



## Interesting interstitial Paramesochridae (Copepoda: Harpacticoida): *Maliithipon wellsi* gen. et sp. nov. from the Philippines, *M. aberrans* (Mielke, 1984) comb. nov. from Panama, and *M. cf. aberrans* (Mielke, 1984) from the Azores

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### Abstract

We propose and describe a new genus of interstitial Paramesochridae, *Maliithipon* gen. nov., to accommodate three species. *Maliithipon wellsi* sp. nov., type species of the genus, is described based on specimens collected in two sandy beaches in Isla Verde, the Philippines. *Apodopsyllus aberrans* Mielke, 1984a described from Panama, is allocated to the herein erected genus as *Maliithipon aberrans* (Mielke, 1984a) comb. nov. *Maliithipon cf. aberrans* is described, based on specimens collected in the Azores and previously identified as *Apodopsyllus aberrans*. The new genus is characterized by several distinct morphological features: mandible with uniramous, 2-segmented palp and gnathobase with thin and pointed teeth; maxillule with reduced armature, lacking endopod and exopod; maxilla large, with three syncoxal endites and endopod with reduced setal number; P5 very reduced in both sexes; caudal rami with six setae, two of which (setae III and VI) transformed; pseudoperculum well-developed, with four-lobed distal margin. The new genus is included in the subfamily Paramesochrinae Lang, 1944 and in the genus-group *Scottopsyllus* (sensu Huys, 1987). It has strong affinities with *Leptopsyllus* (*Leptopsyllus*) *platyspinosus* Mielke, 1984b and *Wellsopsyllus* (*Intermediopsyllus*) *smirnovi* (Kunz, 1992), which are considered as *species inquirendae* in this paper. Some remarks on the ecology and geonomy of the three studied species are provided. We also list the accompanying Paramesochridae obtained from the two new collecting sites of the genus, and all the genera of Paramesochridae recorded from other sites in the Philippines during the same survey.

**Key words:** interstitial meiofauna, mesopsammon, new genus, new species

### Introduction

The family Paramesochridae Lang, 1944 presently includes thirteen genera and 150 species of marine harpacticoids (Walter & Boxshall 2019). No species of this family have ever been recorded from freshwater environments. The family is widespread and more than 80% of the species live in the marine interstitial habitat of sandy beaches (Amorri *et al.* 2010). Less common habitats include the intertidal zone and, with few adapted species, deep sea muds (*e.g.* Vasconcelos *et al.* 2009; Kottman *et al.* 2013). Most species are minute in size, with extremely reduced appendages (Cottarelli & Forniz 1994; Boxshall & Halsey 2004) and such miniaturization is related to their life in the interstitial habitat (Huys 1995). Their very small size, and the difficulties in collecting specimens of both sexes, can make the preparation and observation of these harpacticoids difficult.

The systematics of the family is still partly under debate due to a possible “insufficiency in the present family classification” (Kottmann *et al.* 2013). Based on Huys (1987), the family Paramesochridae is divided in two subfamilies. The Diarthrodellinae Huys, 1987 includes the genera *Diarthrodella* Klie, 1949, *Tisbisoma* Božić, 1964, and *Rossopsyllus* Soyer, 1975, and is the most plesiomorphic subfamily [3-segmented antennary exopod, 3-segmented P2–P4 endopods, inner seta on the proximal segment of P2–P4 exopods, primitive setation of the distal exopodal (7–8 setae) and endopodal (4–5 setae) segments in P2–P4]. The subfamily Paramesochrinae Lang, 1944 is characterized by a large number of apomorphies [2-segmented antennary exopod; 2-segmented P2–P4 endopods;

absence of inner seta on proximal segment of P2–P4 exopods; reduced number of segments of P2–P4 endopods and reduction in setation of distal exopodal (5 setae) and endopodal (3 setae) segments of P2–P4]. Following the revision of Huys (2009), the subfamily Paramesochrinae includes *Remanea* Klie, 1929 and two groups of genera: the *Paramesochra* group, *i.e.* *Paramesochra* Scott, 1892, *Emertonia* Wilson, 1932 (a senior subjective synonym of *Kliopsyllus* Kunz, 1962), *Kunzia* Wells, 1967 and *Meiopsyllus* Cottarelli & Forniz, 1994. The *Wellsopsyllus* group (based on *Wellsopsyllus* Kunz, 1981 replacing the unavailable name *Scottopsyllus* Kunz, 1962; *cf.* Huys 2009) includes the subgenera *Wellsopsyllus* (*Scottopsyllus*) Apostolov & Marinov, 1988, *Wellsopsyllus* (*Intermediopsyllus*) Huys, 2009, *Wellsopsyllus* (*Wellsopsyllus*) Kunz, 1981, *Leptopsyllus* (*Leptopsyllus*) Scott, 1894, *Leptopsyllus* (*Paraleptopsyllus*) Lang, 1944 and the genera *Apodopsyllus* Huys, 2009, *Caligopsyllus* Kunz, 1975, and *Biuncus* Huys, 1996. The type and only species of the latter is morphologically closest to *Leptopsyllus* (*L.*) *typicus* Scott, 1894 (see Huys 1995).

The genus *Apodopsyllus* is strongly adapted to life in the interstitial environment as shown by its cylindrical and slim body, with some body somites completely or partially fused in certain species, adaptations which provide the flexibility required to move between the interstices, and swimming legs (with the exception of P1) without endopods and with transformed exopods. While studying the Paramesochridae collected by the senior author in the mesopsammal of two sandy beaches of a small island near Mindoro Island (Philippines), we re-examined some specimens, which we had previously classified as *Apodopsyllus* sp. These specimens were characterized by several features similar to those of a species collected in Panama, *i.e.* *Apodopsyllus aberrans* Mielke, 1984a. The latter species is peculiar since it is radically different from the “typical” morphology of the other species in the genus *Apodopsyllus*, prompting Mielke to name the species “*aberrans*”. Later on, Huys (1988) stated that “*Apodopsyllus aberrans* Mielke 1984, with its modified caudal rami, reduced mouthparts and an obsolete P5 should undoubtedly be assigned to a new genus”. The results of the present study show that the taxon from the Philippines should be designated as the type species of a new genus, well-characterized by a combination of apomorphies. The newly proposed genus also includes *Apodopsyllus aberrans*, confirming the distinct systematic position of this species.

As a result of our analysis of literature data and examination of paramesochrid specimens in our collection and on loan, we expand our discussion to the main features and the present taxonomic position of other “troublesome” taxa which are morphologically related to the two species from the Philippines and Panama, *i.e.* *Leptopsyllus* (*Leptopsyllus*) *platyspinosus* Mielke, 1984b collected in the Galapagos, and *Wellsopsyllus* (*Intermediopsyllus*) *smirnovi* (Kunz, 1962) from the interstitial habitat of Saplunara beach on Mljet Island (Croatia, Adriatic Sea). Both taxa had already been listed as *incertae sedis* by Wells (2007). We will also discuss *Leptopsyllus* (*L.*) *typicus* and *Biuncus ingens* (Huys, 1995), the latter having been collected from intertidal *Amphioxus*-gravel near Elat (Israel).

The aims of this paper are to define, describe and discuss:

- i) *Maliithipon* **gen. nov.**, a new genus characterized by several autapomorphies, which are compared to those of the most closely related genera, and provide evidence to assign it to the subfamily Paramesochrinae.
- ii) *Maliithipon wellsi* **gen. et sp. nov.**, type species for the genus, defined by comparing it with *Maliithipon aberrans* **comb. nov.** (= *Apodopsyllus aberrans*) and with *M. cf. aberrans*, the latter having been collected in the Azores and previously classified as *Apodopsyllus aberrans* by Packmor & George (2016) and Packmor *et al.* (2015). We provide a morphological description of this taxon, underlining the affinities and differences with the original description of *M. aberrans* from Panama. No distinct taxonomic status was attributed to this taxon for reasons that are presented and discussed below.
- iii) we provide a synthesis of new and published data on the geonemy, habitat and ecology of the newly described species, including new data on the paramesochrid fauna of the Philippines based on the species accompanying *M. wellsi* **gen. et sp. nov.** and of taxa collected in other sites during the same sampling campaign.

## Materials and methods

**Site description and sampling methods.** All material was collected from two coral beaches (stations 1 and 2 thereafter), with medium-coarse sand, pebbles and coral and shell fragments, along the coast of Verde Island. This small island (Batangas Province) is located off the coast of Batangas City, between the islands of Luzon and Mindoro, in the middle of the Verde Island Passage, a strait connecting the South China Sea with the Tayabas Bay

and the Sibuyan Sea. It is noteworthy that this area is a Philippine Marine Reserve and was elected in 2007 a centre of the World's marine biodiversity by the Smithsonian Institute. All specimens of the type species of the new genus and their accompanying fauna were collected by one of us (VC) with the Karaman—Chappuis method (Delamare Deboutteville 1960) *i.e.* by digging a hole in the sand on the beach and decanting water through a plankton net with 40 µm mesh size. Samples were fixed in the field by adding buffered formaldehyde to a final concentration of approximately 4%.

Specimens of *Maliithipon cf. aberrans* were collected in the Azores Archipelago in the North-East Atlantic Ocean; information on the collecting station of this taxon, the collecting methods and the accompanying fauna are listed in Packmor *et al.* (2015).

**Morphological methods.** All specimens of *Maliithipon (M.) wellsi* **sp. nov.** were sorted under a stereomicroscope, placed in 70% ethanol and stored until further morphological analysis. Before morphological analyses, specimens were rinsed in distilled water, dissected and mounted in Faure's or glycerine jelly medium solution between two cover slips to allow observations from both sides. Fragments of glass wool were inserted between the two cover slips of some specimens to allow a better three-dimensional observation. After drying, slides were sealed with transparent nail polish.

Length measurements of the female holotype, the male paratype and other specimens of the type series, and of specimens of *M. cf. aberrans* were taken from the tip of the rostrum to the distal margin of the caudal rami. In some cases, details of appendages and body parts were drawn from undissected specimens because, in accordance with Kottmann *et al.* 2013 "... the animals are very small and the position of mouthparts and reduced swimming legs allows a thorough observation". Illustrations were made at different magnifications up to a maximum of 1250x, using drawing tubes mounted on a Zeiss Axioskop phase-contrast microscope and a Polyvar Reichert-Jung interferential-contrast microscope.

Specimens of the type series are deposited at the Natural History Museum, London (NHMUK) and at the the Department for Innovation in Biological, Agro-food and Forest systems, Tuscia University, Viterbo, Italy, Cottarelli's collection (DIBAF).

The descriptive terminology of Huys *et al.* (1996) was adopted. Abbreviations used in the text and Table 1 are: A1 = antennule; A2 = antenna; aes = aesthetasc; enp = endopod; exp = exopod; enp-1 (2, 3) = proximal (middle, distal) segment of endopod; exp-1 (2, 3) = proximal (middle, distal) segment of exopod; CR = caudal ramus/rami; GF = genital field; Md = mandible; Mx1 = maxillule; Mx = maxilla; Mxp = maxilliped; P1–P6 = first to sixth swimming legs.

## Taxonomic results

### Order Harpacticoida Sars, 1903

#### Family Paramesochridae Lang, 1944

#### Subfamily Paramesochrinae Lang, 1944

#### Genus *Maliithipon* gen. nov.

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**Diagnosis.** Body elongate, cylindrical, slightly depressed dorsoventrally and slightly tapering distally. No distinct separation between prosome and urosome. Cephalotorax approximately quadrangular, larger than somites, longer than the following two somites, with sensilla and several dorsal pores. Dorsal pores present also on the remaining somites. Genital complex of female: genital field small, transversally oval, ventrally at half length of the double genital somite which lacks dorsal suture; P6 reduced to two small arched chitinous plates, apparently not fused; genital pore near the distal margin of the genital field, below the P6. Penultimate somite with well-developed quadrilobate pseudopericulum. Caudal rami approximately cylindrical, tapering distally in lateral view, apparently with six setae. Seta I missing (or not discernible), seta III and VI enlarged and pointed, unipinnate in the distal third on the outer (seta III) or inner (seta VI) margin. Distal setae (IV and V) variable in shape, peculiarly transformed

in short fusiform structures in some specimens; seta VII dorsally inserted at 2/3 of the ramus length, biarticulate at base. Rostrum small, triangular, fused to cephalothorax, with two sensilla. Antennule 8-segmented in female, with large aesthetasc on segment four and small aesthetasc on segment eight. Antennule 7-segmented in male, short, subchirocer, aesthetasc on segments V and VII. Antenna 4-segmented; coxa and basis without ornamentation, enp-1 with strong pinnate abexopodal seta, enp-2 armed with eight elements; exopod 1-segmented with two lateral setae and one or two distal ones, the longest one pinnate. Mandible with uniramous and 2-segmented palp comprising basis, 1-segmented endopod with four setae or three setae and one spine. Coxal gnathobase long, with dorsal seta; cutting edge with a row of thin and pointed teeth along the distal margin, with a stronger tooth at the inner and outer corner. Maxillula: praecoxal arthrite with strong lateral seta and 5-6 distal spiniform setae; coxa with one or two distal setae, basis with one or two to three apical setae; exopod and endopod missing. Maxilla large, with reduced chaetotaxy; syncoxa with three endites: proximal and median ones with one seta, distal one with two or three pinnate setae; basis produced into strong claw; endopod fused with basipodite, carrying four setae, one or two of which are claw-like. Maxilliped: subchelate, syncoxa bare; basis elongate and bare; endopod 1- or 2-segmented. P1: coxa large and bare, basis without outer basal seta, with strong inner seta; rami 2-segmented, endopod slightly longer than exopod, or of about equal length; exp-1 with long pinnate outer seta, exp-2 with four setae; enp-2 with two geniculate apical setae. P2-P4 laterally displaced but coxa and basis not fused and not markedly produced laterally; basis with outer seta. P2 basis with inner setular row in females; exopods 3-segmented, with two spiniform setae on distal segment; endopods absent. P5 very reduced in both sexes, partly incorporated in somite. In females, baseoendopod represented by a lobe with a lateral seta, exopod reduced to a minute subrectangular lobe with two bare and one pinnate setae or exopod reduced to a lobe with one seta. In males, baseoendopodal lobe with one seta, exopodal lobe with two setae or reduced to a small lobe without armature. P6 in male reduced to two asymmetrical round plates with one or no seta.

