mongolia	♀	743		296		1
	♂	651 ± 19.3	605-672	228 ± 15.4	202-249	10
India	♀	624 ± 22.9	600-662	231 ± 6.5	222-240	6
	♂	558 ± 27	527-589	204 ± 3.5	200-207	5
Turkey	♀	776 ± 67.5	707-854	302 ± 15.3	289-326	5
Finland	♀	893 ± 48.4	808-983	329 ± 9.3	313-351	12
	♂	786		262		1
Sweden	♀	923 ± 30.4	901-944	340 ± 27.6	320-359	2
Germany	♀	834 ± 38.2	786-926	336 ± 13.1	318-359	12
	♂	696 ± 31.6	641-728	280 ± 4.5	272-285	7
Japan	♀	862 ± 41.6	777-909	308 ± 13.6	282-328	9
	♂	748 ± 42.4	693-810	259 ± 4.9	247-268	9
Ireland	♀	831 ± 40.9	767-901	336 ± 16.2	311-363	10
	♂	721 ± 22.3	699-757	276 ± 7	268-285	5
Scotland	♀	916 ± 50.9	827-998	337 ± 21.5	295-359	7
	♂	816 ± 80.3	722-913	287 ± 18.7	264-307	5
Palestine	♀	743 ± 48.1	709-777	256 ± 2.8	254-258	2
Uzbekistan	♀	782 ± 32.5	724-846	258 ± 19	234-284	6

double row of strong denticles, plus one naked seta (Fig. 9A, C). Segment 12 armed with minute naked seta, plus short, highly chitinized spine. Segment 13 armed with one short spinulate seta proximally, four short naked setae, plus one modified element attached to segment by short stalk (Fig. 9A); main part of modified element lying along surface of segment and ornamented with longitudinal ridges and small central pore. Geniculation located between segments 13 and 14. Segments 14 and 15 partly fused (Fig. 9B), forming curved subchela-like section: segment 14 armed with two setae and two modified elements each ornamented with longitudinal ridges and a central pore (as proximal element on segment 13). Apical segment tapering distally; armed with eleven setae and one aesthetasc, mostly originating on outer (= posterior) surface. Segmental fusion pattern as follows: I-V, VI-VII, VIII, IX, X, XI, XII, XIII, XIV, XV, XVI, XVII, XVIII-XX, XXI-XXIII, XXIV-XXVIII.

All other appendages as in female except: coxobasis of antenna with additional spinular row near inner spinulose setae (arrowed in Fig. 8E), innermost seta of coxobasis strongly spinulated. One inner seta on endopodal segment 3 of leg 1 spinulose (Fig. 4D). Outer seta of fifth leg plumose and less developed than in

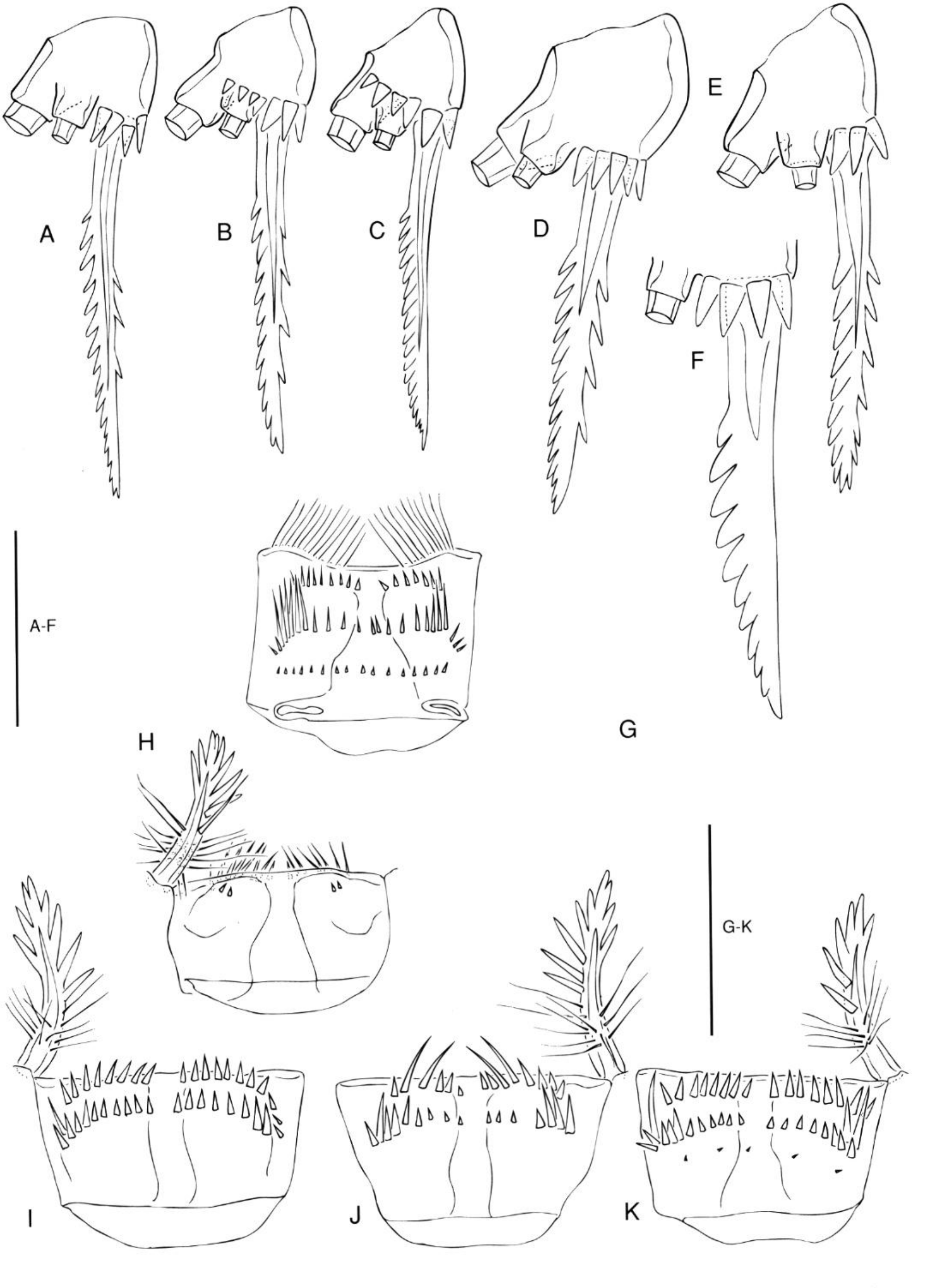

FIG. 6. — *P. fimbriatus*; non-type, adult ♀; **A-C**, leg 5, ventral (India); **D**, **E**, leg 5, ventral (St Petersburg); **F**, leg 5, ventral (Germany); **G**, leg 3, intercoxal sclerite, posterior (Lake Baikal); **H** (anterior), **I** (posterior), leg 4, intercoxal sclerite (Russia); **J**, **K**, leg 4, intercoxal sclerite, posterior (India). Scale bars: A-F, 25 µm; G-K, 50 µm.

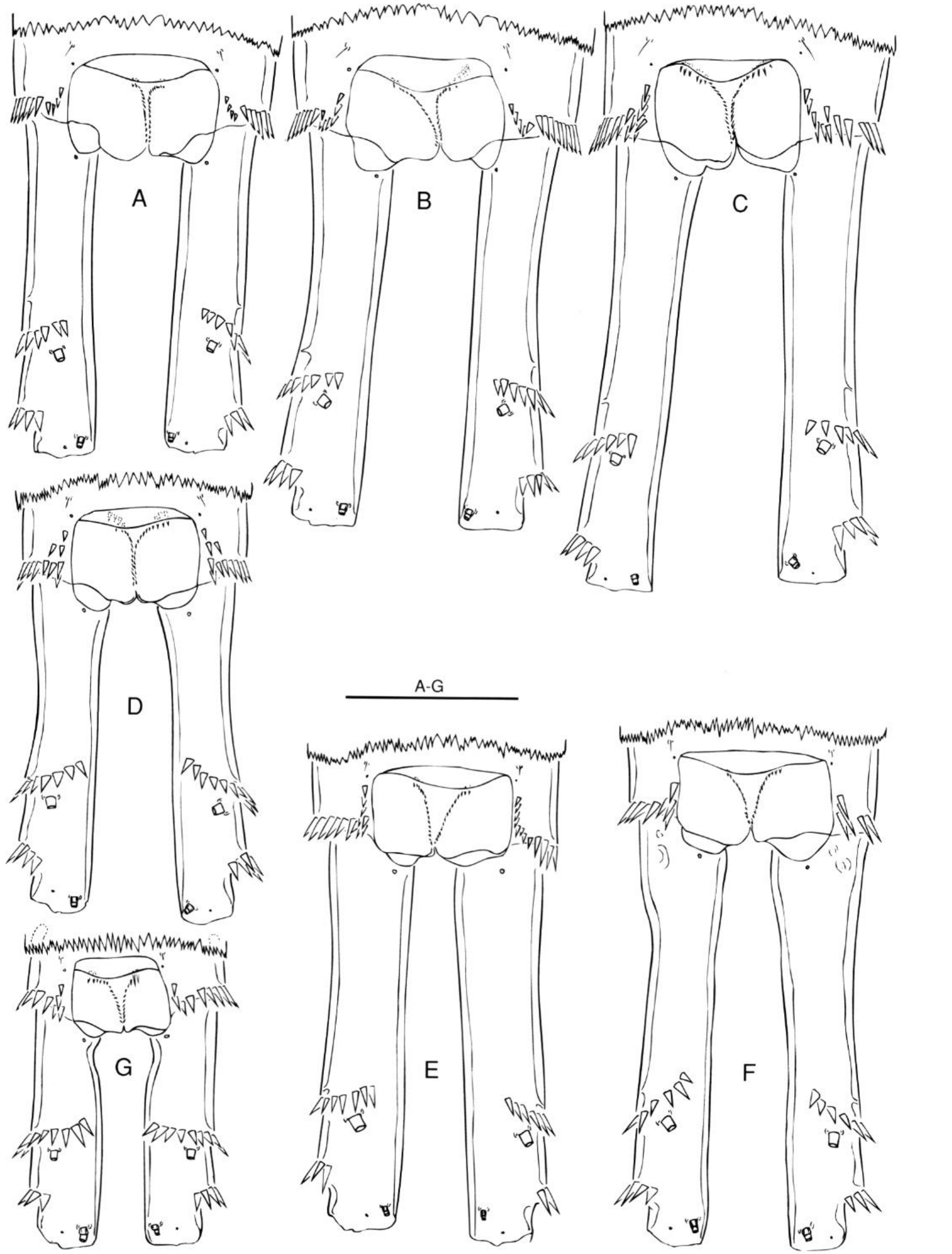

FIG. 7. — *P. fimbriatus*; **A**-**F**, non-type, adult ♀; **G**, adult ♂; **A**-**E** (Europe), **F** (India), caudal rami, dorsal; **G**, caudal rami (India). Scale bar: 50 µm.

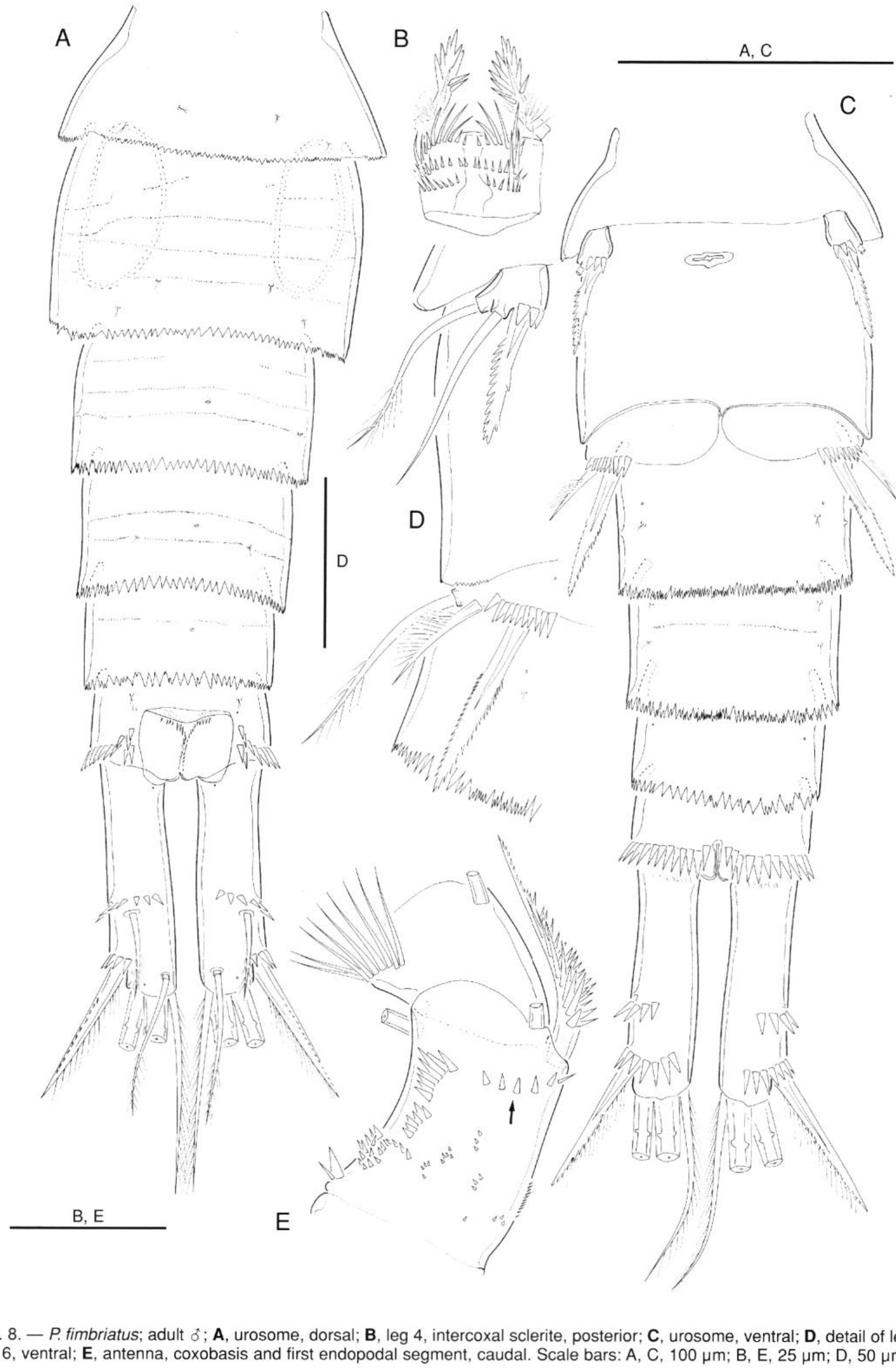

FIG. 8. — *P. fimbriatus*; adult ♂; **A**, urosome, dorsal; **B**, leg 4, intercoxal sclerite, posterior; **C**, urosome, ventral; **D**, detail of leg 5 and leg 6, ventral; **E**, antenna, coxobasis and first endopodal segment, caudal. Scale bars: A, C, 100 µm; B, E, 25 µm; D, 50 µm.

female (Fig. 8D). Sixth leg (Fig. 8D) armed with one inner spine (as long as third urosomal somite and ornamented with about eleven spinules at base) and two outer plumose setae.

