A preliminary review of Parastenheliidae (Crustacea, Copepoda, Harpacticoida) and description of a new species from Victoria, Australia

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Abstract

Prior to this study the family Parastenheliidae contained 10 species of *Parastenhelia* and four species of *Karllangia*. Two "formae" of *P. spinosa* and two subspecies of *K. arenicola* were also recognised. Using cladistic analyses, the monophyly of the Parastenheliidae is tested. Results suggested the genus *Karllangia* should be synonymised with *Parastenhelia* and the two "formae" and two subspecies in the family be given species status. This investigation however, should be considered preliminary as analyses are based largely on information obtained from the literature.

In addition, a new species of *Parastenhelia* is described from Port Phillip Bay, Victoria, Australia and *P. spinosa* (also collected from Port Phillip Bay) is redescribed. A key to the world species is also provided.

Introduction

Harpacticoid copepods are minute crustaceans in the order Harpacticoida, subclass Copepoda (Huys and Boxshall, 1991), class Maxillopoda. There are approximately 50 families and 460 genera of Harpacticoida. The total number of described species has been estimated to be between 3000 (Huys et al., 1996) and 4000 to 4500 (Giere, 1993). Harpacticoids are found in marine, estuarine and freshwater environments and also inhabit the terrestrial realm, occurring in mosses and leaf-litter. The majority are free-living and benthic, although there are a few pelagic and symbiotic species (Hicks and Coull, 1983).

Little is known of the composition of harpacticoid fauna in Australia. In a comprehensive book on meiobenthology, Giere (1993: p. 4) noted the lack of knowledge of Australian Harpacticoida stating "wide areas in Africa, South America, Asia and Australia remain terra incognita in the field of meiobenthology; their coast and inland meiobenthos still awaits description ". Published taxonomic work on marine species (including those from saline lakes) has recorded 94 harpacticoid species in Australia with 64 of these being potentially endemic, as they are yet to be found outside Australian waters. Published records document only five harpacticoid species from Victoria: *Longipedia nichollsi* Wells, 1980, which is also found in South Australian and Fiji; two found associated with the wood boring isopod *Limnoria* (i.e. *Donsiella victoriae* Hicks, 1988 and *Oligoxylora cooksoni* Hicks, 1988), another associated with a sponge (i.e. *Hamondia superba* Huys, 1990) and most recently a species described from seagrass (i.e. *Porcellidium poorei* Walker-Smith, 2001). However, an unpublished survey of the harpacticoid fauna of Port Phillip Bay, Victoria, Australia, has revealed the presence of a large number of species in the seagrass *Heterozostera tasmanica* (Martens ex Ascherson) den Hartog, and on the surrounding sediments (Walker-Smith, 2003). Included in the array of species from Port Phillip Bay was a new species of *Parastenhelia* Thompson & Scott, 1903, as well as specimens of *Parastenhelia spinosa* (Fischer, 1860) (Walker-Smith, 2003).

Parastenhelia is the type genus of the family Parastenheliidae Lang, 1944 but historically the genus has been placed in several other families. Thompson and A. Scott (1903) established *Parastenhelia* to differentiate two new species from *Stenhelia* Boeck, 1865 (i.e. *Parastenhelia hornelli* Thompson and A. Scott, 1903 and *P. similis* Thompson and A. Scott, 1903) and placed it in the family Harpacticidae Sars, 1904. At that time, Harpacticidae was broadly defined by Claus (1863) but in 1904, Sars restricted the definition and is now recognised as the author of Harpacticidae (Lang, 1948). In 1912, T. Scott described *P. antarctica* sp. nov. and acknowledged the presence of three other species of *Parastenhelia* (*P. hornelli*, *P. similis* and *P. angelica* Norman and T. Scott, 1905) all of which he placed in the family Canthocamptidae Sars, 1906. T. Scott (1912) made no mention of *P. gracilis* Brady, 1910 or *P. tenuis* Brady, 1910. In 1927, Gurney synonymised *P. antarctica* with *P. gracilis* and noted *P. tenuis* did not belong in the genus *Parastenhelia*. While Gurney (1927) recognised *Parastenhelia* as a member of the family Canthocamptidae, Monard (1927) moved *Parastenhelia* to the family Diosaccidae Sars, 1906. Lang (1934) synonymised *Microthalestris* Sars, 1905 with *Parastenhelia* and placed *Parastenhelia* in the Thalestridae Sars, 1905. Later, Lang (1936) established the subfamily Parastenheliinae (within the Thalestridae) for *Parastenhelia* in recognition of a combination of characters not seen in other genera of Thalestridae. Lang (1936) suspected elevation to family status was warranted but was unsure if the genus belonged in the Canthocamptidae. He admitted he did not know the Canthocamptidae well enough to eliminate this possibility. In 1944, Lang erected Parastenheliidae for the genus *Parastenhelia* and designated *Harpacticus spinosa* Fischer, 1860 as the type species; Thompson and Scott (1903) had not assigned a type species for *Parastenhelia*. Lang (1944) suggested the diagnosis of the family be the same as that of *Microthalestris* (a junior synonym of *Parastenhelia*) and synonymised *Thalestrella* Monard, 1935 with *Parastenhelia*.

Bodin (1997) and others (e.g. Willen, 2000) attributed the authorship of Parastenheliidae to Lang, 1944. However, Lang (1936) first used in the name Parastenheliinae as a sub-family name and in accordance with the Principle of Coordination applied to family-group names (ICZN Art. 36.1) Lang, 1936 should be considered as the authority of the family Parastenheliidae as authorship and date remain unchanged at every rank. Huys and Boxshall (1991) recognised the correct authorship of Parastenheliidae as Lang, 1936.

Lang (1944) established the Thalestridimorpha for the families Diosaccidae, Balaenophilidae Sars, 1910, Miraciidae Dana, 1846, Parastenheliidae and Thalestridae. In a recent phylogenetic analysis, Parastenheliidae was recognised as the most primitive taxon in the Thalestridimorpha (Willen, 2000). It was the presence of several pleisomorphic characters within the Parastenheliidae that resulted in its placement at the base of the Thalestridimorpha (Willen, 2000). Based on her new diagnosis of the Parastenheliidae Willen (2000) suggested *Karllangia* Noodt, 1964 could be moved from Ameiridae Monard, 1927 to Parastenheliidae. Willen (2000) acknowledged Mielke (1994) had previously questioned the placement of *Karllangia* in Ameiridae.

