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New Macrostylidae Hansen, 1916 (Crustacea: Isopoda) from the Gay Head-Bermuda transect with special consideration of sexual dimorphism

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Abstract

In the Asellota, sexual dimorphism is often characterized by males that show pronounced morphological differences after the final moult compared to females but also to sub-adult males. Such a sexual dimorphism may strongly complicate allocation of these terminal males to conspecifics. Consequently, we regard it to be a likely explanation for why in 50% of the described species of the family Macrostylidae Hansen, 1916, only one sex is known. Based on detailed description of two previously unknown species of the isopod genus *Macrostylis* Sars, 1864, the changes in the morphology that can occur during the final moult of the males are highlighted. *M. dorsaetosa* n. sp. is unlike any other species owing to the row of spine-like setae on the posterior margins of pereonites 5–6. *M. strigosa* Mezhov, 1999 shows remarkable similarity but lacks these setae. In *M. papillata* n. sp., cuticular ridges overlap posteriorly with the margin of the pereonites 1–4 and head forming a warty appearance. This species is easily identifiable and unlike any previously described macrostylid owing to the presence of the tergal articulation between pleonite 1 and pleotelson. Information for the identification of terminal males is provided and implications of our results for future taxonomic and systematic work on this isopod family are discussed.

Key words: Janiroidea, deep sea, benthos, bathyal, abyssal, North Atlantic, DELTA, SEM, new species

Introduction

The phenomenon of sexual dimorphism occurs widely among the animal kingdom. Its evolution is driven by both sexual selection due to mating preferences or competition for mates and natural selection (Darwin 1874; Lande 1980). Sexual dimorphism is common among isopod crustaceans (e.g., Veuille 1980; Jormalainen & Merilaita 1995; Lefebvre *et al.* 2000) and also among deep-sea asellotes (e.g., Svavarsson 1984; Wilson 2008a; Brökeland 2010; Riehl & Brandt 2010). In Asellota, sexual dimorphism is often characterized by mature males showing strong morphological differences when compared to sub-adult males and females only after the final moult.

Since the first description of a species belonging to the deep-sea isopod family Macrostylidae by G.O. Sars (1864), 80 species have been formally described (Riehl & Brandt 2010). 50% of these have been based on only one sex and often (22 species, i.e., 17.6%) only on a single specimen. Observations of behavior (Hessler & Strömberg 1989), morphological characteristics (Thistle & Wilson 1987), as well as sampling evidence (Hessler & Sanders 1967; Wilson 2008b) suggest an infaunal lifestyle for macrostylids. Therefore, macrostylids have probably been undersampled by epibenthic apparatus often used in deep-sea research. Low numbers of specimens available in the samples have been a frequent impediment to their description. Males tend to be especially rare compared to females (personal observation) and this might explain the above mentioned numbers. The morphological evidence presented here suggests that another explanation for descriptions based on only one sex (at least in some cases) can be found in a pronounced sexual dimorphism. Substantial morphological differences may strongly complicate allocation of conspecifics.

The terminal-male concept will be introduced to macrostylid taxonomy in this article. Based on two new species, *Macrostylis dorsaetosa* n. sp. and *M. papillata* n. sp., the changes in the morphology that occur during the

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final moult of the males, especially of the antennulae, are described. Implications for future taxonomic and systematic work on this isopod family and the potential meaning of the sexual dimorphism for the ecology and evolution of Macrostylidae are discussed.

Material & methods

Specimens were collected during the Gay Head–Bermuda transect project (Sanders & Hessler 1969) of the Woods Hole Oceanographic Institution by two different types of gear. Station GH#1 and GH#4 were sampled during the cruise RV Atlantis 273 by means of an Anchor Dredge (Sanders *et al.* 1965). An epibenthic sled (Hessler & Sanders 1967) was deployed at stations WHOI 62 (RV Atlantis II cruise 12), WHOI 121 and WHOI 122 (both RV Atlantis II cruise 24). Specimens were originally fixed in formaldehyde, then preserved and sorted in 70% ethanol. For habitus drawings and dissections of limbs, specimens were transferred into a glycerine-70% ethanol solution (approximately 1:1), and subsequently transferred into glycerine. For illustrations, temporary slides were used following Wilson (2008a). Line drawings were made using an Olympus BH-2 compound microscope fitted with interference-contrast optics and camera lucida. Vector-graphics software was applied (*Inkscape* ver. 0.48 and *Adobe Illustrator* ver. CS4) according to the methods described by Coleman (2003, 2009). Figures were prepared either using *GIMP 2* or *Adobe Photoshop* (ver.CS4). A stage micrometer was used for calibration. Measurements were made from line drawings and are presented as ratios to normalize differences in body size. Where several specimens were used for measurement, ranges are displayed. Measurements were made following Hessler (1970) and using the distance measurement tool imbedded in *Adobe Acrobat Professional*. We use the term subequal to mean ‘within 5% of a measurement’ as described by Kavanagh and Wilson (2007). All appendages article-length ratios are given in proximal to distal order, excluding setae. Descriptions of pereopodal setae (e.g., type, shape and location) are listed in proximal-to-distal and lateral-to-medial order.

Body lengths are given excluding appendages, appendage lengths excluding setae. Terminology is based on Hessler (1970) and Wilson (1989). Setal nomenclature follows Hessler (1970) and Riehl and Brandt (2010) with some modifications for reasons of style and consistency with other sources. The body region “fossosome” is defined as a hardening and fusion of the anterior pereonites 1–3 with a spade-like head inserting into the first pereonite; this apomorphy of the Macrostylidae is presumed to be an adaptation for burrowing (Thistle & Wilson 1987; Hessler & Strömberg 1989). One- and two-sided serrate setae (Riehl & Brandt 2010) are called here mono- and biserrate, unequally bifid setae are simplified as bifid and the setal type bisetulate is introduced for Macrostylidae for the first time. The latter setal type bears two rows of setules apically on opposite sides of the setal shaft. It can be found on all pereopods (Figs 9–10). The terms ‘antennula’ and ‘maxillula’ are preferred over but synonymous to ‘antenna 1’ and ‘maxilla 2’ (Wilson 2009). We introduce a new term, the “pereonal collum”, to describe the shape of the pereonites of macrostylid species. The collum, a Latin term meaning “neck”, refers to a constricted region anterior to the widest section of the pereonite where the preceeding segment over-rides the narrowed anterior region of a segment. Although the collum is present to a degree on pereonites 4–7 posterior to the fossosome, it is most strongly developed on pereonite 4, and is referred to in the descriptions.

Final permanent slides were assembled using *Euparal*. For SEM of whole specimens and fragments methods according to Cunha & Wilson (2006) were applied. An *Evo LS15 Carl Zeiss* microscope was used. The SEM stubs are retained at the Australian Museum (see Materials Examined below). Accession numbers begin with “AM P” and SEM stub numbers have a “MI” prefix.

Descriptions were generated using the taxonomic database system DELTA (Dallwitz 1980). For holotypes, female specimens were chosen and the descriptions are mainly based upon female characters for reasons of applicability (females are more abundant and therefore more easily accessible). Nevertheless, subadult and terminal male specimens were studied extensively. Terminal male characters are described were character states differ from those of the female. Through the description of the latter, a more complex (but also more complete) description could be achieved. In the following descriptions, a great deal of space is devoted to the description of setae on the limbs. The distribution of setae in the Macrostylidae has been found to be essential for identifying species. As a result of our findings, the setal details are a central component of macrostylid descriptions.

Implicit attributes

Unless indicated otherwise, the following attributes are implicit throughout the descriptions, except where the characters concerned are inapplicable.

Female. Body. Elongate. *Ventral spines.* Pereonite 1 spine present. Pereonite 2 spine absent. Pereonite 3 spine directed posteriorly. Pereonite 4 spine present. Pereonite 5–7 spine present. Marsupium with 2 pairs of oostegites. Developing oostegites in preparatory stage absent.

Cephalothorax. Articulation with pereonite 1 present. Posterolateral setae simple. Posterior margins papillae absent, setae absent. *Pereonite 1–2.* Posterolateral setae not on pedestals, posterior tergite margin papillae absent. *Pereonite 3.* Posterolateral margin not produced posteriorly; setae not on pedestals, posterior tergite margin papillae absent. *Pereonite 4.* Subequal to pereonite 5 width. Tergal plates laterally not projecting below coxal articulation and not obscuring view on coxae. Posterior tergite margin papillae absent, setae absent. Posterolateral margin not produced posteriorly. Posterolateral setae absent, not articulating on pedestals. *Pereonite 5.* Posterior tergite margin setulose. Posterolateral margin produced posteriorly. Tergite posterolateral setae present, flexibly articulated, not on pedestals. Coxae posterolateral setae absent, flexibly articulated, not on pedestals. *Pereonite 6.* Posterior tergite margin setae absent. Posterolateral margin similar in shape to pereonite 5. Tergite posterolateral setae present, not articulating on pedestals. Coxae posterolateral setae absent, not articulating on pedestals. *Pereonite 7.* Without posterolateral protrusions, similar to pereonites 5–6. Posterior tergite margin setae absent. Tergite posterolateral setae present, not on pedestals. Coxae posterolateral setae absent, not on pedestals.

Pleonite 1. Tergal articulation with pleotelson absent.

Antennula. Of 5 articles. All articles cylindrical. Article 2 present, shorter than article 1. Article 3 present, shorter than article 1. Article 4 present, shorter than article 1. Article 5 present, shorter than article 1. Article 6–9 absent. Terminal article aesthetascs present, penultimate and antepenultimate articles aesthetascs absent. *Antenna.* Of 5 podomeres. Article 3 squat, globular. Scale absent.

Mandibles. Palp absent. *Maxilliped.* With 2 receptaculi.

Pereopod I. Ischium dorsal margin with row of setae along dorsal ridge. Merus with dorsal row of setae along dorsal ridge. Articular plate on propodus present.

Pereopod II. Ischium with dorsal row of setae along dorsal margin. Merus with dorsal row of setae along dorsal margin. Articular plate present.

Pereopod III. Ischium with small simple seta proximo-dorsally, dorsal lobe present; proximally with setae; apex with prominent apical setae. Articular plate on propodus present.

Pereopod IV. Dactylus present.

Pereopod VII. Fully developed, all segments present.

Operculum (female pleopod II). With pappose setae terminally. *Pleopod III.* Exopod with plumose seta absent.

Uropod. Uniramous. Endopod of 1 article.

Terminal male

Body. Similar to female. *Ventral spines.* Similar to female on all pereonites. *Imbricate ornamentation (IO).* Cephalothorax, pereonites 1–7 and pleotelson IO as in female.

Cephalothorax. Dorsal setation as in female, posterior margins papillae absent, setae absent. *Fossosome.* Lateral tergite margins in dorsal view as in female, tergal plates laterally as in female. Ventrally as in female, sternite articulations as in female.

Pereonite 1–2. Posterolateral setae as in female, without pedestals. *Pereonite 3.* Posterolateral margins as in female, not produced posteriorly; setae as in female, without pedestals. *Pereonite 4.* Width/pereonite 5 width subequal to female, about as wide as pereonite 5, length/width ratio subequal in female and male. Lateral margins as in female; tergal plates laterally as in female; posterolateral margins rounded. Posterior tergite margin as in female, with setae absent. Posterolateral setae as in female, absent, without pedestals. *Pereonite 5.* Posterior tergite margin as in female, setae absent. Posterolateral margins as in female. Posterolateral setae on tergite as in female, present, without pedestals. Posterolateral setae on coxae absent. *Pereonite 6.* Posterior tergite margin as in female, setae absent. Posterolateral margins as in female, similar in shape to pereonite 5. Posterolateral setae on tergite as in female, present, flexibly articulating, without pedestals. Posterolateral setae on coxae absent, without pedestals. *Pereonite 7.* Similar in shape to pereonites 5–6. Posterior tergite margin as in female, setae absent. Posterolateral margins similar to female. Posterolateral setae on tergite as in female, present, without pedestals. Posterolateral setae on coxae absent, without pedestals.

Pleonite 1. Tergal articulation with pleotelson absent.

Pleotelson. Tergite dorsal surface in posterior view uniformly convex. Posterior apex as in female, setation as in female.

Antennula. Of 5 articles, with articles cylindrical, articles decreasing in size; terminal article with several aesthetascs, penultimate article with several aesthetascs, antepenultimate article with no aesthetascs.

Pereopod I. Length/body-length ratio similar female. Ischium with dorsal row of setae in normal position on dorsal ridge. *Pereopod II.* Length/body-length ratio as in female. Ischium with dorsal row of setae along dorsal margin. *Pereopod III.* Length/body-length ratio as in female. Ischium similar to female, with small simple seta proximo-dorsally, dorsal lobe present, proximally with row of setae; with one or two prominent apical setae. Merus setation and carpus setation as in female. *Pereopod IV.* Length/body-length ratio as in female. *Pereopod V.* Length/body-length ratio as in female; ischium setation as in female. *Pereopod VI.* Length/body-length ratio as in female.

Pleopod I. Distally with lateral horns.

Systematics

Asellota Latreille, 1802

Macrostylidae Hansen, 1916

Desmosomidae Sars, 1899
Macrostylini Hansen, 1916, p. 74; Wolff, 1956, p. 99
Macrostylinae Birstein, 1973
Macrostylidae Gurjanova, 1933, p. 411; Menzies, 1962, p. 28, p. 127; Wolff, 1962; Birstein, 1970; Menzies and George, 1972, p. 79–81; Mezhov, 1988, p. 983–994; 1992, p. 69; Brandt, 1992; 2002; 2004; Kussakin, 1999, p. 336; Riehl and Brandt, 2010

Type genus. *Macrostylis* Sars, 1864

Macrostylis Sars, 1864 (Monotypic)

Vana Meinert, 1890
Desmostylis Brandt, 1992

Type species. *Macrostylis spinifera* Sars, 1864

Gender. Female

Composition. See Riehl & Brandt, 2010

Macrostylis dorsaetosa n. sp.

(Figs 1–7)

Etymology. The species name 'dorsaetosa' is feminine and a shortened composition of three words: The first part is the prefix ‘dors-‘ derived from the Latin word 'dorsum'. The prefix is meant to provide position information regarding the second part, 'setae', owing to the presence of conspicuous setae dorsally on the posterior tergites. Finally, the greek suffix ‘-osis’ indicates the condition ‘dorsally setose’, which is the literal translation of the name.

Type fixation. Holotype: adult female, 2.6 mm, AM P.86000, designated here.

Type material examined. Holotype: non-ovigerous female, 2.6 mm, AM P.86000, used for the illustration of the habitus, WHOI 62. Paratypes: sub-adult male, 1.9 mm, AM P.86001, partly dissected for illustration of appendages, WHOI GH1; non-ovigerous female, 2.6 mm, AM P.86002, dissected for illustration of appendages and habitus, WHOI GH1; terminal male, 2.2 mm, AM P.86003, dissected for illustration of appendages, WHOI GH1; terminal male, 2.2 mm, AM P.86004, used for habitus illustration, WHOI 62; sub-adult male, 2.0 mm, AM P.86005, MI 633, gold-coated for SEM, WHOI 62; juvenile female, 1.9 mm, AM P.86006, MI 639, gold-coated for

SEM, WHOI 62; 14 specimens, AM P.86021, male and female, WHOI 62; 4 specimens, AM P.86025, male and female, WHOI GH4.

Type locality. Western North Atlantic off Long Island: 39°25.5'N; 70°35.0'W; 2500 m (WHOI GH #1); 39°28.8'N, 70°34.2'W; 2469 m (WHOI GH#4); 39°26'N; 70°33'W–39°27.2'N; 70°33.2'W; 2496 m (WHOI 62).

Type material — Remarks. Collected on North American slope off Long Island during cruise R/V Atlantis-273, stations WHOI GH1 (27. Septemember 1961) and WHOI GH4 (30. October 1961) and R/V Atlantis II-12, station WHOI 62 (21 August 1964), about 3.4 km apart.

Further records. WHOI G#1, 1 juvenile male (AM P86024); WHOI HH#3, 1 terminal male, AM P86026; WHOI 66, 1 non-ovigerous female, 1 manca, AM P98019; WHOI 128, 7 non-ovigerous females, AM P86007; WHOI 131, 12 specimen, male and female, AM P67257.