**Type species.** *Maliithipon wellsi* **gen. et sp. nov.** (by original designation).

**Other species.** *Apodopsyllus aberrans* Mielke, 1984a = *Maliithipon aberrans* (Mielke, 1984a) **comb. nov.**; *Apodopsyllus aberrans* Mielke, 1984a in Packmor *et al.* (2015) and Packmor & George (2016) = *Malliithipon cf. aberrans* (Mielke, 1984a).

**Etymology.** The generic name is derived from two Tagalog (the official language of the Philippines) words: “maliit” meaning small, and “hipon” meaning shrimp. Gender: masculine.

**Relationships.** Based on the existing classifications, *M. wellsi* **sp. nov.** could have been included in the genus *Apodopsyllus*, as we did when we first examined our specimens, and as it had occurred for the specimens collected from the *locus typicus* and the Azores (Packmor *et al.* 2015; Packmor & George 2016). In fact, *M. wellsi* **sp. nov.** lacks the endopods of swimming legs P2–P4, as is typical of *Apodopsyllus*. However, members of the latter genus have the coxa and basis of P2–P4 fused forming a fusiform segment that is much longer than wide. To our knowledge no author noticed that in *A. aberrans* the coxa and basis are not fused, are wider than long, and that the exopods are inserted laterally. The same conditions occur in the new genus; the P2–P4 of this type are morphologically and functionally different from those of the remaining species of *Apodopsyllus*, possibly providing a very different locomotion modality. A similar type of swimming legs are present in *Leptopsyllus* Scott, 1894 and *Wellsopsyllus* Kunz, 1981, which include species similar to the new ones established in this work (see below). The presence of this type of legs could therefore be a synapomorphic character, shared with other genera, however, *Maliithipon* **gen. nov.** has a set of exclusive (autapomorphic?) characters related to the mouthparts, P5 and caudal rami, the most significant being the following:

- i) Mandibular palp: uniramous and 2-segmented, *i.e.* composed of basis and endopod, armed with few setae. Cutting edge of coxal gnathobase with long, thin and pointed teeth, the innermost and outermost ones being longer and stronger.
- ii) Maxillule of simple structure, coxa and basis with few setae, exopod and endopod missing.
- iii) Maxilla with three endites with reduced armature, the proximal endite can be reduced to a seta; the endopod is 1-segmented and fused to the basis, which is unarmed, at least one of the apical endopodal setae is claw-like. The maxillae are very large compared to the other mouthparts; in lateral view, they typically protrude from the cephalothorax.
- iv) P5 very reduced in both sexes: in *M. aberrans* **comb. nov.** (only females are known for this species) each P5 is represented by two small adjacent plates (one is the baseoendopod, the other the exopod), inserted laterally and

carrying respectively one and three setae; in *M. cf. aberrans* the exopod has three setae in the female but only two in the male, and the endopodal lobe in the male is partly fused with the exopodal lobe to form a structure similar to the one of *Wellsopsyllus (Intermediopsyllus) smirnovi*. The P5 can be further reduced: in *M. wellsi* **sp. nov.** the female has only one lobe (with a small incision, probably representing the boundary between baseoendopod and exopod) with one seta (missing in some specimens), and the male has a single, smaller lobe without setae.

v) Pseudopericulum with multilobate posterior margin.

vi) Caudal rami always with six setae, with peculiar transformation of setae III and VI.

All the above-mentioned characters are absent in the remaining species of *Apodopsyllus* (*A. aberrans* excluded), which share with *Maliithipon* **gen. nov.** only the morphology of P1, the absence of P2–P4 endopods, and the morphology of P2–P2 exopods. These similarities could be due to parallel evolution; however, the morphology of P2–P4 coxa and basis differs between the two genera. Both genera also share the number of setae on the caudal rami, but setae III and VI are not transformed in *Apodopsyllus*, which also has a different shape and ornamentation of the body, caudal rami, and genital field.

In summary, the unique combination of the above-listed characters does, in our opinion, characterize the new genus and separates it from *Apodopsyllus*; as a consequence the two species of *Apodopsyllus* which indeed share such set of characters, *i.e.* *A. aberrans* and *A. cf. aberrans*, are transferred to the new genus *Maliithipon* as *M. aberrans* (Mielke, 1984a) **comb. nov.** and *M. cf. aberrans* (Mielke, 1984a), respectively.

As regards the genera *Wellsopsyllus* and *Leptopsyllus*, the affinities with *Maliithipon* **gen. nov.** can be found with some species whose generic attribution is uncertain, according to their authors. As we discussed for *Apodopsyllus*, there are two unusual species among these genera, *i.e.* *Leptopsyllus (Leptopsyllus) platyspinosus* and *Wellsopsyllus (Intermediopsyllus) smirnovi*, which, according to us, have more morphological characters in common with *Maliithipon* **gen. nov.** than with their respective congeners. The same applies, but to a lesser degree, to *Leptopsyllus (Leptopsyllus) typicus*, *Wellsopsyllus (Wellsopsyllus) antarcticus* Kottmann & Veit-Köhler, 2013, and *Biuncus ingens*. In *Leptopsyllus (L.) platyspinosus* the mandible has a uniramous, 2-segmented palp, including an unarmed basis and a 1-segmented endopod carrying four setae; the morphology of the coxal gnathobase and cutting edge are also similar to those of the new genus. The maxillule and maxilla are very similar to those of the new genus (see Mielke 1984b: Fig. 23). The maxillipedal endopod is 2-segmented, there is a pseudopericulum with a bilobate rather than a quadrilobate posterior margin, the P4 has a 1-segmented endopod, the P5 has a reduced baseoendopod and small exopod, carrying three setae, and the genital field and shape and armature of the caudal rami are very similar to those of *Maliithipon* **gen. nov.** *Leptopsyllus (L.) typicus* has not been redescribed according to modern standards, and only the females are known. Nonetheless, the mandibular palp is uniramous, being represented by the basis and the endopod, and the structure of the maxilla (endites with reduced armature, basis prolonged into a claw, a second claw originates from the partially fused endopod) and maxilliped (with 1-segmented endopod) are characters which indicate a degree of affinity with the new genus. The morphology of the maxilla, pseudopericulum and P5 are unknown for this species, the caudal rami differ in shape and ornamentation and the body size of this species is very large (700 µm). *Wellsopsyllus (L.) smirnovi* has the same transformation/reduction of the mouthparts as in *Leptopsyllus (L.) platyspinosus*, but the three maxillary endites have more setae than the taxa discussed so far, and the P5, “a small plate with three setae, middle lobe not noticeable” (Kunz 1992), is morphologically similar to the one of the new genus but even simpler: it is reduced to a very small exopod, completely fused to the somite, carrying only two setae. Setae III and IV of the caudal rami are not characteristically transformed, the pseudopericulum seems to be missing but it could have been overlooked by Kunz (1992) who, for the male, described only the subchirocer antennule and did not provide any information on the P5 and P6. This species is remarkably long (510 µm). *Wellsopsyllus (W.) antarcticus*<sup>1)</sup> has a 1-segmented antennary exopod, a uniramous (but 3-segmented) mandibular palp, a maxillule without endopod or exopod and the size and armature of the maxilla are similar to those of *Maliithipon* **gen. nov.** Differences with the new genus are expressed in the P2–P4 which have retained the endopod, the genital field with a different structure carrying two setae, the P5 which is not reduced in either sex, the absence of a lobate pseudopericulum and the morphology of the caudal rami. *Biuncus ingens* is a large species, known only from males, and was included by Huys (1995) in the group of species related to *Leptopsyllus* based on

1 We underline that Kottmann *et al.* (2013) provided some interesting remarks on the “uncertainties” regarding the systematic and morphology of this genus and subgenera with which we fully agree.

the mandibular palp (which in *Biuncus* is simple but retains the exopod, represented by a seta, and the endopod is 2-segmented), the structure and size of the maxilla, and the presence of a lobate pseudoperculum. The analysis of all the above-listed taxa, which are morphologically close to *Maliithipon* **gen. nov.**, underlines that only the species of this genus share all the above-mentioned characters. These same characters can be present in other Paramesochridae, but never all of them combined in one species.

Particularly relevant to solving some systematic issues in the Paramesochridae is the analysis of the morphology of mouthparts, P5 and caudal rami. This view is supported by Kottman *et al.* (2013) who, while discussing affinities among species of *Wellsopsyllus*, remarked how “at present, the classification is mainly based on the segmentation of the swimming legs, but there are other important characteristics to be considered (e.g., mouthparts, furcal rami)”. More recently, Back & Lee (2017a) discussed the genus *Leptopsyllus*, underlining how most of the recent classifications for this genus are based on leg characteristics (reduced or absent), and the complete descriptions of mouthparts are lacking for many species. Veit-Köhler (2004, 2005) gave similar remarks for the genus *Kliopsyllus* (now *Emertonia*). Already Kunz (1981) stated that in very specialized Paramesochridae with reduced pereopods, such as *Apodopsyllus* and *Leptopsyllus*, the original components of the mouthparts are still recognizable. Later on, Huys (1987) remarked that *Wellsopsyllus*, *Leptopsyllus* and *Apodopsyllus* have undergone paedomorphic evolution and “can easily be included in a morphological series with increasingly pronounced larval characters”. The new genus *Maliithipon* **gen. nov.** can be added to this “morphological series” but the species included in the latter and the above-discussed species to which it is most closely related (mainly *Leptopsyllus* (*L.*) *platyspinosus*) can represent a further step which characterizes and separates them from the other components of the evolutionary lineages hypothesized by Huys (1987). Possibly, further studies based also on a molecular approach will allow including them in a phylogenetically-valid group.

The discussion of the taxonomic position of *Leptopsyllus* (*L.*) *platyspinosus* and *W. (L.) smirnovi* is outside the scope of this paper. We, however, suggest that these two species should be considered *incertae sedis*, as already proposed by Wells (2007) for *W. (L.) smirnovi*. When and if *Wellsopsyllus* (*L.*) *smirnovi* will be redescribed with more details (the original drawings of *Leptopsyllus* (*L.*) *platyspinosus* are still adequate), it will be possible to include these two species in a taxonomic unit close to *Maliithipon* **gen. nov.**, or possibly in the same genus appropriately reviewed and divided into subgenera. In fact, it is difficult to suppose that complicated structures as those described above could have evolved independently but in a similar way in different genera. It is worthy to remember that Kunz (1992: 90), while discussing the affinities of *W. (L.) smirnovi*, stated that “these observations suggest to separate *L. platyspinosus*, *S. smirnovi* and *S. minutus* as a phylogenetically-related group”.

### ***Maliithipon wellsii* sp. nov.**

(Figs. 1–5)

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**Type locality.** Philippines, Batangas Province, Verde Island. Station 1 (13°31'36.03"N, 121°04'45.68"E), beach in Saint Agapito Village. Station 2 (13°34'02.65"N; 121°03'56.64"E) on the opposite side of the island, on Mahabang Buhangin beach, in the Barangay area, near San Augustin village.

**Type material.** Holotype: female, undissected, mounted on one slide labelled: *Maliithipon wellsii*, holotype female (reg. no. NHMUK 2019.1002), Isla Verde, station 1, 4/VIII/1995. Paratypes: one male, undissected, mounted on one slide labelled: *Maliithipon wellsii*, paratype male (reg. no. NHMUK 2019.1003), Isla Verde, station 1, 4/VIII/1995. One female dissected, mounted on slide labelled: *Maliithipon wellsii*, paratype female (reg. no. NHMUK 2019.1004), Isla Verde, station 1, 4/08/1995. Two females, undissected, each one mounted on one slide labelled: *Maliithipon wellsii*, paratype female (reg. nos NHMUK 2019.1005–1006), Isla Verde station 1, 4/VIII/1995. Two females, undissected, each one mounted on one slide labelled: *Maliithipon wellsii*, paratype female (reg. nos NHMUK 2019.1007–1008), Isla Verde station 2, 4/VIII/1995. Two females, undissected, each one mounted on one slide labelled: *Maliithipon wellsii*, paratype female (DIBAF), Isla Verde station 1, 4/VIII/1995. All material collected by V.C.

**Etymology.** The new species is named in honour of Prof. John B. J. Wells, in appreciation of his outstanding contribution to the study of copepods. The specific epithet is a noun in the genitive singular. Gender masculine.

**Description of female (holotype).** Habitus (Fig. 1A): body elongate, cylindrical and slightly depressed dorsoventrally, naupliar eye absent. Length: 300–350 µm; *n* = 5, mean = 331 µm. Length of the holotype: 349 µm.

Last urosomites tapering posteriorly; prosome to urosome ratio: 0.90; free pedigerous somites without any lateral or dorsal expansions, all connected by well-developed arthrodial membranes. Integument weakly sclerotized, cuticle finely pitted dorsally (Fig. 2D). First pedigerous somite and dorsal cephalic shield fused forming cephalothorax representing about 25% of the total body length. Cephalothorax and somites with few sensilla and several pores on dorsal, lateral and ventral surfaces (pores were difficult to observe, their pattern could not be precisely determined) (Figs. 1A, 2D). Second and third urosomite completely fused to form genital double-somite (Figs. 2A–C). Penultimate body somite without sensilla, carrying a fine, well developed lobate pseudopericulum (Figs. 1A, 2D, 3A–B). Anal somite small, with pair of dorsal sensilla (Fig. 3A–B); anal operculum not visible. Genital field (Fig. 2A–C) small, ellipsoidal, located mid-ventrally and slightly above the mid-length of the genital double-somite, surrounded by eight pores of different size; P6 (Fig. 2B–C) reduced to two small arched plates not fused to each other; copulatory pore opening below them.

Caudal rami (Figs. 1A, 2D). Elongated, slightly tapering posteriorly and slightly divergent, three times the length of the last urosomite; length: 31  $\mu\text{m}$ ; length/width: 2.7. Armature represented by six setae (seta I apparently missing): seta II short and very thin; seta III stout and pointed, unipinnate in approximately one/fifth of the distal outer margin; seta IV very small, bare, enlarged in the first half and thin in the second half; seta V unipinnate, enlarged in the first half and thin in the second half; seta VI as seta III but shorter; seta VII bare, bi-articulate at base and arising distally at two/third of the ramus.