At present Parastenheliidae contains 10 species of *Parastenhelia* and four species of *Karllangia*. Bodin (1997) also recognised two "formae" of *P. spinosa* and two subspecies of *K. arenicola* Noodt, 1964. Bodin (1997) listed *K. arenicola psammophila* Wells, 1967 as a synonym of *K. arenicola arenicola* Noodt, 1964 and attributed the synonymy to Wells and Rao (1987). However, Wells and Rao (1987) assigned subspecific status to *Karllangia psammophila*, placing it in the genus *K. arenicola* and giving it the subspecies name *K. arenicola psammophila* they did not synonymise it. Mielke (1994) disputed Wells and Rao's (1987) assignment of subspecific status to *K. psammophila* and suggested *K. arenicola bengalensis* Wells and Rao, 1987 be a subspecies of *K. psammophila* or a genus in its own right.

The description of a new Australian species of *Parastenhelia* and confusion over the rank of several taxa with Parastenheliidae has prompted the monophyly of the family to be assessed. This investigation of the phylogeny of Parastenheliidae should be viewed as preliminary since the cladistic analyses are based largely on information obtained from the literature. To undertake a more thorough analysis, redescription of several poorly described species needs to be completed but this is beyond the scope of this project. In addition, a key to the world species is presented.

Material and Methods

Specimens were collected from St Leonards and Grassy Point in Port Phillip Bay, Victoria, Australia. Material was collected by hand from the seagrass *Heterozostera tasmanica* and adjacent unvegetated sediments. Harpacticoids were fixed in 4% buffered formalin and transferred to 70% ethanol after at least 48 hours. Harpacticoids were dissected in a drop of glycerol (on a microscope slide) using electrolytically sharpened tungsten needles. Appendages and whole animals were mounted in glycerol on microscope slides and covered with a glass coverslip. Appendages were examined with an Olympus BX50 compound microscope using Nomarski interference contrast and drawn with the aid of a camera lucida (drawing tube). All geographical coordinates were obtained from maps of Victoria and Port Phillip Bay with scale of 1:20,000.

Terminology used follows that of Huys and Boxshall (1991). Abbreviations used are: A1, antennules or first antennae; A2, antennae or second antennae; Mx1, maxillules; Mx, maxillae; and Mxp, maxillipeds. P1–P4 refers to swimming legs 1–4. Individual segments of P1–P4 rami are written (for example) as P1 exopod-3, which refers to the third or terminal segment of the P1 exopod. P5 and P6 refer to the fifth and sixth legs. The term armature elements refer to setae and spines. Total length is measured from the base of the rostrum to the posterior margin of the caudal rami (caudal setae excluded). Setal formulae for swimming legs were derive using the method devised by Lang (1934) (also see Huys and Boxshall, 1991: p. 29). Scale bars on illustrations are labelled with lower case letters that correspond to the figure labelled with the same letter but in an upper case font. Type material has been deposited in the collections of Museum Victoria (NMV). All diagnoses are for females unless otherwise stated.

Phylogenetic analyses

Cladistic analyses were used to generate trees of monophyletic groups as hypotheses of relationships between selected taxa. The relationship between genera was of greatest interest. Thirty-six characters were scored for each taxon (table 1) resulting in a matrix of 21 taxa and 36 characters (table 2). Character states for all described species where scored using available literature. The character states of *P. spinosa* were taken from the literature and from specimens collected in Port Phillip Bay. The new species of *Parastenhelia*, described herein, is referred to in the matrix and the cladograms as *Parastenhelia* sp. nov. All characters were initially treated as unordered and unweighted. A second analysis using unordered, successively weighted characters was conducted in an attempt to obtain a more structured tree (i.e. to remove the two polytomies).

Parastenheliidae has been identified as the most primitive family within the Thalestridimorpha (Willen, 2000). Willen (2000) suggested the monospecific genus *Protolatiremus* Itô, 1974 was a sister taxon to the Thalestridimorpha and thus *Protolatiremus sakaguchii* Itô, 1974 was used as an outgroup in the cladistic analyses of Parastenheliidae. The ancestral harpacticoid, as defined by Huys and Boxshall (1991), was also used as an outgroup.

Cladistic analyses were conducted using the parsimony function in PAUP*4.0b10 (beta-test version for windows) (Swofford, 2001). Heuristic searches were made with the treespace search using tree bisection and reconnection (TBR) with randomised addition of taxa (addseq=random). One thousand replications were completed and the branch swapping option was set to save no more than three trees with length greater than or equal to the shortest tree found in each replicate (nreps=1000, nchuck=3, chuck score=1, randomize=trees). The “reweight” option was used to achieve greater resolution. Characters are “reweighted” to a constant weight base using the rescaled initial consistency indices. Three successive “reweight” runs were conducted (using the heuristic protocol outlined above). A 50% majority-rule and strict consensus tree of the parsimony trees produced using reweighted characters are also presented.

The stability of the clades was assessed using bootstrap. Bootstrap was conducted in PAUP* and analysis was based on 1000 pseudoreplicates. The treespace search used 5 random-addition sequence iterations with 10 trees saved per iteration (nreps=5; addseq=random; nchuck=10).

Character state changes were mapped on tree 2, one of the three shortest trees. Only clades and synapomorphies common to all parsimony trees were labelled. All trees shown were edited using TreeView 1.6.5 (Page, 2001).

Results and Discussion

Phylogenetic analyses

Six equally parsimonious trees (tree length 89) resulted from the first analysis using unweighted characters. The strict consensus tree, produced from these six trees are shown in figure 1.

Automatic reweighting decreased the value of 21 of the 36 characters. Four characters (characters 15, 22, 25, 30) were given a zero weight effectively excluding them from the analysis. Five characters were given a weight less than or equal to 0.2 (characters 10, 11, 17, 20 and 28) leaving Twelve characters (characters 2, 3, 4, 7, 13, 18, 19, 23, 27, 33, 34 and 35) with character weights between 0.2 and one. The 15 characters with a weight of one were: 1, 5, 6, 8, 9, 12, 14, 16, 24, 26, 29, 31, 32 and 36.

Three parsimony trees (tree length 33.05) were produced after successive reweighting of characters and their statistics were: consistency index (CI) = 0.78; homoplasy index (HI) = 0.22; retention index (RI) = 0.88; rescaled consistency index (RC) = 0.68. The strict consensus tree and the 50% majority rule tree were identical, thus only the former is illustrated (fig. 2A)

Hypotheses of the evolution of the family Parastenheliidae and the clades apparent within the family should (theoretically) be discussed with reference to a “real” tree, that is, one of most parsimonious trees and not a consensus tree. Therefore the structure of tree number 2 will be discussed and the character state changes for the undisputed synapomorphies of clades retained in all parsimony trees were mapped on this tree (fig. 3A and table 3). The branch lengths for tree 2 are shown in figure 3B. Bootstrap values (above 50) for clades retained in all shortest trees are shown in figure 2B.