Description, female.

Body (Figs 1A, C, E, 6D, 7B). Length 2.6 mm, 6.5–6.9 width, subcylindrical, tergite surfaces with scattered setae. *Ventral spines.* Pereonite 1 spine acute, prominent. Pereonite 3–4 spine absent. Pereonite 5 spine acute, small, closer to posterior segment border. Pereonite 6 spine acute, prominent, closer to posterior segment border. Pereonite 7 spine small. *Imbricate ornamentation (IO).* Pereonite 4 IO in anterior region of tergite and sternite; pereonite 5–6 IO in anterior dorsal pereonal collum regions.

Cephalothorax. Length 0.82–0.90 width, 0.10–0.11 body length; frons in dorsal view straight, frontal ridge present, straight. Posterolateral setae present. Posterolateral margins blunt. *Fossosome.* Length 1.1–1.2 width, 0.16–0.18 body length. Lateral tergite margins in dorsal view forming almost uninterrupted line, ventral surface with keel, sternite articulations present. *Pereonite 1.* Anterior margin straight; posterolateral setae simple. *Pereonite 2.* Posterolateral setae simple. *Pereonite 3.* Posterolateral setae simple, flexibly articulated. *Pereonite 4.* Width 0.96–1.0 pereonite 5 width, length 0.65–0.90 width; pereonal collum present. Lateral margins in dorsal view curved, narrow in pereonal collum, widest in middle and slightly constricted anterior to posterolateral angles. Posterior tergite margin setae 8–9 altogether, bifid, robust, flexibly articulating, short, not extending beyond posterolateral margin. Posterolateral margins rounded. Posterolateral setae simple, not robust, flexibly articulated. *Pereonite 5.* Length 0.95–1.1 width. Posterior tergite margin setae 8 altogether, bifid, robust, flexibly articulating, long, extending beyond posterolateral margin. Posterolateral margins rounded. Tergite posterolateral setae bifid, robust. *Pereonite 6.* Length 0.90–0.97 width. Posterior tergite margin setae 8–9 altogether, bifid, robust, flexibly articulating, long, extending beyond posterolateral margin. Posterolateral margin produced posteriorly, rounded. Tergite posterolateral setae bifid, robust, flexibly articulated. *Pereonite 7.* Length 0.67–0.73 width. Posterior tergite margin setae 10–12 altogether, bifid, short, not extending beyond posterolateral margin. Posterolateral margin produced posteriorly. Tergite posterolateral setae bifid, robust, flexibly articulated.

Pleonite 1. Sternal articulation with pleotelson absent.

Pleotelson. Ovoid, length 0.21 body length, 1.6 width, narrower than pereonite 7; statocysts present, dorsal slot-like apertures absent. Posterior apex convex, bluntly rounded. Posterior apex setae 2 altogether, simple, positioned lateral to apex. Pleopodal cavity width 0.58 pleotelson width, preanal ridge width 0.42 pleotelson width. Anal opening subterminal, tilted posteriorly relative to frontal plane.

Labrum. Anterior margin in dorsal view concave.

Antennula (Fig. 2K–L). Length 0.41 head width, 0.25 antenna length, width 1.0 antenna width. Articles decreasing in size from proximal to distal. Article 1 distinctly longer than wide, longest and widest, with 2 simple setae. Article 2 distinctly longer than wide, tubular, with 2 simple setae. Article 3 squat, globular. Article 4 squat, globular. Article 5 minute, squat, globular, with 1 simple seta. Terminal article with 1 aesthetasc, penultimate article with 1 aesthetasc, aesthetascs simple, tubular.

Antenna (Fig. 2M–N). Length 0.2 body length. Article 1 squat, globular. Article 2 elongate, longer than article 1. Article 3 elongate, longer than article 1. Article 4 longer than articles 1–3 together, distally with 1 simple seta. Article 5 shorter than article 4, distally with 6 simple setae, distally with 1 broom seta. Flagellum with 5 articles.

Mandibles (Fig. 2A–D). In medial view strongly narrowing from proximal to distal, sub-triangular, with lateral setae; left mandible incisor process distal margin flattened and curved (shovel-like), with 3 cusps, lacinia mobilis grinding, with 4 cusps; right mandible incisior process with shovel-like appearance, with 3 cusps, lacinia mobilis grinding, clearly smaller than left lacinia, with 8 cusps.

Maxillula (Fig. 2F). Lateral lobe with 14 robust setae.

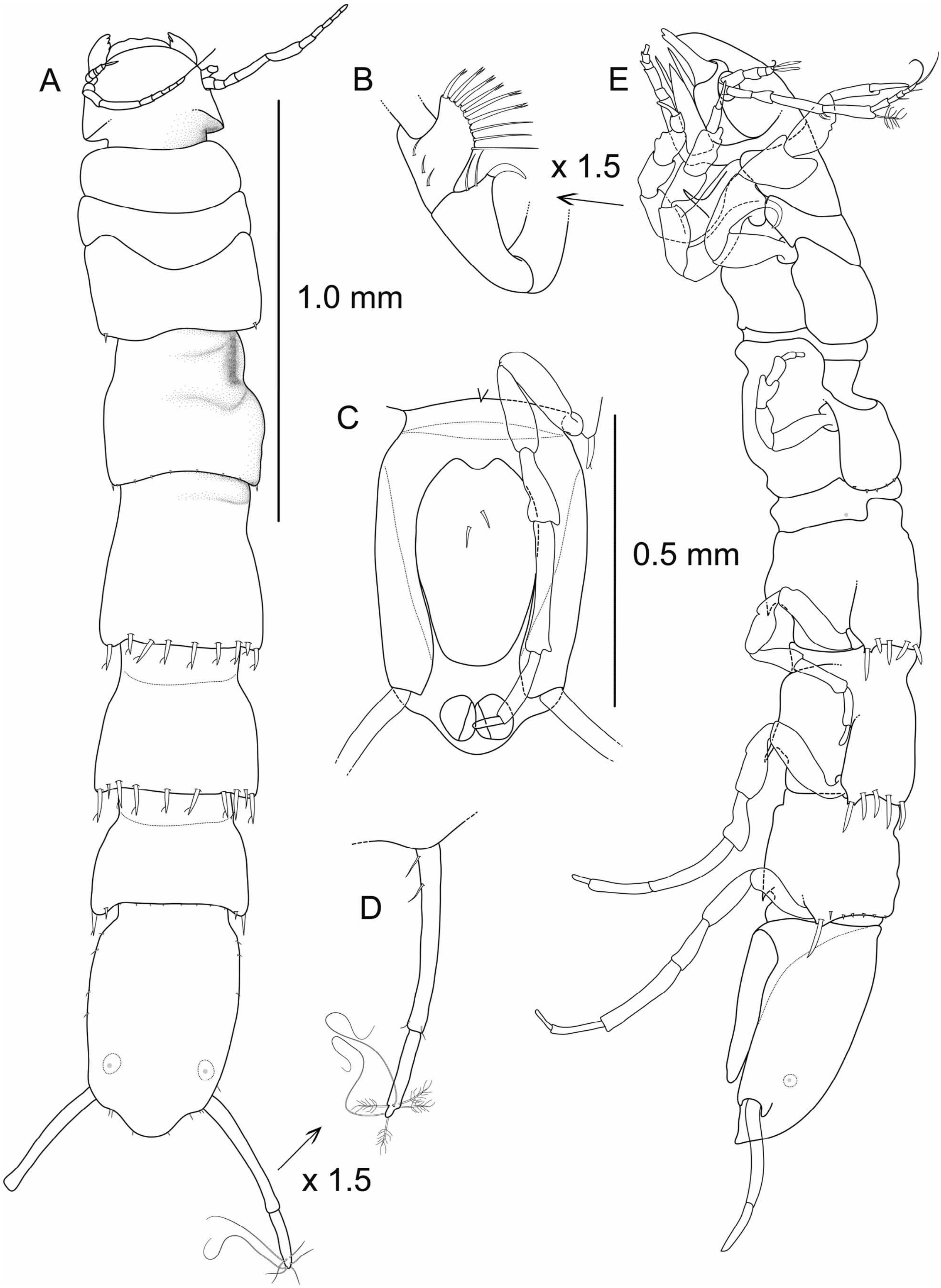

FIGURE 1. ***Macrostylis dorsaetosa*** **n. sp. A–E, holotype ♀ (AM P86000). A,** dorsal habitus, imbricate ornamentation and fine setation omitted. **B,** left pereopod III ischium, close-up. **C,** pleotelson, ventral. **D,** right uropod, close-up. **E,** lateral habitus. Scales: A, D–E = 1 mm, B–C = 0.5 mm.

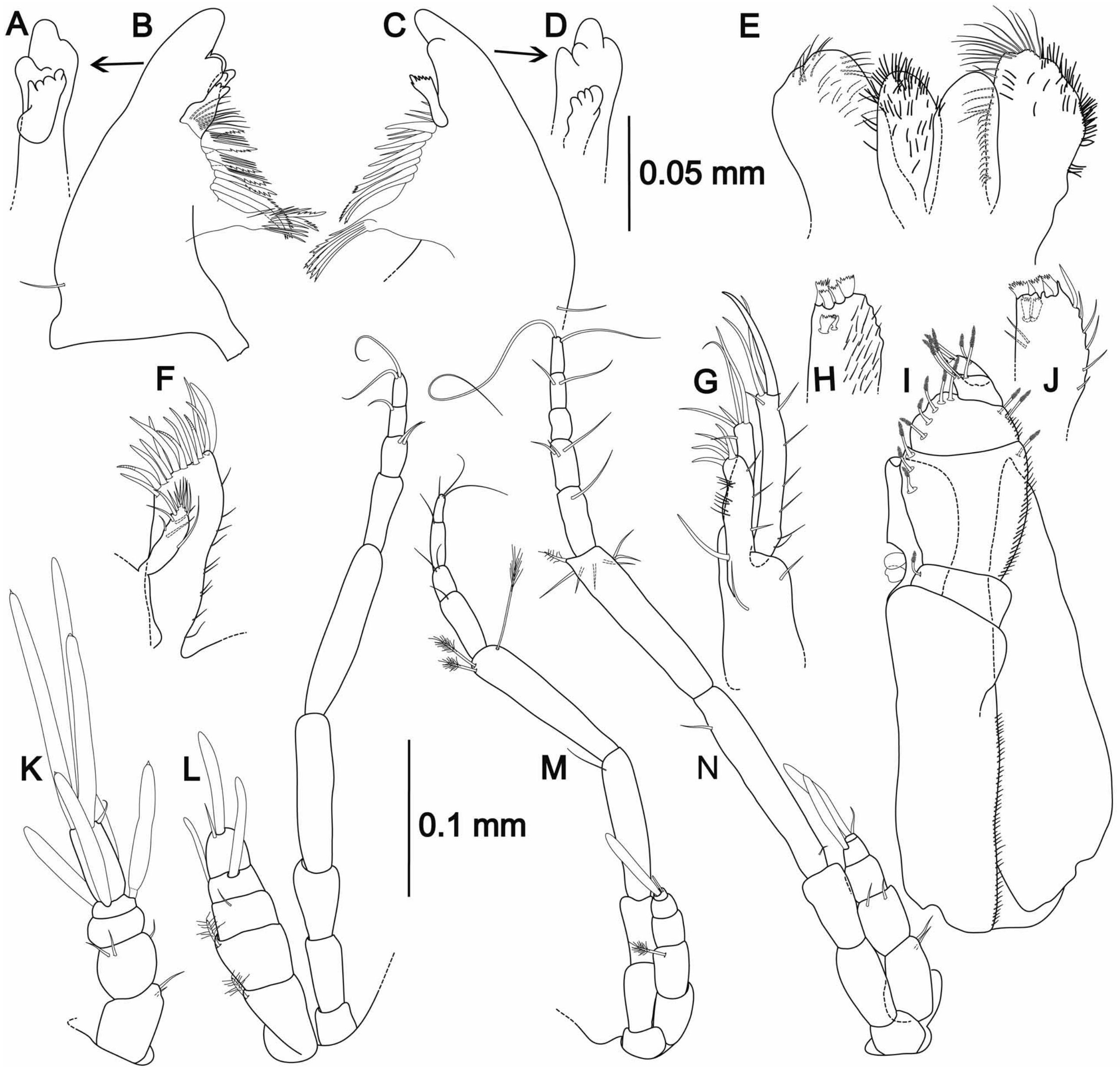

FIGURE 2. ***Macrostylis dorsaetosa*** **n. sp. A–C, E, N, paratype adult (non-ovigerous) ♀ (AM P86002). M, paratype juvenile ♀ (AM P86006). D, F–G, K, paratype terminal ♂ (AM P86003). L, paratype juvenile ♂ (AM P86005). A,** left mandible, medial view of incisor process and lacinia mobilis. **B,** left mandible, dorsal. **C,** right mandible, dorsal. **D**, right mandible, incisor process and lacinia mobilis, medial view. **E,** paragnaths, ventral view, ventral setae omitted in right lateral lobe, all setae omitted in left medial lobe, dorsal setae omitted in left lateral lobe. **F,** right maxillula, dorsal. **G,** left maxilla, ventral. **H,** left maxilliped, endite setation, ventral. **I,** left maxilliped, ventral. **J,** right maxilliped, endite setation, dorsal. **K** right antennula, lateral. **L** left antennula and antenna, lateral. **M,** right antennula and antenna, lateral. **N,** right antennula and antenna, lateral. Scales: A–J = 0.05 mm, K–N = 0.1 mm.

Maxilla (Fig. 2G). Lateral lobe with 4 setae terminally; middle endite with 3 setae terminally; inner endite with 8 setae terminally.

Maxilliped (Fig. 2H–J). Basis endite length 4.2 width; epipod length 4 width, 1.0 basis-endite length; palp wider than endite, article 2 wider than articles 1 and 3, article 1 shorter than article 3.

Pereopod I (Fig. 3A). Length 0.25 body length. Ischium dorsal margin with 5 setae, simple, in row, row of setae laterally to margin. Merus dorsal margin with 6 setae, 5 simple, 1 prominent, split, ventral margin with 4 setae, 3 biserrate, 1 split, with dorsal row of setae laterally to margin. Carpus dorsally with 3 setae, 2 simple, 1 prominent, split. Dactylus distally with 3 sensillae.