VARIABILITY

Females

Measurements of body lengths and widths are given in Table 1. One female from St Petersburg possessed an extra spinular row on the anal somite ventrally (Fig. 2D). Specimens from Finland consistently had two spinular rows on exopodal segment 1 of leg 4 on posterior surface (Fig. 5D). These rows appeared inconsistently on specimens from St Petersburg and Turkey. This variability is also illustrated in Damian-Georgescu's (1963) drawings based on material from Romania. The exopodal spines of the swimming legs and the inner spine of leg 5 (Fig. 6F) of some specimens from Oldenburg (Germany) appeared to be stouter than in other populations. Despite the fact that material from Germany had stouter spines on swimming legs, as did the Finish material, the two posterior spinular rows on the first exopodal segment of leg 4 were not consistently present in German material. Additional variability was noted for the spinules on anterior surface of the intercoxal sclerite of leg 3 which may be present or absent in any population examined (Fig. 5F, G) and some specimens from the vicinity of Lake Baikal had three rows of spinules posteriorly on the intercoxal sclerite (Fig. 6G).

Variability in the arrangement and number of posterior spinular rows on the intercoxal sclerite of leg 4, as well as in the shape of the inner coxal spine (degree of curvature) on leg 4 was also noted in some specimens from the vicinity of Lake Baikal (Fig. 6H, I) and from India (Fig. 6J, K). The material from India especially showed interesting variability in leg 5 (*cf.* Fig. 6A-C) as the inner spine was usually longer than in other material examined and there were spinules present at the base of the middle seta in some specimens (Fig. 6B, C). Variability in the structure of the inner spine of leg 5 in specimens from St Petersburg region is shown in Figure 6D, E, but no consistent pattern was observed in this variability.

Males

In material from Japan, a group of spinules (arrowed in Fig. 8E) on the coxobasis of antenna can be very small or absent in some specimens.

DIFFERENTIAL DIAGNOSIS

P. fimbriatus is distinguished by the following unique combination of characters: the structure of leg 5 (Fig. 2C), the spinular ornamentation of coxobasis of antenna in both sexes (Figs 3B, C, 8E), the structure of the receptaculum seminis (Fig. 2B), the absence of the aesthetasc on the first segment of the male antennule (Fig. 9A).

P. fimbriatus and *P. imminuta* are easily confused as a result of their close morphological similarity. Nevertheless, the absence of the well-developed spinular row on the frontal surface of the coxobasis of the antenna in *P. fimbriatus* (Fig. 3C) can be used unequivocally to separate females of *P. fimbriatus* from *P. imminuta*. The spinular row is sexually dimorphic and, in the adult male of *P. fimbriatus* (Fig. 8E), the spinules are less well-developed than in *P. imminuta* (arrowed in Fig. 15D). In addition, the ornamentation of the mid-distal spinular ornamentation on the posterior surface of leg 1 in *P. imminuta* is significantly different (arrowed in Fig. 13B) from that of *P. fimbriatus* (Fig. 4F). *P. fimbriatus* can easily be separated from *P. chiltoni* by the length of outer seta of leg 5 in the female (Fig. 2C), by the absence of cuticular depressions on the ventral surface of the caudal rami in the female and by the structure of the seminal receptacle (Fig. 2B).

REMARKS

Most early descriptions of this species lack detail and several subspecies have been described on the basis of characters that are very variable. Most early records are, therefore, unreliable. Below, comparisons are made only with the important descriptions that conform to *P. fimbriatus* as described above. However, one record of "*P. fimbriatus*" from Iran (Lindberg 1941) should be mentioned here because the material described by Lindberg appears to be significantly different from the typical form described in detail above, on the basis of very short inner spine of leg 5 (Lindberg 1941: 477, figs a, c). This record does

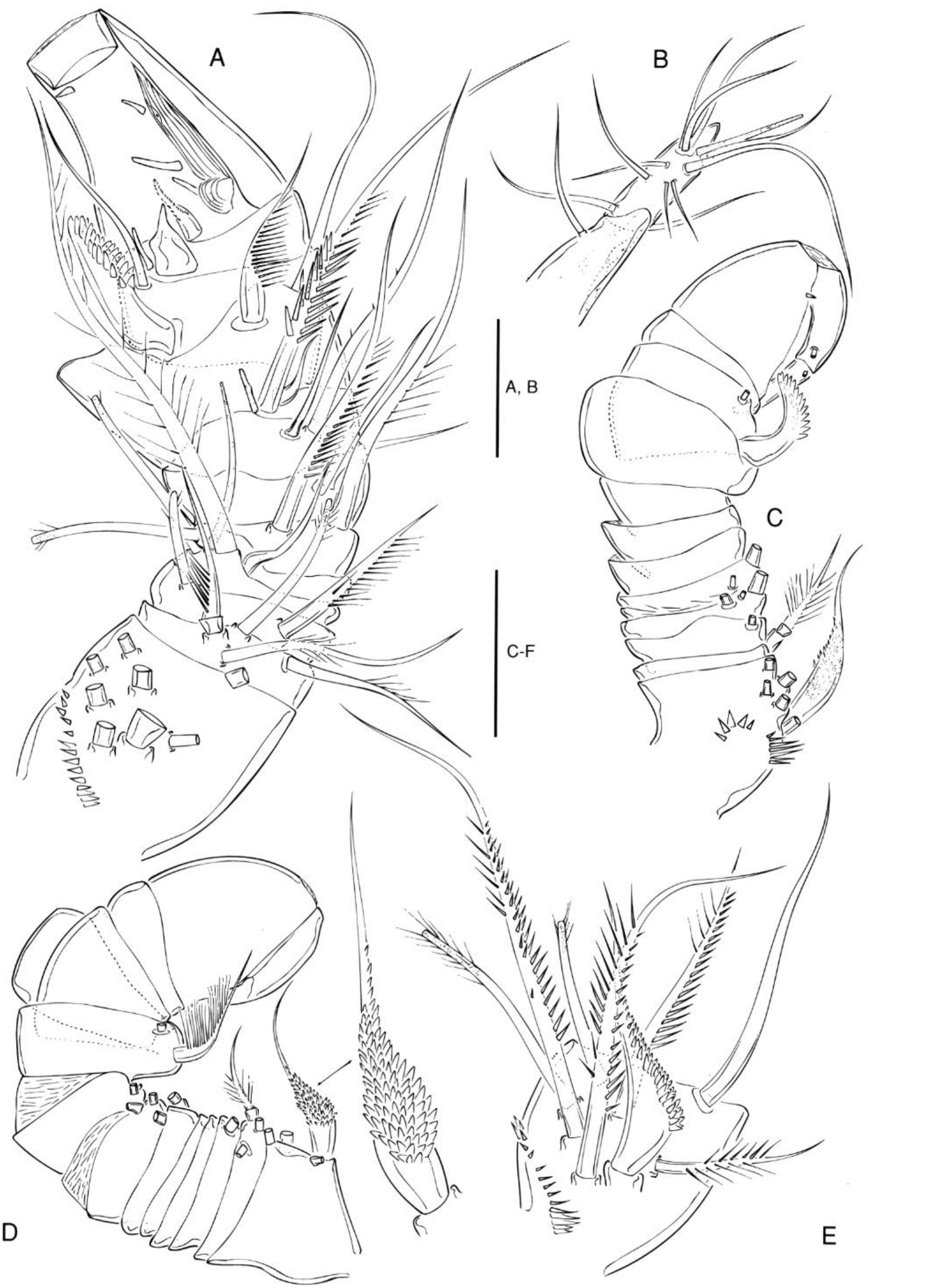

FIG. 9. — *P. fimbriatus*; adult ♂, antennule; **A**, anteroventral showing setation; **B**, terminal segment, posterior; **C**, ventral showing segmentation; **D**, dorsal showing segmentation; **E**, first segment showing setation, anteroventral. Scale bars: A, B, 25 µm; C-E, 50 µm.

not conform to *P. fimbriatus* as defined here and may represent a new species.

After Fischer (1853), a more detailed description of *P. fimbriatus* was given by Brady (1878). In Brady's drawings the caudal rami are inserted very wide apart. This character is typical of *P. fimbriatus* and is never found in *P. imminuta*. Later, further improved illustrations were provided by Schmeil (1892) showing long caudal rami, the structure of leg 5 and the seminal receptacle. These characters, though variable, help to confirm the identity of his material as *P. fimbriatus*. After Schmeil, similar descriptions were given by Sars (1913-1918) as *Platycyclops fimbriatus* and by Pesta (1928) under the name *Cyclops* (*Paracyclops*) *fimbriatus*.

Although Kokubo (1912) presumably overlooked the third seta of leg 5 or possibly examined an aberrant specimen, his description of *Cyclops soli* indicates that it is a synonym of *P. fimbriatus*.

Kiefer (1929) separated *P. abnobensis* from *P. fimbriatus* on the basis of shorter (not quite 4 times as long as broad) but widely separated caudal rami. In addition, in leg 4 the inner apical spine is twice as long as the third endopodal segment and the outer seta of leg 5 is relatively long. These characters do not differ significantly from those of *P. fimbriatus*. It is now widely accepted that the length of caudal rami is a very variable feature within species of Cyclopidae in general. Individual examination of specimens in samples of *P. fimbriatus* from several localities in Europe, especially those specimens with short caudal rami (see Fig. 7A), revealed no consistent variation in characters other than length of caudal rami to support the validity of *P. abnobensis*. Consequently, *P. abnobenis* is treated here as a synonym of *P. fimbriatus*, following Dussart & Defaye (1985). Variation in the length of caudal rami was also indicated by Monchenko's (1974) description of *P. fimbriatus* in which the caudal rami are shown as very short and widely separated.

Lindberg (1939) described *P. vagus* as a new species from India but later synonymized it with *P. fimbriatus* (Lindberg 1958). Study of material from India that was identified as *P. vagus* by Ranga Reddy & Radhakrishna (1984) revealed variation in leg 5 (*cf.* Fig. 6A-C), as the inner spine was usually longer than in other material examined and there were spinules present at the base of the middle seta in some specimens (Fig. 6B, C). Consistent variation, however, was not observed and no additional characters supporting the status of *P. vagus* as a distinct species or subspecies were found. In accordance with Lindberg (1958) *P. vagus* is treated here as a synonym of *P. fimbriatus*.

Paracyclops imminuta Kiefer, 1929
(Figs 10-16)

Original description:
Paracyclops fimbriatus f. *imminuta* Kiefer, 1929 [Zur Kenntnis einiger Artgruppen der Süsswasser-Cyclopiden. *Z. wiss. Zool.* 133: 1-56, figs 1-61].

Synonymy:
Cyclops fimbriatus Fischer var: Kiefer, 1926: 278.

Paracyclops fimbriatus f. *imminuta* Kiefer, 1929: 49, 50, Abb. 54-56.

Paracyclops fimbriatus Fischer, 1853 *sensu* Gurney 1933: 121-126, figs 1438-1458.

Paracyclops fimbriatus orientalis Alekseev, 1995: 133-138, figs 1, 2.

TYPE LOCALITY. — Germany: Mains water system of Oefingen (Kiefer 1929).

MATERIAL EXAMINED. — It has not been possible to examine the type material of *Paracyclops fimbriatus* f. *imminuta* Kiefer, 1929. It is not listed in the catalogue of the Kiefer collection (Franke 1989) and may not be extant.

England. Co. Durham: 26 ♀♀, 10 ♂♂ (Norman Collection, NHM 1911.11.8.40884-903). — Richmond Park, Surrey, 5.VI.1967, coll. A. J. Bruce: 9 ♀♀, 3 ♂♂ (NHM 1967.9.1.242). — Rainton Meadows, Durham: 34 ♀♀, 11 ♂♂ (Norman Collection, NHM 1900.3.29.261). — Somerset: 2 ♀ (NHM 1953.6.29.1). — Beechwood Park: 1 ♀ (NHM 1965.4.1.1.5). — Langness Cave, Deep Threshold, partly dried up pool, pH 6.7, t 21.5 °C, conductivity 725 ms/cm, coll. M. Moseley: 3 ♀♀. — Highgate: 3 ♀♀ (NHM 1951.11.9.3). — Derby Power Station: 1 ♀ (NHM 1963.7.16.3). — Manchester: 2 ♀♀, 1 ♂ (NHM 1961.3.10.1). — Langness Peninsula (NGR SC 281653) from damp pebble/gravel on floor, 2"-3" below ground, (material was collected from a sea cave which is only inundated by the sea during storms, freshwater enters as seepage at other times), 30.VII.1994: 3 ♀♀, 4 ♂♂.