The family level clade in tree 2 (fig. 3A), clade 39, had good bootstrap support (100%). It was defined by ten synapomorphies, including eight that were unique to the clade: maxilliped exopod 1-segmented; P1 exopod-3 with four armature elements; P1 endopod 2-segmented; P1 endopod-3 with three setae; P2 endopod-2, inner margin with one seta; P3 endopod-2, inner margin with one seta; P4 endopod-2 with one seta; caudal rami with six setae. Within clade 39 there were two major clades, clade 27 and 38.

Clade 27 contained all the species of *Karllangia* (except *Karllangia tertia*), as well as two species of *Parastenhelia* and was defined by seven apomorphies. Although the bootstrap support for this clade was strong there were no characters, unique to this clade, on which generic status could be based. Within clade 27 there was a sub-clade of *Karllangia* species (clade 25) which had good bootstrap support (71%) and was defined by a character unique to the clade: A2 exopod sexually dimorphic. However, clade 25 (*Karllangia* spp.) could not be given the rank of genus, as this would have resulted in the other species in clade 27 becoming paraphyletic. Therefore, *Karllangia* must be synonymised with its senior synonym, *Parastenhelia*.

Clade 38 contained the remaining species of *Parastenhelia*. Clade 38 was defined by two apomorphies: A2 exopod with seven setae and P2 endopod of male 2-segmented. However, these characters changed within this clade. There was no bootstrap support for this clade.

Conversely, clade 36 had good bootstrap support (78%) and was defined by four apomorphies, including one unique to the clade: P1 exopod-3 with the setal formula 123. Although this clade contained most of the species originally assigned to *Parastenhelia*, this clade could not be give the rank of genus as this would have created paraphyletic taxa within the family.

This hypothesis for the evolution of the species within Parastenheliidae also indicated the formae *Parastenhelia spinosa bulbosa* and *Parastenhelia spinosa bulgarica* and the subspecies *Karllangia arenicola bengalensis* and *Karllangia arenicola psammophila* should be elevated to species status.

As *Parastenhelia spinosa bulbosa* and *Parastenhelia spinosa bulgarica* were not sister taxa to *Parastenhelia spinosa spinosa* there is not justification for maintaining the subspecific status of these taxa. The sister taxon to *Parastenhelia spinosa bulbosa* was *P. costata* and the possession (by *P. costata*) of the P3 endopod-3 with the setal formula 321 separated it from *P. spinosa bulbosa*. *Parastenhelia spinosa bulgarica* was separated from its sister taxon (*P. gracilis*) by the possession of four apomorphies: P2 exopod-1 with no inner seta; P2 endopod-1 with no inner seta; P4 exopod-1 with no inner seta; P5 exopod of female with seven setae. Therefore I give *P. spinosa bulbosa* and *P. spinosa bulgarica* species status.

Karllangia arenicola psammophila was separated from its sister taxon, *Karllangia arenicola bengalensis*, by the possession of three apomorphies: P1 endopod-1 inner seta extending beyond the distal margin of endopod-1; P2 exopod-3 with the setal formula 323; P4 exopod-1 inner seta present. Thus I believe both these species of *Karllangia* should be elevated to species level. As it has already been shown that *Karllangia* is a junior synonym of *Parastenhelia, Karllangia arenicola psammophila* should become *Parastenhelia psammophila* (Noodt, 1964) and *Karllangia arenicola bengalensis* should be known as *Parastenhelia bengalensis* (Wells and Rao, 1987).

In summary, the cladistic analyses suggested Parastenheliidae is a monogeneric family containing 19 species. The genus *Karllangia* has been synonymised with its senior synonym *Parastenhelia*.

Systematics

Family **Parastenheliidae** Lang

Parastenheliinae Lang, 1936: 23, 52.

Parastenheliidae.—Lang, 1944: 13.—Lang, 1948: 584–586.—Apostolov and Marinov, 1988: 134–135.—Willen, 2000: 43–44.

Type genus. Parastenhelia Thompson and A. Scott, 1903.

Composition. Parastenhelia.

Remarks.—Parastenheliidae is a monogeneric family and thus the diagnosis and description of the family is the same as for *Parastenhelia*.

Genus **Parastenhelia** Thompson and A. Scott

Parastenhelia Thompson and A. Scott, 1903: 263.—Lang, 1934: 22–25.—Lang, 1936: 23, 52.—Lang, 1944: 13.—Lang, 1948: 584–588.—Pallares, 1968: 63.

Microthalestris Sars 1905: 122–124.—Wilson, 1932: 204.

Thalestrella Monard, 1935: 4.

Karllangia Noodt, 1964: 143.—Kunz, 1975: 199.

Type species. Harpacticus spinosa Fischer, 1860.

Composition. P. spinosa (Fischer, 1860); *P. hornelli* Thompson and A. Scott, 1903; *P. angelica* Norman and T. Scott, 1905; *P. gracilis* Brady, 1910; *P. ornatissima* (Monard, 1935); *P. bulbosa* Wells, 1963; ***P. arenicola*** (Noodt, 1964) comb. nov.; *P. bulgarica* Apostolov, 1968; *P. reducta* Apostolov, 1975; ***P. tertia*** (Kunz, 1975) comb. nov.; *P. megarostrum* Wells, Hicks and Coull, 1982; *P. costata* Pallares, 1982; *P. minuta* Pallares, 1982; *P. oligochaeta* Wells and Rao, 1987; ***P. bengalensis*** (Wells and Rao, 1987) comb. nov.; ***P. pulchra*** (Mielke, 1994) comb. nov.; *P. obscura* (Mielke, 1994) comb. nov.; ***P. jenkinsi*** sp. nov. (described herein).

Diagnosis

Female. Body elongate, strong flexure between prosome and urosome. A1 with 8–9 segments, but commonly with 9; A1 segment 4 and terminal segment with an aesthetasc. A2 exopod generally 2-segmented, rarely 3-segmented, with 5–7 setae, proximal seta on exopod-1 miniaturised. Mandible endopod 1-segmented with 7 setae at most; exopod 1-segmented, shorter than endopod and with 4 setae at most. Mx1 basis with 6 setae at most; endopod with 4 setae at most; exopod lost (except in *P. jenkinsi* sp. nov.) but represented by 3 setae at most. Mx endopod represented by 3 setae at most; praecoxal endite bilobed, each lobe with 2 setae at most. Mxp coxa with 3 setae at most. P1 endopod

2-segmented; endopod-1 elongate; endopod-2 with 2 spines and 1 seta. P1 exopod segments approximately equal or exopod-2 distinctly longer than exopod-1 and exopod-3; exopod-3 with 3 spines and 1 seta. P2 endopod-2 inner margin with 1 seta; endopod-3 with 1 plumose seta and 1 spinose seta terminally and 1 spinose spine subterminally or P2 endopod-3 with 2 plumose seta terminally and 1 spinose spine subterminally. P3 endopod-2 inner margin with 1 seta; endopod-3 with 2 setae. P4 endopod-2 inner margin with 1 seta. For setal formulae for swimming legs see table 4. P5 baseoendopod, endopodal lobe small, triangular, with 5 setae (rarely with 4 setae); exopod elongate, at least twice as long as wide, most commonly with 6 setae (occasionally with 7 or 8). Genital double-somite sometimes with an epicopulatory bulb. Caudal rami with 6 setae, seta I lost.