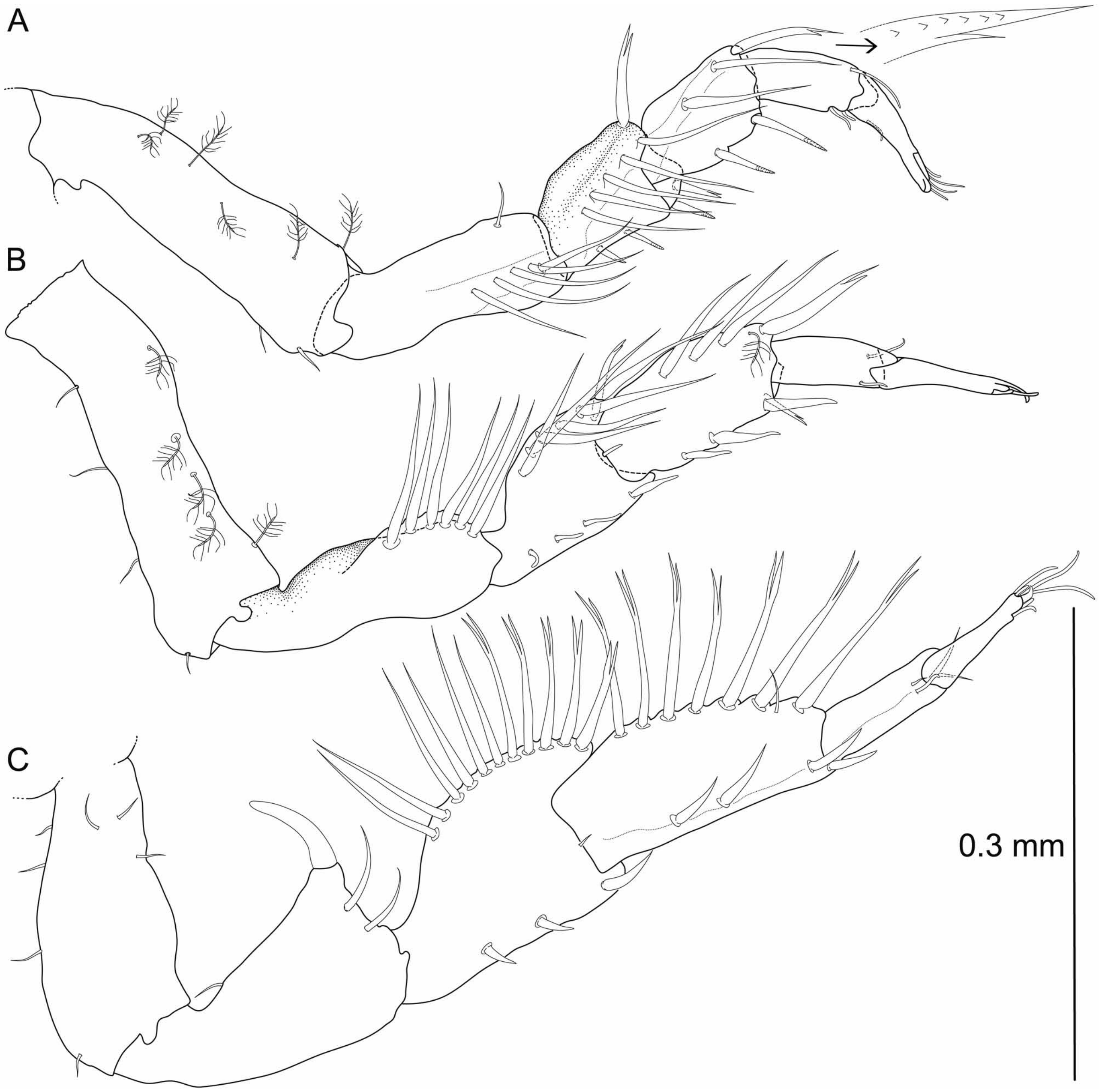

FIGURE 3. ***Macrostylis dorsaetosa*** **n. sp. A–C, paratype ♀ (AM P86002). A,** pereopod I, lateral, close-up of split and monoserrate seta. **B,** pereopod II, lateral. **C,** pereopod III, lateral. Scale = 0.3 mm.

Pereopod II (Fig. 3B). Longer than pereopod I, length 0.29 body length. Ischium dorsally with 6 setae, simple, with dorsal row of setae laterally to margin. Merus dorsally with 8 setae, 6 simple in row, 2 split disto-medially, with dorsal row of setae laterally to margin, ventrally with 4 setae, biserrate. Carpus dorsally with 5 setae, 3 simple, 1 broom, 1 prominent split, serrate, ventrally with 4 setae, 3 biserrate, 1 split. Dactylus distally with 3 sensillae.

Pereopod III (Fig. 3C). Length 0.26 body length. Ischium dorsal lobe tapering; proximally with no setae; apex with 1 prominent seta; apical seta robust, robust sensillate, bent towards proximal, spine-like; distally with 2 simple setae. Merus dorsally with 11 setae, 6 simple, 5 split, serrate, ventrally with 3 setae, biserrate. Carpus dorsally with 7 setae, split, serrate, ventrally with 4 setae, 3 biserrate, 1 split. Dactylus with 3 sensillae. *Pereopod IV (Fig. 4A).* Length 0.15 body length, carpus laterally flattened.

Pereopod V (Fig. 4B). Length 0.25 body length. Ischium mid-ventrally with 3 setae, simple, disto-ventrally with 3 setae, simple. Merus disto-dorsally with 4 setae, split, mid-ventrally with 3 setae, 1 split, 2 simple, disto-ventrally with 2 setae, 1 short, split, serrate, 1 long, simple. Carpus disto-dorsally with 3 setae, 1 split, 1 broom, 1 split, serrate, disto-ventrally with 3 setae, split.

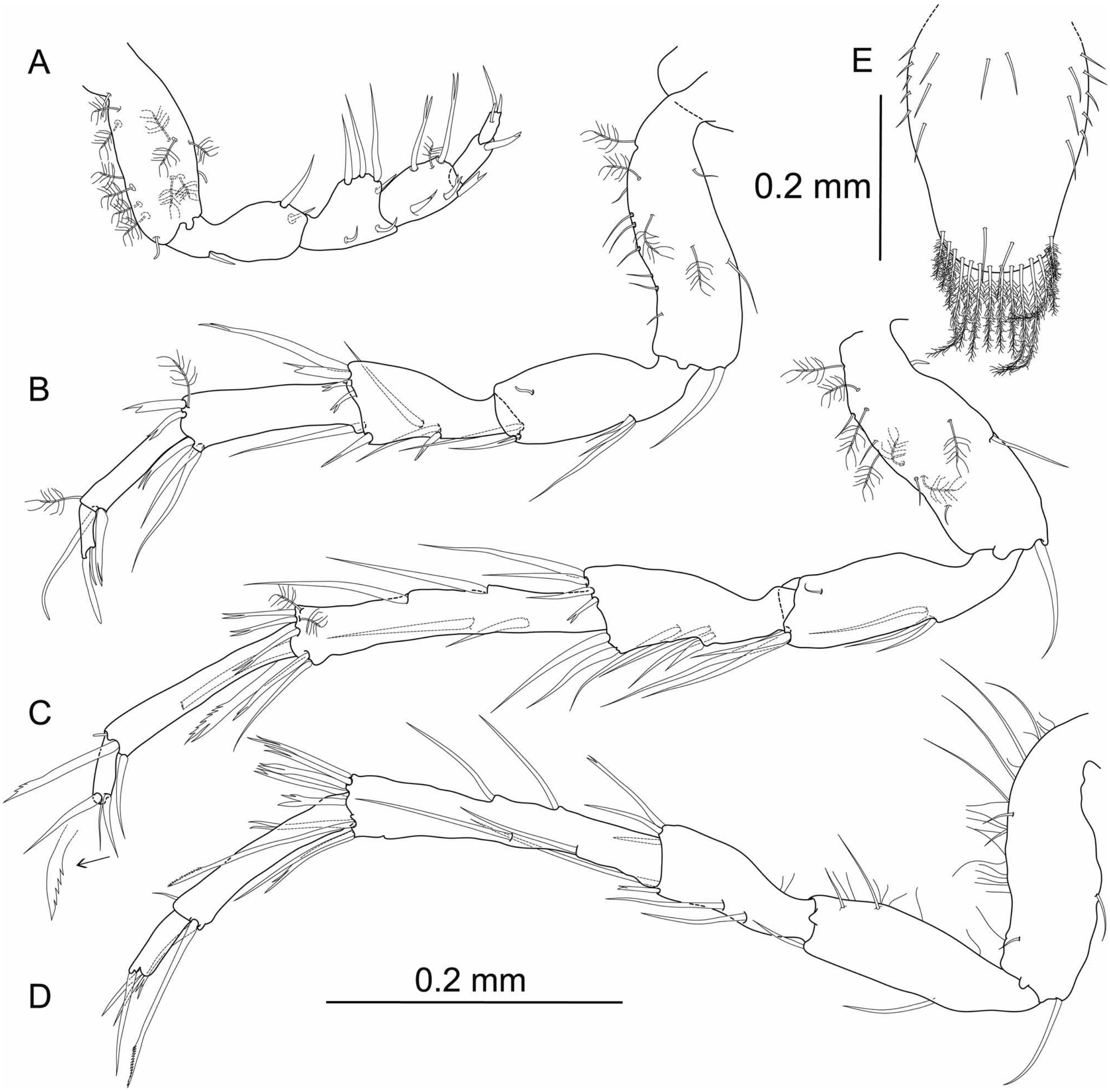

FIGURE 4. ***Macrostylis dorsaetosa*** **n. sp. A–E, paratype ♀ (AM P86002). A,** pereopod IV, posterior. **B,** pereopod V, lateral. **C,** pereopod VI, lateral. **D,** pereopod VII, lateral. **E,** operculum, ventral. Scales = 0.2 mm.

Pereopod VI (Fig. 4C). Length 0.32 body length; ischium mid-ventrally with 3 setae, simple, disto-ventrally with 3 setae, all simple; merus disto-dorsally with 4 setae, 2 short, split, 1 simple, 1 long split, mid-ventrally with 4 setae, simple, disto-ventrally with 2 setae; carpus mid-dorsally with 2 setae, simple, disto-dorsally with 5 setae, 1 split, 2 broom, 1 split, serrate, 1 split, mid-ventrally with 2 setae, simple, disto-ventrally with 4 setae, 2 split, 2 prominent, split, serrate.

Pereopod VII (Fig. 5D). Length less than pereopod VI length, 0.33 body length. Basis length 2.7 width; with row of elongate setae on posterior margin. Ischium length 3 width, mid-dorsally with 2 setae, simple, mid-ventrally with 1 seta, simple, disto-ventrally with 1 seta, simple. Merus length 2.2 width, disto-dorsally with 3 setae, 1 split, 2 simple, mid-ventrally with 2 setae, simple, disto-ventrally with 2, 1 simple, long, 1 split, short. Carpus length 5.5 width, mid-dorsally with 2 setae, simple, disto-dorsally with 5 setae, all split, possibly all serrate or biserrate, mid-ventrally with 2 setae, simple, disto-ventrally with 4 setae, 1 long, split, serrate, 1 simple, 2 split. Propodus length 4.3 width. Dactylus length 2.5 width.

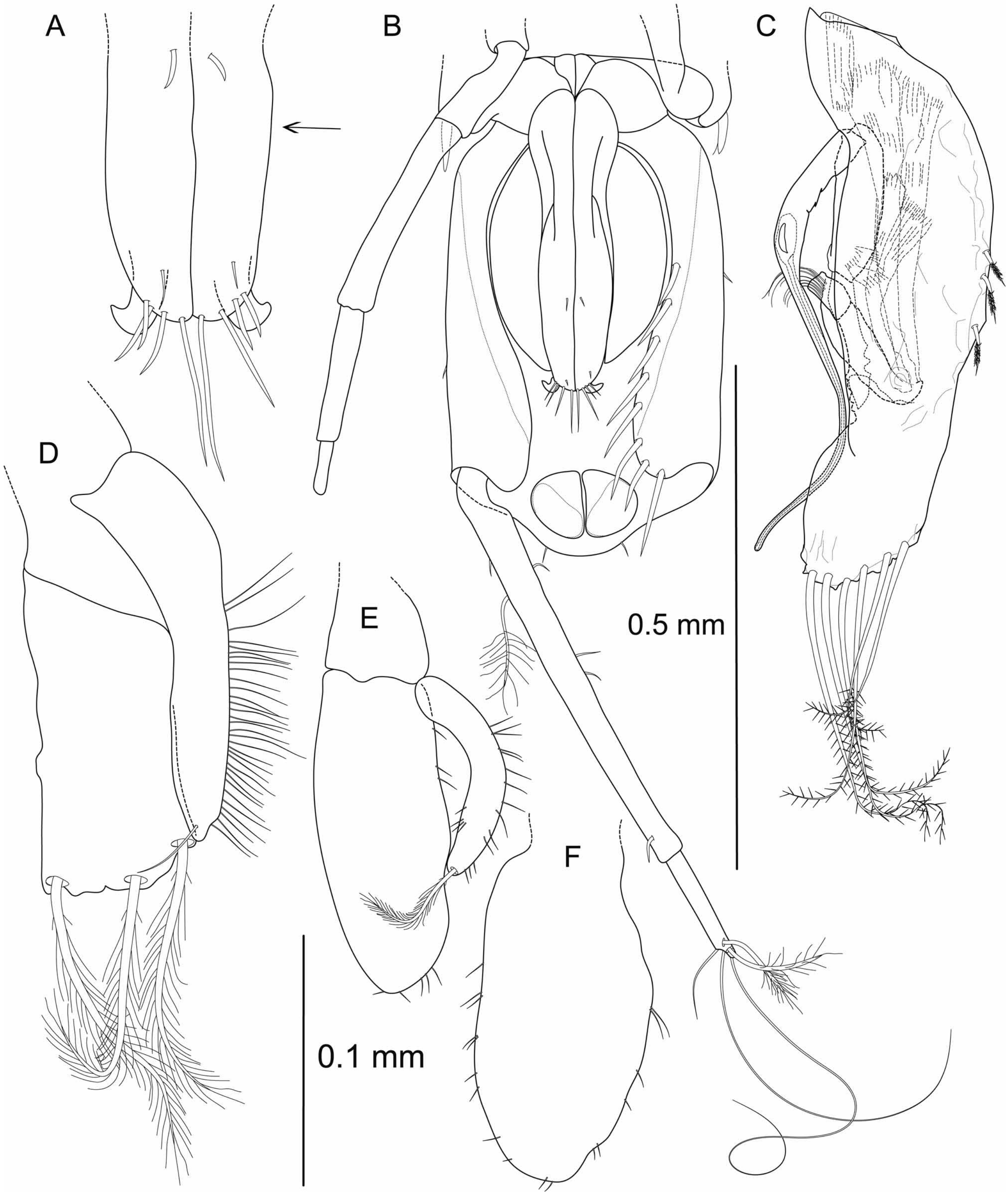

FIGURE 5. ***Macrostylis dorsaetosa*** **n. sp. A–B, paratype terminal ♂ (P86004). C–F, paratype terminal ♂ (AM P86003). A,** close-up of pleopods I, ventral. **B,** pleotelson, ventral. **C,** left pleopod II, ventral. **D–F,** right pleopods III–V, dorsal. Scales: A, C–F = 0.1 mm, B = 0.5 mm.

Operculum (female pleopod II; Fig. 4E). Elongate, length 1.6 width, 0.60 pleotelson length, distally tapering, without keel, with 14 pappose setae on apex, completely covering anal opening.

Pleopod III (Fig. 5D). Length 2.5 width, protopod length 1.6 width, 0.46 pleopod III length; exopod with fringe of fine setae, about as long as pleopod III exopod width, with simple seta subterminally, exopod length 0.77 pleopod III length.

Pleopod V (Fig. 5F). Present.

Uropod (Figs 1A, D, 7B). Length 0.79–0.82 pleotelson length; protopod length 0.55–0.56 pleotelson length, inserting on pleotelson ventrally on posterior margin. Protopod distal margin blunt, endopod insertion terminal, length 7.5–8.1 width; endopod length 4.7–6.1 width, 0.46–0.47 protopod length, endopod width subequal protopod width.

Description, terminal male.

Body. Length 2.2 mm, 6.6 width. *Cephalothorax.* Frons smooth, frontal ridge present, straight; length/width ratio greater than in female, length 0.96 width, 0.12 body length; with conspicious dorsal array of setae, posterolateral corners rounded, posterolateral setae absent. *Fossosome.* Length/width ratio greater than in female, length 1.4 width, length/body-length ratio greater than in female, length 0.21 body length. *Pereonite 4.* Lateral margins in dorsal view convex; posterolateral margin not produced posteriorly. Pereonal collum present, medially convex.

Pleonite 1. Sternal articulation with pleotelson present.

Pleotelson. In dorsal view approximately rectangular, length/width ratio in male greater than in female, length 1.8–2.1 width, 0.23 body length, width less than pereonite 7 width. Pleopodal cavity width 0.69 pleotelson width, preanal ridge width 0.37 pleotelson width.

Antennula (Figs 2K–L, 6A–B, E). Length 0.52 head width, 0.33 antenna length, width 2.0 antenna width, articles 1, 2 and 5 elongate, tubular; articles 3–4 squat or noticeably shorter; terminal article with 3 aesthetascs, penultimate article with 4 aesthetascs, aesthetascs simple, tubular. Article 1 elongate, subequal in width and length compared to more distal articles, with 1 simple seta and 1 broom seta. Article 2 squat, globular, shorter than article 1, with 1 simple seta and 2 broom setae. Article 3 squat, globular, shorter than article 1, article 4 squat, globular, shorter than article 1. Article 5 elongate, longer than article 1, with 2 simple setae.