Rostrum (Fig. 1A). Small, approximately triangular, with round tip, fused to cephalic shield, armed with two sensilla.

Antennule (Figs. 1A, 3E). Short, robust, 8-segmented. First segment longest, without armature, with a row of inner spinules. Second segment with three pinnate and one bare seta on the inner margin, one long seta on the outer margin. Third segment provided with three pinnate and two bare setae. Inner distal corner of fourth segment forming a sub-cylindrical process provided with a group of one long slender bare seta, one short spindle-like pinnate seta, one long and thick aesthetasc, fused at base with a long slender seta. Fifth segment smallest, with one pinnate and one bare seta arising from a sub-cylindrical inner outgrowth. Sixth segment with five bare setae; seventh segment with five bare setae, the longest and strongest one originating from a ventral cylindrical outgrowth. Last segment wider than long, furnished with seven bare setae and a lateral acrothek formed by a slender aesthetasc and a seta fused at base. Armature formula: 1–[0], 2–[2 bare + 3 pinnate], 3–[2 bare + 3 pinnate], 4–[2 bare + 1 pinnate + ae], 5–[1 bare + 1 pinnate], 6–[5 bare], 7–[5 bare], 8–[7 bare + acrothek].

Antenna (Fig. 3C–D). 4-segmented; coxa small and bare; basis approximately three times longer than wide, without any surface ornamentation; exopod (Fig. 3D) 1-segmented, with a constriction at half-length (trace of segmentation?), two bare setae laterally, one bare and one pinnate seta apically. Endopod 2-segmented, proximal segment with one pinnate abexopodal seta; distal endopodal segment ornamented with two groups of spinules on lateral margin and armed with one bare spiniform seta sub-distally, four long and geniculate setae, two shorter bare ones.

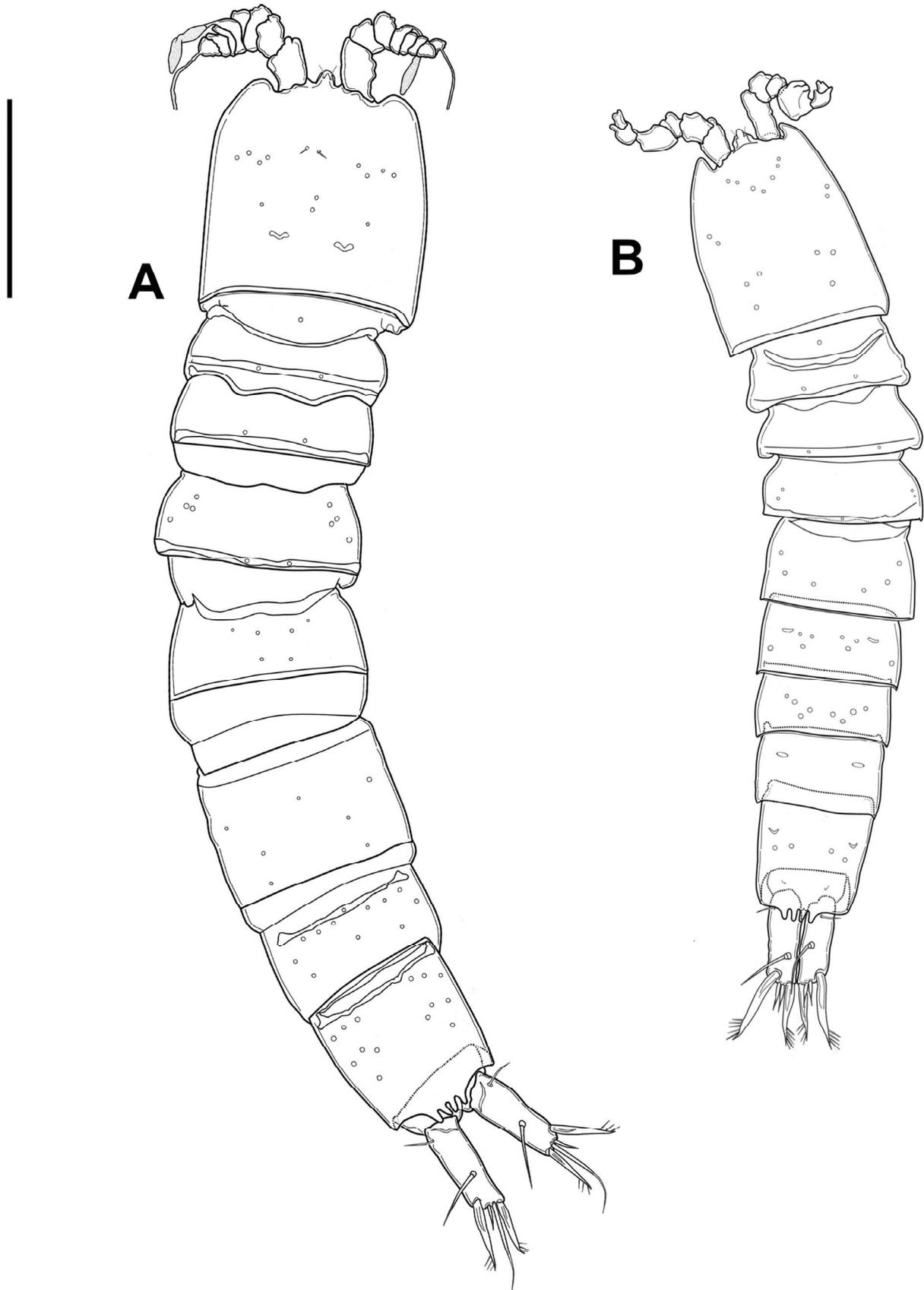
Mandible (Fig. 4A). Coxa with well-developed gnathobase bearing one pinnate seta at dorsal corner; cutting edge provided with one long pointed tooth on outer corner, four apical long needle-like teeth, and one pointed, strong tooth on inner corner, half as long as coxal length. Palp reduced, 2-segmented, comprising basis with distal pinnate seta, 1-segmented endopod with two distal setae of subequal length, two short lateral pinnate setae.

Maxillule (Fig. 4B). Praecoxal arthrite well developed, quadrangular, with one pinnate proximal seta on lateral margin, three thin bare setae, three pointed teeth at distal margin. Coxa prolonged in a cylindrical endite with apical pinnate seta; basis with one subapical unipinnate seta and one apical unipinnate spiniform seta. Exopod and endopod missing.

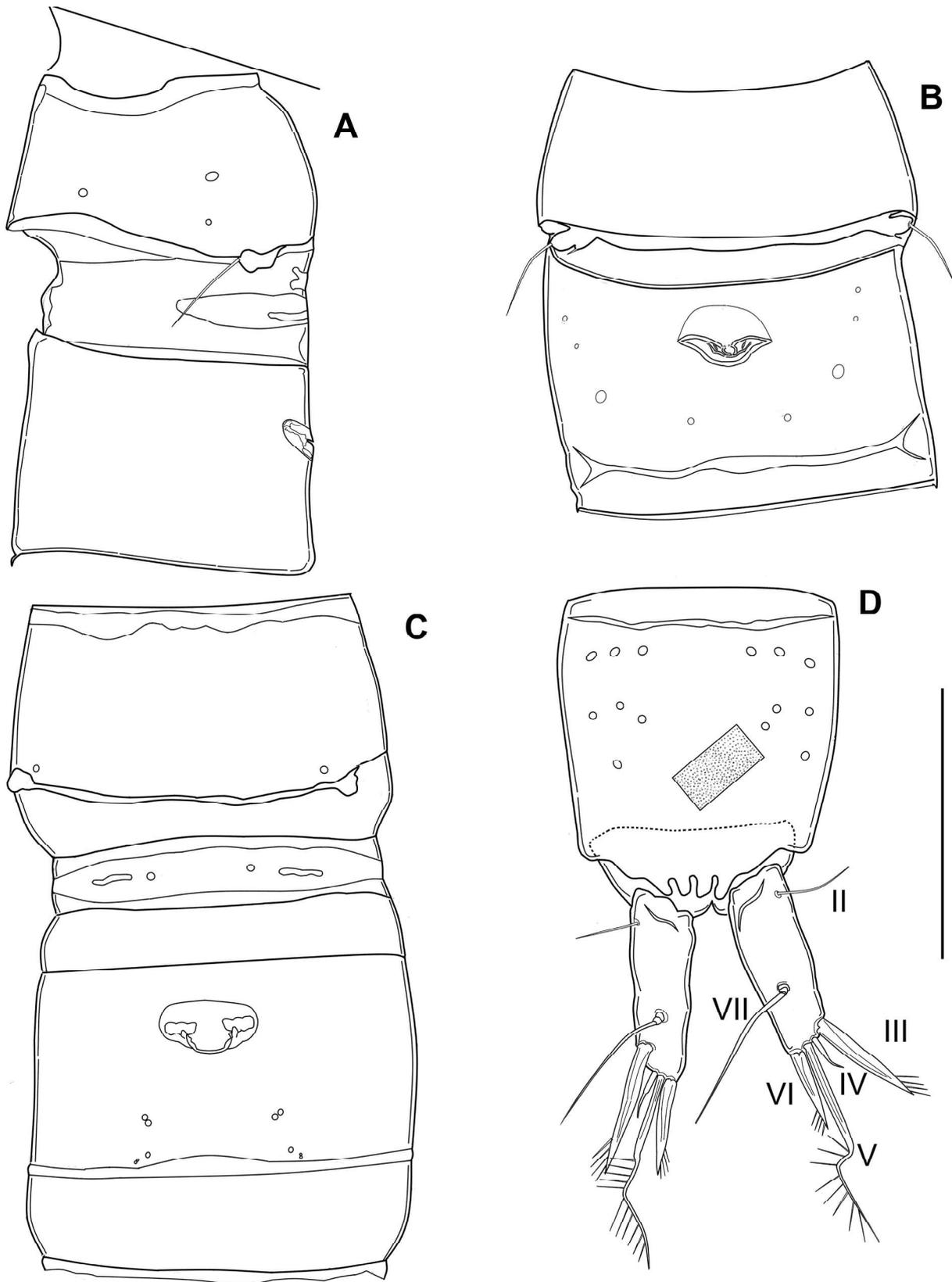
Maxilla (Fig. 4C). Overall very large compared to the other mouthparts; syncoxa with three endites, proximal one reduced to a large pinnate seta, median endite with one apical pinnate seta, distal coxal endite with one bare and one pinnate apical seta. Allobasis prolonged into strong denticled claw; endopod fused to basis and armed with one claw-like unipinnate seta and four naked setae distally.

Maxilliped (Fig. 4F). 3-segmented, comprising syncoxa, basis, and 1-segmented endopod; syncoxa bare, basis more than twice the length of coxa and bare, length/width: 2.9; endopod small, with one small subapical spine, one strong claw-like pinnate seta and two thinner bare ones distally.

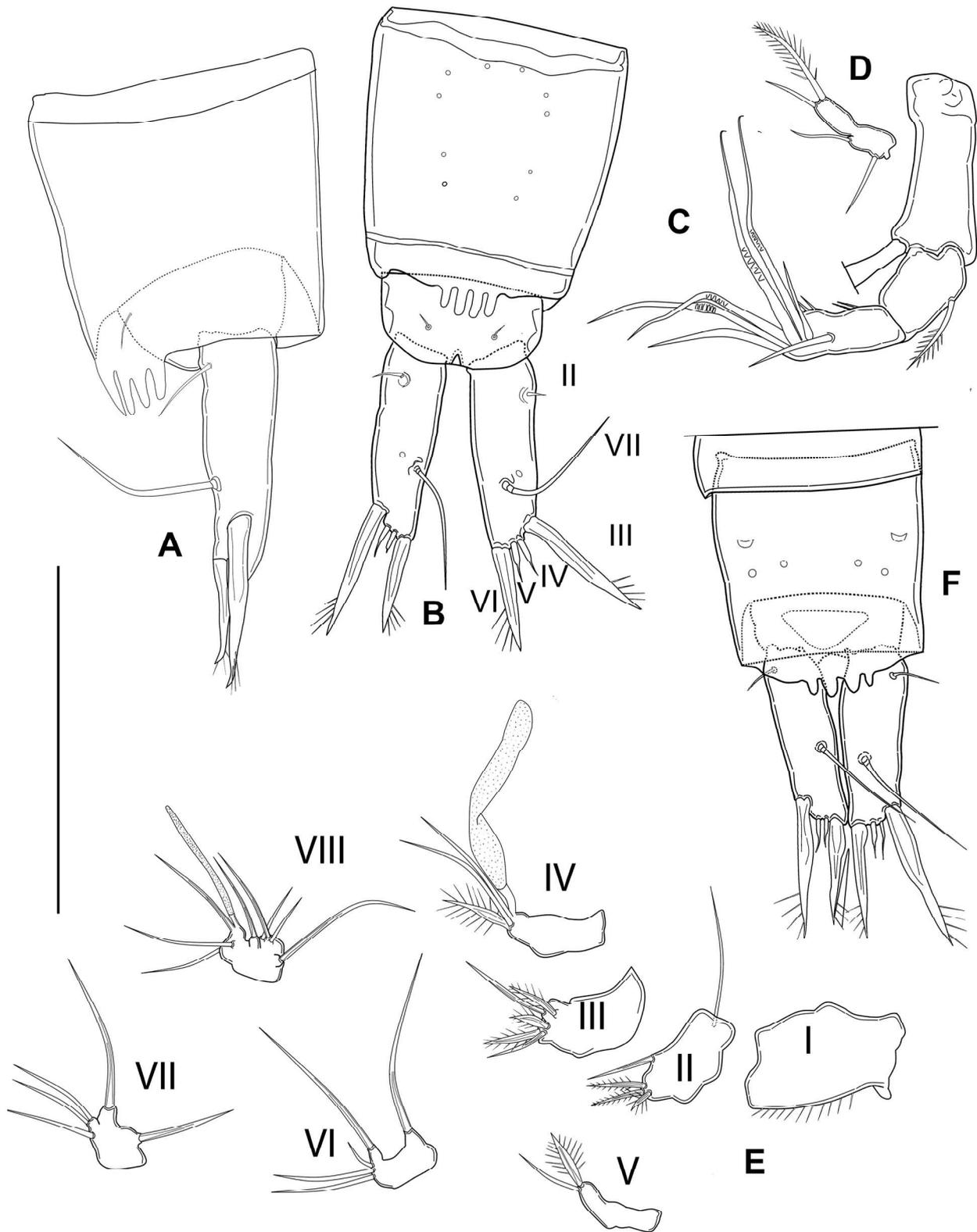
P1 (Fig. 4G). Intercoxal sclerite long and thin, slightly concave; coxa bare, well-developed and pyramidal; basis without outer seta, with bare inner seta at half length of the inner margin; exopod and endopod 2-segmented,