Male. A1 haplocer, with 7–9 segments. A2 sexually dimorphic in some species, where by male exopod-1 has only 1 (well-developed) seta instead of 2 lateral setae also 1 terminal seta more highly developed than in female. P2 endopod-2 and -3 sometimes fused. P2 without modified setae; endopod 2- or 3-segmented. P3 endopod-3 sometimes with a spine-like projection. P5 baseoendopod, endopodal lobe with 2 setae (but occasionally with 1 seta); exopod sometimes 3-segmented, usually 1-segmented.

Remarks

Karllangia is synonymised with its senior synonym *Parastenhelia.*

Parastenhelia jenkinsi sp. nov.

(Figs 4–9)

Material examined

Holotype. Ovigerous female (NMV J47099, on 8 slides). Collected from sand near the seagrass *Heterozostera tasmanica* in 1 metre of water at St Leonards (38°11'S 144°42'E), Port Phillip Bay, Victoria. Collected by G. Walker-Smith, 24 October 1997.

Paratypes. NMV J47098 (1 male, on 6 slides, *allotype*); NMV J47097 (1 female, on 1 slide); NMV J47096 (1 female, on 2 slides); NMV J47095 (1 female, on 3 slides); NMV J47094 (1 female, on 1 slide); NMV J47093 (1 female, on 2 slides); NMV J47092 (10 females, 4 males). All paratypes collected with holotype.

Diagnosis

Rostrum large, extending at least to A1 segment 5. A1 9-segmented. A2 exopod 2-segmented, with 6 setae. Mxp syncoxa with 3 plumose setae. P1 exopod-2 approximately same length as exopod-1 and exopod-3; endopod at most one third longer than exopod; endopod-1 inner seta long, extending beyond endopod-2. P1 basis of male with a modified seta. P2 and P3 endopod longer than exopod.

P2–P4 endopod-3 with 1 plumose seta and 1 spinose seta terminally and 1 spinose spine subterminally. P3 endopod-3 of male with a spine-like projection. P5 baseoendopod of male, endopodal lobe with 1 spinose seta and 1 small, smooth seta; exopod 1-segmented. Genital field without epicopulatory bulb.

Adult measurements

Females: mean length 0.83±0.02 mm (*n*=6). *Males*: mean length 0.47±0.01 mm (*n*=8).

Description of holotype

Total length 0.81 mm. Rostrum (figs 4A, 4B and 5A) defined at base, elongate, extending at least to A1 segment 5, with parallel margins, tip with rounded subterminal cuticular outgrowth and a pair of sensillae. Somites of prosome with marginal sensillae. Urosome with rows of spinules, dorsally (fig. 4B) and ventrally (fig. 9E). Genital field (fig. 9E) without epicopulatory bulb. Anal operculum with pointed cuticular outgrowths. Caudal ramus short, broader than long, with 6 setae.

Antennule (fig. 5B). 9-segmented, segment 1 longest. Aesthetasc on segment 4 and segment 9.

Antenna (fig. 5C). Allobasis with spinose setae. Exopod 2-segmented, segment-1 with smooth setae and 1 spinose seta, segment 2 with 2 spinose seta and 3 smooth setae. Endopod with 3 geniculate, spinose setae, 3 setae with fine setules along outer margin and 1 long, smooth seta joined at the base to a spinose seta.

Mandible (fig. 6A). Coxa robust, tapering to cutting edge. Basis with 1 smooth seta and 1 spinose seta. Endopod 1-segmented, with 3 plumose setae along lateral margin, and 3 smooth setae terminally (2 are joined basally). Exopod 1-segmented, with 2 plumose setae.

Maxillule (fig. 6B). Arthrite of praecoxa with apical and subapical spines. Coxa with 3 smooth setae and 1 spinulose seta representing the epipodite. Basis with 4 setae. Endopod with 3 setae. Exopod small, with 1 long, spinulose seta and 2 shorter smooth setae.

Maxilla (fig. 6C). Syncoxa with 3 endites. Basis with strong claw. Endopod 1-segmented, with 2 smooth setae.

Maxilliped (fig. 6D). Prehensile. Syncoxa with 3 setae. Basis with 2 rows of spinules and 2 rows of fine setules, inner margin with 1 plumose seta. Endopod with spinose claw with 1 plumose seta inserted proximally.

P1 (fig. 7A). Intercoxal sclerite naked. Coxa with 2 rows of robust spinules and 2 rows of delicate spinules. Basis with 1 spinulose seta and spinules on outer margin and 1 spinose seta above endopod, this seta has 2 or 3 small spinules basally (figs 7A and 7B). Exopod-2 approximately same length as exopod-1 and exopod-3. Exopod-1 and -2 with marginal spinules and 1 spinulose spine. Exopod-2 inner margin with 3 fine, naked setae and 1 slightly larger, naked seta. Exopod-3 with 2 subterminal spinulose setae and 1 spinulose, geniculate seta and 1 plumose seta terminally. Endopod-1 with spinules along inner margin and 1 long, plumose seta inserted above midpoint and reaching beyond endopod-2. Endopod-2 with 2 spinulose setae and 1 plumose seta terminally.

P2 (fig. 7B). Intercoxal sclerite naked. Basis with rows of spinules and a short seta. Endopod longer than exopod. Exopod-1 outer margin with spinules and 1 spinulose seta, inner margin with a fine seta. Exopod-2 outer margin with spinules and 1 spinulose seta, inner margin with 1 long, plumose seta. Exopod-3 outer margin with 3 spinulose setae, inner margin with 1 long, plumose seta, 1 plumose seta and 1 spinulose seta terminally. Endopod-1 with 1 plumose seta. Endopod-2 with 1 long, plumose seta. Endopod-3 with 1 long, plumose seta on inner margin, 1 spinose seta subterminally and 1 spinose seta and 1 plumose seta terminally.