Antenna (Figs 2L, 6A, E). Length 0.2 body length, flagellum of 4 articles. Article 1 squat, globular. Article 2 elongate, longer than article 1. Article 3 elongate, longer than article 1. Article 4 shorter than articles 1–3 together, distally with 1 simple seta. Article 5 longer than article 4, with 3 broom setae.

Pereopod I (Fig. 6F). Ischium dorsally with 4 setae, all simple, with dorsal row of setae shifted laterally. Merus dorsally with 5 setae, 4 simple in row, 1 split distally, ventrally with 3 setae, 2 biserrate, 1 split seta distally. Carpus dorsally with 2 setae, 1 simple, 1 split distally, ventrally with 2 setae, biserrate.

Pereopod II. Ischium dorsally with 5 setae, all simple, with dorsal row of setae shifted laterally. Merus dorsally with 8 setae, 6 simple in row, 2 split disto-medially, ventrally with 3 setae, all two-sided serrate. Carpus setation as in female.

Pereopod V. Merus disto-dorsally with 3 setae, split, mid-ventrally with 2 setae, simple; disto-ventrally with 2 setae. Carpus disto-dorsally with 4 setae, 1 small, split, 1 broom, 2 serrate, split.

Pereopod VI. Ischium setation as in female. Merus disto-dorsally with 4 setae, 2 short, split, 1 simple, 1 long split, mid-ventrally with 2 setae, simple, disto-ventrally with 1 seta, split. Carpus mid-dorsally with 2 setae, simple, disto-dorsally with 3 setae, 1 split, serrate, 1 broom, 1 split; mid-ventrally with 2 setae, simple, disto-ventrally with 4 setae, 3 split, 1 long, split, serrate.

Pereopod VII. Length/body-length ratio as in female, segment L/W ratios sexually dimorphic; basis length 2.6–2.8 width; ischium length 2.6 width, mid-dorsally with 2 setae, simple, mid-ventrally with 1 seta, simple, disto-ventrally with 2 setae, simple; merus length 2.2–2.8 width, merus setation as in female; carpus length 4.8–5 width, carpus mid-dorsally with 2 setae, simple, disto-dorsally with 5 setae, split, mid-ventrally with 2 setae, simple, disto-ventrally with 3 setae, split; propodus length 7 width; dactylus length 4 width.

Pleopod I (Fig. 5A–B). Length 0.64 pleotelson length, with simple setae ventrally.

Pleopod II (Fig. 5C). Protopod apex rounded, with setae on proximal lateral margin, 3 pappose setae altogether, with 6 pappose setae distally. Endopod distance of insertion from protopod distal margin 0.54 protopod length. Stylet sinuous, extending near to distal margin of protopod, length 0.84 protopod length.

Uropod (Figs 5B, 6H). Length 0.88–1.1 pleotelson length; protopod length/width ratio greater than in female, 9.6–10.3 width, with endopod inserting terminally; endopod/protopod length ratio less than in female, endopod length 0.29–0.3 protopod length, length 5.4–6 width, width less than protopod.

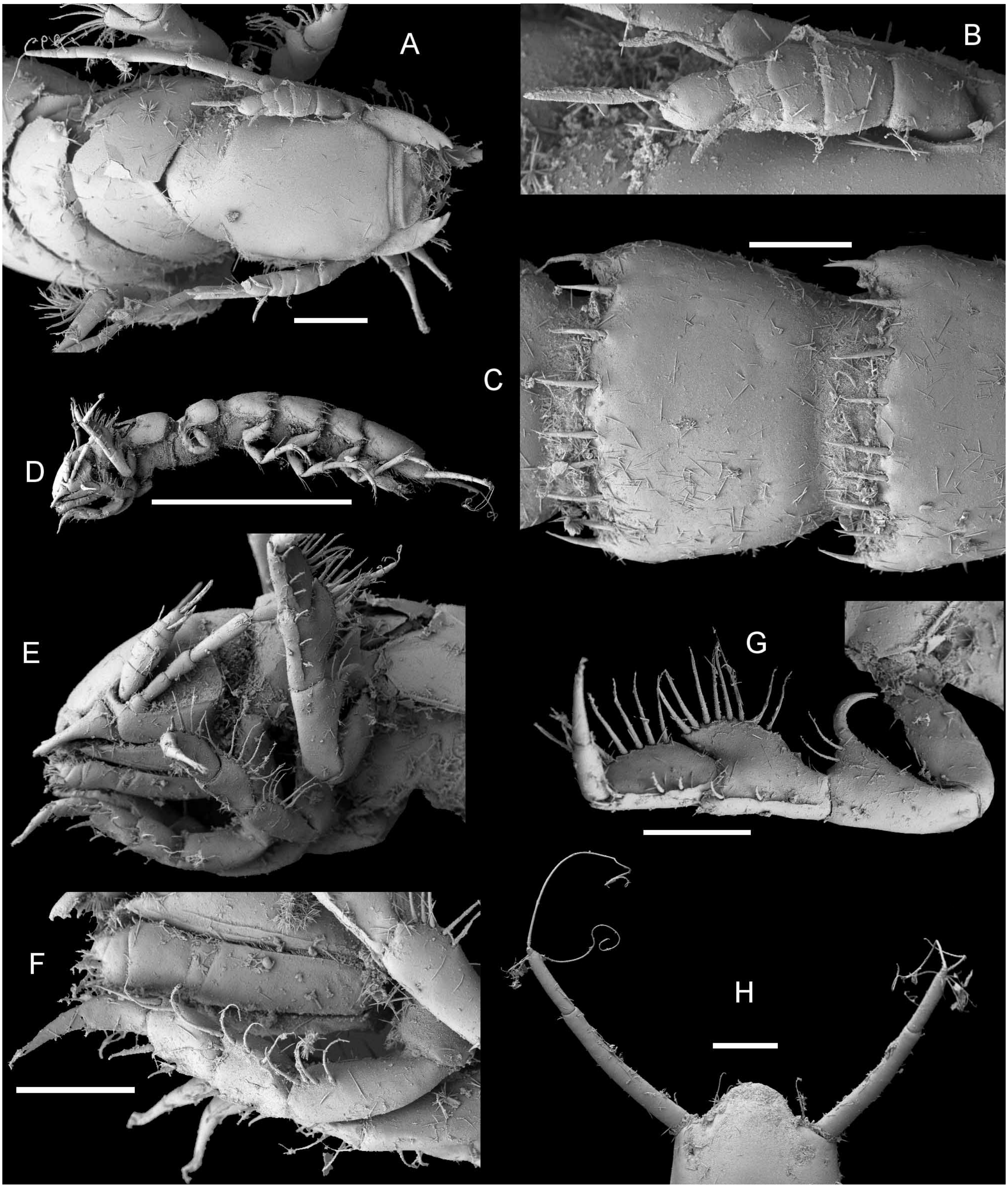

FIGURE 6. ***Macrostylis dorsaetosa*** **n. sp. A–H, paratype juvenile ♂ (AM P86005). A,** cephalothorax, dorsal. **B,** antennula close-up, dorsal. **C,** pereonites 5–6, dorsal. **D,** habitus, lateral. **E,** cephalothorax close-up, lateral. **F,** pereopod I, lateral. **G,** pereopod III, lateral. **H,** posterior apex of pleotelson and uropods, dorsal. Scales: **A–B, F–H = 0.1 mm, D = 1 mm.**

Remarks. *Macrostylis dorsaetosa* n.sp. is unlike any other species in the genus owing to the row of bifid setae on the posterior margins of pereonites 5–6 (Figs 1A, E, 6C). *M. strigosa* Mezhov, 1999 shows remarkable similarity in important characters such as the ischium setation of pereopod III, a character often applied for differentiation of macrostylid species, and body shape. This latter species could therefore be regarded as closely related to *M. dorsaetosa* n. sp. However, the above mentioned dorso-marginal setae are missing in *M. strigosa*. *M. grandis* Birstein,

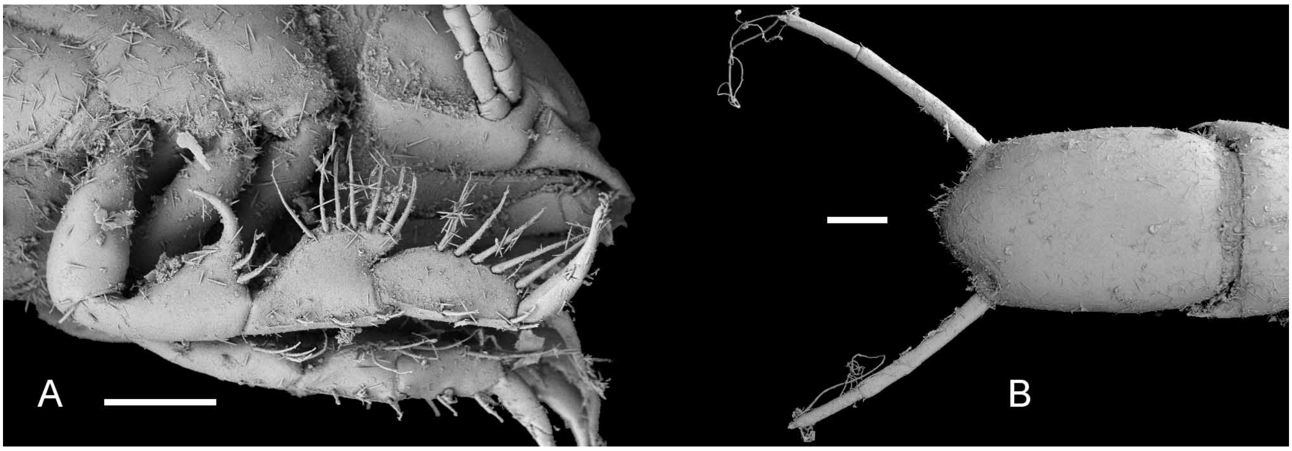

FIGURE 7. ***Macrostylis dorsaetosa*** **n. sp. A–B, paratype non-ovigerous ♀ (AM P86006; MI 639). A,** pereopod III, lateral. **B,** pleotelson and uropods, dorsal. Needle-like objects are crystalline artifacts. Scales = 0.1 mm.

1970 has smaller marginal setae on pereonites 4–6 and the pleotelson, but this latter species is also unusual in having pereonite 6 laterally overlapping pereonite 7. The chaetotaxy of the pereopod III ischium is substantially different in the two species as well, with *M. dorsaetosa* having one robust proximally curving seta on the apex and 2 simple setae on the distal slope of the dorsal projection (Figs 3C, 6G, 7A).

Macrostylis papillata n. sp.

Etymology. The name 'papillata' is derived from the Latin word ‘papilla’, meaning 'wart' because this species is characterized by warty posterior margins of the cephalothorax' and the anterior four pereonites' tergites.

Type fixation. Holotype: ovigerous female, 1.5 mm, AM P.86009, designated here.

Type material examined. Holotype: ovigerous female, 1.5 mm, AM P.86009, used for habitus illustrations, WHOI 121. Paratypes: juvenile female, 1.3 mm, AM P86008, partly used for illustration of habitus and antennae, WHOI 121; non-ovigerous female, 1.5 mm, AM P86010, used for habitus illustrations and dissected for illustration of appendages, WHOI 121; terminal male, 1.3 mm, AM P86011, used for habitus illustrations and dissected for illustration of appendages, WHOI 121; ovigerous female, 1.5 mm, AM P86013, MI 638, gold-coated for SEM, WHOI 121; terminal male, AM P86014, MI 635–MI 637, dissected and gold-coated for SEM, WHOI 121; immature male, 1.3 mm, AM P86015, partly used for illustration of habitus and antennae, WHOI 121.

Type locality. Western North Atlantic abyssal plain between Long Island and Bermuda: 35°50.0'N; 65°11.0'W; 4800 m (WHOI 121), 35°51.0'N; 64°58.2'W; 4833 m (WHOI 122).

Type material – Remarks. Collected during cruise R/V Atlantis II-24 (21 August 1966).

Further records. 1 terminal male, AM P.86016, WHOI LL1; 4 specimen, female and male, AM P.67254, WHOI 58; 1 terminal male, AM P.83030, WHOI 83; 1 non-ovigerous female, AM P.86028, WHOI 85; 8 specimen, female and male, AM P.86029, WHOI 95; 2 ovigerous female, AM P.86055, WHOI 120; 1 terminal male, AM P.86012, WHOI 125; terminal male, 1.3 mm, AM P.86012, MI 630, gold-coated for SEM, WHOI 125.

Description, female

Body (Figs 8A–D, 15A–E). Length 1.5 mm, 4.5 width, subcylindrical, without setation. *Ventral spines.* Pereonite 1 spine acute, prominent. Pereonite 3 spine blunt, small, closer to anterior segment border. Pereonite 4 spine directed posteriorly, acute, small, closer to posterior segment border. Pereonite 5 spine blunt, closer to posterior segment border. Pereonite 6 spine acute, prominent, closer to posterior segment border. Pereonite 7 spine small. *Imbricate ornamentation (IO).* Pereonite 1 IO along anterior tergite margin and medially on tergite from anterior to posterior, covering whole sternite; pereonites 2 and 3 IO in an hourglass-shaped band medially on tergite, wider in pereonite 3 than in pereonite 2, covering whole sternite; pereonite 4–7 and pleotelson IO covering all tergites, sternites and operculum.

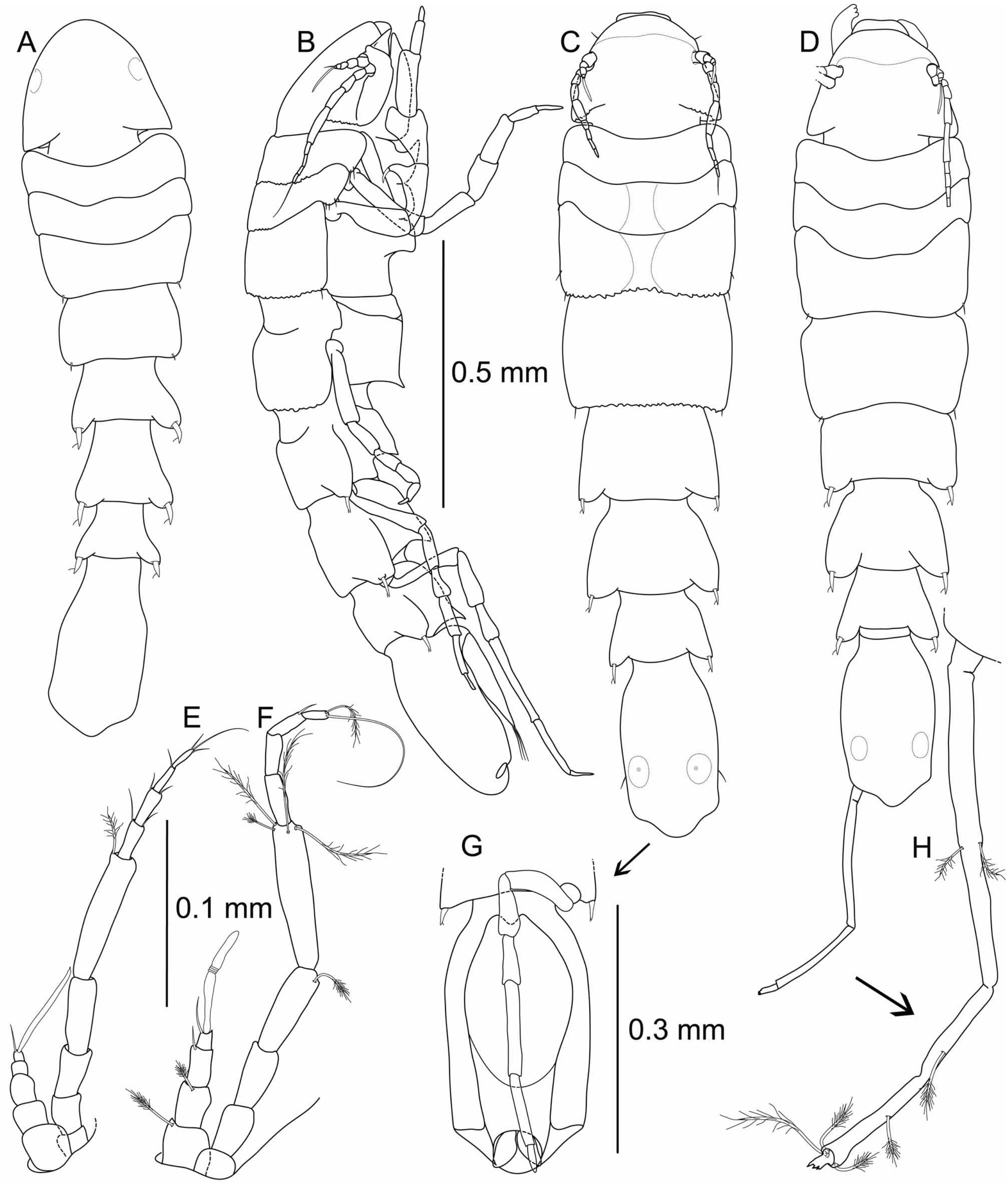

FIGURE 8. ***Macrostylis papillata*** **n. sp. A, E, paratype juvenile ♀ (AM P86008). B–C, F–G, paratype adult, non-ovigerous ♀ (AM P860010). D, H, holotype ovigerous ♀ (AM P86009). A–D,** dorsal and lateral habitus, cuticle ornamentation and appendages mostly omitted, uropods missing where not illustrated. **D,** uropod endopod, damaged. **E–F,** left antennula and antenna, in situ, lateral. **G,** pleotelson, ventral. **H,** uropod, close-up, endopod damaged. Scales: A–D = 0.5 mm, E–F = 0.1 mm, G = 0.3 mm.