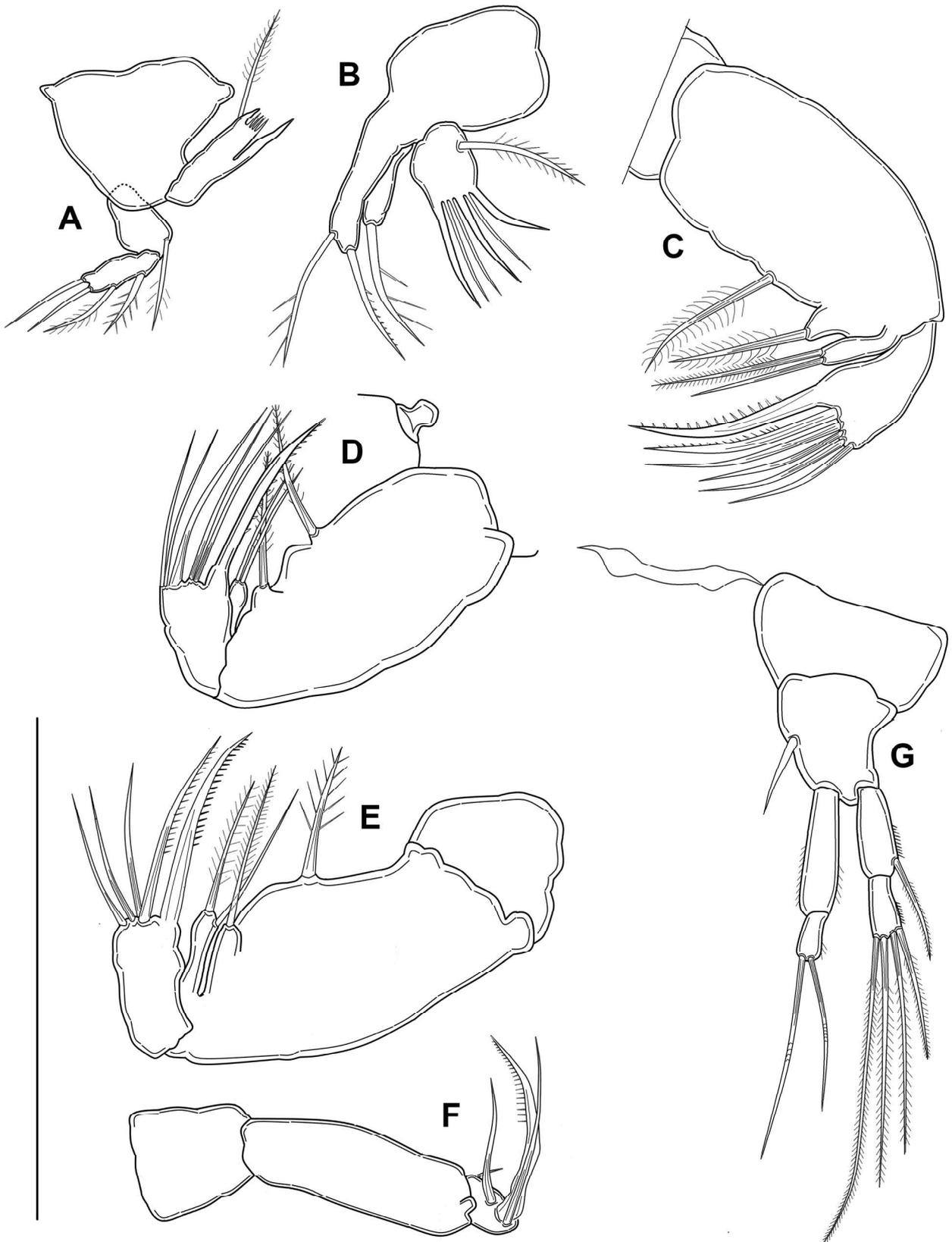
**FIGURE 1.** *Maliithipon wellsi* sp. nov. A, female, habitus, dorsal. B, male, habitus, dorsal. Scale bar: 50  $\mu$ m.



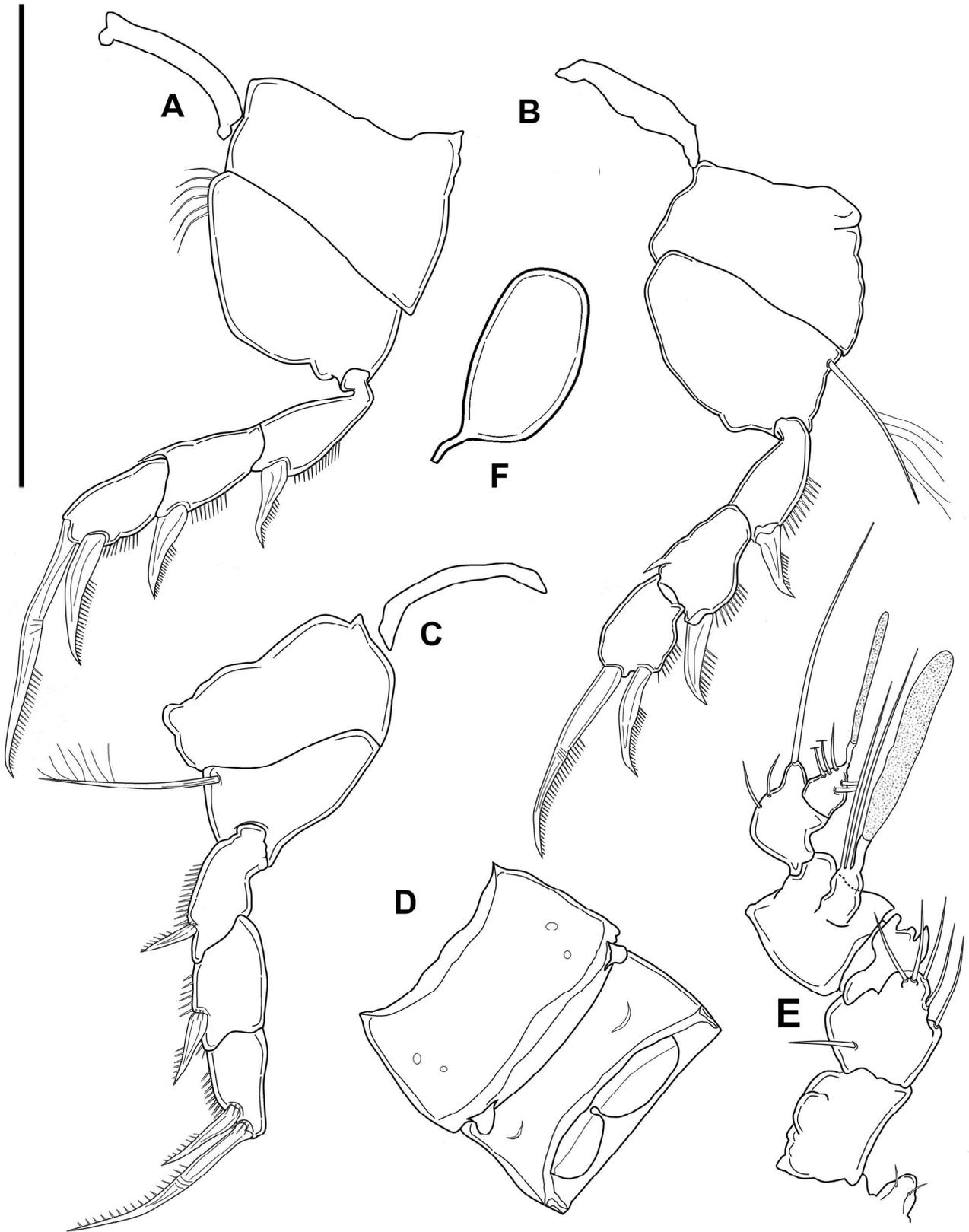
**FIGURE 2.** *Maliithipon wellsi* sp. nov., female. A, first urosomite, P5, genital double-somite, genital field, lateral. B, first urosomite, P5, genital double-somite, genital field, ventral. C, first urosomite, P5 (variability), genital double-somite, genital field, ventral. D, last urosomite, anal somite, pseudoperculum, caudal rami, dorsal (insert representing microstructure of cuticle; setae marked with Roman numerals). Scale bar: 50  $\mu$ m.



**FIGURE 3.** *Maliithipon wellsi* sp. nov. A, female, last urosomite, anal somite, pseudoperculum, caudal rami, lateral (variability). B, female, last urosomite, anal somite, pseudoperculum, caudal rami, dorsal (variability, setae marked with Roman numerals). C, female, antenna. D, female, antennary exopod. E, female, antennule, disarticulated (antennulary segments marked with Roman numerals). F, male, last urosomite, anal somite, pseudoperculum, anal operculum, caudal rami, dorsal. Scale bar: 50  $\mu$ m.



**FIGURE 4.** *Maliithipon wellsi* sp. nov. A, female, mandible. B, female, maxillule. C, female, maxilla. D, male, maxilla. E, female, maxilla (variability). F, female, maxilliped. G, female, P1. Scale bar: 50  $\mu$ m.



**FIGURE 5.** *Maliithipon wellsi* sp. nov. A, female, P2. B, female, P3. C, female, P4. D, male, first and second urosomites, P5, P6, ventral. E, male, rostrum and antennule. F, male, spermatophore. Scale bar: 50  $\mu$ m.

exopod slightly shorter than endopod. First exopodal segment longer than the second one, with spinular row along outer margin, strong pinnate seta on distal outer corner; second segment with spinular row along outer margin, four distal pinnate setae, the innermost is the longest. First endopodal segment bare, 2.5 times longer than the second one, with spinules along inner and outer margin; second segment with spinules along the distal part of the outer margin, two long geniculate apical setae.

P2–P4. (Fig. 5A–C). Intercoxal sclerites long and thin. P2 basis without outer seta and with a proximal inner row of hair-like spinules; P3 and P4 basis with outer pinnate seta. Exopods 3-segmented, first, second and third segments with spinular row along outer margin; first segment with outer unipinnate, curved spine at distal corner; third segment also with long geniculate apical seta. Endopods missing. Setal formula provided in Table 1.

P5 (Fig. 2A–B). Reduced to a lobed plate, with one short seta (ancestral baseoendopodal seta) and a tiny tip.

**Description of male (paratype).** Habitus (Fig. 1B) General body shape and ornamentation as in female, but slightly smaller and more slender than in female, body length 252 µm; largest width measured at posterior margin of cephalic shield: 44 µm; prosome to urosome ratio: 0.83. Cephalothorax representing about 26% of total body length. Antenna, Mdb, Mx1, Mxpd, P1–P4 as in female, sexual dimorphism in separation of genital somite, A1, Mx, P5, and P6, P2 basis ornamentation and P3–P4 basis armature.

Caudal rami (Fig. 3F). Shape and armature as in female but proportionally longer (length/width = 3.2).

Antennule (Fig. 5E). Strong, short, subchirocer, 7-segmented. Armature cannot be described since some of the setae are damaged or missing in the only existing specimen. First segment apparently without distal seta. Fifth segment enlarged, square, with longer and thinner aesthetasc than in female; seventh segment with thin distal aesthetasc, two of the observable four setae are small.

Maxilla (Fig. 4D). Structure and ornamentation as in female, but endopodal setae all bare.

P2. Basis without proximal row of hair-like spinules.

P3–P4. Basis with outer bare seta.

P5 (Fig. 5D). Extremely reduced, represented by a small round lobe without armature.

P6 (Fig. 5D). Two asymmetrical (the right one is larger) roundish plates without armature.

Spermatophore (Fig. 5F). Ellipsoidal, slightly longer than the somite carrying the P5.

**Variability.** In one female paratype the caudal seta V is reduced in size (it equals seta IV) and there is a pore near seta VII (Fig. 3B). In a second female paratype, the maxillary endopod carries one seta less (Fig. 4E). In a third female paratype the P5 is unilobed and unarmed and the number and position of pores on the ventral surface of the genital somite differ (Fig. 2C).

### ***Maliithipon aberrans* (Mielke, 1984a) comb. nov.**

This species was described as *Apodopsyllus aberrans* by Mielke (1984a) based on three female specimens collected in two sandy beaches on the Pacific Coast of Panama: “Isla Naos” (two specimens) and “Isla Melones” (one specimen). The description and the drawings clearly show how this species shares all the characters listed for *Maliithipon gen. nov.* This species can be distinguished from the type species *M. wellsi sp. nov.* by several characters (Table 1), some of which are easy to observe, such as the shape and size of caudal rami (shorter and wider in *M. aberrans*, length/width: 1), the structure of P5 (more reduced in *M. wellsi sp. nov.*). To expand the comparison of the two species, we report here the antennular armature deduced from Mielke’s (1984a: 227) original drawings: 1–[ 0 ], 2–[3 bare + 5 pinnate], 3–[3 bare + 3 pinnate], 4–[1 bare + 1 + ae], 5–[1 bare ], 6–[1 pinnate], 7–[4 bare + 1 pinnate], 8–[4 bare + ae (acrothek?)].

### ***Maliithipon cf. aberrans* (Mielke 1984a) = *Apodopsyllus aberrans* Mielke 1984a in Packmor *et al.* (2015) and Packmor & George (2016)**

(Figs. 6–11)

**Material examined.** Two male and four female specimens, each one undissected and mounted on one slide labelled respectively: *Apodopsyllus aberrans*, adult female. Prainha, ST 1/3 (Madeira Island); *Apodopsyllus aberrans*, adult female, Prainha, ST 1/4 (Madeira Island); *Apodopsyllus aberrans*, adult male. Prainha, ST 1/6 (Madeira Island);

*Apodopsyllus aberrans*, adult male. Calheta, ST1/1 (Madeira Island); *Apodopsyllus aberrans*, adult female, Puerto Santo Island East, ST 3/6; *Apodopsyllus aberrans*, adult female, Puerto Santo Island East, ST 3/6. Details on the collecting methods, collecting sites and dates in Packmor *et al.* (2015).