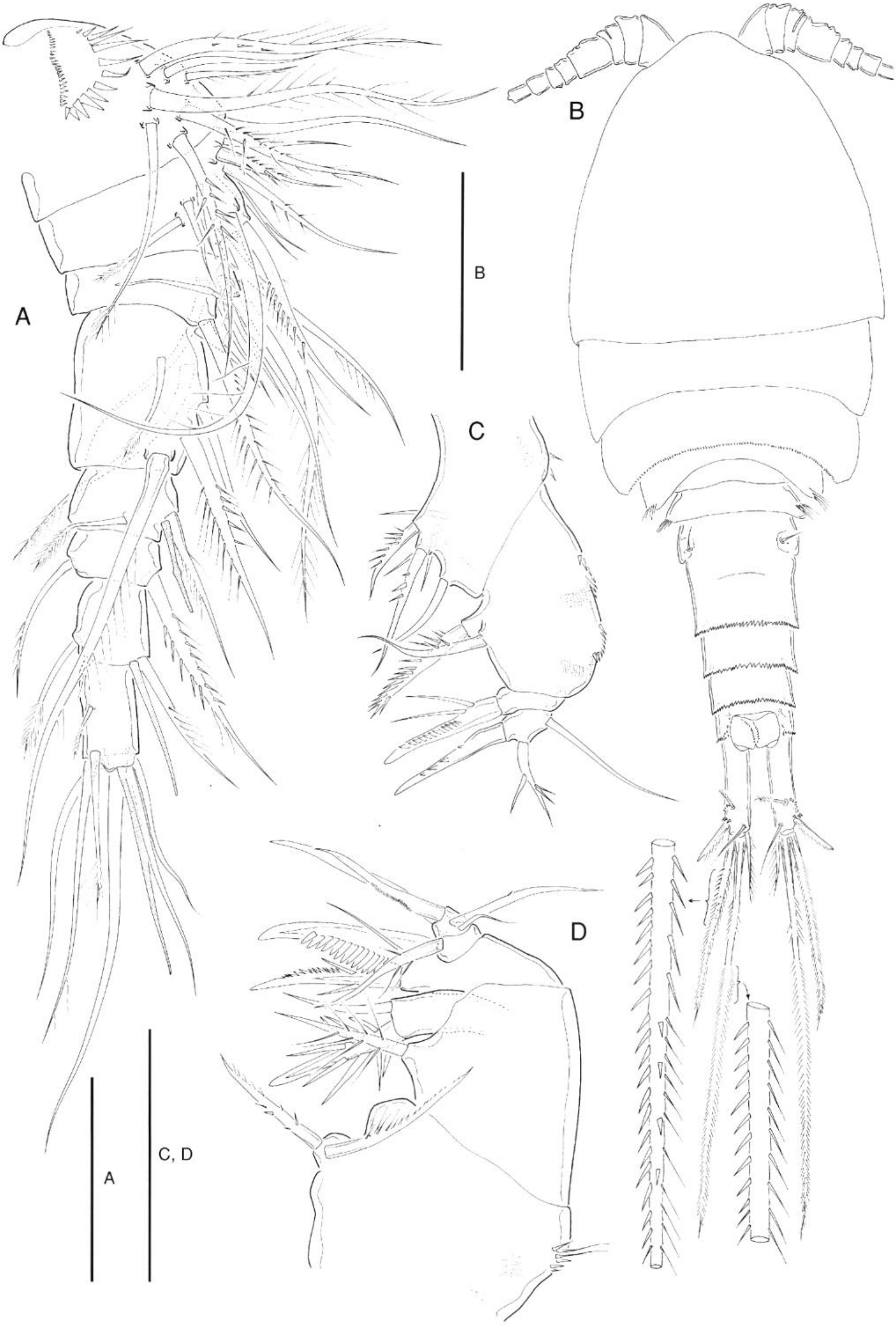

FIG. 10. — *P. imminuta*; adult ♀; **A**, antennule; **B**, body, dorsal; **C**, maxilliped; **D**, maxilla. Scale bars: A, C, D, 50 µm; B, 200 µm.

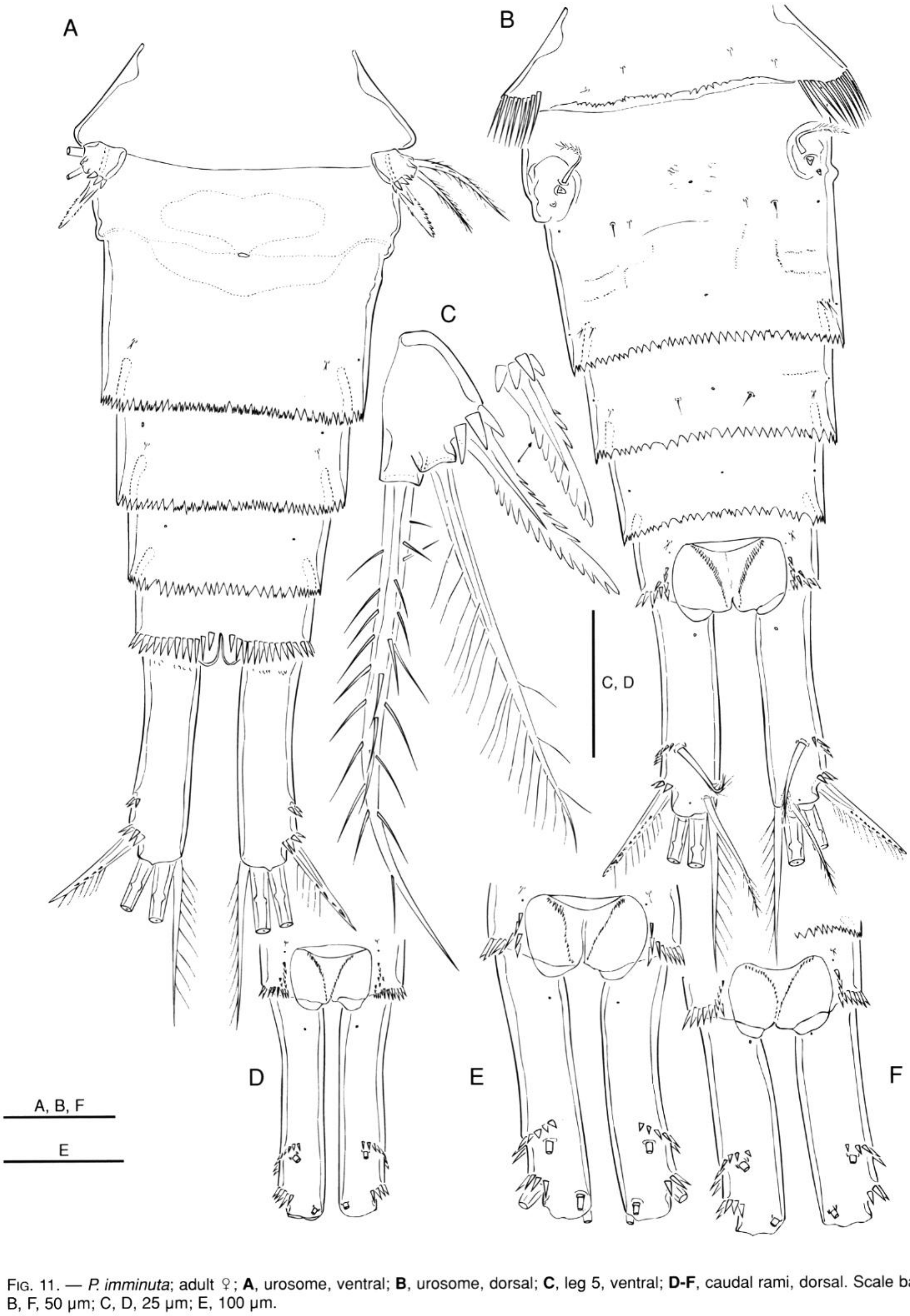

FIG. 11. — *P. imminuta*; adult ♀; **A**, urosome, ventral; **B**, urosome, dorsal; **C**, leg 5, ventral; **D-F**, caudal rami, dorsal. Scale bars: A, B, F, 50 µm; C, D, 25 µm; E, 100 µm.

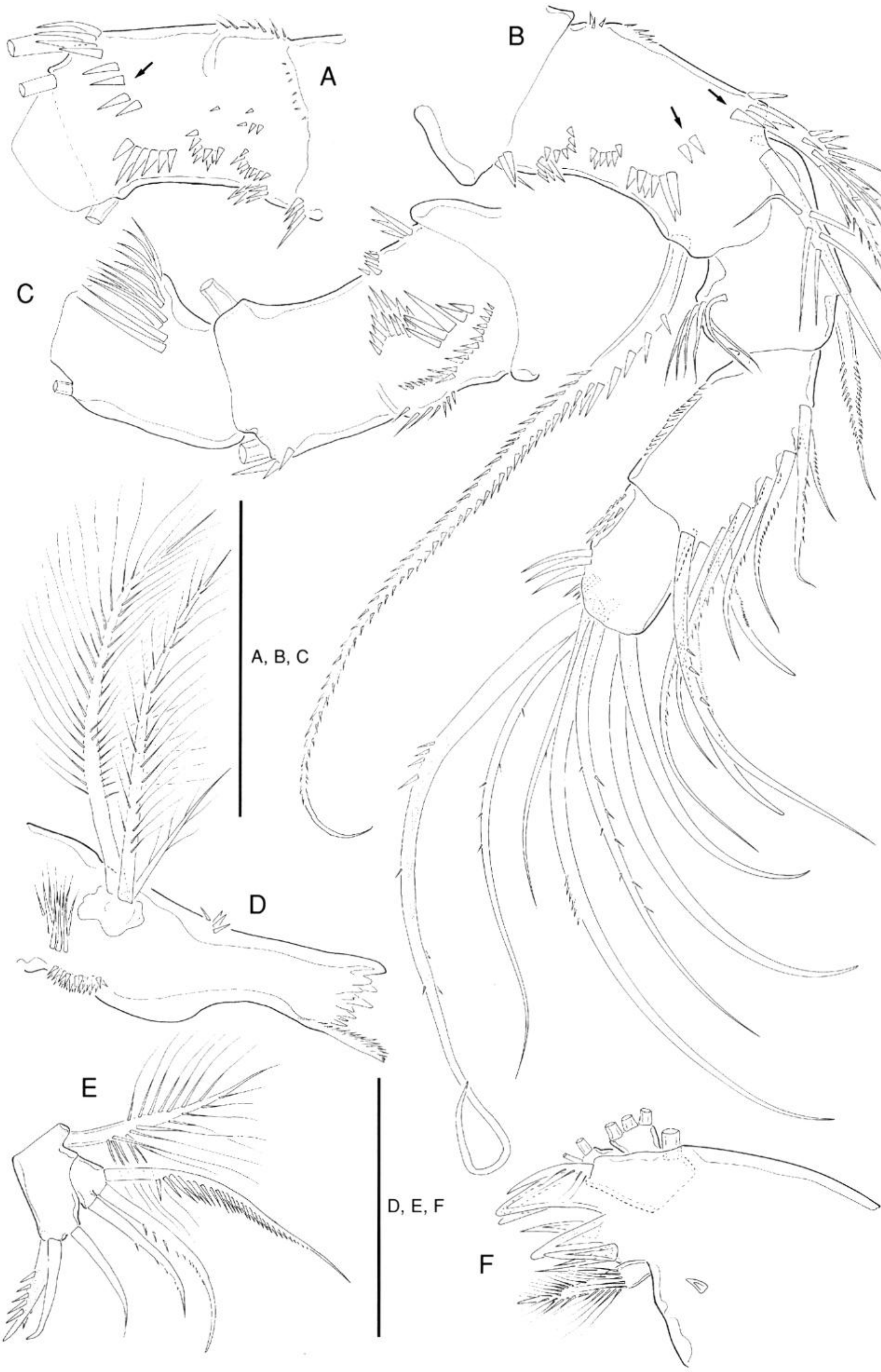

FIG. 12. — *P. imminuta*; adult ♀; **A**, antenna, coxobasis showing variant pattern of spinulation, caudal; **B**, antenna, caudal; **C**, antenna, coxobasis and first endopodal segment, frontal; **D**, mandible; **E**, maxillulary palp; **F**, maxillule. Scale bars: 50 µm.