Cephalothorax. Length 0.82 width, 0.15 body length; frons in dorsal view convex, with wrinkles, frontal ridge absent; dorsal surface with array of setae, 1 pair on frons between anterior rims of antennulae articulations, 1 pair dorsally and 1 pair at back of cephalothorax. Posterolateral setae absent. Posterolateral corners acute. Posterior margin papillose. *Fossosome*. Length 0.85 width, 0.19 body length. Lateral tergite margins in dorsal view forming almost uninterrupted line, ventral surface without keel. *Pereonite 1.* Anterior margin concave; posterolateral setae simple, posterior tergite margin papillose. *Pereonite 2.* Posterolateral setae simple, posterior tergite margin papillose. *Pereonite 3*. Posterolateral setae simple, flexibly articulated, posterior tergite margin papillose. *Pereonite 4.* Width 1.2 pereonite 5 width, length 0.66 width; pereonal collum present. Lateral margins in dorsal view simple convex. Posterior tergite margin papillose. Posterolateral margin rounded. Posterolateral setae simple, not robust, flexibly articulated. *Pereonite 5*. Length 0.69 width. Posterolateral margin rounded. Tergite posterolateral setae bifid, robust. *Pereonite 6.* Length 0.72 width. Posterolateral margin produced posteriorly, rounded. Tergite posterolateral setae bifid, robust, flexibly articulated. *Pereonite 7*. Length 0.63 width. Posterolateral margin produced posteriorly, rounded. Tergite posterolateral setae bifid, robust, flexibly articulated.

Pleonite 1. Tergal articulation with pleotelson present.

Pleotelson (Figs 8D, G, 15C). Ovoid, constricted anteriorly to uropod articulations, length 0.22 body length, 1.8 width, narrower than pereonite 7; statocysts present, dorsal slot-like apertures absent. Posterior apex convex, bluntly rounded. Posterior apex setae absent. Pleopodal cavity width 0.72 pleotelson width, preanal ridge width 0.44 pleotelson width. Anal opening terminal, tilted posteriorly relative to frontal plane.

Labrum (Fig. 14F). Anterior margin in dorsal view concave.

Antennula (Fig. 8E–F). Length 0.25 head width, 0.25 antenna length, width 1.5 antenna width. Articles decreasing in size from proximal to distal. Article 1 squat, globular, widest but not longest, with 1 broom seta. Article 2 distinctly longer than wide, tubular, subequal article 1 length, with 1 broom seta. Article 3 distinctly longer than wide, tubular, length subequal article 1 length, with 1 simple seta. Article 4 squat, globular. Article 5 minute, squat, globular, with 1 simple seta. Terminal article with 1 aesthetasc, aesthetasc with intermediate belt of constrictions.

Antenna (Fig. 8E–F). Length 0.18 body length. Article 1 squat, globular. Article 2 squat, globular, longer than article 1. Article 3 elongate, longer than article 1. Article 4 shorter than articles 1–3 together, distally with 1 broom seta. Article 5 longer than article 4, distally with 4 broom setae. Flagellum with 4 articles.

Mandibles (Fig. 11A–D). In medial view dorsoventrally flattened, with lateral setae; left mandible incisor process distal margin flattened and curved (shovel-like), with 4 cusps, lacinia mobilis grinding, with 4 cusps; right mandible incisior process with shovel-like appearance, with 3 cusps, lacinia mobilis grinding, clearly smaller than left lacinia, with 6 cusps.

Maxillula (Fig. 11E). Lateral lobe with 13 robust setae.

Maxilla (Fig. 11H, 15F–G). Lateral lobe with 4 setae terminally, simple; middle endite with 5 setae terminally, simple; inner endite with 9 setae terminally, 4 monoserrate, 5 slim, simple.

Maxilliped (Figs 11F–G, 15F). Basis endite length 3.5 width; epipod length 3.5 width, 1.2 basis-endite length; palp width subequal endite width, article 2 wider than article 1, article 2 wider than article 3, article 1 shorter than article 3.

Pereopod I (Fig. 9A). Length 0.33 body length. Ischium dorsal margin with 1 seta, split, bisetulate, latero-distally. Merus dorsal margin with 3 setae, bisetulate, distally, ventral margin with 2 setae, bisetulate, placed distally. Carpus dorsally with 1 seta, bisetulate, placed distally. Dactylus distally with 2 sensillae.

Pereopod II (Fig. 9B–C). Longer than pereopod I, length 0.39 body length. Ischium dorsally with 3 setae, bisetulate, placed distally. Merus dorsally with 3 setae, bisetulate, placed distally. Carpus dorsally with 3 setae, 1 bisetulate and 1 broom medially, 1 split distally, ventrally with 2 setae, 1 medially, 1 distally. Dactylus distally with 2 sensillae.

Pereopod III (Fig. 9D). Length 0.41 body length. Ischium with no seta proximo-dorsally, dorsal lobe tapering; proximally with 1 bisetulate seta; apex with 1 prominent seta; apical seta robust, bifid, bent towards proximal, spine-like; distally with 1 bisetulate seta. Merus dorsally with 4 setae, 2 bisetulate, 2 split, bisetulate, ventrally with 2 setae, simple. Carpus dorsally with 5 setae, 1 bisetulate, 2 split, bisetulate, 1 broom, 1 split, bisetulate, ventrally with 3 setae, simple. Dactylus with 2 sensillae.

Pereopod IV (Fig. 10A). Length 0.24 body length.

Pereopod V (Fig. 10B). Length 0.33 body length. Ischium mid-ventrally with 1 seta, bisetulate, disto-ventrally with 2 setae, bisetulate. Merus disto-dorsally with 2 setae, 1 short, bisetulate, 1 long, bisetulate, disto-ventrally with 2 setae, 1 long, bisetulate, 1 short, bisetulate. Carpus disto-dorsally with 1 seta, bisetulate, disto-ventrally with 2 setae, bisetulate.

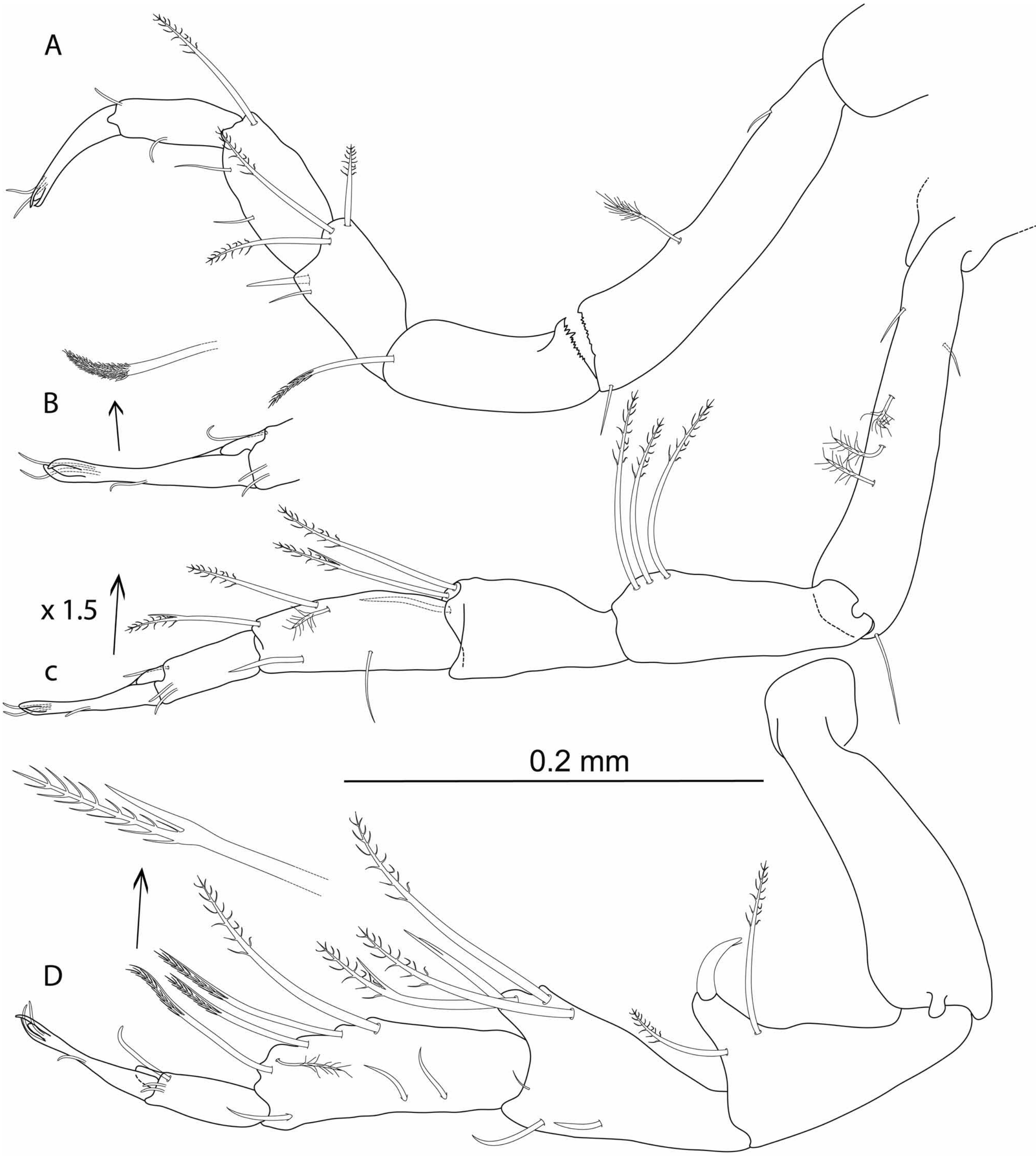

FIGURE 9. ***Macrostylis papillata*** **n. sp. A–D, paratype non-ovigerous ♀ (AM P860010). A,** pereopod I, lateral, baso-ischial articulation damaged. **B,** pereopod II dactylus, lateral with close up of distally pappose fringe-like sensilla. **C,** pereopod II, lateral. **D,** pereopod III, lateral with close up of bisetulate split seta. Scale = 0.2 mm.

Pereopod VI (Fig. 10C). Length 0.41 body length; ischium mid-ventrally with 2 setae, bisetulate, disto-ventrally with 2 setae, bisetulate; merus disto-dorsally with 2 setae, bisetulate, disto-ventrally with 2 setae, bisetulate; disto-dorsally with 3 setae, 1 broom, 1 prominent, split, bisetulate, 1 small, bisetulate, mid-ventrally with 1 seta, bisetulate, disto-ventrally with 2 setae, 1 short, bisetulate, 1 long, bisetulate.

Pereopod VII (Fig. 10D). Length less than pereopod VI length, 0.33 body length. Basis length 4.3 width; with no elongate setae. Ischium length 3.5 width, disto-ventrally with 1 seta, bisetulate. Merus length 3.0 width, disto-dorsally with 1 seta, bisetulate, disto-ventrally with 1 seta, short, bisetulate. Carpus length 6.0 width, disto-dorsally

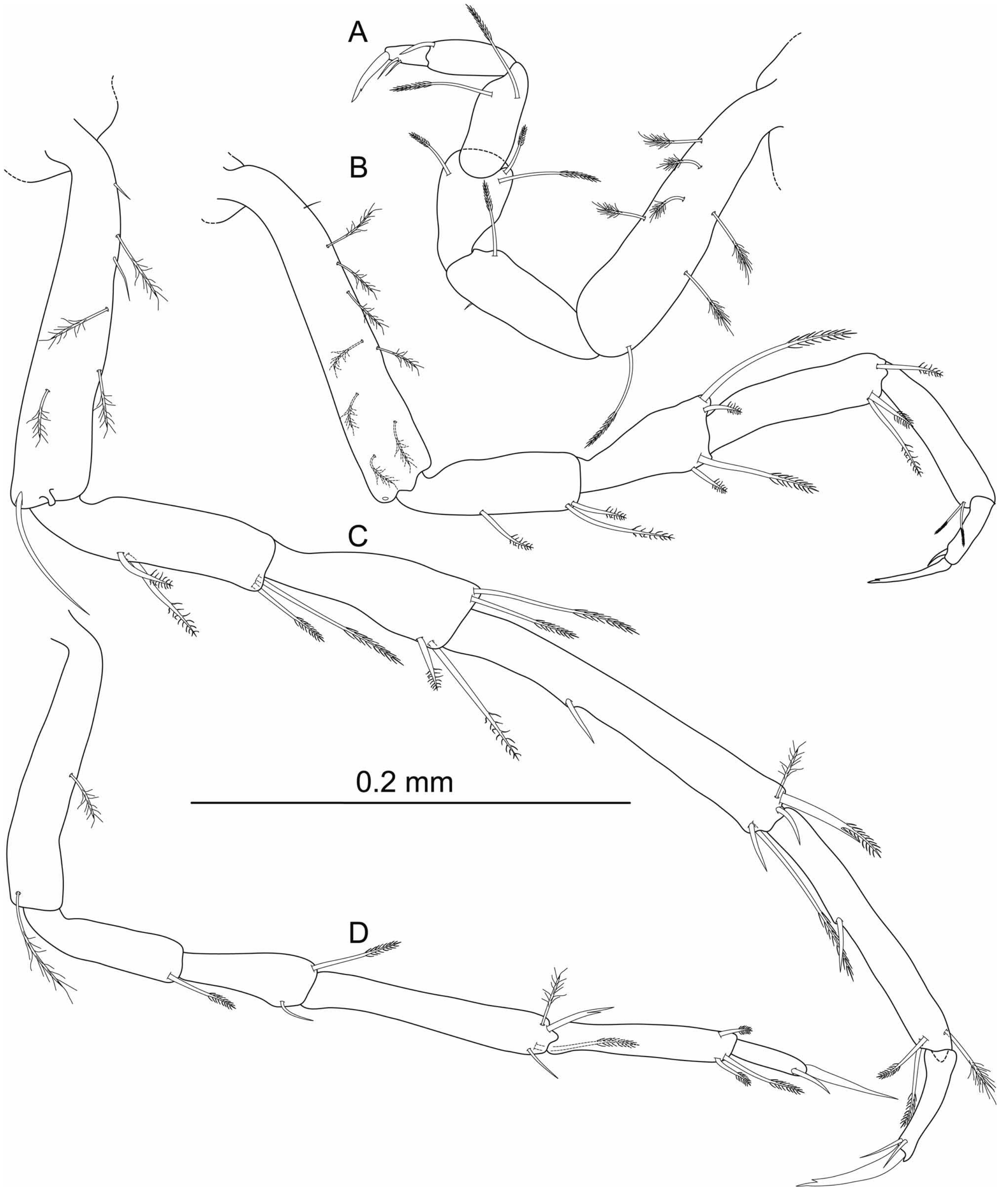

FIGURE 10. ***Macrostylis papillata*** **n. sp. A–D, paratype non-ovigerous ♀ (AM P860010). A,** pereopod IV, posterior. **B,** pereopod V, lateral. **C,** pereopod VI, lateral. **D,** pereopod VII, lateral**.** Scale = 0.2 mm.

with 2 setae, 1 broom, 1 split, bisetulate, disto-ventrally with 2 setae, 1 short, bisetulate, 1 long bisetulate. Propodus length 4.0 width. Dactylus length 4.0 width.