P3 (fig. 8A). Intercoxal sclerite naked. Basis with spinules and outer margin with 1 plumose seta. Endopod slightly longer than exopod. Exopod-1 outer margin with spinules and 1 spinulose seta, inner margin with 1 short, plumose seta. Exopod-2 outer margin with spinules and 1 spinulose seta, inner margin with 1 long, plumose seta. Exopod-3 with 3 spinulose setae along outer margin, inner margin with 3 plumose setae, the distal most one being very reduced; 1 plumose seta and 1 spinulose seta terminally. Endopod-1 with 1 short, plumose seta. Endopod-2 with 1 long, plumose seta. Endopod-3 with 3 plumose setae on inner margin (proximal 2 reduced in size), 1 spinose seta on outer margin and 1 plumose seta and 1 spinose seta terminally.

P4 (fig. 8B). Intercoxal sclerite naked. Basis with spinules and outer margin with plumose seta. Endopod shorter than exopod. Exopod-1 outer margin with spinules and 1 spinulose seta, inner margin with 1 plumose seta. Exopod-2 outer margin with spinules and 1 spinulose seta, inner margin with 1 plumose seta. Exopod-3 with 3 spinulose setae along outer margin, inner margin with 3 plumose setae, the distal most one being very reduced, 1 plumose seta and 1 spinulose seta terminally. Endopod-1 with 1 short, plumose seta. Endopod-2 with 1 long, plumose seta. Endopod-3 with 1 short seta and 1 long, plumose seta on inner margin; 1 spinose seta on outer margin and 1 plumose seta and 1 spinose seta terminally. Variation was observed in the holotype: endopod-3 of the right leg had only 1 inner seta but endopod-3 of the left leg exhibited the normal condition (as seen in paratypes) of 2 inner setae.

Setal formulae for swimming legs, see table 5.

P5 (fig. 9A). Baseoendopod endopodal lobe triangular, with distinctive chitinous striae along inner edge, and with 4 setae. Exopod elongate, twice as long as wide, tapering distally, with 4 spinulose setae and 2 small, naked setae.

P6 (fig. 9E). With 3 setae.

Urosome. As in figures 4B and 9E.

Colour unknown.

Description of male paratype J47098 (allotype)

As for female except: body length 0.47 mm; antennule (fig. 5D) haplocer 9-segmented; P1 inner seta on basis transformed into robust bent, hook-like structure (fig. 7C); P2 endopod-2 and endopod-3 fused, resulting in a 2-segmented endopod (fig. 7E); P3 endopod-2 with 1 smooth, inner seta and 1 longer, plumose seta, endopod-3 with a spine-like outgrowth (fig. 8D); P5 baseoendopod, endopodal lobe with 1 spinose seta, 1 small, smooth seta and small spinules along margins (fig. 9B); P5 exopod with 3 spinose setae along outer margin, 1 small, smooth seta subterminally, 1 long, spinose seta terminally, 1 shorter spinose seta on inner subterminal margin and 5 smooth setules along inner margin (fig. 9B); P6 with 3 setae (fig. 9C); urosome as in fig. 9C.

Variability

Holotype with P4 endopod-3 of left leg with one inner seta (fig. 10B) and right leg with two inner setae (fig. 10C). The normal condition as seen in other paratypes is two inner setae.

Etymology

Parastenhelia jenkinsi after Dr Greg Jenkins, who provided me with guidance and logistical support during my PhD.

Remarks

Parastenhelia jenkinsi differs from other *Parastenhelia* species in the following ways: rostrum large, extending to A1 segment 5 (also in *P. megarostrum* but all other species of *Parastenhelia* have a short rostrum that does not reach beyond the end of A1 segment-2); antennule 9-segmented (8-segmented in *P. arenicola*, *P. ornatissima,* and *P. reducta*); genital field without an epicopulatory bulb (present in *P. hornelli, P. megarostrum* and *P. oligochaeta*); A2 exopod with 6 setae (7 in *P. spinosa*, P. *tertia*; 5 in *P. obscura*, *P. pulchra* and *P. reducta*; 3 in *P. arenicola* and *P. bengalensis*); P1 exopod-2 approximately equal in length to P1 exopod-1 and exopod-3 (P1 exopod-2 more than double the length of P1 exopod-1 or P1 exopod-2 in *P. bulbosa*, *P. bulgarica*, *P. costata*, *P. gracilis, P. minuta* and *P. spinosa*); P3 male, endopod-3 with a spine-like projection, (no spine-like projection in *P. arenicola*, *P. bengalensis, P. megarostrum, P. obscura, P. pulchra, P. reducta* and *P. tertia*). P5 male, baseoendopod with 1 spinose seta and 1 small, smooth seta (1 smooth spine and 1 smaller, smooth seta in *P. bengalensis*, 1 smooth seta in *P. arenicola* and 2 spinose setae in all other *Parastenhelia*).

Parastenhelia jenkinsi is most similar to *P. megarostrum* as these are the only two species of *Parastenhelia* that have P2 and P3 endopods longer than the exopods and a rostrum that extends to A1 segment 5. *Parastenhelia jenkinsi* and *P. megarostrum* also have P3 and P4 endopod-3 with 1 plumose seta and 1 setose seta terminally and 1 spinose spine subterminally (*P. costata, P. arenicola*, *P. pulchra*, *P. obscura*, *P. spinosa* and *P. hornelli sensu* Wells and Rao, 1987 all have P3 and P4 endopod-3 with 2 plumose setae terminally; *P. oligochaeta* has P3 endopod-3 with 1 plumose seta and 1 spinose seta terminally and P4 endopod-3 with 2 plumose setae terminally; *P. tertia and P. bulgarica* P4 endopod-3 with 2 plumose setae but setal type for P3 is unknown; for *P. reducta*, *P. ornatissima*, *P. angelica*, *P. minuta* and *P. gracilis* the setal type is unknown.).

Parastenhelia spinosa (Fischer)

(Figs 10–16)

Material examined

NMV J47091 (ovigerous female, on 6 slides); NMV J47090 (1 male, on 6 slides); NMV J47089) 1 female, on 6 slides); NMV J47088 (1 female, on 1 slide); NMV J47087 (1 female, on 1 slide); NMV J47086 (1 female, on 2 slides), NMV J47085 (1 female, on 1 slide); NMV J47244 (3 females and 2 males); NMV J52500 (20 specimens); NMV J47084 (*aberrant female*, on 1 slide). All material collected, from seagrass (*Heterozostera tasmanica*) in approximately 1 metre of water at Grassy Point, Port Phillip Bay, Victoria, Australia (38°07'S 144°41'E) by G. Walker-Smith, 05 November 1997.