Russia. River Igora (Neva system), about 10-15 km east of St Petersburg, 22.VII.1996, depth 0.5 m, t 18 °C, coll. V. Alekseev: 1 ♀. — P. Dudergofka, St Petersburg, 27.VII.1996, depth 0.5 m, t 18 °C, coll. V. Alekseev: 1 ♀. — St Petersburg water supply system pond, August 1984, coll. V. Alekseev: 2 ♀♀.
Ireland. Several females and males selected from more than 200 specimens (Norman Collection, NHM 1911.11.8.40915-934).
Norway. 69 ♀♀, 16 ♂♂ (G. O. Sars Collection, ZM F20478; no locality is given by G. O. Sars on the original label but on a second label is written: "Norv", which indicates that the material is probably from Norway; this material contains a mixture of *P. fimbriatus* and *P. imminuta*.).
Sweden. Lake Malar, Upland: 4 ♀♀, 2 ♂♂ (Norman Collection, NHM 1911.11.8.40935-939).
Greece. Delphi: 1 ♀, 1 ♂ (Gurney Collection, NHM 1937.11.16.620-1).
Israel. 3 ♀♀ on two slides (Glassman Collection; En Qumran, IES cop 226301); 1 ♀ on 1 slide (Glassman Collection; En Ziv, IES cop 200701).
Azores. Pico, 12.X.1971: 2 ♀♀ dissected on three slides (Th. Monod Collection n° 15190, MNHN); 2 ♂♂ mounted on one slide (Th. Monod Collection n° 15188, MNHN). — Terceira, 15.X.1971: 1 ♀

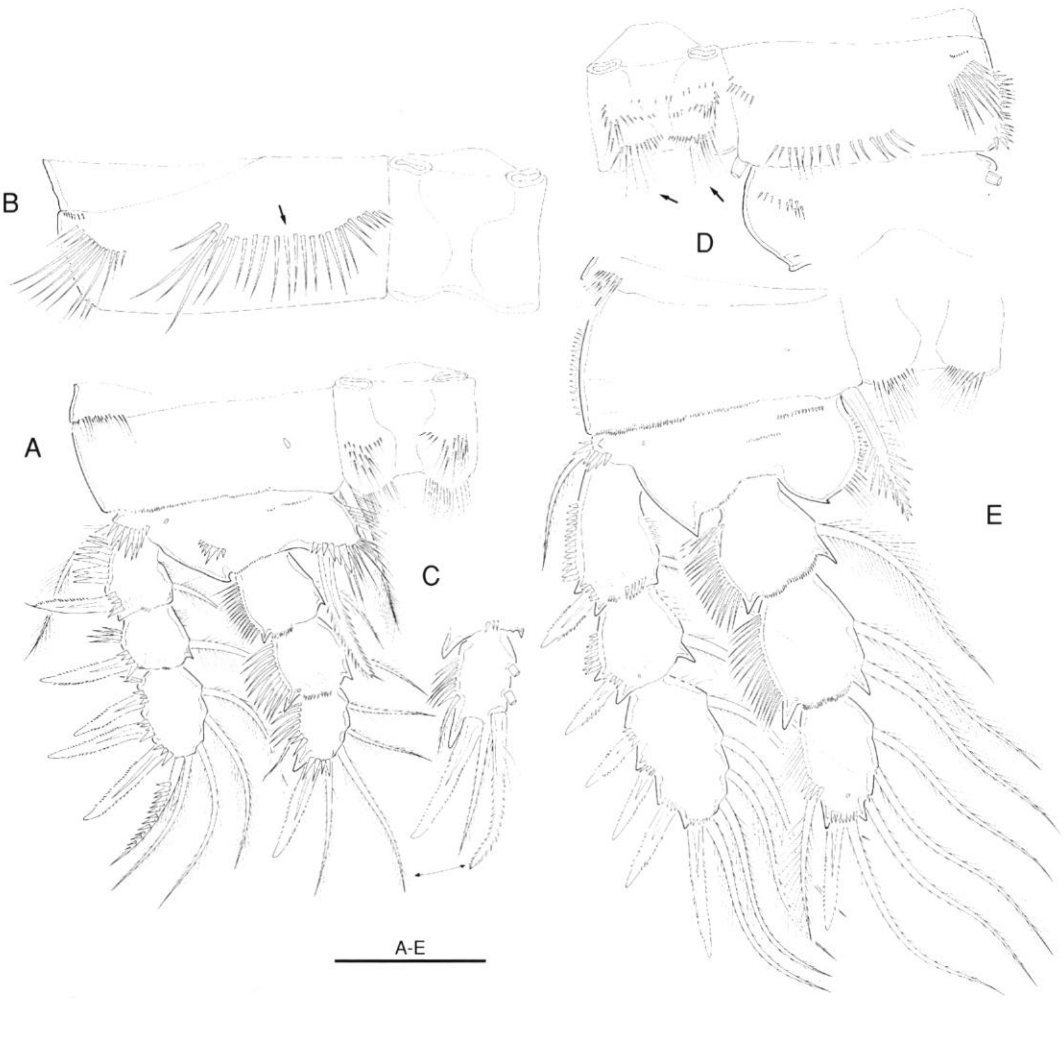

FIG. 13. — *P. imminuta*; **A**, **B**, **D**, **E**, adult ♀; **C**, adult ♂; **A**, leg 1, anterior; **B**, intercoxal sclerite and coxa of leg 1, posterior; **C**, terminal endopodal segment of leg 1; **D**, intercoxal sclerite and coxa of leg 3, posterior; **E**, leg 3, anterior. Scale bar: 50 µm.

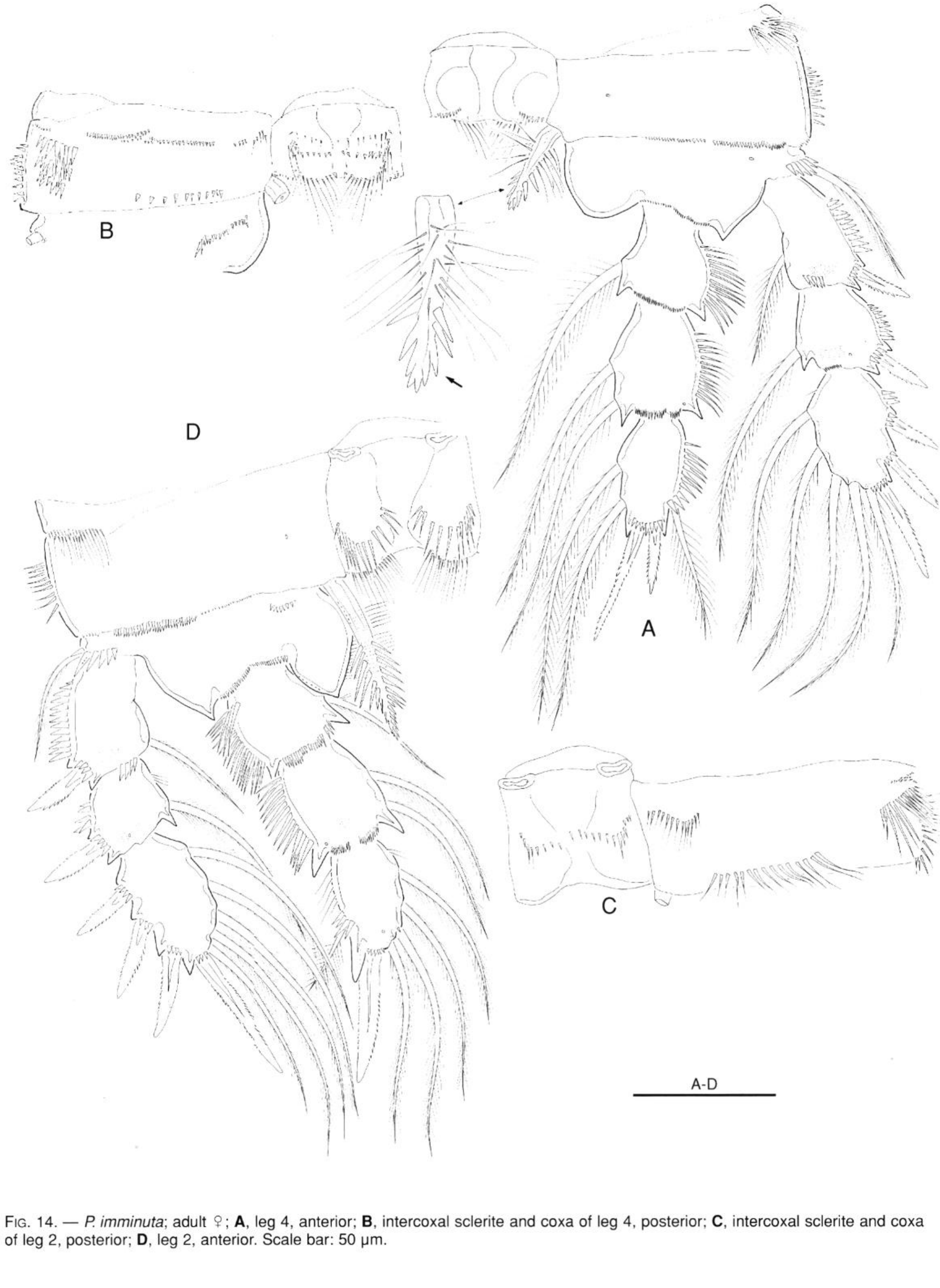

FIG. 14. — *P. imminuta*; adult ♀; **A**, leg 4, anterior; **B**, intercoxal sclerite and coxa of leg 4, posterior; **C**, intercoxal sclerite and coxa of leg 2, posterior; **D**, leg 2, anterior. Scale bar: 50 µm.

dissected on one slide (Th Monod n° 15208, MNHN Collection).
Gibraltar. Leonora Cave, from pool with rotten rope in it: 1 ♀, 5 ♂♂ (NHM 1958.8.5.1).
France. Lac Léman, August 1962, coll. B. Dussart: 3 ♀♀ (MNHN-Cp897).

DISTRIBUTION. — On the basis of examined material only, the distribution of *P. imminuta* extends across Europe to central Russia, and southwards to include Israel.

REDESCRIPTION
Adult female
Body lengths and widths are given in Table 2. Urosome ornamented with finer surface pits dorsally than *P. fimbriatus* as figured (compare Figs 11A, B and 2A). Genital double-somite hardly increasing in width anteriorly, whereas in *P. fimbriatus* genital-double somite increasing in width anteriorly. Seminal receptacles divided into broad anterior and narrower posterior lobes (Fig. 11A), lobes narrower and more distinctly separated than those of *P. fimbriatus*. Caudal rami positioned in parallel configuration, and frequently very close to each other; in some specimens slightly converging proximally, parallel distally (Fig. 11A, B, D-F).
Coxobasis of antenna with complex ornamentation on caudal and frontal surfaces as figured (Fig. 12A-C); well-developed spinular row present on caudal surface (arrowed in Fig. 12A, B).
Coxa of leg 1 ornamented with long continuous spinular row across posterior surface (arrowed in Fig. 13B). Intercoxal sclerite ornamented with group of spinules on anterior surface (Fig. 13A). Leg 3 (Fig. 13E) with intercoxal sclerite ornamented with three spinular rows on posterior surface (Fig. 13D); distal row of spinules (arrowed in Fig. 13D) longer than that of *P. fimbriatus*. Leg 4 with inner coxal spine slightly stouter than that of *P. fimbriatus* (Fig. 14A); distal spinular row on posterior surface of intercoxal sclerite hair-like and much longer than that of *P. fimbriatus* (Fig. 14B); inner apical spine of endopodal segment 3 as long as segment, ratio of length of inner apical spine relative to outer apical spine usually smaller than in *P. fimbriatus*.

Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-I	I-1; I-1; III, 5	0-1; 0-1; 1, I, 4
Leg 2	0-I	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 4
Leg 3	0-I	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 4
Leg 4	0-I	1-0	I-1; I-1; II, I, 5	0-1; 0-2; 1, II, 2

Leg 5 with inner spine serrate-like, usually stouter than in *P. fimbriatus* (Fig. 11C). Leg 6 (Fig. 11B) represented by one plumose seta and two tiny spinules located dorsolaterally.

Adult male
Body lengths and widths excluding caudal setae are given in Table 2. Differing from adult female as follows: urosomal somites (Fig. 15C) ornamented with cuticular pits dorsally as figured. Caudal rami slightly curved inwards proximally, usually parallel for most of length. Coxobasis of antenna with spinular row near base of inner setae (arrowed in Fig. 15D). Innermost seta of coxobasis more strongly spinulated than in female (arrowed in Fig. 15D). Antennule similar to that of male *P. fimbriatus* except aesthetasc on first segment (arrowed in Fig. 16E, F) present and setiform. Aesthetasc on ancestral segment XIV much longer than in *P. fimbriatus* (arrowed in Fig. 16E). Segmental fusion pattern as follows: I-V, VI-VII, VIII, IX, X, XI, XII, XIII, XIV, XV, XVI, XVII, XVIII-XX, XXI-XXIII, XXIV-XXVIII.

VARIABILITY
Females
The relative width, length and shape of caudal rami can vary between specimens from any population as illustrated in figure 11B, D-F. The arrangement of the spinular row on the caudal surface of the antenna (arrowed in Fig. 12A, B) may also vary slightly. The length ratio of the outer apical spine relative to the inner apical spine on the distal endopod segment of leg 4 can be very variable. The form and length of the inner spine of leg 5 can also be variable with some populations or individuals having a stouter spine (Fig. 11C) than others.