**Description of female.** Habitus (Fig. 6A). Body unpigmented, elongate, cylindrical and slightly depressed dorsoventrally, naupliar eye absent. Length 228  $\mu\text{m}$ ,  $n = 4$ , mean = 229  $\mu\text{m}$ . Last urosomites tapering posteriorly. Free pedigerous somites without any lateral or dorsal expansions, all connected by well-developed arthrodial membranes. Ventrolateral margin of first, second, and fourth free thoracic somites with row of denticles (Fig. 6B). Integument weakly sclerotized, without cuticular pits. First pedigerous somite and dorsal cephalic shield fused forming cephalothorax representing about 26% of total body length. Cephalothorax and somites with few sensilla and several pores on dorsal, lateral and ventral surfaces (pores were difficult to observe, their pattern could not be precisely determined). Second and third urosomite completely fused to form genital double-somite. Penultimate body somite without sensilla, carrying a fine, well developed lobate pseudopericulum (Figs. 6A, 7C). Anal somite small, with pair of dorsal sensilla (Fig. 7B); anal operculum not visible. Genital field (Fig. 6C–D) small, ellipsoidal with two small lateral lobes, located mid-ventrally and at mid-length of the genital double-somite, surrounded by eight pores of different size; P6 not discernible (morphology probably as in *M. wellsi*).

Caudal rami (Fig. 7<sup>o</sup>–B). Parallel, slightly longer than the last urosomite; length: 14  $\mu\text{m}$ ; length/width: 1.8. Approximately rectangular in shape, slightly tapering posteriorly, the distal outer corner is prolonged in a ventral cuticular outgrowth; armature represented by six setae (seta I apparently missing): seta II short and very thin, seta III stout and pointed, unipinnate along approximately one/fifth of the distal outer margin; seta IV unipinnate, seta V bare and very reduced; seta VI as seta III but shorter; seta VII bare, bi-articulate at base and arising distally at two-thirds of the ramus length.

Rostrum (Fig. 6A, 8A). Small, approximately triangular, with round tip, fused to cephalic shield, armed with two sensilla.

Antennule (Fig. 8A–B). Short, robust, 8-segmented. First segment longest, without armature; second segment with ten setae, four of which pinnate, the one on the outer distal corner longest. Third segment provided with two pinnate and five bare setae. Inner distal corner of fourth segment forming a sub-cylindrical process carrying a long and thick aesthetasc fused at base with one long bare seta, and two short, basally-enlarged setae, the outer one pinnate. Fifth segment smallest, with one bare seta. Sixth segment with two bare setae; seventh segment with one bare and one pinnate seta. Eighth segment with seven bare setae and one pinnate and acrothek formed by a slender aesthetasc and a seta fused at base. Armature formula: 1–[0], 2–[6 bare + 4 pinnate], 3–[5 bare + 2 pinnate], 4–[1 bare + 1 pinnate + (1 + ae)], 5–[1 bare ], 6–[2 bare], 7–[1 bare + 1 pinnate], 8–[8 bare + 1 pinnate + acrothek].

Antenna (Fig. 8C–D). 4-segmented; coxa small and bare; basis approximately twice longer than wide, without any surface ornamentation; exopod (Fig. 8D) 1-segmented, with two bare setae laterally, one pinnate seta and one short spine apically. Endopod 2-segmented, proximal segment with one pinnate abexopodal seta; distal endopodal segment armed with two subdistal bare spiniform setae, distal margin carrying three bare geniculate setae and three bare normal setae, one of which very short.

Mandible (Fig. 8E). Coxa long and narrow, with well-developed gnathobase bearing one bare seta at dorsal corner; cutting edge provided with three apical needle-like teeth, one long pointed tooth on inner and on outer corner, one tooth has double the size of the other. Palp reduced, 2-segmented, comprising roundish basis, 1-segmented endopod with one seta, one pinnate spiniform seta, and one spinule distally, and one lateral unipinnate spiniform seta.

Maxillule (Fig. 8F). Difficult to discern. All setae bare. Praecoxal arthrite roundish, with one seta at half of the lateral margin (marked with asterisk in Fig. 8F), two thin and two stronger setae at distal margin. Coxa prolonged in a cylindrical endite with two apical setae; basis with one apical seta. Exopod and endopod missing.

Maxilla (Fig. 9A). Overall very large compared to the other mouthparts (in lateral view, it projects from the cephalothoracic margin); syncoxa with three endites, proximal one small with one apical pinnate seta, median endite small with one apical pinnate seta, distal coxal endite with two apical bare setae. Allobasis prolonged into strong denticled claw; endopod fused to basis and armed with four strong setae distally.

Maxilliped (Fig. 9C). 3-segmented, comprising syncoxa, basis, and 1-segmented endopod; syncoxa bare, basis slightly longer than coxa and bare; endopod short, distally one normal and two slightly geniculated bare setae.

P1 (Fig. 9D). Intercoxal sclerite long and thin, slightly concave; coxa bare, well-developed; basis without outer seta, with bare inner seta at half length of the inner margin; exopod and endopod 2-segmented, exopod slightly shorter than endopod. First exopodal segment longer than the second one, with spinular row along outer margin,

strong pinnate seta on distal outer corner; second segment with spinular row along outer margin, four distal pinnate setae, the innermost is the longest. First endopodal segment bare, 2.5 times longer than the second one, with spinules along outer margin; second segment with spinules along the distal part of the outer margin, two long geniculate apical setae.

P2–P4. (Figs. 9E–F, 10A). Intercoxal sclerites long and thin. P2 basis with small bare outer seta and with a row of spinules on inner margin; P3 and P4 basis with outer pinnate seta. Exopods 3-segmented, first, second and third segments with spinular row along outer margin and outer unipinnate, curved spine at distal corner, longest in P4 exp-2; third segment also with apical long geniculate pinnate seta. Endopods missing. Setal formula provided in Table 1.

P5 (Fig. 6C). Reduced to two adjacent lobed plates laterally inserted; the outermost plate with a pinnate seta (ancestral basal seta), the innermost plate, roundish, with three setae, the longest middle one unipinnate.

**Description of male.** General body shape and ornamentation as in female, but slightly smaller and more slender, body length 220  $\mu\text{m}$ ; prosome to urosome ratio: 0.85. Last urosomites tapering posteriorly. Cephalothorax representing about 25% of total body length. Antenna, Mdb, Mx1, Mx, Mxp, P1–P4 (Figs. 10D, 11–C) as in female. Sexual dimorphism in separation of genital somite, A1, P5, and P6, ventrolateral margin of free thoracic somites without row of denticles; P2 basis ornamentation, P3–P4 basis armature; P4 exp-2 armature. Anal somite small, anal operculum and dorsal sensilla of the anal somite not visible.

Caudal rami (Fig. 11E). Shape and armature as in female but proportionally longer and thinner (length/width = 2).

Antennule (Fig. 10C). Strong, short, subchirocer, 7-segmented. First segment without distal seta, as in female; second segment with long lateral seta, as in female, two short pinnate lateral setae, five bare setae. Third segment with four bare setae of different lengths, one short pinnate seta. Fourth segment small, with two short setae; fifth segment enlarged, square, with long aesthetasc fused at base with long seta. Fifth segment with lateral tubercle carrying one thick aesthetasc and two setae of same length; inner distal corner produced in a tubercle carrying one bare seta and three shorter ones, the middle one is enlarged in the first half and pinnate. Sixth segment with one long and three short setae, one of which pinnate; seventh segment with eight bare setae and one small seta fused to aesthetasc to form apical acrothek. Armature formula: 1–[0], 2–[6 bare + 2 pinnate], 3–[4 bare + 1 pinnate], 4–[4 bare], 5–[4 bare + 1 pinnate + (1 + ae)], 6–[3 bare + 1 pinnate], 7–[8 bare + acrothek].

P2 (Fig. 11A). Basis without inner row of spinules.

P3 (Fig. 11B). Basis with outer bare seta.

P4 (Fig. 11C). Basis with outer bare seta; exp-2 with distal spine of normal size.

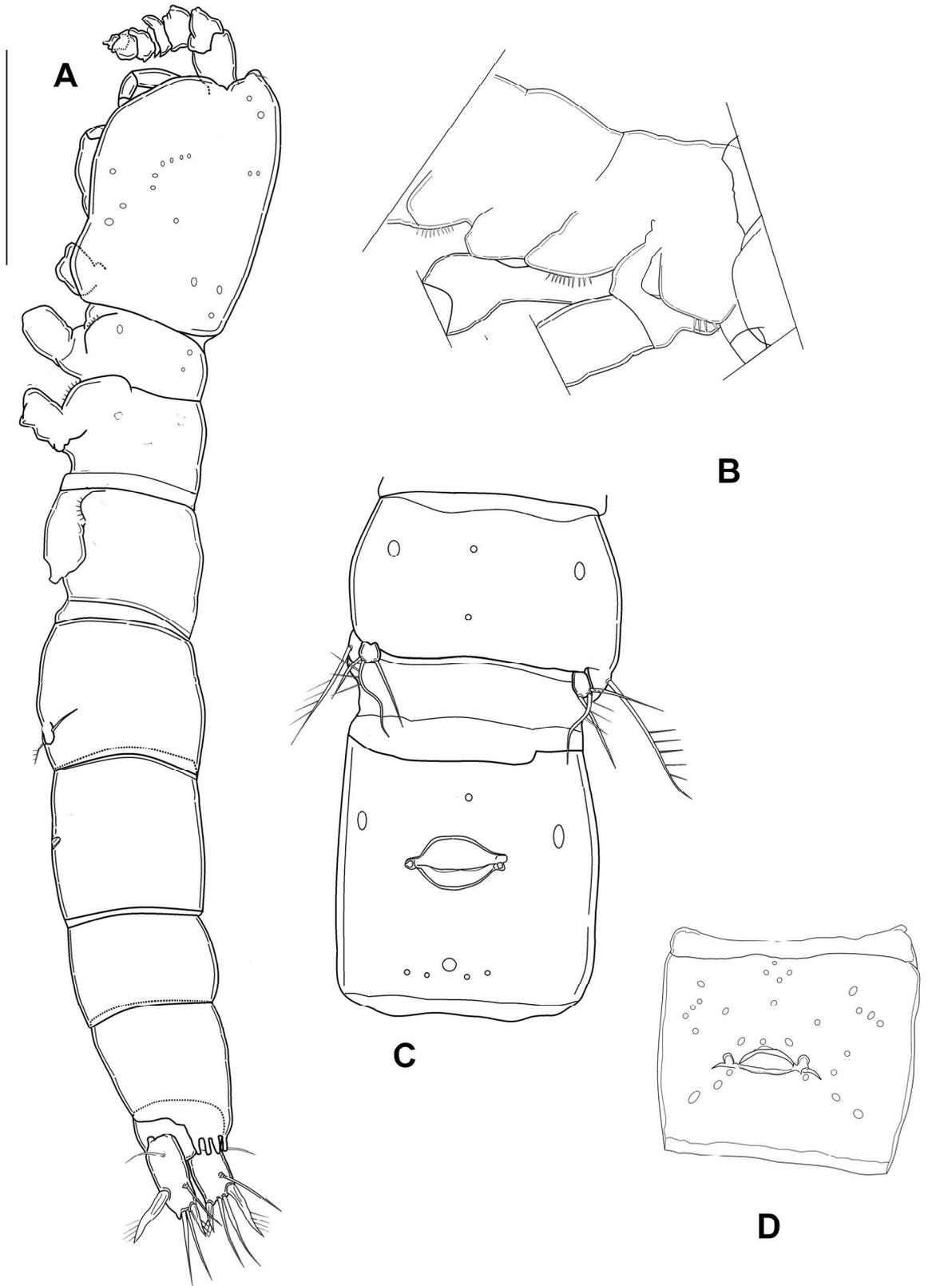
P5 (Fig. 10E). Similar to female but the two lobes are merged, smaller, and with bare setae; the exopod is merged with the somite and carries two setae (one less seta than in the female).

P6 (Fig. 11D) represented by two asymmetrical (the right one is larger) roundish plates with one seta, the one on the right is longer.