Operculum (female pleopod II; Figs 8G, 11J). Stout, length 1.5 width, 0.48 pleotelson length, ovoid, without keel, with 10 pappose setae on apex, extending to anal opening.

Pleopod III (Fig. 11I). Length 2.2 width, protopod length 2.0 width, 0.55 pleopod III length; exopod with fringe of fine setae, about as long as pleopod III exopod width, with simple seta subterminally, exopod length 0.73 pleopod III length.

Uropod (Fig. 8D, H). Protopod length 1.3 pleotelson length; inserting on pleotelson on posterior margin. Protopod distal margin blunt, endopod insertion terminal, length 24.0 width.

Description, terminal male

Body (Figs 12A–B, E, 14A–B, D). Length 1.3 mm, 5.0 width. *Ventral spines.* Pereonite 3 spine acute, prominent, located closer to anterior segment border. Pereonite 4 spine directed ventrally and posteriorly, blunt, prominent, located closer to posterior segment boder.

Cephalothorax. Frons with wrinkles, frontal ridge present, as cluster of slight transversal scratches between antennulae articulations; length/width ratio subequal to female, 0.16 body length; with conspicious array of setae, posterolateral corners acute, posterolateral setae absent, posterior margins papillose. *Fossosome.* Length/width ratio greater than in female, length 0.94 width, length/body-length ratio subequal to female; keeled. *Pereonite 4.* Narrower than pereonite 5, length/width ratio subequal to female; pereonal collum present. Lateral margins in dorsal view medially convex. Posterolateral margin not produced posteriorly.

Pleonite 1 (Fig. 14B). Tergal and sternal articulations with pleotelson present.

Pleotelson (Figs 12B, D–F, 14A–B). In dorsal view, approximately rectangular, length/width ratio in male subequal to female, 0.23 body length, width subequal pereonite 7 width. Posterior apex convex, more obtusely-angled compared to female, without setae on margin, pleopodal cavity width 0.75 pleotelson width, preanal ridge width 0.43 pleotelson width.

Antennula (Figs 12C, G, 14C). Length 0.35 head width, 0.27 antenna length, width 1.2 antenna width; terminal article with 2 aesthetascs, penultimate article with 2 aesthetascs, aesthetascs with intermediate belt of constrictions; article 1 squat, globular, longest and widest, 1 broom seta, article 2 squat, globular, shorter than article 1, 2 broom setae, article 3 squat, globular, shorter than article 1, 1 broom seta, article 4 squat, globular, minute, article 5 squat, globular, minute, with 1 simple seta.

Antenna (Figs 12C, G, 14C). Length 0.22 body length, flagellum of 4 articles, article 1 elongate, article 2 elongate, longer than article 1, article 3 elongate, longer than article 1, article 4 shorter than articles 1–3 together, 1 broom seta, article 5 longer than article 4, distally with 1 simple seta, 4 broom setae.

Pereopod I. Length 0.37 body length. Merus setation as in female. Carpus dorsally with 2 setae, 1 broom, 1 bisetulate, carpus ventrally with 3 setae, 1 simple, 2 split.

Pereopod II. Ischium setation as in female. Merus dorsally with 4 setae, dorso-distally, bisetulate, ventrally with 2 setae, along margin, distally, bisetulate. Carpus dorsally with 4 setae, 2 bisetulate along margin, 2 split distally, bisetulate, ventrally with 3 setae, 1 bisetulate, 1 broom, 1 split, bisetulate.

Pereopod III. Length 0.44 body length.

Pereopod V. Length 0.35 body length. Merus disto-dorsally with 2 setae; 1 short, bisetulate, 1 long, bisetulate; mid-ventrally with 1 seta; bisetulate; disto-ventrally with 2 setae; 1 short, bisetulate, 1 long, bisetulate. Carpus disto-ventrally with 2 setae, 1 short, bisetulate, 1 long, bisetulate.

Pereopod VI. Length 0.51 body length; ischium, merus and carpus setation as in female.

Pereopod VII. Length 0.35 body length, less than pereopod VI length, segment L/W ratios sexually dimorphic; basis length 4.3 width; ischium length 2.8 width, setation as in female; merus length 1.7 width, disto-dorsally with 1 seta, bisetulate, disto-ventrally with 2 setae, 1 short, bisetulate, 1 long, bisetulate; carpus length 5 width, carpus setation as in female; propodus length 4.0 width; dactylus length 3.0 width.

Pleopod I (Fig. 13A). Length 0.58 pleotelson length, distally with fringe-like sensillae. *Pleopod II (Fig. 13B).* Protopod apex tapering, with setae on proximal lateral margin, 3 pappose setae altogether, with 5 pappose setae distally. Endopod distance of insertion from protopod distal margin 0.38 protopod length. Stylet weakly curved, not extending to distal margin of protopod, length 0.52 protopod length.

Uropod (Fig. 12F). Length 2.0 pleotelson length; protopod length/width ratio greater than in female, length1.5 width, with endopod inserting terminally; endopod length 0.31 protopod length, 11.5 width, width less than protopod.

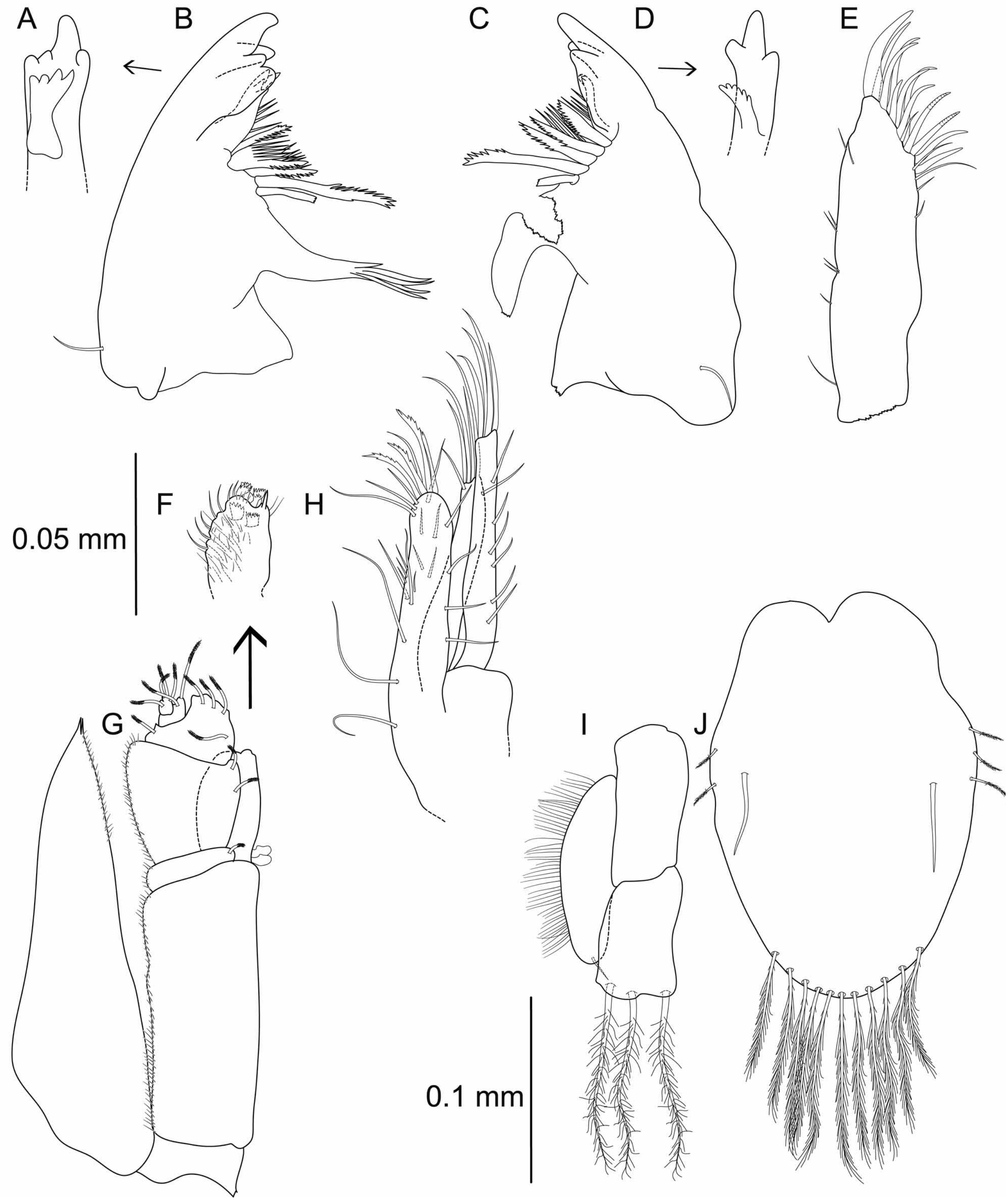

FIGURE 11. ***Macrostylis papillata*** **n. sp. A–J, paratype non-ovigerous ♀ (AM P860010). A,** left mandible, medial view of incisor process and lacinia mobilis. **B,** left mandible, dorsal, setal row damaged. **C,** right mandible, dorsal, setal row and molar process damaged. **D,** right mandible, incisor process and lacinia mobilis, medial view. **E,** right maxillula, ventral, inner lobe broken off. **F,** right maxilliped, endite setation, ventral. **G,** right maxilliped, ventral. **H,** left maxilla, ventral. **I,** right pleopod III, ventral. **J,** operculum, ventral. Scales: A–H = 0.05 mm, I–J = 0.1 mm.

other authors, *M. reticulata* Birstein, 1963 has strongly developed imbricate ornamentation and could thus potentially show marginal wartyness as well. This latter species is substantially different from *M. papillata* n. sp. because it has the ornamentation on all somites. Both species differ in the shape of their pereopod III ischium, in that *M. papillata* has an narrow dorsal projection bearing a robust proximally curved seta with two flanking bisetulate setae, whereas *M. reticulata* has a more rounded projection with only 3 straight non-robust setae.

Remarks. *M. papillata* differs from any previously described macrostylid owing to the presence of a tergal pleonite 1 articulation with the pleotelson. Furthermore, the ridges that create the imbricate ornamentation in this species overlap posteriorly with the margin of the pereonites 1–4 and head. As a result, the margins of these somites have a warty appearance that is most evident in the SEM images (Figs 14–15), but can be seen in the light microscope (Fig. 12B). Although this subtlety of the imbricate ornamentation may not have been fully noted by

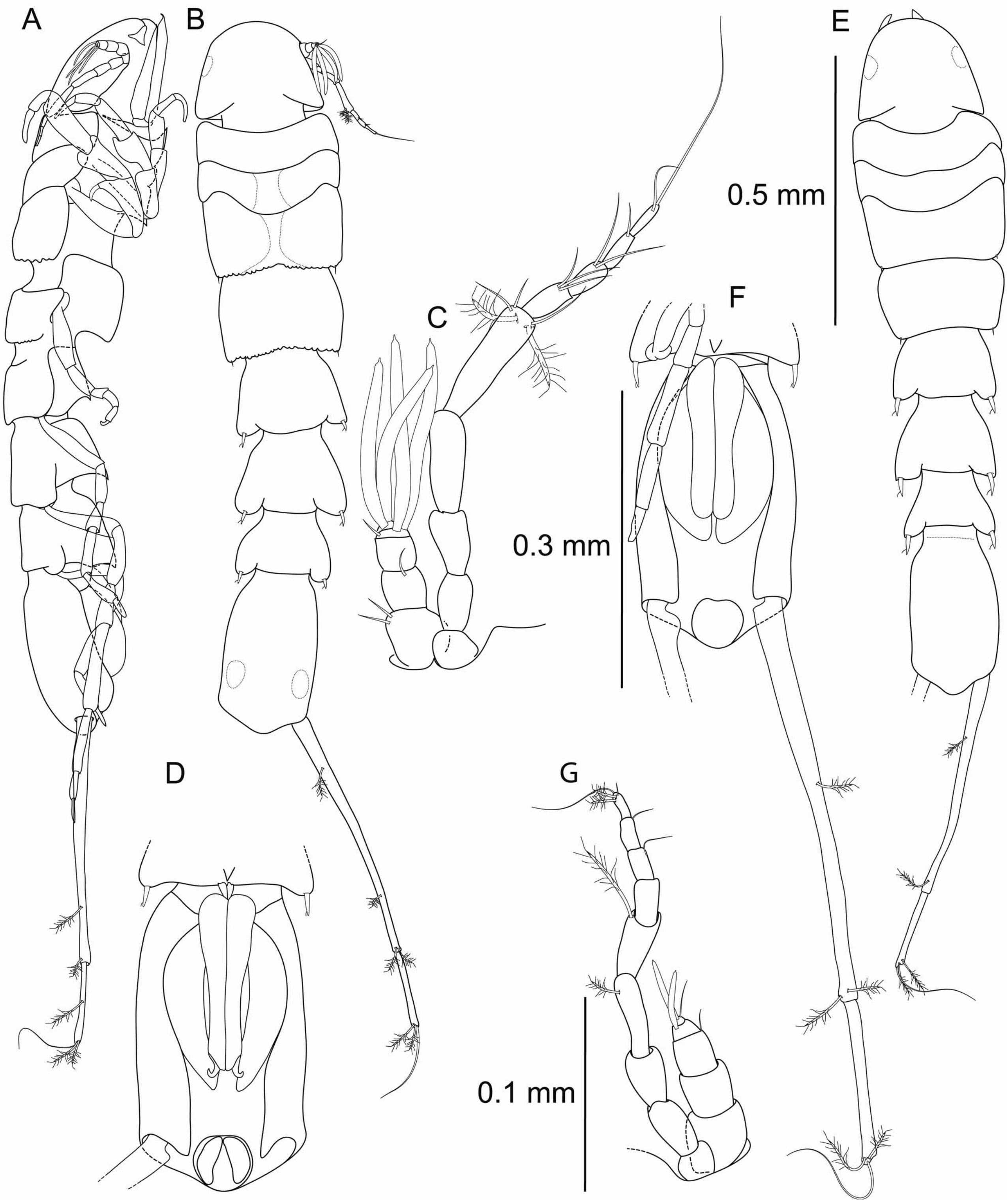

FIGURE 12. ***Macrostylis papillata*** **n. sp. A–D, paratype terminal ♂ (AM P860011). E–G, paratype subadult ♂ (AM P860015). A–B, E,** dorsal and lateral habitus, cuticle ornamentation and appendages mostly omitted, uropods missing where not illustrated. **C, G,** antennula and antenna, in situ, lateral. **D, F,** pleotelson, ventral. Scales: A–B, E = 0.5 mm, C, G = 0.1 mm, D, F = 0.3 mm.