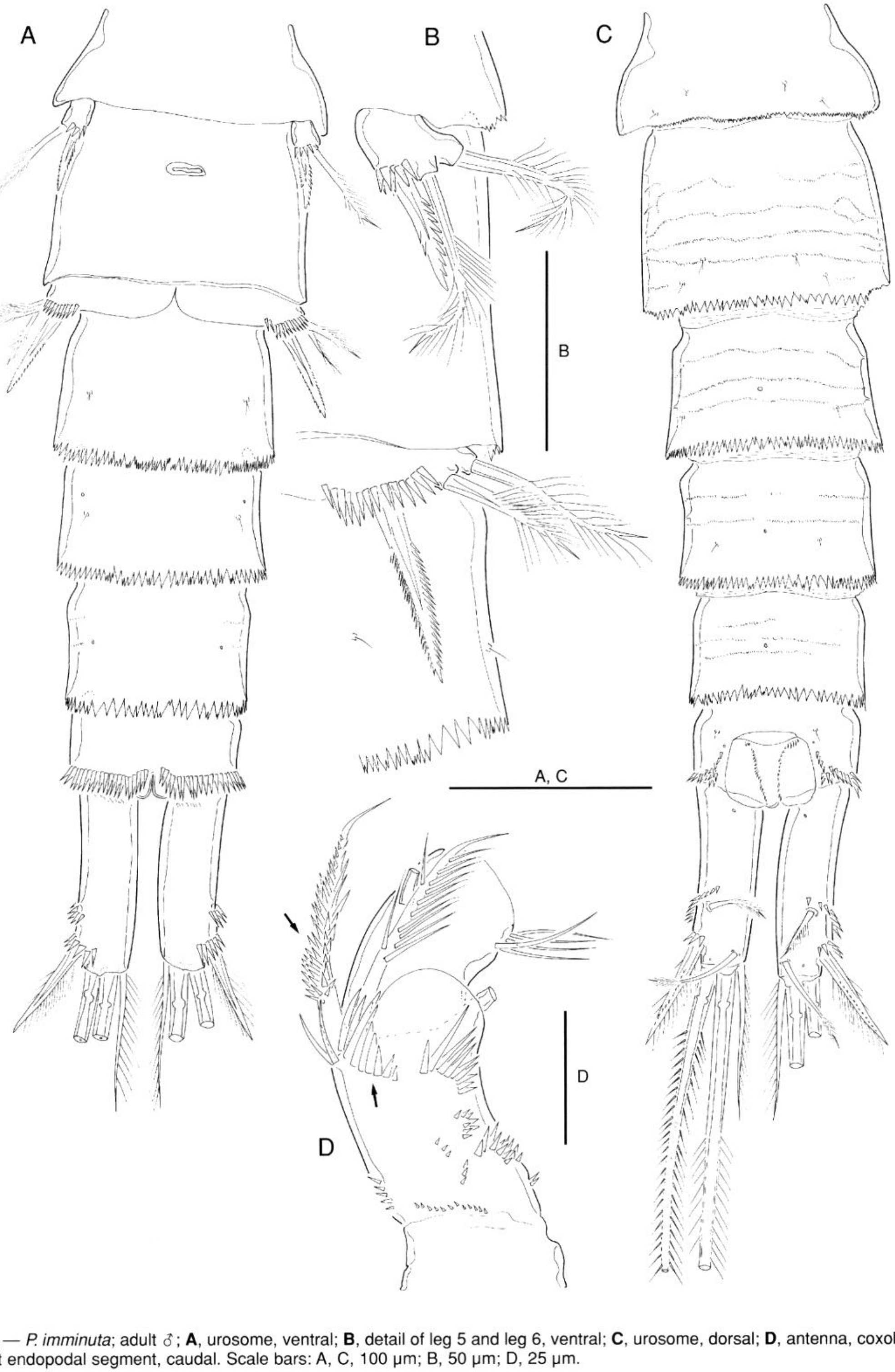

FIG. 15. — *P. imminuta*; adult ♂; **A**, urosome, ventral; **B**, detail of leg 5 and leg 6, ventral; **C**, urosome, dorsal; **D**, antenna, coxobasis and first endopodal segment, caudal. Scale bars: A, C, 100 µm; B, 50 µm; D, 25 µm.

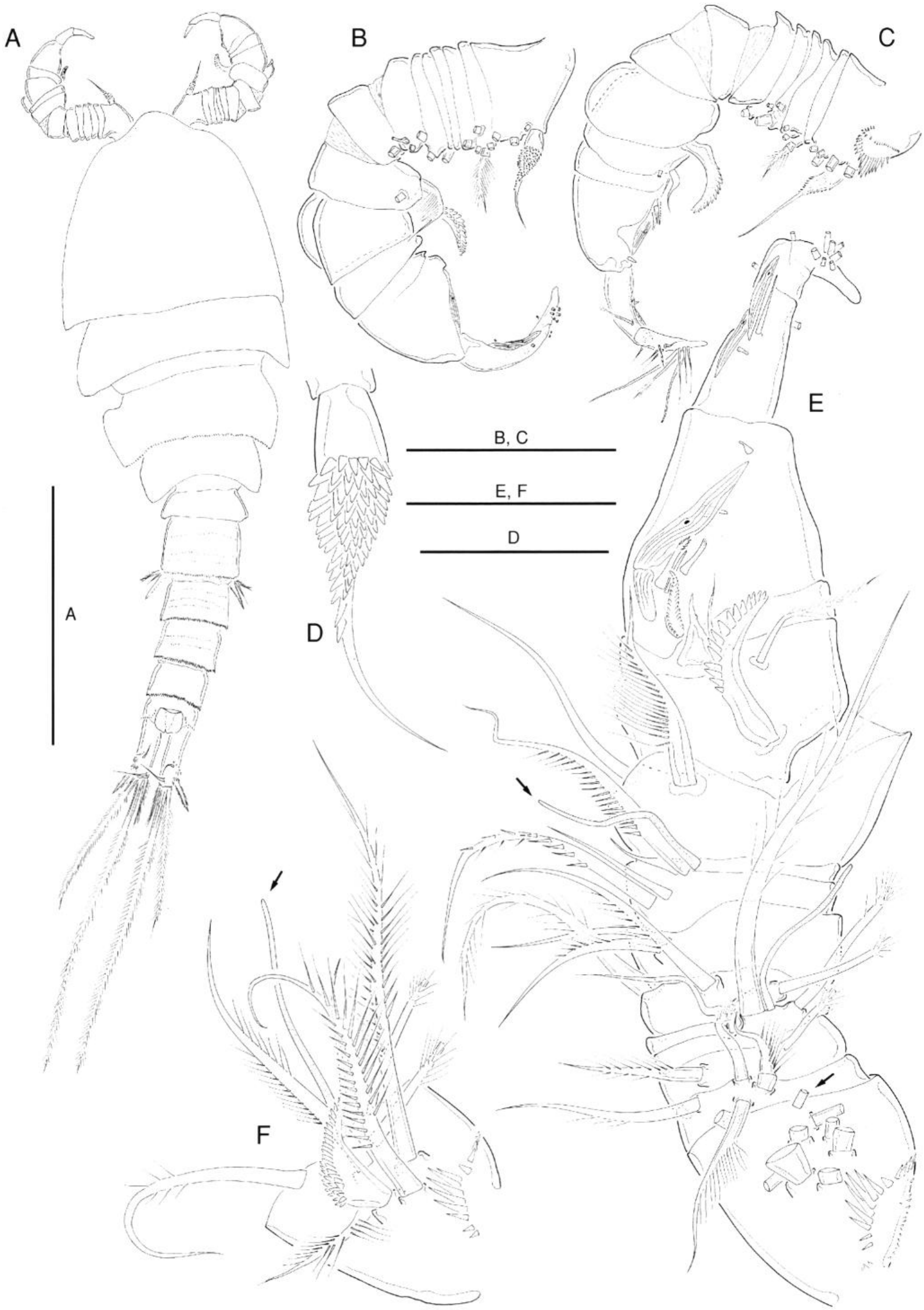

FIG. 16. — *P. imminuta*; adult ♂; **A**, body, dorsal; **B**, antennule showing segmentation, dorsal; **C**, antennule showing segmentation, ventral; **D**, detail of modified seta on first segment of the antennule; **E**, antennule showing setation, anteroventral; **F**, antennule, first segment showing setation, anteroventral. Scale bars: A, 400 µm; B, C, 100 µm, D, 25 µm; E, F, 50 µm.

TABLE 2. — Body length (BL) and width (BW) measurements (in µm) of adult *Paracyclops imminuta* from different localities (N, number of specimens measured).

LOCALITY	SEX	BL (mean ± SD)	RANGE	BW (mean ± SD)	RANGE	N
St Petersburg	♀	846 ± 26.2	827-864	310 ± 1.4	309-311	2
England	♀	1014 ± 51.7	918-1082	343 ± 15.4	305-359	10
	♂	960 ± 60.3	872-1079	321 ± 23.6	275-354	10
Ireland	♀	835 ± 32	781-880	318 ± 14.2	293-342	10
	♂	805 ± 30.6	757-858	292 ± 9.4	282-311	10
Sweden	♀	1072 ± 128.7	981-1163	351 ± 23.3	334-367	2
	♂	819		299		1
Greece	♀	670		247		1
	♂	670		243		1
Azores (Pico)	♂	791 ± 74.2	738-843	298 ± 7.1	293-303	2
Israel	♀	777 ± 82.7	718-835	286 ± 1.4	285-287	2
Gibraltar	♂	910 ± 37	849-946	292 ± 7.5	280-301	5
France	♀	921 ± 143.8	835-1087	315 ± 25.4	299-344	3

DIFFERENTIAL DIAGNOSIS

The close morphological similarity between *P. fimbriatus* and *P. imminuta* makes it easy to confuse them, however, there are two characters that have proven to be extremely constant both within and between populations of *P. imminuta*. These characters are the spinular ornamentation on the caudal surface of the antennary coxobasis (arrowed in Fig. 12A, B) and the presence of the mid-distal spinular row on the posterior surface of leg 1 (arrowed in Fig. 13B). The latter character also distinguishes *P. imminuta* from other *Paracyclops* species. In addition, the following combination of five characters also separates *P. imminuta* from *P. fimbriatus*: (1) the spinular row near the base of inner setae on the coxobasis of antenna which is better developed in the male of *P. imminuta* (arrowed in Fig. 15D) than in *P. fimbriatus* (Fig. 8E); (2) the aesthetasc on the first segment of male antennule (arrowed in Fig. 16E, F) which is present only in *P. imminuta*; (3) the inner coxal spine of leg 4 (Fig. 14A), which is stouter than in *P. fimbriatus*; (4) the form of the distal spinular row on the posterior surface of the intercoxal sclerite of legs 3-4 (Fig. 14A, B), the spinules of which are hair-like and much longer than in *P. fimbriatus*; (5) the aesthetasc on ancestral segment XIV (arrowed in Fig. 16E) which is much longer than that of *P. fimbriatus*.

REMARKS

Kiefer (1929) first separated this form from *P. fimbriatus* on the basis of the shorter caudal rami which are about 3-4 times longer than broad. *P. fimbriatus* forma *imminuta* sensu Šramek-Hušek (1939), *Paracyclops fimbriatus* var. *imminutus* sensu Rylov (1963) and *Paracyclops fimbriatus* f. *imminutus* sensu Štěrba (1955) may be considered as conspecific with *P. imminuta* on the basis of the caudal rami which are illustrated as being close to each other and slightly converging in the proximal part. The usefulness of this character is however limited since it is known to be extremely variable.

Borutzky's (1930) usage of the caudal rami and the leg 5 of male in his identification of *P. fimbriatus*. f. *imminuta* is very doubtful since Kiefer did not refer to male characters in his original drawings. Perhaps the most complete description of *P. imminuta* was given by Gurney (1933) under the name *P. fimbriatus*. Fortunately, Gurney figured the coxa of leg 1 in posterior view and it can be seen that the pattern of the spinular row is very similar to that of *P. imminuta* (arrowed in Fig. 13B). Also, there is one relatively large spinule at the base of the outer seta of the antennary coxobasis in the position corresponding to the spinular row in *P. imminuta* (arrowed in Fig. 12A, B) and probably representing the end of this spinular row. As remarked earlier, these two characters unequivocally separate *P. imminuta* from *P. fimbriatus* and strongly indicate that Gurney's material belonged to the former species. In addition, other less significant characters which serve to separate *P. imminuta* from *P. fimbriatus* can be observed in Gurney's drawings, such as the shape of the caudal rami in both sexes, the structure of the seminal receptacle and the relatively short inner spine on the female leg 5 (Fig. 11C), all of which are more characteristic for *P. imminuta* than *P. fimbriatus*.

The validity of *P. fimbriatus orientalis* is problematic. This subspecies was incompletely described (Alekseev 1995). Apart from the spinular ornamentation on the coxobasis of the antenna, the illustrations of this species lack sufficient detail. No type material was designated by Alekseev (1995) but four females and three males collected and identified as *P. fimbriatus orientalis* by V. Alekseev were re-examined. None of these specimens matched Alekseev's original drawings of *P. fimbriatus orientalis*. In fact the material represented *P. fimbriatus* and showed variation in the shape of the caudal rami and in the spinular ornamentation on the posterior surface of the intercoxal sclerite of leg 4, as also found in Indian, Mongolian and Uzbekistani material. From the original drawings alone it is extremely difficult to assign *P. fimbriatus orientalis* to any of the species recognised herein. The pattern of spinulation on the coxobasis of antenna is the only indication that Alekseev might have been dealing with the species redescribed here as *P. imminuta*.

Paracyclops chiltoni (Thomson, 1882)
(Figs 17-23)

Original description:
Cyclops chiltoni Thomson, 1882 [*Trans. Proc. New Zealand. Inst.* 15: 93-116].

Synonymy:
Cyclops chiltoni Thomson, 1882: 97, pl. IX, figs 11-19.

Paracyclops finitimus Kiefer, 1929: 51, Abb. 60, 61.

Paracyclops fimbriatus Fischer, 1853 *sensu* Karaytug & Boxshall 1996: 42-66, figs 1-22.

TYPE LOCALITY. — New Zealand, Eyreton.

MATERIAL EXAMINED. — It has not been possible to locate Thomson's type material. It is not stored in the collection of the National Museum of New Zealand. One vial with forty-seven specimens from New Zealand is stored in the Smithsonian Institution, Washington, D. C. The redescription is based on this material.

New Zealand. South Island, Southland, Te Anau, Upakerora River, New Zealand, 45°21'18S - 167°43'18E, 15.IV.1990, coll. T. Ishida: 33 ♀♀, 8 ♂♂, 6 copepodids (USNM. cat. 250692).

Easter Island. Rano Aroi crater (almost completely overgrown by *Polygonum*), small puddle of open water in littoral zone, 19.IX.1990, coll. H. J. Dumont: 2 ♀♀, 21 ♂♂.

South Africa. 52 ♀♀, 44 ♂♂, coll. A. D. Harrison (NHM 1966.3.22.9).

England. Hertfordshire, percolating filters of sewage works: 50 ♀♀, 65 ♂♂ (NHM 1968.7.1.1). — London, Regent's Park pond. Numerous specimens examined from cultured material.