Rediagnosis

Rostrum defined at base, triangular, extending at most to end of A1 segment-2. A1 8-segmented. A2 exopod 2-segmented, with 7 setae. Mxp syncoxa with 2 setae. P1 exopod-2 distinctly longer that exopod-1 and exopod-3; endopod is not much longer than the exopod; endopod-1 inner seta short and placed proximally. Male P1 basis without modified seta. P2 and P3 endopod shorter than exopod. P2–P4 endopod-3 with 2 plumose setae terminally. P3 endopod-3 of male with a spine-like projection. P5 exopod of male generally 1-segmented but sometimes 3-segmented. Female genital field without epicopulatory bulb.

Adult measurements

Females: mean length 0.61±0.04 mm (*n*=11). *Males*: mean length 0.45±0.01 mm (*n*=4).

Description of adult female (NMV J47091)

Body (figs 10 and 11D). Total length 0.65 mm. Rostrum (figs 11B and 11D) defined at base, extending only to A1 segment 2, triangular, rounded at end and with a pair of sensillae. Somites of prosome with marginal sensillae, margins of somites serrate. Urosome with rows of spinules dorsally (fig. 11D) and ventrally. Genital field (fig. 16C) without epicopulatory bulb. Anal operculum with fine setules. Caudal ramus short, broader than long, with 6 setae.

Antennule (fig. 11A). 8-segmented, segments 2 and 3 approximately equal in length and longer than segment 1. Aesthetasc on segment 4 and segment 8.

Antenna (fig. 11C). Allobasis with spinose setae. Exopod 2-segmented, segment 1 with 2 setae, segment 2 with 2 setae on lateral margin; and 1 spinose seta and 2 smooth setae terminally. Endopod with 3 geniculate, terminally setose setae; 3 setae with fine setules on outer margin and 1 naked seta joined at the base to a spinose seta.

Mandible (fig. 12A). Coxa robust, tapering to cutting edge. Basis with patch of short, smooth setae, a row of spinules and 3 plumose setae. Endopod 1-segmented, with 1 plumose seta on lateral margin, and 4 smooth setae terminally. Exopod 1-segmented, with 2 plumose setae.

Maxillule (fig. 12B). Arthrite of praecoxa with 6 apical spines, distally spinose, 1 plumose seta subapically and surface with 2 plumose setae and a row of spinules. Coxa with 4 smooth setae and 1 plumose seta representing the epipodite. Basis with 4 setae. Endopod with 3 setae. Exopod represented by 3 setae.

Maxilla (fig. 12C). Syncoxa with 3 endites. Basis with strong spinose claw and 1 geniculate seta. Endopod reduced, represented by 2 smooth setae.

Maxilliped (fig. 12D). Prehensile. Syncoxa with 2 long, plumose setae. Basis with 2 rows of long spinules and 2 rows of shorter spinules, including 1 on inner edge, inner edge also with a spinulose seta. Endopod with fimbriate (fringed) claw.

P1 (fig. 13A). Intercoxal sclerite naked. Coxa with 2 rows of robust spinules and 3 rows of tiny spinules. Basis with 1 spinulose seta and spinules on outer margin and 1 spinose seta above endopod. Exopod-2 elongate, more than 3 times length of exopod-1. Exopod-1 with marginal spinules and 1 spinulose seta. Exopod-2 outer margin with tiny spinules and 1 smooth seta distally, inner margin with 3 fine naked setae proximally and 1 fine, naked seta distally. Exopod-3 with 2 subterminal fimbriate (fringed) setae and 1 geniculate seta with fine setules along distal half. Endopod-1 with fine setules along inner margin and 1 short, plumose seta inserted proximally, reaching to midpoint of endopod-1. Endopod-2 with 2 fimbriate spines and 1 small, naked seta terminally.

P2 (fig. 13B) intercoxal sclerite naked. Basis with rows of spinules and 1 spinulose seta on outer margin. Exopod-1 outer margin with spinules and 1 spinulose seta, inner margin without seta. Exopod-2 outer margin with spinules and 1 spinulose seta, inner margin with 1 seta. Exopod-3 outer margin with 3 spinulose setae, inner margin with 1 long, plumose seta; 1 plumose seta and 1 spinulose seta terminally. Endopod-1 with 1 short, inner seta. Endopod-2 inner margin with 1 distally serrate seta. Endopod-3 inner margin with 1 plumose seta, outer margin with 3 small spinules and 1 spinulose seta; 2 plumose setae terminally.

P3 (fig. 14A) intercoxal sclerite naked. Basis with spinules and outer margin with 1 plumose seta. Exopod-1 outer margin with spinules and 1 spinulose seta, inner margin without a seta. Exopod-2 outer margin with spinules and 1 spinulose seta, inner margin with 4 short, smooth setae and 1 plumose seta (fig. 14B), inner plumose seta absent on right P3 (fig. 14A) but present on left one, the normal condition in Port Phillip Bay specimens is 1 plumose seta. Exopod-3 with 3 spinulose setae along outer margin, inner margin with 3 plumose setae, the distal most one being slightly reduced in size, 1 plumose seta and 1 spinulose seta terminally. Endopod-1 with 1 small, naked seta. Endopod-2 inner margin with 1 serrate seta. Endopod-3 inner margin with 1 serrate seta and 1 plumose seta, outer margin with 1 spinulose seta; 2 plumose setae terminally.

P4 (fig. 14D) intercoxal sclerite naked. Basis with spinules and outer margin with 1 plumose seta. Exopod-1 outer margin with spinules and 1 spinulose seta, inner margin without seta. Exopod-2 outer margin with spinules and 1 spinulose seta, inner margin with 3 setules and 1 plumose seta. Exopod-3 with 3 spinulose setae along outer margin, inner margin with 3 setae, proximal one plumose, middle one serrate and the distal most one smooth and reduced in size; 1 plumose seta and 1 spinulose seta terminally. Endopod-1 with 1 small, naked seta. Endopod-2 inner margin with 1 serrate seta. Endopod-3 inner margin with 2 plumose setae, outer margin with 1 spinulose seta; 2 plumose setae terminally.

Setal formulae for swimming legs, see table 6.

P5 (fig. 16E). Baseoendopod, endopodal lobe triangular, without distinctive chitinous striae along inner edge; with 2 serrate setae and 3 spinose setae on inner margin, outer margin with 1 naked seta. Exopod elongate, length three times width, tapering distally; with 3 spinulose setae and 3 smooth setae.

P6 (fig. 16C). With 3 setae.

Colour unknown.

Description of adult male (NMV J47090)

As for female except: body length 0.45 mm; antennule haplocer, 9-segmented (fig. 11B); P2 (fig. 13C); P3 endopod-3 with a spine-like outgrowth (fig. 14C); P4 endopod-1 inner margin with 1 seta (fig. 14E); P5 baseoendopod, endopodal lobe with 2 spinose setae and small spinules along inner margin, outer margin with 1 naked seta (fig. 16D); P5 exopod with 4 spinose setae and 2 naked setae; urosome as in figures 16A and 16B.