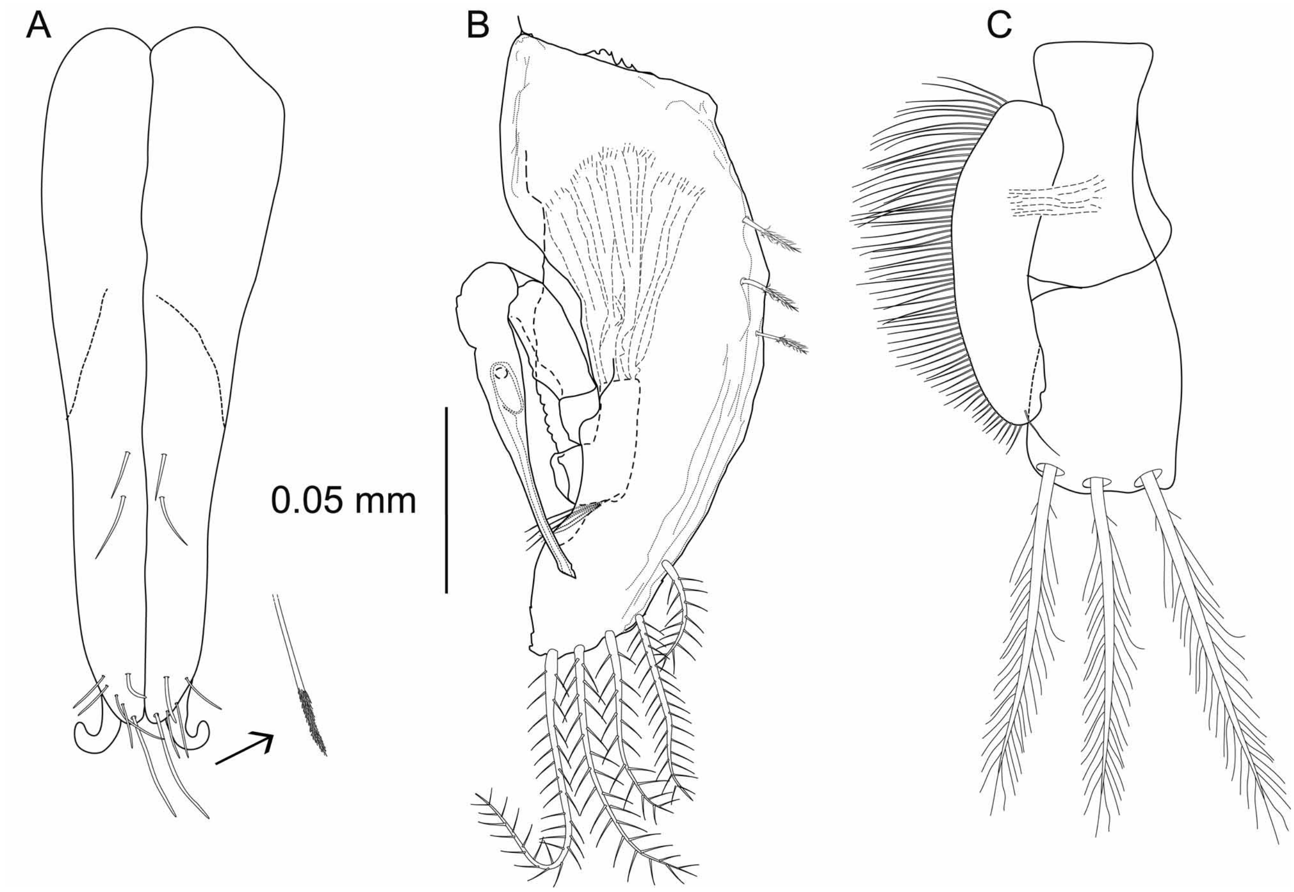

FIGURE 13. ***Macrostylis papillata*** **n. sp. A–C, paratype terminal ♂ (AM P860011). A,** pleopods I, ventral. **B,** right pleopod II, dorsal, with indicated endopod musculature and sperm duct. **C,** left pleopod III, dorsal. Scale = 0.05 mm.

Discussion

Sexual dimorphism and terminal male stages. Sexual dimorphism has led (and still leads) to significant taxonomic problems across a wide range of taxa (e.g., Sibley 1957; Kelley 1993; Brökeland 2010). Morphological differences between conspecific males and females vary between and within species during ontogeny. In macrostylid isopods, juvenile stages typically show high similarity to adult females except from developing first pleopods and enlarged antennulae in males. Although so far discussed only for the Macrostylidae (discussion below) and the Paramunnidae (Just & Wilson 2004), a male that transforms substantially to the last instar occurs frequently among the Asellota. In the Ischnomesidae, the males can have substantially more elongate pereonites 4 and 5 (e.g., *Heteromesus calcar* Cunha & Wilson, 2006) and often have distinctly different spination patterns from the females (e.g., *Cornuamesus longiramus* (Kavanagh & Sorbe, 2006)). Some Desmosomatidae and Nannoniscidae show important transformations of the head (e.g., *Pseudomesus pitombo* Kaiser & Brix, 2007; *Nannoniscoides latediffusus* Siebenaller & Hessler, 1977). Among common shallow water taxa such as Janiridae (species of *Ianiropsis*, see Doti & Wilson 2010) and Munnidae (e.g., *Munna spicata* Teodorczyk & Wägele 1994) a transformation in the last instar of the male is characterized by the male pereopod I changing substantially, being typically longer and more robust, with corresponding changes in pereonite 1. Such transformations of the male can result in wrong identification; i.e., females and males are classified as different species, or at least not associated in ecological studies. This transformation in *Macrostylis* is parallel to the “terminal-male” stage (T male) in *Paramunna* Sars (compare Just & Wilson 2004) and hence this term will be applied to the Macrostylidae, too. As we show below, one is still able to place males with females of the same species by using other characters that may not be related to the male transformation.

In adults of *Macrostylis*, the antennulae bear more aesthetascs in males (three in *Macrostylis dorsaetosa* n. sp., two in *M. papillata* n. sp.). The available dataset was not sufficient to reconstruct the whole development trajectory

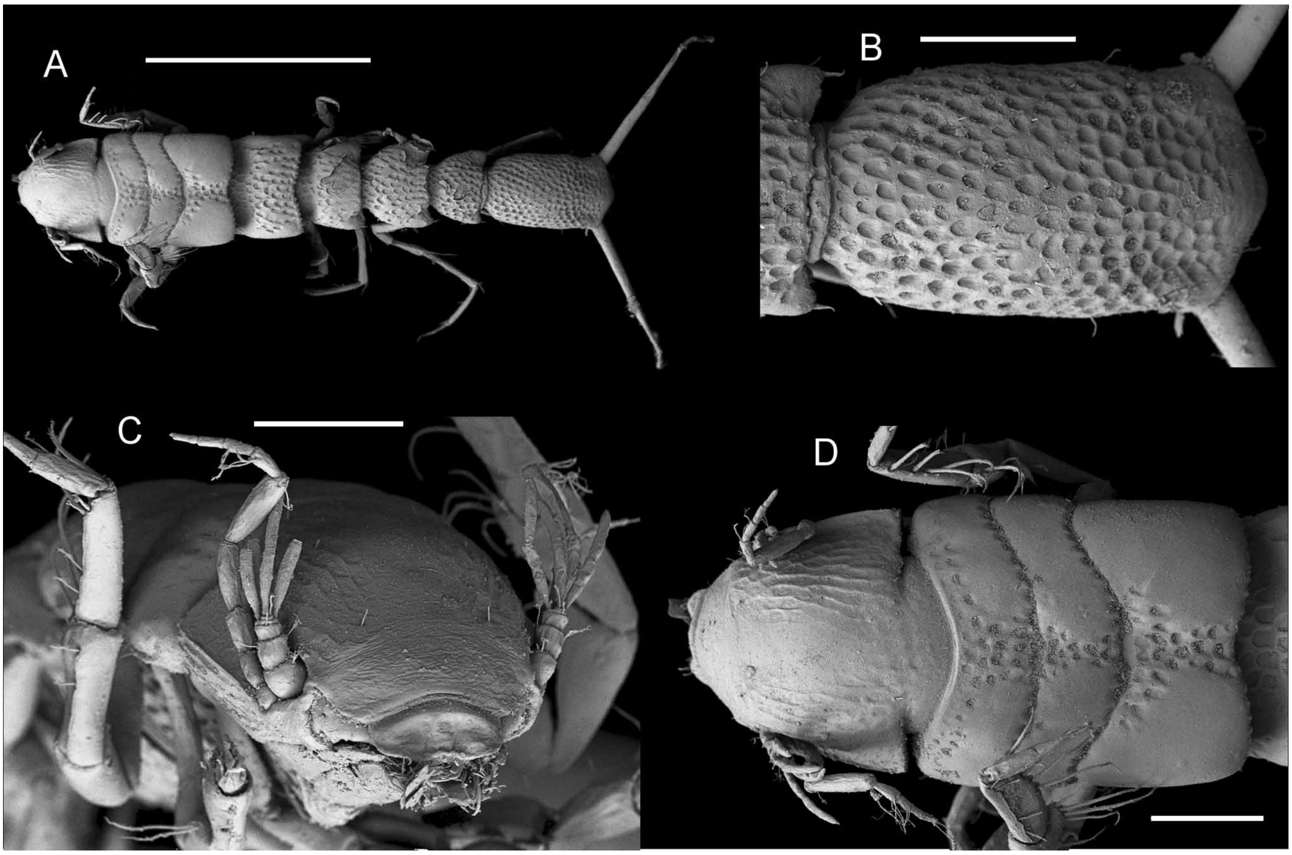

FIGURE 14. ***Macrostylis papillata*** **n. sp. A–D, paratype terminal ♂ (AM P860012, MI630). A,** habitus dorsal. **B,** pleotelson, dorsal. **C,** cephalothorax, anterio-lateral view. **D,** anterior habitus. Scales: A = 0.5 mm, B–D = 0.1 mm.

for these species. The largest size class of males in the samples, however, shares important characters with females, providing good support for the males and females to be conspecific. Nevertheless, a transformation affecting large parts of the male anatomy can be observed. The collections at hand (Riehl, unpublished data) suggest that those changes appear during the final moult, as intermediate stages are generally missing.

In detail, T male appear to be more slender (larger length-width ratio). In *M. dorsaetosa* and *M. papillata*, the pleotelson shows differences in shape: while the pleotelson in the female and juvenile male is widest in the anterior half and rather rounded, the pleotelson in T male appears almost parallel or trapezoidal with the greatest width just anterior to the uropod articulations (Fig. 14). In the antennulae of the males, the transformation can be dramatic. Length-width ratios and length ratios of subsequent articles in T male of *M. dorsaetosa* are much unlike those found in juvenile males and all female instars. Antennular articles 3 and 4 are short and article 5 elongated and narrow. This is not a general pattern for Macrostylidae, as in (e.g.) *M. papillata* only the number of aesthetascs is increased, while the relative article sizes show no change. Thus, the high number of aesthetascs relative to the female condition is probably the most reliable indication for the T male stage. Uropods in T males in relation to the pleotelson are longer than in the female. A similar pattern has been described for *M. spinifera* Sars, 1864. Because the uropods in macrostylids are often broken and missing, generality of this pattern cannot be tested at the moment.

In the species described here, characters that are not affected by the sexual dimorphism and useful for allocation of conspecifics (without dissection of appendages) include: ventral spination; shape of pleotelson posterior apex; setation on posterolateral angles of pereonites; setation of the anterior pereopods; especially the ischium of pereopod III (not only number but especially arrangement and type of setae). Studies on intraspecific variability and allometry of these characters would further support these results.

Ecological and evolutionary implications. Sexually dimorphic sensory systems can be found across various Arthropoda (e.g. Schafer & Sanchez 1976; Martens 1987; Jourdan *et al.* 1995; Koh *et al.* 1995; Fernandes *et al.* 2004). In most of these cases, males show an increased size of sensory organs (e.g., antennae) and number of olfactory sensillae (i.e. chemoreceptors), which has been attributed to the search for and location of (receptive) females.

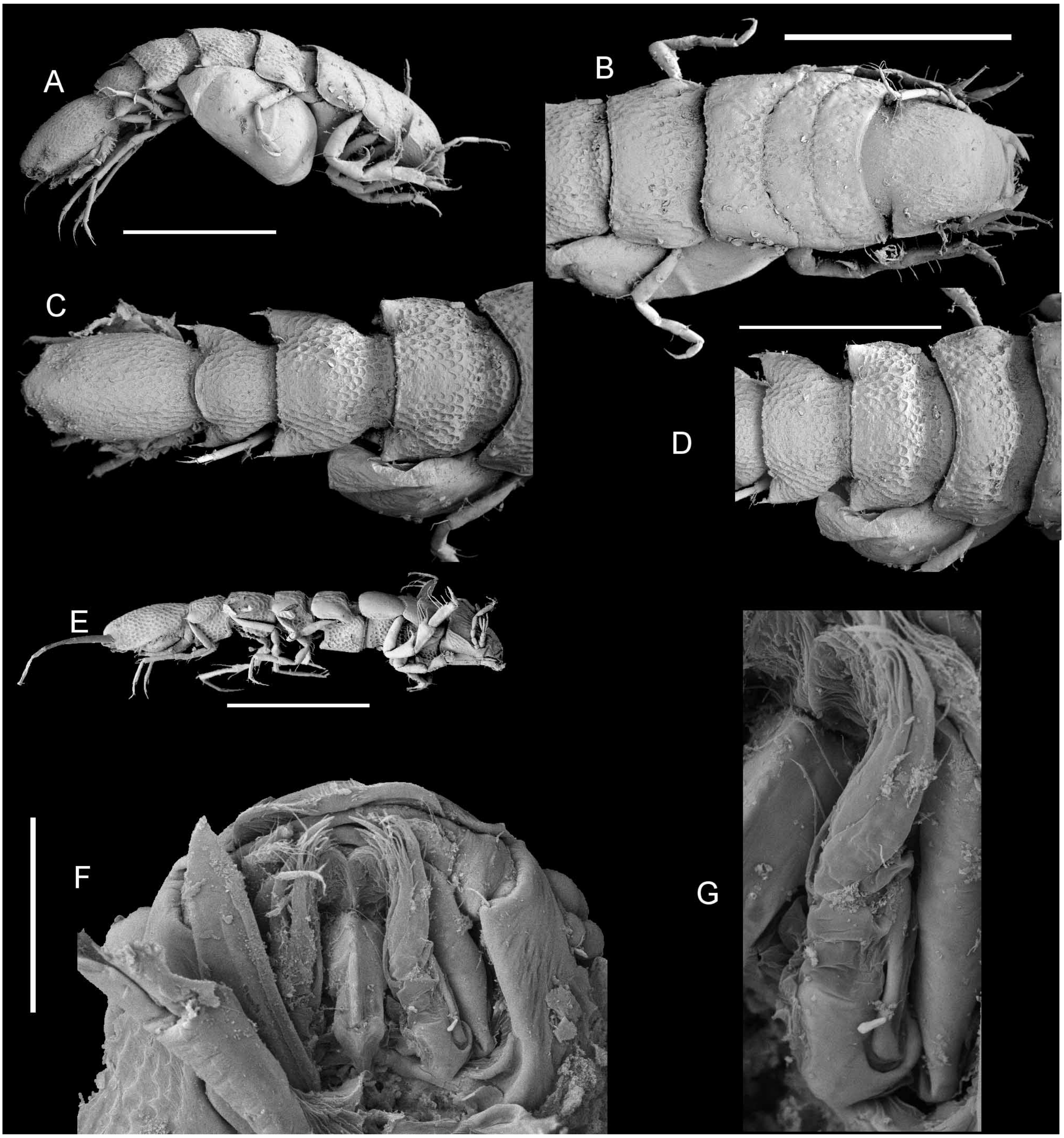

FIGURE 15. ***Macrostylis papillata*** **n. sp. A–D, paratype ovigerous ♀ (AM P860013, MI638). E, paratype terminal ♂ (AM P860012, MI630). F–G, paratype subadult ♀ (AM P860014, MI635). A,** habitus, lateral. **B–D** habitus, dorsal. **E,** habitus, lateral. **F,** mouthparts, ventral. **G,** maxilla, ventral, close up. Scales: A–E = 0.5 mm, F–G = 0.1 mm.

As an example, for several species of oniscid isopods, Lefebvre *et al.* (2000) found evidence for scramble-competition polygyny (Alcock 1980) as the prevalent mating system. Males compete indirectly by fertilizing as many mates as they can find in their fertile period. They bear longer antennae compared to the females that they apply to compete intensively in searching and locating receptive females (Lefebvre *et al.* 2000).

Mating strategies for Macrostylidae cannot be inferred from morphological data only. Because of the unavailability of genetic data (as discussed below) and the difficulties associated with keeping live specimens, morphology and collection data make our primary sources for ecological and evolutionary implications.

However, given low densities in the deep-sea benthic environment (Sanders & Hessler 1969), the search for a mating partner itself is likely to be among the dominating forces for the evolution of sexually dimorphic traits in olfactory organs. The evolution of the dimorphism found in the males' enlarged antennulae and increased number of aesthetascs implies importance of this chemosensory organ for mating in general and would hence be driven by sexually selective pressure (Lande 1980).