Russia. P. Dudergofka, St Petersburg, 27.VII 1996, depth 0.5 m, t 18 °C, coll. V. Alekseev: 4 ♀♀.

Crozet Island. 28.II.1969: 2 ♂♂ dissected on two slides (NHM 1970.4.30.3).

Tahiti. 20.I.1981: 2 ♀♀, 6 ♂♂ (MNHN, unregistered material).

Brazil. Leaf litter and small quantity of moist superficial soil collected from bank of a rill near to the entrance of Gruta da Tapagem (Tapagem Cave), 24°38'12"S - 48°23'50"W, Eldorado Paulista, State of São Paulo, 31.VIII.1988, coll. Carlos E. F. Rocha: 18 ♀♀, 17 ♂♂ obtained from a culture.

Azores. Terceira, mounted on three slides (undissected), 2 ♀, 1 ♂ (Th. Monod Collection n° 15210, MNHN). — Flores, mounted on one slide (undissected), all Th. Monod Collection: 1 ♀ (n° 15324, MNHN); 2 ♀♀, 1 ♂, mounted on two slides (1 ♀ dissected) (n° 15292, MNHN); 1 ♀, partially dissected on one slide (n° 15079, MNHN); 1 ♀, dissected and mounted on one slide (n° 15087, MNHN); 1 ♀, mounted on one slide (n° 15138, MNHN); 1 ♀, dissected and mounted on one slide (n° 15317, MNHN); 1 ♀, dissected and mounted on one slide (n° 15335, MNHN); 1 ♂, mounted on one slide (n° 15274, MNHN). — Pico, 12.X.1971, coll. Th. Monod: 1 ♀, mounted on one slide (Th. Monod Collection n° 15189, MNHN).

DISTRIBUTION. — *P. chiltoni* shows the widest distribution within the genus *Paracyclops* and is the only true cosmopolitan species at present (Karaytug 1998). It occurs at extremely isolated sites such as Easter Island and Hawaii in the Pacific Ocean, Crozet Island in southern Indian Ocean, and in New Zealand. However records of *P. chiltoni* from some other regions could not be confirmed because material was unavailable.

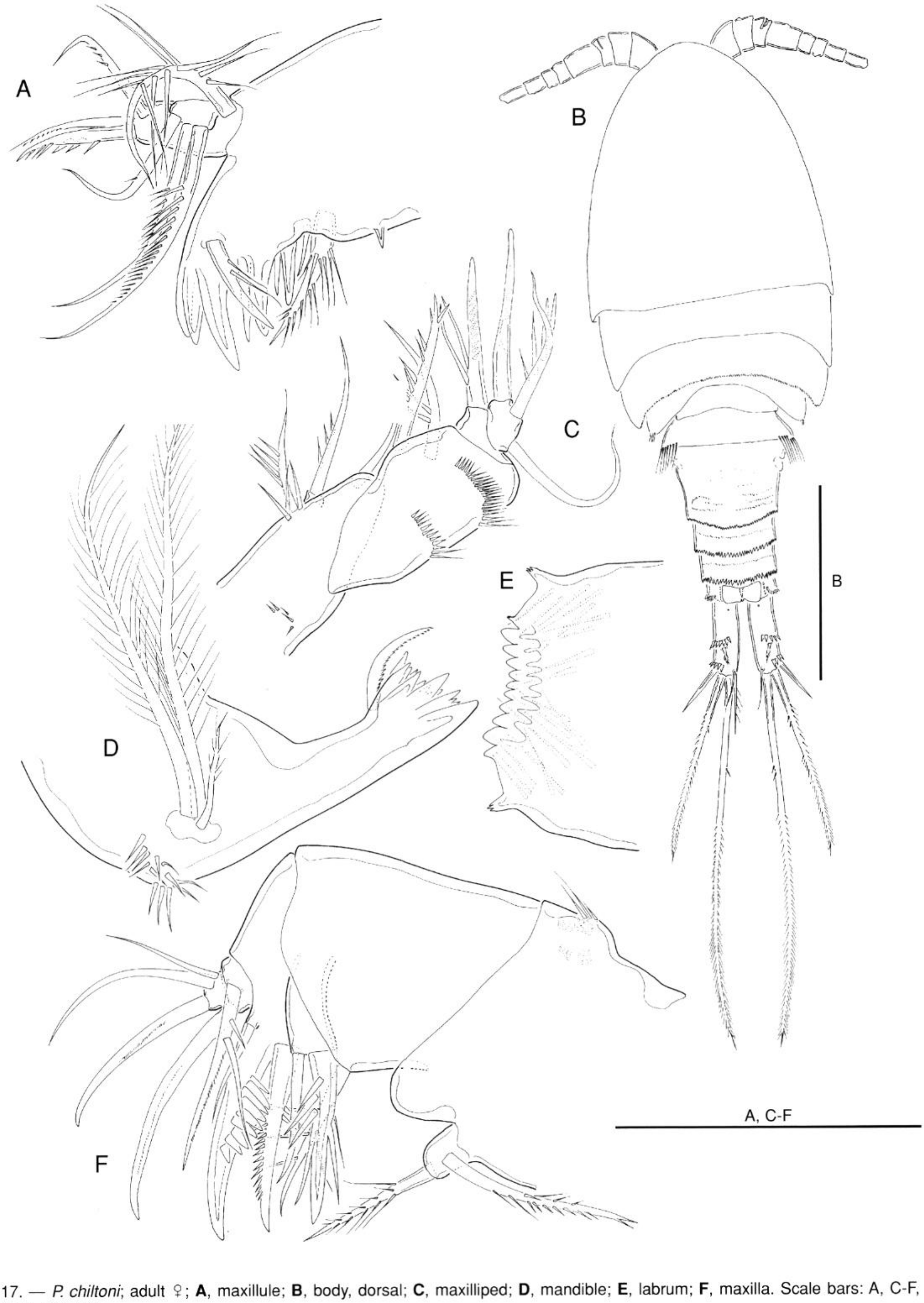

FIG. 17. — *P. chiltoni*; adult ♀; **A**, maxillule; **B**, body, dorsal; **C**, maxilliped; **D**, mandible; **E**, labrum; **F**, maxilla. Scale bars: A, C-F, 50 µm; B, 200 µm.

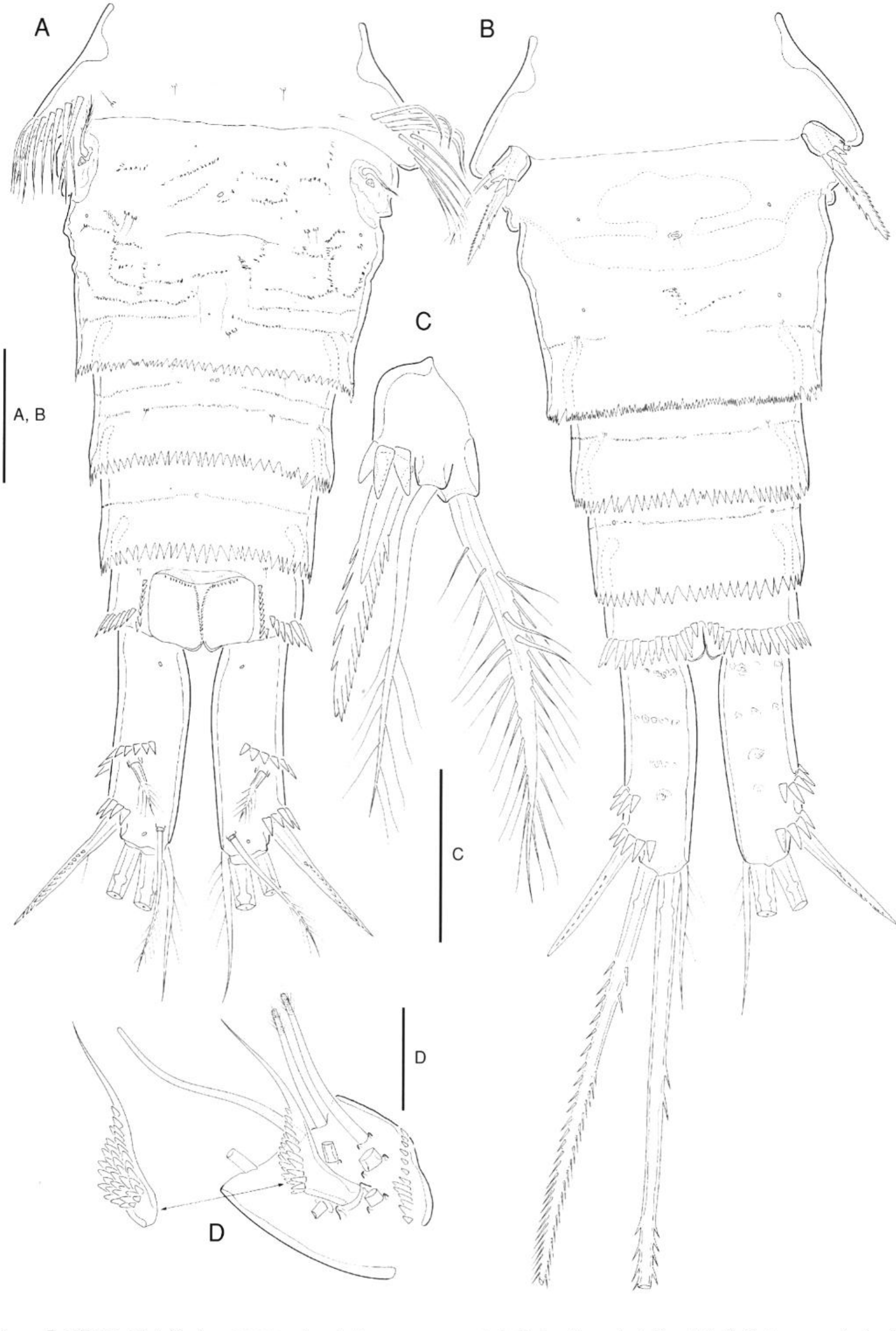

FIG. 18. — *P. chiltoni*; adult ♀; **A**, urosome, dorsal; **B**, urosome, ventral; **C**, leg 5, ventral; **D**, adult ♂, first segment of antennule showing setation, anteroventral, with inset showing detail of modified seta, dorsal. Scale bars: A, B, 50 µm; C, D, 25 µm.

FIG. 19. — *P. chiltoni*; adult ♀; **A**, antenna, coxobasis, frontal; **B**, antenna, caudal; **C**, antennule. Scale bars: A, B, 25 µm; C, 50 µm.

TABLE 3. — Body length (BL) and width (BW) measurements (in μm) of *Paracyclops chiltoni* from different localities. (N, number of specimens measured).

LOCALITY	SEX	BL (mean ± SD)	RANGE	BW (mean ± SD)	RANGE	N
New Zealand	♀	627 ± 36.1	556-738	251 ± 14.9	230-291	30
	♂	581 ± 29.2	531-630	214 ± 5.1	207-222	8
England	♀	713 ± 61.2	588-802	289 ± 24.6	237-353	30
(Hertfordshire)	♂	649 ± 52.5	598-751	240 ± 7.8	227-254	10
Easter Island	♀	555		210		1
	♂	618 ± 22.9	575-664	225 ± 10.9	200-239	12
South Africa	♀	722 ± 49.5	606-798	262 ± 17.9	223-291	14
	♂	655 ± 25.2	606-699	237 ± 8.7	225-252	7
Russia (St Petersburg)	♀	797 ± 68.7	738-857	308 ± 9.8	299-316	4
Tahiti	♀	636 ± 15.6	625-647	232 ± 7.1	227-237	2
	♂	642 ± 25.6	614-676	205 ± 5.4	196-214	6
Brazil	♀	611 ± 42.7	567-703	237 ± 17.8	217-282	10
	♂	548 ± 25.8	505-588	201 ± 12.1	183-217	10

REDESCRIPTION

Adult female

Body width and length are given in Table 3. Genital double-somite, second and third abdominal somites densely ornamented with distinct pits dorsally (Fig. 18A) and ventrally (Fig. 18B) as figured. Genital double-somite about as long as broad; seminal receptacle divided into narrow anterior and broad posterior lobes (Fig. 18B). Row of spinules present in anal cleft either side of midline (Fig 18A). Caudal rami short, parallel, with ornamentation comprising rows of pits or cuticular depressions on ventral surface (Fig. 18B). Length and width of caudal rami from different populations given in Table 4. Antennule 8-segmented (Fig. 19C): setal formula 8, 12, 6, 5, 2 + aesthetasc, 2, 2 + aesthetasc, 7 + aesthetasc. Third segment with two partial suture lines ventrally. Coxobasis of antenna with complex ornamentation on caudal and frontal surfaces as figured (Fig. 19A, B) and lacking spinular row near inner setae caudally (arrowed in Fig. 19B).

Leg 1 intercoxal sclerite ornamented with dense spinules on anterior surface (Fig. 20B). Leg 2 with outer apical spine of distal endopodal segment stout (Fig. 20C); intercoxal sclerite ornamented with dense spinules on anterior surface, single row small spinules on posterior (Fig. 21A). Leg 3 (Fig. 21D, E) intercoxal sclerite ornamented with two spinular rows on posterior surface; inner coxal spine stouter than that of *P. fimbriatus*. Leg 4 (Fig. 21B, C) inner coxal spine stouter than in *P. fimbriatus*; intercoxal sclerite with two spinular

TABLE 4. — Caudal rami length (CL), caudal rami width (CW) and ratio of length relative to width (L:W) of *Paracyclops chiltoni* from different localities (measurements in μm). (N = number of specimens measured).