Variability

An aberrant female (NMV J47084) with P1 exopod longer than endopod was found (fig. 15A). This specimen also had P2 (right leg) and P3 (left leg) with only two exopod segments (figs 15B and 15C). For the holotype the P3 exopod-2 of the right leg does not have an inner seta (fig. 14A) but the left leg shows the normal condition (as seen in other Port Phillip Bay specimens) of one inner seta (fig. 14B).

Remarks

Parastenhelia spinosa is recognised as a highly variable species (Monard, 1928; Lang, 1936, 1948; Mielke, 1974). The presence of *Parastenhelia spinosa* in Australia was first documented by Nicholls (1945a) collected who *P. spinosa* from algae on a reef fringing Leander Point at the southern end of the bay at Port Denison (near Dongarra), Western Australia. Nicholls (1945a) recorded his specimens as *Parastenhelia forficula* (Claus) and *Parastenhelia forficula* var. *littoralis* (Sars) but these names have since been synonymised (by Lang, 1948) with *P. spinosa*.

Key to the world species of *Parastenhelia*

(Character states are for female specimens except where males are explicitly referred to. Note triplet at 1)

1. P1 exopod segments approximately equal in length 2
— P1 exopod-2 approximately twice length of P1 exopod-3 .... *P. angelica*
— P1 exopod-2 more than 3 times length of P1 exopod-3 13
2. A1 8-segmented 3
— A1 9-segmented 4
3. P4 exopod-3 with the setal formula 323 5
— P4 exopod-3 with the setal formula 223 7
4. P3 exopod-3 with the setal formula 223 8
— P3 exopod-3 with the setal formula 323 9
5. P5 exopod of female, with 6 setae; P5 baseoendopod of male, endopodal lobe with 1 seta .... *P. arenicola*
— P5 exopod of female, with 5 setae; P5 baseoendopod of male, endopodal lobe with 2 setae ... 6
6. A2 exopod 1-segmented (or indistinctly 2-segmented); P2 expopod-3 with the setal formula 323 .... *P. psammophila*
— A2 exopod distinctly 2-segmented; P2 expopod-3 with the setal formula 223 .... *P. bengalensis*
7. P3 endopod-3 with the setal formula 221; P4 endopod-1 with 1 inner seta; P4 endopod-3 with the setal formula 221 .... *P. ornatissima*
— P3 endopod-3 with the setal formula 121; P4 endopod-1 without inner seta; P4 endopod-3 with the setal formula 121 .... *P. reducta*
8. A2 sexually dimorphic; P3 endopod-3 of male without distal spine-like projection; P2 exopod-3 with the setal formula 223; P2 endopod-1 with 1 inner seta 10
— A2 not sexually dimorphic; P3 endopod-3 of male with distal spine-like projection; P2 exopod-3 with the setal formula 123; P2 endopod-1 without inner seta .... *P. oligochaeta*
9. P1 endopod-1 inner seta shorter than endopod-1; P5 exopod of male with 4 or 7 setae 11
— P1 endopod-1 inner seta longer or as long as than endopod-1; P5 exopod of male with 6 setae 12
10. P2 endopod of male 2-segmented (segments 2 and 3 fused); P5 exopod of male with 5 setae; P2 exopod-1 with 1 seta on inner margin; P2 endopod-3 with the setal formula 221; P3 expopod-1 and P4 exopod-2 with 1 inner seta .... *P. tertia*
— P2 endopod of male 3-segmented; P5 exopod of male with 4 setae; P2 exopod-1 without inner seta. P2 endopod-3 with the setal formula 121; P3 expopod-1 and P4 exopod-1 without inner seta .... *P. pulchra*
11. A2 sexually dimorphic .... *P. obscura*
— A2 not sexually dimorphic .... *P. hornelli*

12.	Genital field with pear-shaped epicopulatory bulb; P2 and P3 not sexually dimorphic; P3 endopod-3 with the setal formula 221	*P. megarostrum*
—	Genital field without epicopulatory bulb; P2 and P3 sexually dimorphic (P2 of male 2-segmented (segments 2 and 3 fused); P3 of male, endopod-3 with spine-like outgrowth distally); P3 endopod-3 with the setal formula 321	*P. jenkinsi*
13.	P2 exopod-1 and endopod-1 with 1 inner seta	14
—	P2 exopod-1 and endopod-1 without inner seta	*P. bulgarica*
14.	Caudal rami outer apical seta with a bulbous base	*P. bulbosa*
—	Caudal rami outer apical seta without a bulbous base	15
15.	P1 endopod-1 without suture line; P2 endopod-3 with the setal formula 121	16
—	P1 endopod-1 with suture line; P2 endopod-3 with the setal formula 021	*P. minuta*
16.	P3 exopod-1 with 1 inner seta	17
—	P3 exopod-1 without inner seta	*P. spinosa*
17.	P3 exopod-3 with the setal formula 223	*P. gracilis*
—	P3 exopod-3 with the setal formula 323	*P. costata*

Discussion

The recognition of *Karllangia* as a junior synonym of *Parastenhelia* and the elevation of "formae" and two subspecies to species level, in addition to the discovery of a new species of *Parastenhelia* in Port Phillip Bay means Parastenheliidae is now a monogeneric family containing 19 species.

Although both *P. spinosa* and *P. jenkinsi* were collected in Port Phillip Bay their ecological niches overlap little. In Port Phillip Bay *P. spinosa* was common among the seagrass *Heterozostera tasmanica* but was rarely collected from the surface of the adjacent unvegetated sand. Conversely, *P. jenkinsi* was 12 times more common on the unvegetated sediment, adjacent to seagrass beds, than among the seagrass itself (Walker-Smith, 2003). World-wide *Parastenhelia* species have been recorded from coralline, filamentous and encrusting red algae (Pallares, 1982); *Durvillea* (brown alga) (Pallares, 1982), seagrass (Walker-Smith, 2003) and sand (e.g. Apostolov, 1975; Wells et al., 1982; Mielke, 1994).

Parastenhelia jenkinsi and *P. spinosa* are the only *Parastenhelia* species recorded from Australia, thus far.

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I would like to thank Dr Rony Huys for his useful suggestions regarding this family and two anonymous reviewers for their critical comments of this manuscript. This research was funded in part by a grant from the Australian Biological Resources Study.

Table 1. Character transformations used in the PAUP* analyses of Parastenheliidae.
Characters are for females unless otherwise stated.