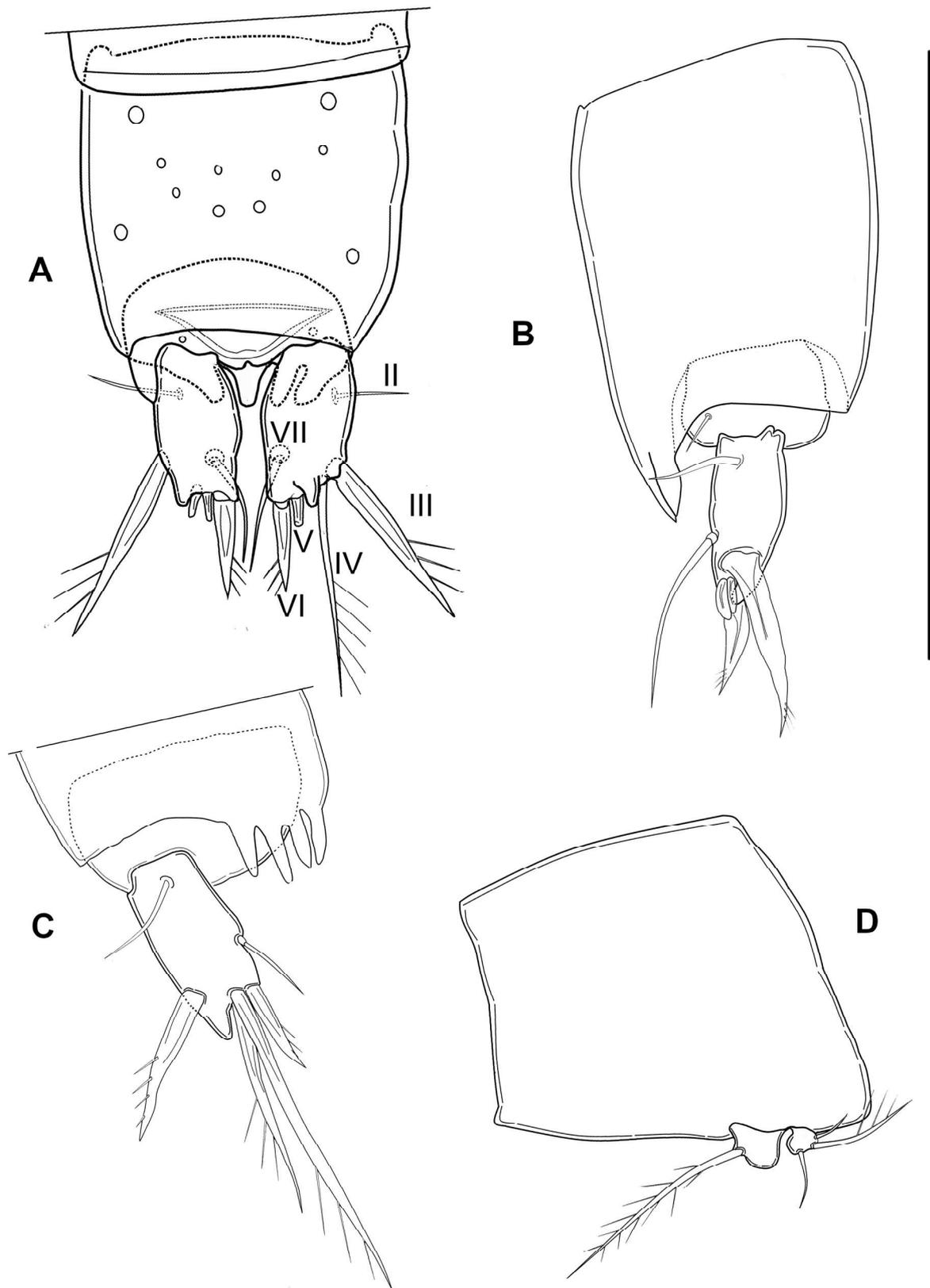
Spermatophore (Fig. 11D). Ellipsoidal, approximately as long as the somite carrying the P5.

**Variability.** In one female paratype the maxillary distal endite is longer and carries three setae instead of two (Fig. 9B). In a second female paratype the P5 exopod carries one seta less (Fig. 10B) and setae IV and V on the caudal rami are normally developed (Fig. 7C). In one male seta V is normal on the right caudal ramus, and extremely reduced on the left caudal ramus (Fig. 11F).

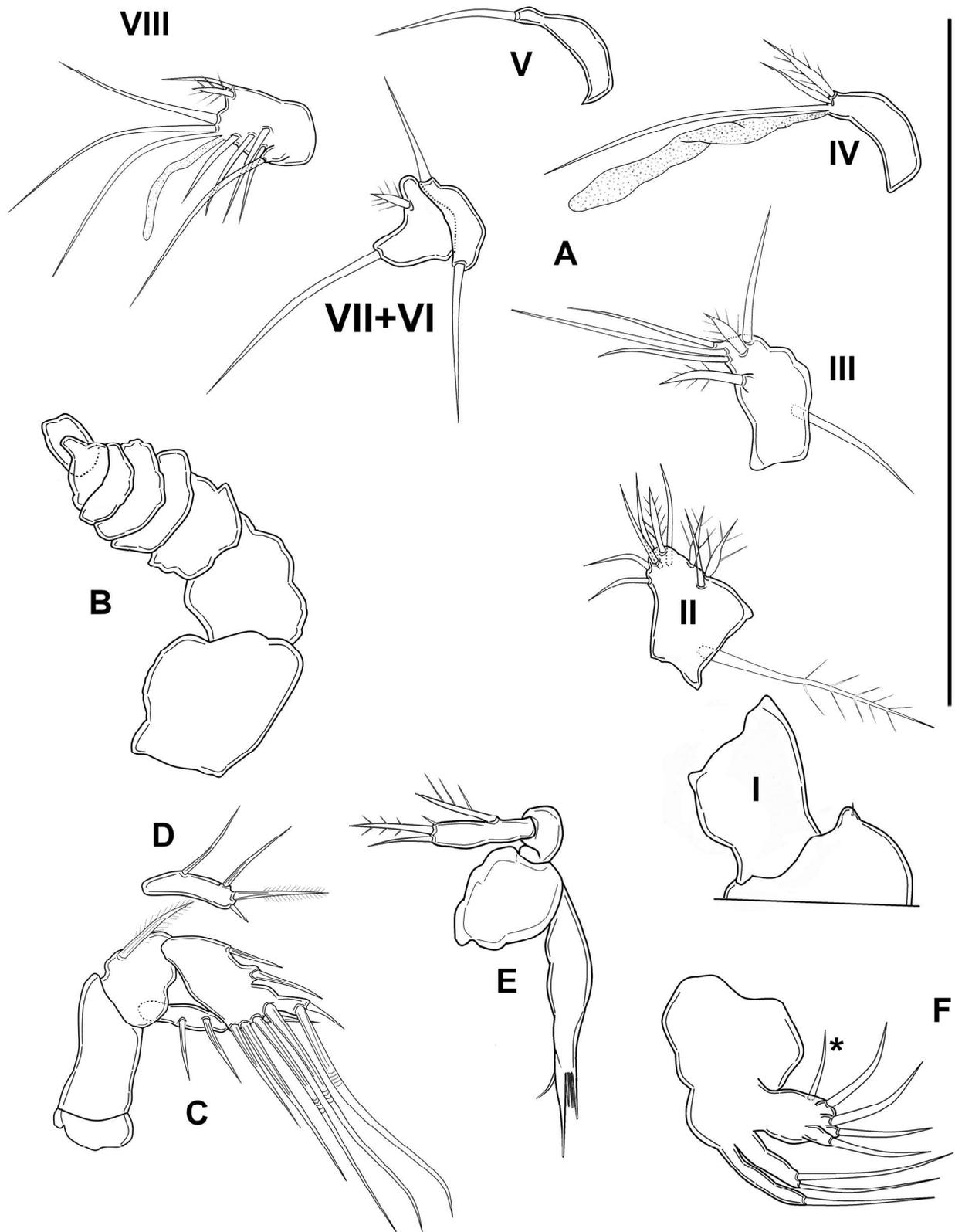
**Remarks.** Since the description of the new genus *Maliithipon* is based exclusively on morphological characters, *M. cf. aberrans* can be included in the new genus (Table 1). Females and males of *M. cf. aberrans* can be distinguished from those of *M. wellsi* **sp. nov.** by easily-observable characters, e.g. the caudal rami, P5 and P6. The distinction of *M. cf. aberrans* from *M. aberrans* **comb. nov.** is more difficult, mainly due to the lack of males in the type series of *M. aberrans*. As a consequence, the males collected in the Azores, initially listed as *A. aberrans* in Packmor *et al.* (2015) and Packmor & George (2016), cannot be compared with males of the type series, and could potentially belong to a different taxon. However, because the females collected in the Azores share the main discriminant features with *M. aberrans*, but differ in some minor features which are more difficult to observe (Table 1), we have chosen to be more conservative in the attribution of the taxonomic status to this population of *Maliithipon*, and not to follow Packmor *et al.* (2015) and Packmor & George (2016). The discovery of new populations, or the availability of new knowledge on the taxonomy of the existing populations (based for instance on scanning and/or confocal laser scanning microscopy; developmental study, molecular analysis) will hopefully allow to attribute a final taxonomic status to this taxon.



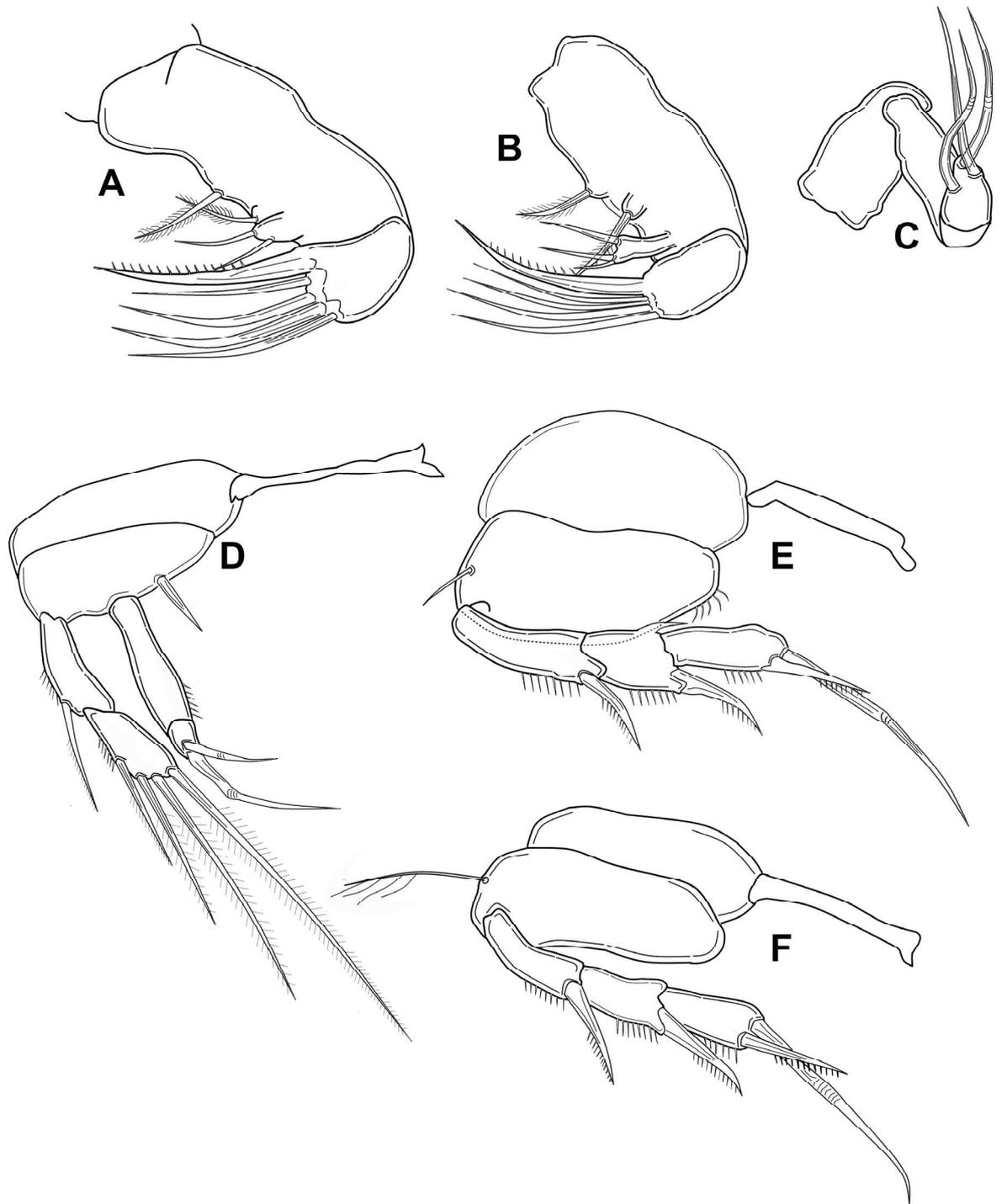
**FIGURE 6.** *Maliithipon cf. aberrans* (Mielke, 1984a) **comb. nov.** Female. A, habitus (cuticular ornamentation partly omitted). B, free thoracic somites, lateral. C, first urosomite, P5, genital double-somite, genital field, ventral. D, genital double-somite, ventral. Scale bar: 50  $\mu$ m.



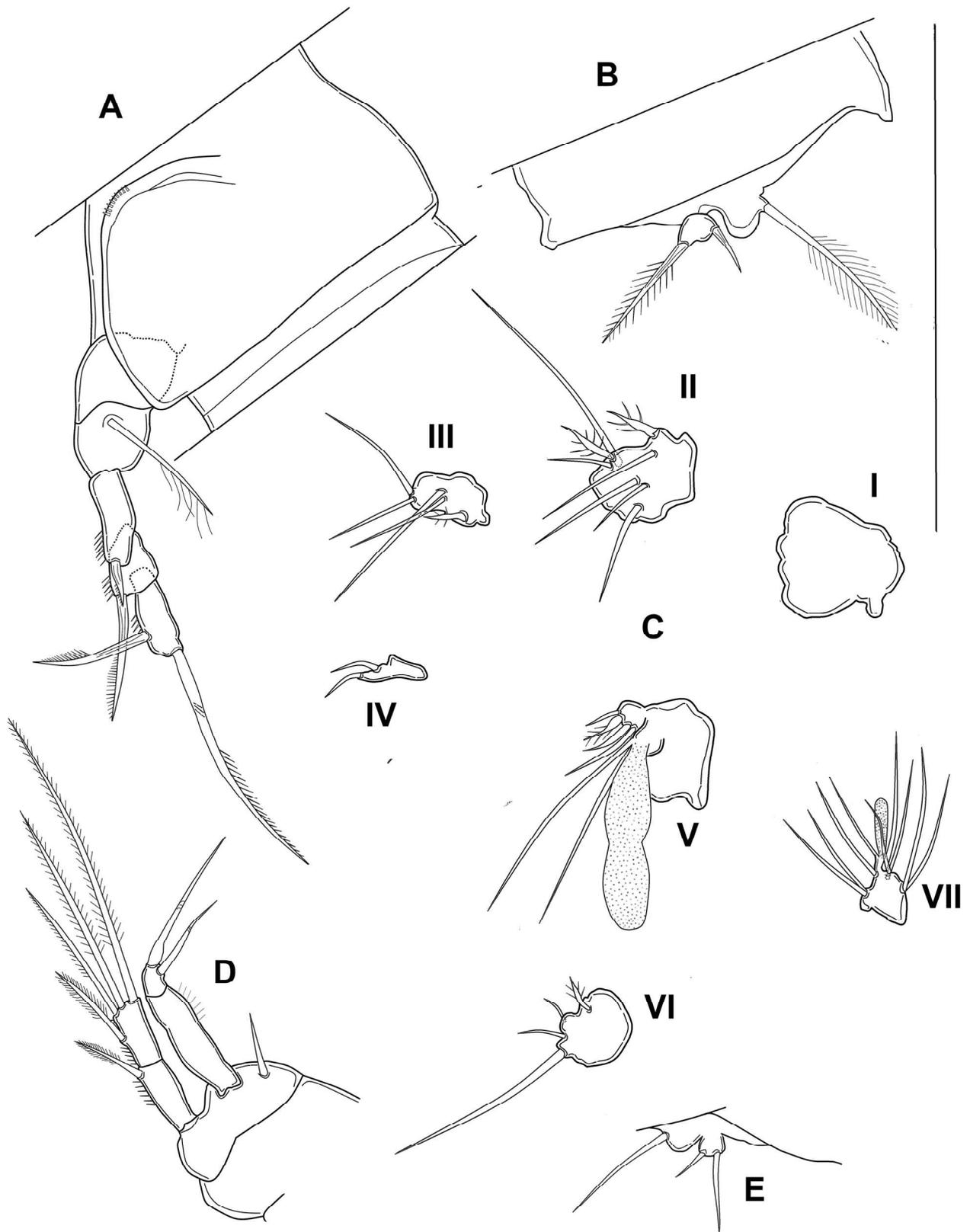
**FIGURE 7.** *Maliithipon* cf. *aberrans* (Mielke, 1984a) **comb. nov.** Female. A, last urosomite, anal somite, pseudoperculum, caudal rami, ventral (setae marked with Roman numerals). B, last urosomite, anal somite, pseudoperculum, caudal rami, lateral. C, anal somite, pseudoperculum, caudal rami, lateral (variability). D, P5 and first abdominal somite, lateral. Scale bar: 50  $\mu$ m.