LOCALITY	SEX	CL (mean ± SD)	RANGE	CW (mean ± SD)	RANGE	N	L:W
New Zealand	♀	79 ± 8.4	68-96	26 ± 1.4	25-30	28	3
England	♀	95 ± 12.8	77-116	28 ± 1.6	26-30	10	3.4
South Africa	♀	94 ± 10.8	78-115	27 ± 1.4	25-29	10	3.5
Russia (St Petersburg)	♀	97 ± 5.9	88-101	25 ± 3.5	20-28	4	3.9
Tahiti	♀	68 ± 14.1	58-78	23 ± 1.4	22-24	2	2.9
Brazil	♀	80 ± 13.5	60-109	25 ± 1.6	23-29	20	3.2
Azores	♀	94 ± 10	84-109	28 ± 1.5	26-30	6	3.4
Easter Island	♀	63		25		1	2.5

rows on posterior surface (Fig. 21C). The outer spinulose seta of leg 5 was equal in length to the inner spine in most specimens from New Zealand and in all specimens examined from other localities (Fig. 22A) but distinctly longer than the inner spine in a few specimens from New Zealand (Fig. 18C).

Adult male

Urosomal somites ornamented with cuticular pits dorsally and ventrally as figured (Fig. 23B, C). Caudal rami about 2.3 times longer than broad. Coxobasis of antenna with well-developed spinular row near base of inner setae (arrowed in Fig. 23E); innermost seta of coxobasis more strongly spinulate than female. First segment of the antennule (Fig. 18D) with large seta and modified by ornamentation of strong spinules in proximal and midsections, tapering to fine point distally (Fig. 18D). First segment with long setiform aesthetasc (Fig. 18D). The setal elements similar to those of *P. imminuta*. Segmental fusion pattern as follows I-V, VI-VII, VIII, IX, X, XI, XII, XIII, XIV, XV, XVI, XVII, XVIII-XX, XXI-XXIII, XXIV-XXVIII.

VARIABILITY

Unless stated the following variability applies to the females. The cuticular pits on the ventral surface of the caudal rami may not be as well defined in some specimens from outside the Palaearctic zoogeographical region. The outer spinulose seta of leg 5 was equal in length to the inner spine in most specimens from New Zealand and in all specimens examined from other localities (Fig. 22A) but distinctly longer than the inner spine in a few specimens from New Zealand (Fig. 18C). The structure of the

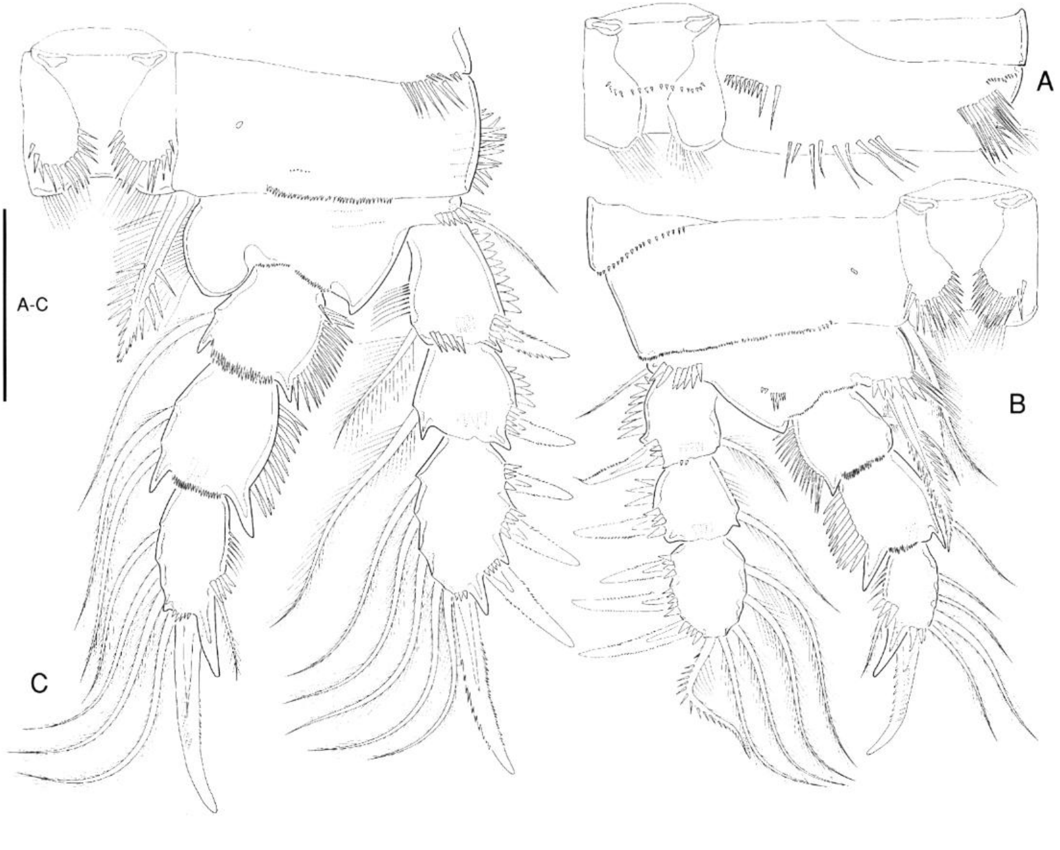

FIG. 20. — *P. chiltoni*; adult ♀; **A**, intercoxal sclerite and coxa of leg 1, posterior; **B**, leg 1, anterior; **C**, leg 2, anterior. Scale bar: 50 µm.

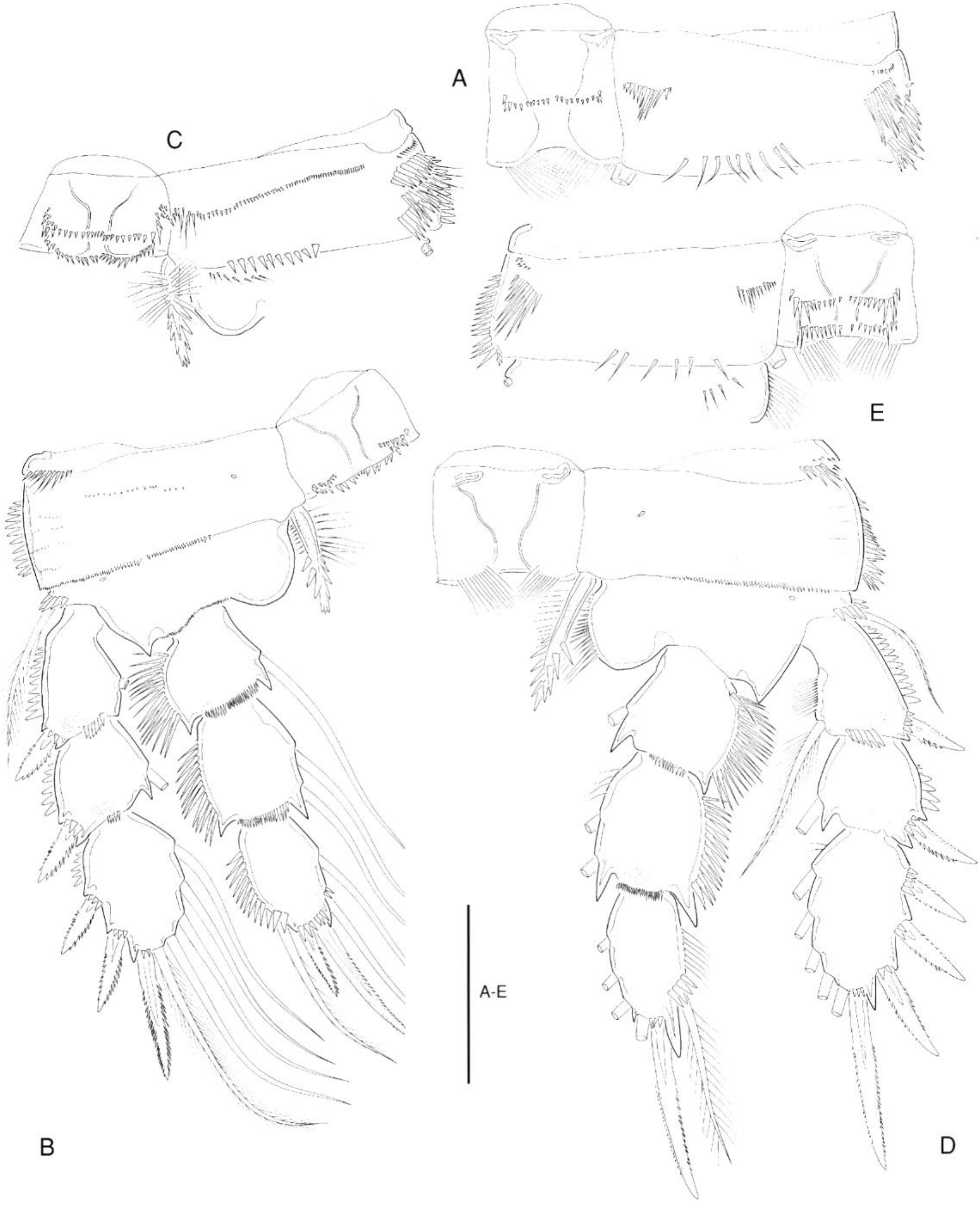

FIG. 21. — *P. chiltoni*; adult ♀; **A**, intercoxal sclerite and coxa of leg 2, posterior; **B**, leg 4, anterior; **C**, intercoxal sclerite and coxa of leg 4, posterior; **D**, leg 3, anterior; **E**, intercoxal sclerite and coxa of leg 3, posterior. Scale bar: 50 µm.

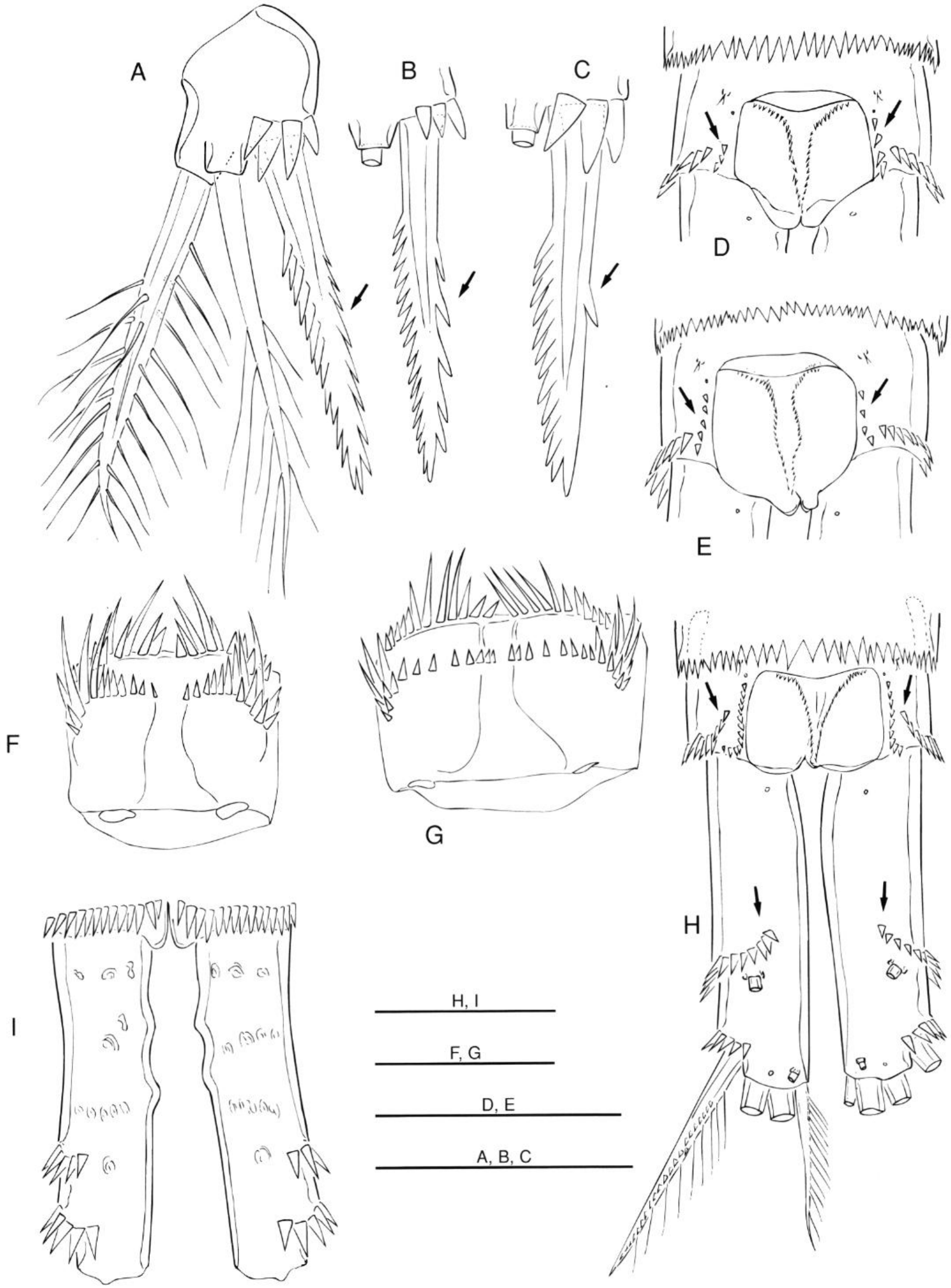

FIG. 22. — *P. chiltoni*; **A** (New Zealand), adult ♀, leg 5, ventral; **B** (U.K.), **C** (Brazil), adult ♀, inner spine of leg 5, ventral; **D**, adult ♂, **E**, adult ♀, anal somite, dorsal (Tahiti); **F**, adult ♂; **G**, adult ♀, leg 4, intercoxal sclerite, posterior (Brazil); **H**, adult ♀, anal somite and caudal rami, dorsal (Brazil); **I**, adult ♀, caudal rami, ventral (St Petersburg). Scale bars: A-C, F, G, 25 µm; D, E, H, I, 50 µm.

inner spine of leg 5 was slightly different in some specimens from England (Fig. 22B) and from the State of São Paulo, Brazil (Fig. 22C). In material from Tahiti, the number of spinules in the anal cleft, either side of the midline (arrowed in Fig. 22D, E), was very small in both sexes. In specimens from the State of São Paulo, Brazil (Fig. 22H) with relatively longer caudal rami, the terminal accessory seta (VI) is shorter than the posterolateral seta (III), and the spinular row at the base of the anterolateral seta (II) is slightly curved anteriorly (arrowed in Fig. 22H). In some specimens from New Zealand, England and Russia (St Petersburg), the inner margins of the caudal rami may be irregular, not smooth (Fig. 22I). The distal spinules on the posterior surface of the intercoxal sclerite of leg 4 are especially well-developed in females from the State of Rio Grande in Brazil (Fig. 22G) and in males from the State of São Paulo in Brazil (Fig. 22F).