Other than that, dimorphic body measures can be interpreted as consequence of the different reproductive roles: i.e., ovigerous females with relatively wider bodies due to resource storage and breeding. Experimental tests would be required to verify these hypotheses. However, due to their remote habitats and infaunal lifestyle (Hessler & Strömberg 1989), detailed observations on living macrostylids remain difficult.

Implications for future systematic work. Some evidence (Riehl, unpublished data) suggests that in other species the sexual dimorphism is even more developed than in *Macrostylis dorsaetosa* n. sp. and *M. papillata* n. sp. Furthermore, in those species characters other than those mentioned above are affected. Herein, the reason might be found that some species, such as *M. longipes* Hansen, 1916 or *M. longipedis* Brandt, 2004, have been described without recognition of females. Genetic data would be helpful in such cases, as demonstrated by Brix *et al.* (2011), and allow reciprocal illumination sensu Hennig (1965). DNA studies on decades old, formaldehyde-fixed deep-sea samples, though, can be accomplished only with difficulty (France & Kocher 1996; Boyle *et al.* 2004; Skage & Schander 2007). Consequently, careful examination of the morphology remains to date the best way to deal with sexual dimorphism.

On the other hand, Brökeland (2010) and Riehl and Brandt (2010) pointed out that, while females of haploniscid and macrostylid isopods are difficult to distinguish in some cases using morphology, the adult males usually are distinguishable.

Consequently, the various characters affected by the expression of dimorphisms may hold valuable information for systematic research. We recommend the use of integrative approaches to the taxonomy including morphology as well as DNA data where possible for multiple-evidence based allocation of sexually dimorphic conspecifics (see also Pilgrim & Pitts 2006; Brix *et al.* 2011). Once the expression of dimorphism has been described, the characters involved will hold valuable information for inferring the lifestyle and evolution of those taxa. The above mentioned characters also should be evaluated for species that show stronger dimorphism. We argue that the inclusion of sexually dimorphic characters will most likely result in improved phylogenetic and taxonomic resolution.

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References

Alcock, J. (1980) Natural selection and the mating systems of solitary bees. *American Scientist*, 68(2), 146–153.

Birstein, Y.A. (1963) *Deep Sea Isopod Crustaceans of the Northwestern Part of the Pacific Ocean.* Institute of Oceanology, Academy of Sciences, USSR: Moscow. (*In Russian with English summary)*.

Birstein, Y.A. (1970) New Crustacea Isopoda from the Kurile-Kamchatka Trench area. *Fauna of the Kurile–Kamchatka Trench and its environment, VG Bogorov (ed.)*, 86, 308–356. (*In Russian)*.

Birstein, Y.A. (1973) Deep water isopods (Crustacea. Isopoda) of the north-western part of the Pacific Ocean. *Akademiya Nauk, SSSR: Moscow*, 1–213. (*In Russian)*.

Boyle, E.E., Zardus, J.D., Chase, M.R., Etter, R.J. & Rex, M.A. (2004) Strategies for molecular genetic studies of preserved deep-sea macrofauna. *Deep-Sea Research I*, 51(10), 1319–1336.

Brandt, A. (1992) New Asellota from the Antarctic deep sea (Crustacea, Isopoda, Asellota), with descriptions of two new genera. *Zoologica Scripta*, 21(1), 57–78.

Brandt, A. (2002) *Desmostylis gerdesi*, a new species (Isopoda: Malacostraca) from Kapp Norvegia, Weddell Sea, Antarctica. *Proceedings of the Biological Society of Washington*, 115(3), 616–627.

Brandt, A. (2004) New deep-sea species of Macrostylidae (Asellota: Isopoda: Malacostraca) from the Angola Basin off Namibia, South West Africa. *Zootaxa*, 448, 1– 35.

Brix, S., Riehl, T. & Leese, F. (2011) First genetic data for *Haploniscus rostratus* and *Haploniscus unicornis* from neighbouring deep-sea basins in the South Atlantic. *Zootaxa*, 2838, 79–84.

Brökeland, W. (2010) Description of four new species from the *Haploniscus unicornis* Menzies, 1956 complex (Isopoda:Asellota: Haploniscidae). *Zootaxa*, 2536, 1–35.

Coleman, C.O. (2003) ”Digital inking”: how to make perfect line drawings on computers. *Organisms Diversity & Evolution*, 3(4), 303–304.

Coleman, C.O. (2009) Drawing setae the digital way. *Zoosystematics and Evolution*, 85(2), 305–310.

Cunha, M.R. & Wilson, G.D.F. (2006) The North Atlantic genus *Heteromesus* (Crustacea: Isopoda: Asellota: Ischnomesidae). *Zootaxa*, 1192, 1–76.

Dallwitz, M.J. (1980) A general system for coding taxonomic descriptions. *Taxon*, 29(1), 41–46.

Darwin, C. (1874) *The descent of man, and selection in relation to sex*. Second Edition. John Murray, London, 797 pp.

Doti, B.L. & Wilson, G.D.F. (2010) The genera *Carpias* Richardson, *Ianiropsis* Sars and *Janaira* Moreira & Pires (Isopoda: Asellota: Janiridae) from Australia, with description of three new species. *Zootaxa*, 2625, 1–39.

Fernandes, F. de F., Pimenta, P.F.P. & Linardi, P.M. (2004) Antennal sensilla of the New World screwworm fly, *Cochliomyia hominivorax* (Diptera: Calliphoridae). *Journal of Medical Entomology*, 41(4), 545–551.

France, S.C. & Kocher, T.D. (1996) DNA sequencing of formalin-fixed crustaceans from archival research collections. *Molecular Marine Biology and Biotechnology*, 5(4), 304–313.

Gandon, S. (1999) Kin competition, the cost of inbreeding and the evolution of dispersal. *Journal of Theoretical Biology*, 200(4), 345–364.

Gurjanova, E. (1933) Die marinen Isopoden der Arktis. *Fauna Arctica*, 6(5), 391–470.

Hansen, H.J. (1916) Crustacea Malacostraca: The order Isopoda. *Danish Ingolf Expedition*, 3(5), 1–262.

Hennig, W. (1965) Phylogenetic systematics. *Annual Review of Entomology*, 10(1), 97–116.

Hessler, R.R. (1970) The Desmosomatidae (Isopoda, Asellota) of the Gay Head–Bermuda Transect. *Bulletin of the Scripps Institution of Oceanography*, 15, 1–185.

Hessler, R.R. & Sanders, H.L. (1967) Faunal diversity in the deep sea. *Deep-Sea Research*, 14, 65–78.

Hessler, R.R. & Strömberg, J.O. (1989) Behavior of janiroidean isopods (Asellota), with special reference to deep sea genera. *Sarsia*, 74(3), 145–159.

Jormalainen, V. (1998) Precopulatory mate guarding in crustaceans: male competitive strategy and intersexual conflict. *The Quarterly Review of Biology*, 73(3), 275–304.

Jormalainen, V. & Merilaita, S. (1995) Female resistance and duration of mate-guarding in three aquatic peracarids (Crustacea). *Behavioral Ecology and Sociobiology*, 36(1), 43–48.

Jourdan, H., Barbier, R., Bernard, J. & Ferran, A. (1995) Antennal sensilla and sexual dimorphism of the adult ladybird beetle *Semiadalia undecimnotata* Schn. (Coleoptera: Coccinellidae). *International Journal of Insect Morphology and Embryology*, 24(3), 307–322.

Just, J. & Wilson, G.D.F. (2004) Revision of the *Paramunna* complex (Isopoda: Asellota: Paramunnidae). *Invertebrate Systematics*, 18(4), 377–466.

Kaiser, S. & Brix, S. (2007) Two new species of the genus *Pseudomesus* Hansen, 1916 (Isopoda, Asellota) from the southern hemisphere: *Pseudomesus pitombo* sp. nov. and *Pseudomesus satanus* sp. nov. *Zootaxa*, 1658, 21–38.

Kaiser, S., Barnes, D.K.A. & Brandt, A. (2007) Slope and deep-sea abundance across scales: Southern Ocean isopods show how complex the deep sea can be. *Deep-Sea Research Part II*, 54(16–17), 1776–1789.

Kavanagh, F.A. & Sorbe, J.-C. (2006) *Haplomesus longiramus* sp. nov. (Crustacea: Isopoda: Asellota), a new ischnomesid species from the Bay of Biscay, North East Atlantic Ocean. *Zootaxa*, 1300, 51–68.

Kavanagh, F.A. & Wilson, G.D.F. (2007) Revision of the genus *Haplomesus* (Isopoda: Asellota: Ischnomesidae) with erection of four new genera. *Invertebrate Systematics*, 21(5), 487–535.

Kelley, J. (1993) Taxonomic implications of sexual dimorphism in *Lufengpithecus*. *In:* Kimbel, W. H. & Martin, L. B. (Eds), *Species, Species Concepts, and Primate Evolution*, Plenum Press, New York, pp. 429–458.

Koh, Y.H., Park, K.C. & Boo, K.S. (1995) Antennal sensilla in adult *Helicoverpa assulta* (Lepidoptera: Noctuidae): morphology, distribution, and ultrastructure. *Annals of the Entomological Society of America*, 88(4), 519–530.

Kussakin, O.G. (1999) *Morskye I solonovatovodnye ravnonogie rakoobrasnye (Isopoda) cholodnix I umerennix vod severnogo polushariya [Marine and brackishwater likefooted Crustacea (Isopoda) from the cold and temperate watersof the Northern Hemisphere] Suborder Asellota. Part 2. Families Joeropsididae, Nannoniscidae, Desmosomatidae, Macrostylidae).*(Alimov, A. F., Ed.), Izdavaemye Zoologischeskim Institutom Rossiiskiya Akademiya Nauk, St. Petersburg, 383 pp

Lande, R. (1980) Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, 34(2), 292–305.

Latreille, P.A. (1802) Histoire naturelle générale et particuliè re des Crustacés et des Insectes. *In:* de Buffon, G. L. L. (Ed.), *Histoire Naturelle, nouvelle edition, accompagnee des notes.* Paris, 467 pp.

Lefebvre, F., Limousin, M. & Caubet, Y. (2000) Sexual dimorphism in the antennae of terrestrial isopods: a result of male contests or scramble competition? *Canadian Journal of Zoology,* 78(11), 1987–1993.

Martens, K. (1987) Homology and functional morphology of the sexual dimorphism in the antenna of *Sclerocypris* Sars, 1924 (Crustacea, Ostracoda, Megalocypridinae). *Bijdragen tot de Dierkunde*, 57(2), 183–190.

Meinert, F.V.A. (1890) Crustacea malacostraca. *Videnskabelige udbytte af kanonbaden "Hauchs Dogter"* pp. 147–230.

Menzies, R.J. (1962) The isopods of abyssal depths in the Atlantic Ocean. *In:* Barnard, J. L., Menzies, R. J., & Bacescu, M. C. (Eds), *Abyssal Crustacea*. pp 79–206. Columbia University Press, New York.

Menzies, R.J. & George, R.Y. (1972) Isopod Crustacea of the Peru–Chile Trench. *Anton Bruun Report,* 9, 1–124.

Mezhov, B.V. (1988) The first findings of Macrostylidae (Isopoda, Asellota) in the Indian Ocean. *Zoologicheskii Zhurnal*, 67(7), 983–994. (*In Russian)*.

Mezhov, B.V. (1992) Two new species of the genus *Macrostylis* G.O.Sars, 1864 (Crustacea Isopoda Asellota Macrostylidae from the Antarctic. *Arthropoda Selecta,* 1(2), 83–87. (*In Russian with English summary)*.

Mezhov, B.V. (1999) Four new species of the genus *Macrostylis* (Crustacea, Isopoda, Macrostylidae) from the Atlantic Ocean abyssal zone. *Zoologicheskii Zhurnal*, 78(12), 1417–1423. (*In Russian with English summary)*.

Pilgrim, E.M. & Pitts, J.P. (2006) A molecular method for associating the dimorphic sexes of velvet ants (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society,* 79, 222–230.

Riehl, T. & Brandt, A. (2010) Descriptions of two new species in the genus *Macrostylis* Sars, 1864 (Isopoda, Asellota, Macrostylidae) from the Weddell Sea (Southern Ocean), with a synonymisation of the genus *Desmostylis* Brandt, 1992 with *Macrostylis*. *ZooKeys,* 57, 9–49.

Sanders, H.L. & Hessler, R.R. (1969) Ecology of the deep-sea benthos. *Science,* 163(874), 1419.

Sanders, H.L., Hessler, R.R. & Hampson, G. R. (1965) An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head–Bermuda transect. *Deep Sea Research and Oceanographic Abstracts*, 12(6), 845–867.

Sars, G.O. (1864) Om en anomal Gruppe af Isopoder. *In: Forhandhlinger Videnskapsselskapet I Kristiania, Anar 1863,* pp. 205–221.

Sars, G.O. (1899) *An account of the Crustacea of Norway: with short descriptions and figures of all the species: Vol. 2, Isopoda*. Bergen Museum, Bergen, Norway, 270 pp.

Schafer, R. & Sanchez, T.V. (1976) The nature and development of sex attractant specificity in cockroaches of the genus *Periplaneta*. I. Sexual dimorphism in the distribution of antennal sense organs in five species. *Journal of Morphology,* 149(2), 139–157.

Shuster, S.M. (2008) The expression of crustacean mating strategies. In: Brockmann, H. J. & Oliveira, R. F. (Eds), *Alternative reproductive tactics: an integrative approach*, Cambridge University Press, Cambridge, pp. 224–250.

Sibley, C.G. (1957) The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. *The Condor,* 59(3), 166–191.

Siebenaller, J. & Hessler, R.R. (1977) The Nannoniscidae (Isopoda, Asellota): *Hebefustis* n. gen. and *Nannoniscoides* Hansen. *Transactions of the San Diego Society of Natural History,* 19(2), 17–43.

Skage, M. & Schander, C. (2007) DNA from formalin-fixed tissue: extraction or repair? That is the question. *Marine Biology Research*, 3(5), 289–295.

Svavarsson, J. (1984) Ischnomesidae (Isopoda: Asellota) from bathyal and abyssal depths in the Norwegian and North Polar Seas. *Sarsia*, 69(1), 25–36.

Teodorczyk, W. & Wägele, J. (1994) On Antarctic species of the genus *Munna* Kroeyer, 1839 (Crustacea, Isopoda, Asellota, Munnidae). *Bulletin of the National Museum of Natural History, Paris*, 16, 111–201.

Thistle, D. & Wilson, G.D.F. (1987) A hydrodynamically modified, abyssal isopod fauna. *Deep-Sea Research. Part A. Oceanographic Research Papers*, 34(1), 73–87.

Veuille, M. (1980) Sexual behaviour and evolution of sexual dimorphism in body size in *Jaera* (Isopoda Asellota). *Biological Journal of the Linnean Society*, 13(1), 89–100.

Wilson, G.D.F. (1989) A systematic revision of the deep-sea subfamily Lipomerinae of the isopod crustacean family Munnopsidae. *Bulletin of the Scripps Institution of Oceanography*, 27, 1–138.

Wilson, G.D.F. (1991) Functional morphology and evolution of isopod genitalia. *Crustacean Sexual Biology. Columbia University Press, New York*, 228–245.

Wilson, G.D.F. (2008a) A review of taxonomic concepts in the Nannoniscidae (Isopoda, Asellota), with a key to the genera and a description of *Nannoniscus oblongus* Sars. *Zootaxa*, 1680, 1–24.

Wilson, G.D.F. (2008b) Local and regional species diversity of benthic Isopoda (Crustacea) in the deep Gulf of Mexico. *Deep-Sea Research Part II,* 55, 2634–2649.

Wilson, G.D.F. (2009) The phylogenetic position of the Isopoda in the Peracarida (Crustacea: Malacostraca). *Arthropod Systematics & Phylogeny,* 67(2), 159–198.

Wolff, T. (1956) Isopoda from depths exceeding 6000 meters. *Galathea Report,* 2, 85–157.

Wolff, T. (1962) The systematics and biology of bathyal and abyssal Isopoda Asellota. *Galathea Report*, 6(3), 1–320.