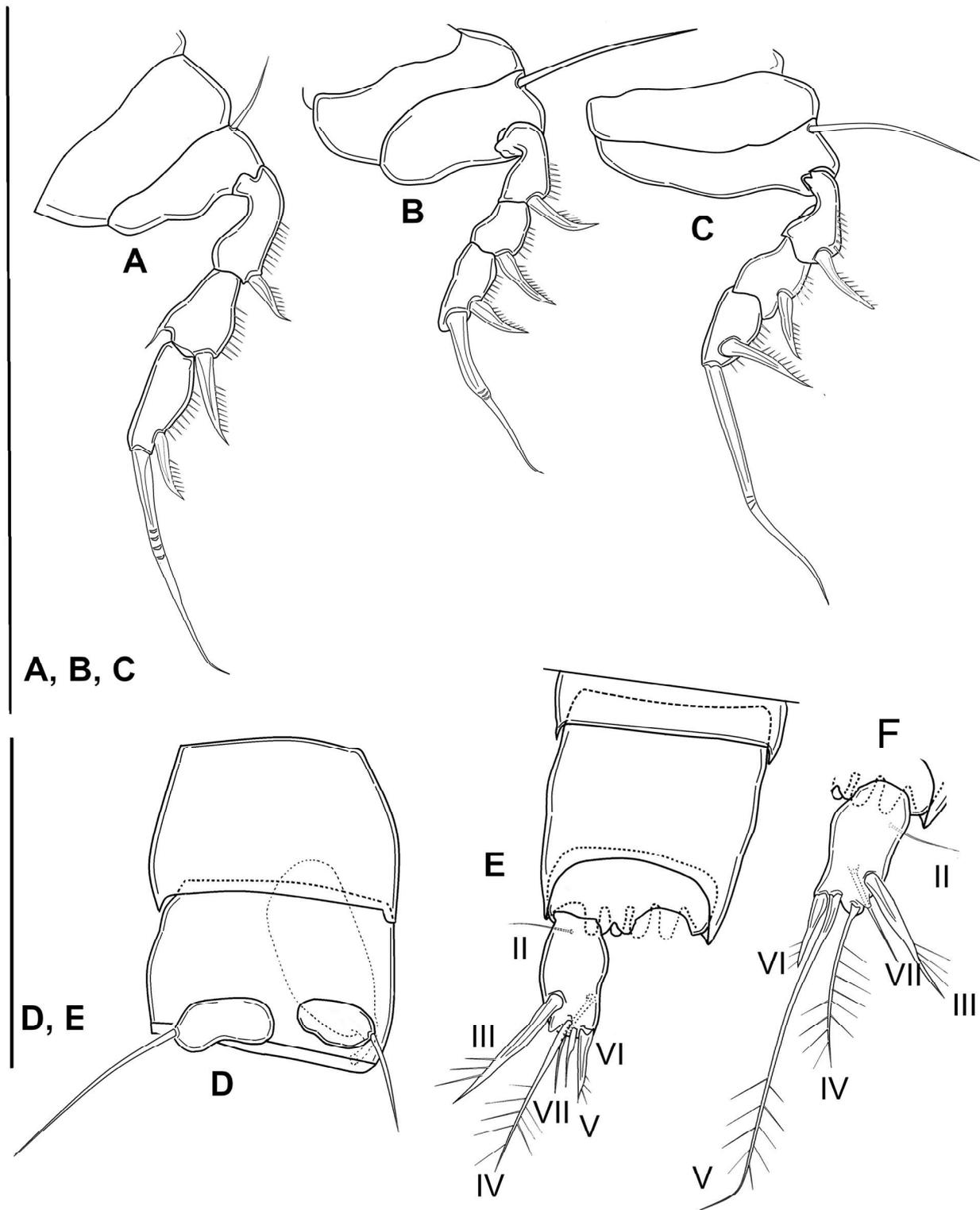
**FIGURE 8.** *Maliithipon cf. aberrans* (Mielke, 1984a) **comb. nov.** Female. A, rostrum and antennule, disarticulated (antennulary segments marked with Roman numerals). B, antennule, schematic. C, antenna. D, antennary exopod. E, mandible. F, maxillule. Scale bar: 50  $\mu$ m.



**FIGURE 9.** *Maliithipon* cf. *aberrans* (Mielke, 1984a) **comb. nov.** Female. A, maxilla. B, maxilla (variability). C, maxilliped. D, P1. E, P2. F, P3. Scale bar: 50  $\mu$ m.



**FIGURE 10.** *Maliithipon cf. aberrans* (Mielke, 1984a) **comb. nov.** A, female, third free thoracic somite and P4, lateral. B, female, P5 (variability). C, male, antennule, disarticulated (antennular segments marked with Roman numerals). D, male, P1. E, male, P5. Scale bar: 50 µm.



**FIGURE 11.** *Maliithipon cf. aberrans* (Mielke, 1984a) **comb. nov.** Male. A, P2. B, P3. C, P4. D, second and third urosomites, P6, spermatophore. E, anal somite, pseudoperculum, right caudal ramus, ventral (setae marked with Roman numerals). F, left caudal ramus, ventral (variability, setae marked with Roman numerals). Scale bar: 50  $\mu$ m.

**TABLE 1.** List of micro- and macro-characters differing among the three species. (\*) Numbers represent the number of setae on the proximal, middle and distal syncoxal endites, and on the endopod.

	<i>M. wellsi</i> <b>sp. nov.</b>	<i>M. aberrans</i> <b>comb. nov.</b> (male unknown)	<i>M. cf. aberrans</i> <b>comb. nov.</b>
A2 (both sexes)	exp-1 with 4 setae	exp-1 with 4 setae	exp-1 with 3 setae and 1 small spine
Md (both sexes)	basis with seta; endopod with 4 setae; cutting edge with 6 teeth	basis bare; endopod with 4 setae; cutting edge with 7 teeth	basis bare; endopod with 3 setae; cutting edge with 5 teeth
Mx1 (both sexes)	arthrite with 6 setae; basis with 2 setae; coxa with 1 seta	arthrite with 5 setae; basis with 3 setae; coxa with 2 setae	arthrite with 4 setae; basis with 1 seta; coxa with 2 setae
Mx (*) (both sexes)	1.1.2; 5	1.1.3; 6	1.1.2; 4
Mxp (both sexes)	enp 1-segmented, with 1 small spine and 3 setae	enp 2-segmented, distal segment with 3 setae	enp 1-segmented with 3 setae
P2 setal formula	basis: 0–0 (proximal inner row of hair-like spinules in females); exopod: 0, 0, 01I; endopod: missing	basis: 0–1; exopod: 0, 0, 01I; endopod: missing	basis: 0–1 (seta bare, proximal inner row of hair-like spinules in females); exopod: 0, 0, 01I; endopod: missing
P3 setal formula	basis: 0–1 (seta pinnate in females, bare in males); exopod: 0, 0, 01I; endopod: missing	basis: 0–1; exopod: 0, 0, 01I; endopod: missing	basis: 0–1 (seta pinnate in females, bare in males); exopod: 0, 0, 01I; endopod: missing
P4 setal formula	basis: 1–1 (seta pinnate in females, bare in males); exopod: 0, 0, 01I; endopod: missing	basis: 0–1; exopod: 0, 0, 01I; endopod: missing	basis: 1–1 (seta pinnate in females, bare in males); exopod: 0, 0, 01I; endopod: missing
P4 females	normal seta on exp-2	transformed spiniform seta on exp-2	transformed spiniform seta on exp-2
P5 females	one lobe with 1 seta	two separate lobes; baseoendopodal lobe with 1 seta, exopodal lobe round, with 3 setae	two fused lobes; baseoendopodal lobe with 1 seta, exopodal lobe subrectangular, with 3 setae
P5 males	small round lobe without armature		two lobes fused together and with the somite; baseoendopodal lobe with 1 seta, exopodal lobe subrectangular, with 2 setae
P6 males	two small unarmed lobes		two unequal small lobes, each one with 1 seta
CR (both sexes)	long, L/W = 2.7; no ventral cuticular outgrowth	short, L/W = 1.8; ventral cuticular outgrowth	very short, L/W = 1.1; ventral cuticular outgrowth

### Accompanying paramesochrid fauna

In station 1, the few specimens of *Maliithipon wellsi* **sp. nov.** were collected with numerous specimens of *Emertonia* sp. 1 (the most abundant paramesochrid in this station), and several specimens of *Emertonia* sp. 2 and *Apodopsyllus* sp. In station 2, *M. wellsi* **sp. nov.** was collected with numerous specimens of *Emertonia* sp. 2 (the most abundant paramesochrid in this station), *Apodopsyllus* sp., and a few specimens of *Leptopsyllus* sp. These are the first records for the Philippines of the genera *Emertonia* and *Leptopsyllus*.

Research on the presence and distribution of Paramesochridae along the coasts and sea of the Philippines has so far been scarce. The discovery of the new genus described herein strengthens the opinion that the large range of habitats (typically inhabited by members of this family) present in this country probably support a large number of still-unknown taxa. To expand the scarce published knowledge on paramesochrid biodiversity in the Philippines, we provide a preliminary list of the taxa collected in three more islands during 1995:

- 1) Mindoro Island: *Apodopsyllus* sp. 1 (intertidal, 3 m depth); *Apodopsyllus* sp. 2 (intertidal, 3 m depth); *Emertonia* sp. 1 (intertidal, 3 m depth); *Emertonia* sp. 2 (mesopsammal); *Emertonia* sp. 3 (mesopsammal); *Emertonia* sp. 4 (mesopsammal); *Paramesochra* sp. 1 (mesopsammal); *Wellsopsyllus* (*L.*) sp. 1 (intertidal, 3 m depth);
- 2) Siquijor Island: *Apodopsyllus* sp. 1 (intertidal, 2.5 m depth); *Apodopsyllus* sp. 2 (mesopsammal); *Emertonia* sp. 1 (intertidal, 2.5 m depth); *Emertonia* sp. 2 (intertidal, 2.5 m depth); *Emertonia* sp. 3 (mesopsammal); *Emertonia* sp. 4 (mesopsammal); *Emertonia* sp. 5 (mesopsammal); *Emertonia* sp. 6 (mesopsammal); *Leptopsyllus* (*L.*) sp. 1 (intertidal, 2.5 m depth); *Leptopsyllus* (*L.*) sp. 2 (mesopsammal); *Paramesochra* sp. 1 (mesopsammal); *Wellsopsyllus* (*L.*) sp. 2 (mesopsammal);
- 3) Sumilon Island: *Apodopsyllus* sp. 1 (mesopsammal); *Diarthrodella* sp. (mesopsammal); *Emertonia* sp. 1 (mesopsammal); *Emertonia* sp. 2 (mesopsammal).

We underline that *Emertonia* was the species-richest genus, an observation similar to that made by Back & Lee (2017b) for Korea. The genera *Paramesochra*, *Wellsopsyllus* and *Diarthrodella* are new records for the Philippines.

### Notes on the autecology and distribution

The reduced body size and the structure of the swimming legs in *Maliithipon* **gen. nov.** are typical of harpacticoids that are highly specialized for life in the interstitial habitat, *i.e.* animals which can easily move in the spaces between the substrate particles. Miniaturization is a well-known adaptation to such habitat (Delamare Deboutteville 1960); the species of this genus are among the smallest known free-living harpacticoids (*M. wellsii*: 331  $\mu\text{m}$  average length, *M. aberrans*: 303  $\mu\text{m}$ , *M. cf. aberrans*: 229  $\mu\text{m}$ ). The mouthparts are also transformed in this genus: the mandibular palp segmentation and armature are reduced while the gnathobase is highly specialized, being provided apically with both strong tips and acuminate thin teeth. When the undissected animal is observed in ventral view, the small maxillules are almost completely covered by the large maxillae, suggesting a loss of functionality for the former, somewhat counterbalanced by the over-development of the latter. Although the maxillae are also simplified (reduced armature, basis structure, fused endopod), they probably are the functionally dominant mouthparts. The strong reduction and simplification of the P5 of *M. wellsii* are known for other harpacticoids which can completely lack these pereopods (*e.g.* *Simplicaris* Galassi & De Laurentiis, 2004 among groundwater Parastenocarididae) and could be caused by paedomorphic heterochronic events which are well-known for harpacticoids (Galassi *et al.* 2009). A further specialization could be represented by the caudal rami setae III and VI, which are transformed and stronger than normal setae (seta III is similarly transformed in *Emertonia coreana* Back & Lee, 2017b), and could help pushing the animal forward, or represent an anchoring/leverage structure. An analogous transformation of caudal setae has been reported in some Canthocamptidae that are specialized for life in the epikarst (Brancelj 2006, 2009), where these structures can provide anchorage of the animal to the substrate, preventing vertical drift. Cottarelli *et al.* (2012) reported the presence of an apical dorsal curved apophysis on the caudal rami of some epikarstic Parastenocarididae that could fulfil the same function. Such dorsal apophyses are present in *L. (L.) typicus* and *Biuncus ingens*, supporting the hypothesis of a functional role for the modification in the structure/armature of the caudal rami related to locomotion in the reduced space of the mesopsammic sediment, or the epikarstic microfractures. The peculiar morphology and size of the mouthparts in *Maliithipon* (*i.e.* morphology and armature of mandibular palp and cutting edge, simplified maxillules, claws and size of maxillae) hint at a peculiar trophic role of these species. The type species is apparently rare; in each of the collection sites in Isla Verde, the populations of *M. wellsii* **sp. nov.** had low densities, and only eight females and one male were collected overall, whereas all the other paramesochrids collected with the new species were abundant and both sexes were present in similar percentages.