Differential diagnosis

P. chiltoni can be differentiated from other *Paracyclops* species by the combination of the following four characters: (1) the structure of leg 5 (Figs 18C, 22A); (2) the presence of the conspicuous, well-developed spinular row near the base of two setae on the coxobasis of antenna in the male (arrowed in Fig. 23E), this spinular row is not present in the female (arrowed in Fig. 19B); (3) the obvious, dense, cuticular ornamentation of pits on the dorsal and ventral surfaces of the genital double-somite, and second and third urosomal somites (Fig. 18A); (4) the presence of similar cuticular depressions on the ventral surface of the caudal rami (Fig. 18B). The last character may be less pronounced in some specimens from outside the Palearctic region and should therefore be used with caution.

P. chiltoni also differs from *P. fimbriatus* and *P. imminuta* in the much shorter outer seta of leg 5 (Figs 18C). In the male of *P. chiltoni*, aesthetasc G on the first antennulary segment is present (Fig. 18D) but this aesthetasc is absent in *P. fimbriatus*.

Remarks

Paracyclops chiltoni (Thomson, 1882) was originally described from New Zealand. Later, Kiefer (1928) described *P. finitimus*, which matches well with *P. chiltoni* described herein, on the basis of the very short caudal rami, only three times as long as broad, and the short outer seta of leg 5 which is about as long as the inner spine. Kiefer (1931) expressed the opinion that Thomson (1882) likewise had found *P. finitimus* and therefore synonymized *P. chiltoni* with *P. finitimus*. However, according to the rules of Zoological Nomenclature, *P. chiltoni* takes priority and consequently *P. finitimus* is here ranked as a junior subjective synonym of *P. chiltoni*. Dussart & Defaye (1985) had earlier accepted *P. finitimus* as a synonym of *P.* f. *chiltoni*.

DISCUSSION

Currently, seven species of *Paracyclops* occur in the Palearctic region of which *P. baicalensis*, *P. dilatatus*, *P. affinis* and *P. poppei* are each quite distinct in their morphology (Karaytug 1998). *P. fimbriatus*, *P. imminuta* and *P. chiltoni* are, however, very closely related and the failure to separate *P. imminuta* from the other two of the species complex was the main reason behind the taxonomic confusion concerning all three. This taxonomic problem could not have been solved by using traditional features such as proportional measurements of the caudal rami and the terminal spines of the third endopodal segment of leg 4, because these characters vary considerably within populations as well as between populations. Since there is extensive overlap in variability expressed between these three variable species, it is concluded that most early records are unreliable.

The type material of none of the three species is extant. In the absence of types it was concluded that the best option would be to redescribe *P. fimbriatus* from the vicinity of St Petersburg, one of the listed type localities, on the basis of newly collected topotypic material. Examination of three unsorted samples from the vicinity of St Petersburg revealed four distinct *Paracyclops* species, *P. fimbriatus*, *P. poppei*, *P. chiltoni* and *P. imminuta*. It is interesting to note that the sample from P. Dudergofka (St Petersburg)

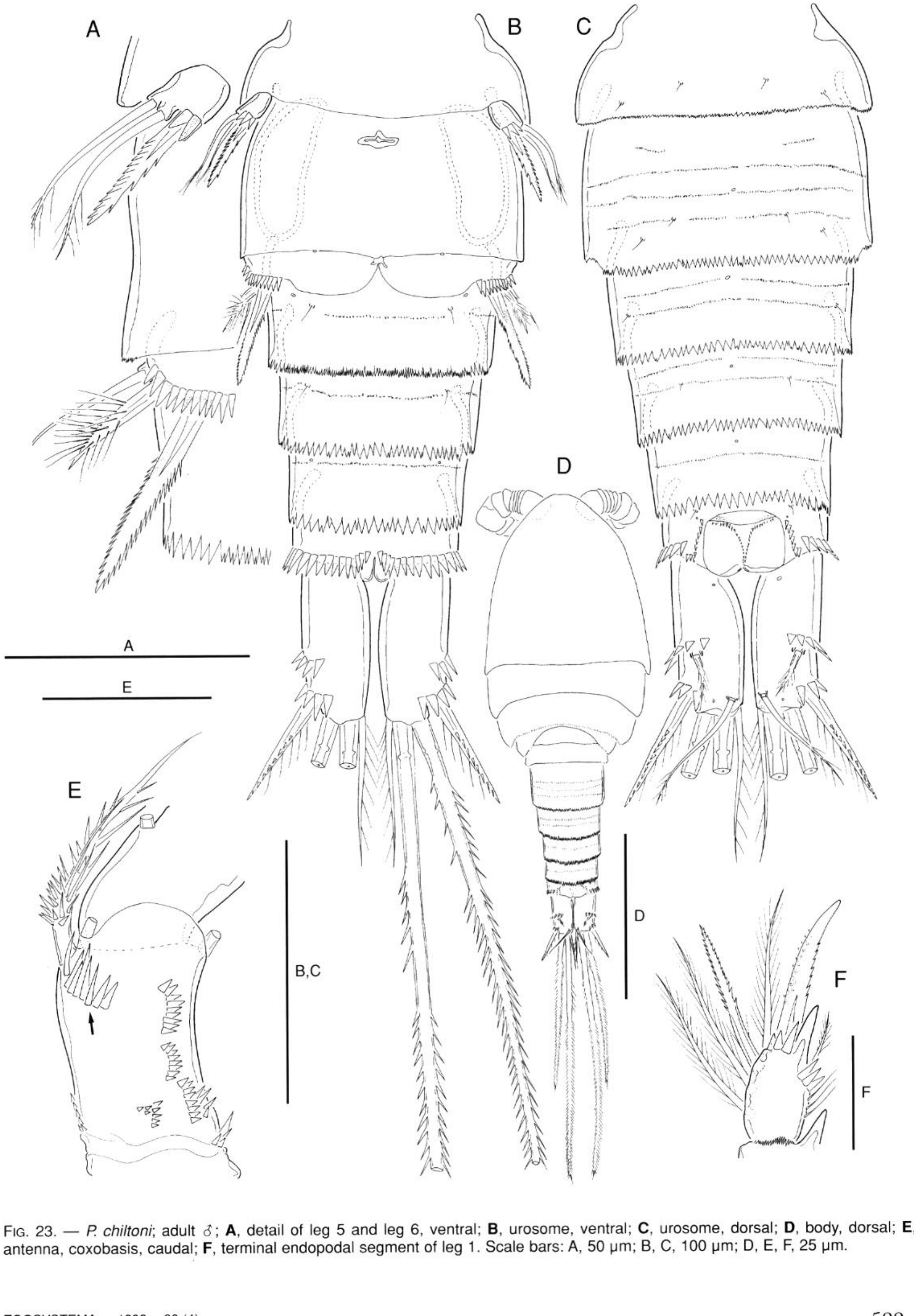

FIG. 23. — *P. chiltoni*; adult ♂; **A**, detail of leg 5 and leg 6, ventral; **B**, urosome, ventral; **C**, urosome, dorsal; **D**, body, dorsal; **E**, antenna, coxobasis, caudal; **F**, terminal endopodal segment of leg 1. Scale bars: A, 50 µm; B, C, 100 µm; D, E, F, 25 µm.

contained four females of *P. fimbriatus*, one female of *P. imminuta*, and four females of *P. chiltoni*. The sample from the River Igora (St Petersburg) contained fourteen females of *P. fimbriatus* and one female of *P. imminuta*. The sample from River Ravan (St Petersburg) contained two females of *P. fimbriatus* and seven females, three males of *P. poppei*. A single female of *P. fimbriatus* from P. Dudergofka (St Petersburg, Russia) was selected as the neotype.

Detailed redescriptions of *P. chiltoni* and *P. poppei* left no doubt that they are distinct species. The fourth taxon present in the St Petersburg samples was very problematic. It closely resembled the rather variable *P. fimbriatus* but could be distinguished on the basis of the arrangement of spinular row on the posterior surface of coxa of leg 1 and the presence of the spinular row near the base of two inner setae on the coxobasis of antenna.

Historically there have been some questions concerning the validity of several of the named species and subspecies of the *Paracyclops fimbriatus* complex. Gurney (1933) expressed certain doubts about the validity of *P. abnobensis* Kiefer, 1929 and *P. finitimus* Kiefer, 1928. Rylov (1963) agreed with Gurney's doubts and treated these two nominal species as varieties of *P. fimbriatus*. Lindberg (1958) synonymized *P. fimbriatus* forma *imminuta* Kiefer, 1929 with *P. fimbriatus chiltoni* which he accepted as a valid subspecies. Lindberg (1958) also synonymized the previously described species and subspecies on the basis of similarities between old descriptions, apparently without comparing type material and without giving detailed redescriptions.

Few workers have considered the possibility that the underlying reason for the gross variability found in particular populations of *P. fimbriatus* is the co-existence of closely related sympatric species. A first indication was given by Frenzel (1976) who studied a number of populations of *P. fimbriatus* from locations in Germany and Tenerife in which both "typical" and "*chiltoni*-type" specimens co-occurred. Using the "Furcal index" [Length (L): Width (W) ratio of the caudal rami in which W is measured halfway L] he recognized a distinct discontinuity separating two groups which were also distinguished – be it to a lesser extent – on the basis of the distance measured proximally between both caudal rami. Frenzel (1976) remarked that the P5 was remarkably constant in the group with short caudal rami and agreed in form and shape with Lindberg's (1958) illustrations of *P. fimbriatus chiltoni*. Because both groups still showed overlap in several other morphometric parameters, Frenzel (1976) left the matter undecided and concluded that only breeding experiments or more sophisticated techniques such as chromosome research could elucidate the problem. In a later paper Frenzel (1977) conducted various breeding experiments and succeeded in proving that at least three reproductive isolates ("Kreuzungsisolate") occurred in his samples, of which two could be identified with already described species, i.e. *P. fimbriatus* and *P. chiltoni*. The author also found that for each of these the morphometry of the caudal rami and the morphology of the P5 remained largely constant during successive generations and temperature did not seem to have any significant influence on these characters. All three had the same chromosome number in the female (2n = 13) which is identical to that found in *P. affinis* (Braun, 1909). It has to be remarked here that Frenzel did not study any possible differences in chromosome structure. Frenzel (1977) concluded that although the three types were entirely intersterile, clearcut distinction on purely morphological grounds was as yet impossible since an intermediate form was also separated during the breeding experiments. He recommended further cross-breeding experiments with other species such as *P. abnobensis*, *P. poppei* and *P. andinus* in order to test the distinctiveness of the three German types. In the absence of type material, it was impossible to assign Fischer's (1853) *Cyclops fimbriatus* to either *P. fimbriatus* or *P. imminuta* or even to *P. chiltoni*. The two critical characters that best separate *P. fimbriatus* from the other two species cannot be discerned from Fischer's original drawings. These characters are:

1. The spinular ornamentation on the frontal surface of the coxobasis of the antenna of both sexes.

2. The pattern of spinular ornamentation on the posterior surface of the coxa of leg 1.

The shape and length-width ratio of the caudal ramus of *P. fimbriatus* and *P. imminuta* as well as their geographical distributions overlap to a certain extent. Unfortunately, Fischer's original drawings of caudal rami fall within that degree of overlap. For the sake of nomenclatural stability the species that has been believed to be true *Paracyclops fimbriatus* by the majority of workers dealing with Palaearctic material, which occurs in St Petersburg and which could be represented by Fischer's figures, has been chosen here for redescription as typical *P. fimbriatus*.

The morphology of *P. fimbriatus* from Asia differs slightly from that of European specimens. Some variation is noted in the arrangement and number of spinular rows on the posterior surface of the intercoxal sclerite of leg 4 as well as in the shape of the inner coxal spine (slightly curved) on leg 4 in some specimens from the vicinity of Lake Baikal (Fig. 6H, I), Mongolia, Uzbekistan and India (Fig. 6G, K). Material from India especially showed remarkable variability on the inner spine of leg 5 as shown in figure 6A-C. The inner spine was usually longer than in other material examined and spinules were present at the base of the middle seta in some specimens (Fig. 6B, C). It is possible that Asian specimens of *P. fimbriatus* tend to show a greater degree of variability in these characters. Examination of more *P. fimbriatus* material from Asia, and the opportunity to carry out breeding experiments between them, would provide valuable new information on the taxonomy of *P. fimbriatus* in this part of the Palaearctic.

P. fimbriatus and *P. imminuta* are, at present, distributed probably throughout the Palaearctic. However, the biogeography of *P. chiltoni* is remarkable because it is the only species of the genus with very wide distribution (Karaytug 1998). It occurs, for example, in very remote locations, such as Easter Island, as well as in Europe. Breeding experiments between geographically isolated populations would provide new insights into the possible involvement of several sibling species of *P. chiltoni*.

Acknowledgements

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