The discovery of *M. wellsii* **sp. nov.** in the Indian Ocean widens the distribution of the genus, which was so far known restricted to the Pacific Ocean (Panama; Mielke 1984a) and the Atlantic Ocean (Azores; Packmor *et al.* 2015). One specimen of *M. aberrans* was also collected in Sant'Andrea beach, Elba Island, Mediterranean Sea (Werner 2006; Packmor *et al.* 2015), but the re-examination of these specimens was not possible, hence we suggest considering this record with caution.

If the geonemy of the genus is well-defined, the one of each species is not: if the populations from Panama

and the Azores (and Elba Island?) will prove to be attributable to the same taxon *M. aberrans*, this species would have a very vast distribution, ranging across two oceans and would support the theory of the “meiofaunal paradox” (Giere 2009) and the important role of seamounts and oceanic islands as staging post and stepping stones in the dispersal of harpacticoid copepods (Packmor *et al.* 2015). Following what is described by these authors, in fact, *M. aberrans* would be one of those taxa that prove the theory according to which “seamounts located within a critical dispersion distance from a shallow-water habitat play an important role as staging posts, supporting meiobenthic steady state dispersion”. If, on the contrary, *M. cf. aberrans* is a different and new taxon, the genus would have three representatives, each one in one different ocean. The systematic position of the Mediterranean “*Maliithipon aberrans*” strictly depends on the exact definition of the taxon from the Azores (it is more parsimonious to suppose that two geographically close populations belong to the same species) besides, obviously, the collection of new material from the same site.

In summary, *Maliithipon* **gen. nov.** is a genus with a wide distribution, known from few species, all of them characterized by low densities and spanandry. This could be due to an ongoing rarefaction and imminent extinction of the genus, but more likely these data are the result of the scarcity in collections for wide geographical areas. This is a recurring issue in systematic studies; it can be expected that new future research and sampling campaigns will increase the number of known taxa for this interesting copepod genus.

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## References

- Amorri, J., Veit-Köhler, G., Drewes, J. & Aïssa, P. (2010) *Apodopsyllus gabesensis* n. sp.: a new species of Paramesochridae (Copepoda: Harpacticoida) from the Gulf of Gabès (south-eastern Tunisia). *Helgoland marine Research*, 64, 191–203.  
<https://doi.org/10.1007/s10152-009-0178-3>
- Apostolov, A. & Marinov, T.M. (1988) Copepoda Harpacticoida (morski kharpaktikoidi). [Copepoda, Harpacticoida (marine harpacticoids)]. *Fauna Bolgarii [Fauna Bulgarica]*, 18, 1–384. [In Bulgarian]
- Back, J. & Lee, W. (2017a) Two new species of *Leptopsyllus* from Korea (Copepoda, Harpacticoida, Paramesochridae). *ZooKeys*, 665, 37–57.  
<https://doi.org/10.3897/zookeys.665.6150>
- Back, J. & Lee, W. (2017b) Two new species of the genus *Emertonia* Wilson, 1932 from Korean waters (Copepoda, Harpacticoida, Paramesochridae). *ZooKeys*, 718, 35–64.  
<https://doi.org/10.3897/zookeys.718.19959>
- Boxshall, G.A. & Halsey, S.H. (2004) *An Introduction to Copepod Diversity*. The Ray Society, London, 966 pp.
- Božić, B. (1964) *Tisbisoma spinisetum* n. gen., n. sp., Copépode Harpacticoidé de la Réunion. *Bulletin de la Société zoologique de France*, 89, 219–225.
- Brancelj, A. (2006) The epikarst habitat in Slovenia and the description of a new species. *Journal of natural History*, 40, 403–413.  
<https://doi.org/10.1080/00222930600646608>
- Brancelj, A. (2009) Fauna of an unsaturated karstic zone in Central Slovenia: two new species of Harpacticoida (Crustacea: Copepoda), *Elaphoidella millennii* n. sp. and *E. tarmani* n. sp., their ecology and morphological adaptations. *Hydrobiologia*, 621, 85–104.  
<https://doi.org/10.1007/s10750-008-9634-3>
- Cottarelli, V., Bruno, M.C., Spena, M.T. & Grasso, R. (2012) Studies on subterranean copepods from Italy, with descriptions of two new epikarstic species from a cave in Sicily. *Zoological Studies*, 51, 556–82.
- Cottarelli, V. & Forniz, C. (1994) *Meiopsyllus marinae*: a new genus and a new species of Paramesochridae from the meiobenthos of Asinara and S. Pietro Islands (Sardinia). *Annali Museo Civico Storia naturale Giacomo Doria*, 90, 577–589.
- Delamare Deboutteville, C. (1960) *Biologie des eaux souterraines littorales et continentales*. Hermann, Paris, 740 pp.
- Galassi, D.M.P. & De Laurentiis, P. (2004) Towards a revision of the genus *Parastenocaris* Kessler, 1913: establishment of *Simplicaris* gen. nov. from groundwaters in central Italy and review of the *P. brevipes*-group (Copepoda, Harpacticoida, Parastenocarididae). *Zoological Journal of the Linnean Society*, 140, 417–436.

- <https://doi.org/10.1111/j.1096-3642.2003.00107.x>
- Galassi, D.M.P., Huys, R. & Reid, J.W. (2009) Diversity, ecology and evolution of groundwater copepods. *Freshwater Biology*, 54, 691–708.
- <https://doi.org/10.1111/j.1365-2427.2009.02185.x>
- Giere, O. (2009) *Meiobenthology. The Microscopic Motile Fauna of Aquatic Sediments. 2<sup>nd</sup> Edition*. Springer-Verlag, Berlin and Heidelberg, 548 pp.
- Huys, R. (1987) *Paramesochra* Scott, T. 1892 (Copepoda, Harpacticoida) – a revised key, including a new species from the SW Dutch coast and some remarks on the phylogeny of the Paramesochridae. *Hydrobiologia*, 144, 193–210.
- <https://doi.org/10.1007/BF00005554>
- Huys, R. (1995) A new genus of Paramesochridae (Copepoda: Harpacticoida) from *Amphioxus*-sand, Elat, Israel. *Journal of natural History*, 29, 673–684.
- <https://doi.org/10.1080/00222939500770231>
- Huys, R. (1996) *Biuncus* nom. nov., a replacement name for *Singularia* Huys, 1995 (Copepoda: Harpacticoida: Paramesochridae). *Journal of natural History*, 30, 1261.
- <https://doi.org/10.1080/00222939600770691>
- Huys, R. (2009) Unresolved cases of type fixation, synonymy and homonymy in harpacticoid copepod nomenclature (Crustacea: Copepoda). *Zootaxa*, 2183 (1), 1–99.
- <https://doi.org/10.11646/zootaxa.2183.1.1>
- Huys, R., Gee, J.M., Moore, C.G. & Hamond, R. (1996) *Synopses of the British Fauna (New Series) No. 51. Marine and brackish water harpacticoid copepods. Part I*. Field Studies Council, Shrewsbury, 352 pp.
- Klie, W. (1929) Die Copepoda Harpacticoida der südlichen und westlichen Ostsee mit besonderer Berücksichtigung der Sandfauna der Kieler Bucht. *Zoologische Jahrbücher, Systematik*, 57, 329–386.
- Klie, W. (1949) Harpacticoida (Cop.) aus dem Bereich von Helgoland und der Kieler Bucht. 1. *Kieler Meeresforschungen*, 6, 1–40.
- Kottmann J., Kihara, T.C., Glatzel, T. & Veit-Köhler, G. (2013) A new species of *Wellsopsyllus* (Copepoda, Harpacticoida, Paramesochridae) from the deep Southern Ocean and remarks on its biogeography. *Helgoland marine Research*, 67, 33–48.
- <https://doi.org/10.1007/s10152-012-0302-7>
- Kunz, H. (1962) Revision der Paramesochridae (Crust. Copepoda). *Kieler Meeresforschungen*, 18, 245–257.
- Kunz, H. (1975) Copepoda Harpacticoida aus dem Litoral des südlichen Afrika. I. Teil. *Kieler Meeresforschungen*, 31, 179–212.
- Kunz, H. (1981) Beitrag zur Systematik der Paramesochridae (Copepoda, Harpacticoida) mit Beschreibung einiger neuen Arten. *Mitteilungen aus dem Zoologischen Museum der Universität Kiel*, 1 (8), 2–33.
- Kunz, H. (1992) Beitrag zur Kenntnis mariner Copepoda Harpacticoida (Fam. Paramesochridae Lang) mit Beschreibung zweier neuer Arten und einer neuen Unterart. *Crustaceana*, 62, 85–97.
- <https://doi.org/10.1163/156854092X00073>
- Lang, K. (1944) *Monographie der Harpacticiden (Vorläufige Mitteilung)*. Almqvist & Wiksells, Uppsala, 39 pp.
- Mielke, W. (1984a) Einige Paramesochridae (Copepoda) von Panama. *Spixiana*, 7, 217–243.
- Mielke, W. (1984b) Interstitielle Fauna von Galapagos. XXXI. Paramesochridae (Harpacticoida). *Microfauna marina*, 1, 63–147.
- Packmor, J. & George, K.H. (2016) Littoral Harpacticoida (Crustacea: Copepoda) of Madeira and Porto Santo (Portugal). *Journal of the marine biological Association of the United Kingdom*, 98, 171–182.
- <https://doi.org/10.1017/S0025315416001168>
- Packmor, J., Müller, F. & George, K.H. (2015) Oceanic islands and seamounts as staging posts for Copepoda Harpacticoida (Crustacea)—Shallow-water Paramesochridae Lang, 1944 from the North-East Atlantic Ocean, including the redescription of three species and one subspecies from the Madeiran Archipelago. *Progress in Oceanography*, 131, 59–81.
- <https://doi.org/10.1016/j.pocean.2014.11.012>
- Sars, G.O. (1903) Copepoda Harpacticoida. Parts I & II, Misophriidae, Longipediidae, Cerviniidae, Ectinosomidae (part). *An account of the Crustacea of Norway, with short Descriptions and Figures of all the Species*, 5, 1–28, pls. I–XVI.
- Scott, T. (1892) Additions to the fauna of the Firth of Forth. Part IV. *Reports of the Fishery Board for Scotland, Edinburgh*, 10 (3), 244–272.
- Scott, T. (1894) Additions to the fauna of the Firth of Forth. Part VI. *Reports of the Fishery Board for Scotland, Edinburgh*, 12 (3), 231–271.
- Soyer, J. (1975) Harpacticoides (Crustacés Copépodes) de l'archipel de Kerguelen. I. Quelques formes mésopsammiques. *Bulletin du Muséum national d'Histoire naturelle, Paris, Series 3*, 244 (= Zoologie, 168), 1169–1223.
- Vasconcelos, D.M., Veit-Köhler, G., Drewes, J. & Santos, P.J.P. (2009) First record of the genus *Kliopsyllus* Kunz, 1962 (Copepoda Harpacticoida, Paramesochridae) from Northeastern Brazil with description of the deep-sea species *Kliopsyllus minor* sp. nov. *Zootaxa*, 2096 (1), 327–337.
- <https://doi.org/10.11646/zootaxa.2096.1.19>
- Veit-Köhler, G. (2004) *Kliopsyllus andeep* sp. n. (Copepoda: Harpacticoida) from the Antarctic deep sea—a copepod closely related to certain shallow-water species. *Deep-Sea Research II*, 51, 1629–1641.

- <https://doi.org/10.1016/j.dsr2.2004.06.027>
- Veit-Köhler, G. (2005) First deep-sea record of the genus *Kliopsyllus* Kunz, 1962 (Copepoda: Harpacticoida) with the description of *Kliopsyllus diva* sp. n.—the most abundant member of Paramesochridae at two different sites of the Angola Basin. *Organisms, Diversity and Evolution*, 5, 29–41.  
<https://doi.org/10.1016/j.ode.2004.10.003>
- Walter, T.C. & Boxshall, G. (2019) World of Copepods database. Paramesochridae Lang, 1944. World Register of Marine Species. Available from: <http://www.marinespecies.org> (accessed 6 May 2019)
- Wells, J.B.J. (1967) The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. *Transactions of the Royal Society of Edinburgh*, 67 (7), 189–358.  
<https://doi.org/10.1017/S0080456800024017>
- Wells, J.B.J. (2007) An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea). *Zootaxa*, 1568 (1), 1–872.  
<https://doi.org/10.11646/zootaxa.1568.1.1>
- Werner, A.R. (2006) Vergleich von Abundanzen und Tiefenverteilung der Meiofauna, im Speziellen der Harpacticoida (Copepoda, Crustacea), in sublitoralen Kalk- und Quarzsedimenten (Mittelmeer). Diploma thesis, Carl von Ossietzky Universität Oldenburg, Oldenburg, Lower Saxony, 69 pp.
- Wilson, C.B. (1932) The copepods of the Woods Hole region, Massachusetts. *Bulletin of the United States National Museum*, 158, 1–635.  
<https://doi.org/10.5479/si.03629236.158.i>