Character no.	Character states
1	*Rostrum length*: (1) reaching beyond distal margin of A1 segment 2; (2) reaching to segment 1 or segment 2 of A1
2	*A1 number of segments*: (1) 9; (2) 8; (3) 7; (4) 5
3	*A1 segment 2*; (1) shorter than A1 segment 1; (2) at least 2 times length of A1 segment 1; (3) approximately equal in length or slightly longer (but not shorter) than A1 segment 1
4	*A2 exopod with*: (1) 3 setae; (2) 4 setae; (3) 5 setae; (4) 6 setae; (5) 7 setae
5	*A2 exopod of male*: (1) modified (different from that of females); (2) not modified (same as for females)
6	*Maxilliped exopod*: (1) multi-segment; (2) 1-segmented
7	*P1 exopod-2*: (1) approximately the same length as P1 exopod-3; (2) approximately twice length of P1 exopod-3; (3) elongate (more than three times length of P1 exopod-3)
8	*P1 exopod-3 with*: (1) 5 armature elements; (2) 4 armature elements
9	*P1 endopod*: (1) 3-segmented; (2) 2-segmented
10	*P1 endopod-1, inner seta situated*: (1) in proximal third of segment; (2) in middle third of segment; (3) seta absent
11	*P1 endopod-1 inner seta length*: (1) long (extending beyond the distal margin of endopod-1; (2) short (not extending beyond the distal margin of endopod-1)
12	*P1 endopod-3 with*: (1) 4 setae; (2) 3 setae
13	*P2 exopod-1 inner margin, seta*: (1) present; (2) absent
14	*P2 exopod-3 setal formula*: (1) 223; (2) 123; (3) 023; (4) 323
15	*P2 endopod-1 inner margin, seta*: (1) present; (2) absent
16	*P2 endopod-2 inner margin, with*: (1) 1 seta; (2) 2 setae
17	*P2 endopod-3 setal formula*: (1) 321; (2) 221; (3) 121; (4) 021
18	*P2 endopod of male*: (1) 3-segmented; (2) 2-segmented
19	*P3 exopod-1 inner margin, seta*: (1) present; (2) absent
20	*P3 exopod-3 setal formula*: (1) 323; (2) 223; (3) 023
21	*P3 endopod-2 inner margin, with*: (1) 2 setae; (2) 1 seta
22	*P3 endopod-3 setal formula*: (1) 321; (2) 221; (3) 121; (4) 021
23	*P3 of male*: (1) without spine-like terminal outgrowth; (2) with spine-like terminal outgrowth
24	*P3 endopod-3 of male, outer seta*: (1) normal (as in female); (2) reduced (compared to female)
25	*P3 endopod of male, setal formula*: (1) 321; (2) 221; (3) 121
26	*P2 and P3 endopod*: (1) longer than exopod; (2) shorter than exopod
27	*P4 exopod-1 inner margin, seta*: (1) present; (2) absent
28	*P4 exopod-3 setal formula*: (1) 323; (2) 223
29	*P4 endopod-2 with*: (1) 2 setae; (2) 1 seta
30	*P4 endopod-3 setal formula*: (1) 221; (2) 121; (3) 021; (4) 211
31	*P2–P4 endopod-3 with*: (1) 2 thin setae (approximately equal width); (2) 1 thin plumose seta and 1 larger, spinose seta (more the twice as wide as plumose seta)
32	*P3 and P4 exopod-3, inner margin*: (1) without a reduced seta; (2) with a reduced seta
33	*P5 exopod of female, number of setae*: (1) 8; (2) 7; (3) 6; (4) 5; (5) 4
34	*P5 exopod of male, number of setae*: (1) 8; (2) 7; (3) 6; (4) 5; (5) 4
35	*P5 exopod of male, number of segments*: (1) 3; (2) 2; (3) 1
36	*Caudal rami with*: (1) 7 setae; (2) 6 setae

Table 2. Character matrix used in phylogenetic analysis of Parastenheliidae.

When multiple states of a character were recorded for a taxon, superscript and subscript numbers were used to denote the range of applicable states. For example $^{2}_{4}$ indicates that character states 2, 3 and 4 had been recorded. ? denotes unknown character states, – indicates inapplicable characters.

Character numbers →		10	20	30
Taxa ↓	1234567891	1234567892	1234567893	123456
Ancestral harpacticoid	?1?521111?	?111121111	11111?1111	?11111
Protolatiremus sakaguchii	2134211112	1111122112	1211221211	113331
Karllangia arenicola	2231121222	2221113122	221?222121	1?3532
Karllangia arenicola bengalensis	2221121221	2221113121	221???2121	1?4532
Karllangia arenicola psammophila	2221121221	1224113121	2211221121	114532
Karllangia obscura	?123121222	2221113121	2212222121	114532
Karllangia pulchra	2123121222	2221113121	2212222121	113532
Karllangia tertia	2135221221	2211112211	22111?1121	113432
Parastenhelia angelica	2125221222	2211112211	212--21121	1?3$^{4}_{5}$32
Parastenhelia costata	2135222222	2212113211	212--21121	113212
Parastenhelia gracilis	?1?5222222	2212113212	2$^{1}_{2}$2--21222	??3232
Parastenhelia hornelli	2135221221	2212$^{1}_{2}$132$^{1}_{2}$1	222--2$^{1}_{2}$121	223$^{2}_{3}$$^{1}_{3}$2
Parastenhelia sp. nov.	1115221221	1212113211	212--11121	223332
Parastenhelia megarostrum	1114221221	12$^{1}_{2}$2$^{1}_{2}$131$^{1}_{2}$1	2211311121	223332
Parastenhelia minuta	?135222221	2212114112	232--21121	??3232
Parastenhelia oligochaeta	2135221221	2222214221	242--21123	223332
Parastenhelia ornatissima	2234?21223	-221113?22	22???22221	113??2
Parastenhelia reducta	2233221221	2221113122	231??22222	113432
Parastenhelia spinosa	2$^{1}_{3}$35222221	22121132$^{1}_{2}$$^{1}_{2}$	222--2$^{1}_{2}$$^{1}_{2}2^{1}_{2}$	12$^{1}_{3}$$^{2}_{3}$$^{1}_{3}$2
Parastenhelia spinosa f. *bulbosa*	21?522222?	?212113 2??	222--2$^{1}_{2}$$^{1}_{2}$2?	1?3212
Parastenhelia spinosa f. *bulgarica*	2??5222221	2222213 2??	222--22221	112232

Table 3. Synapomorphies of the clades labelled in tree 2 (fig. 3) generated by PAUP*. Character transformations listed are those common to all parsimony trees for the clades retained in all three shortest trees (with reweighted characters). Superscript numbers are states, derived from 1 unless otherwise indicated (e.g. 6^{2-1} indicates character 6 changing from state 2 to state 1). Characters in bold have CI=1.0. Characters in Italics have CI between 0.5 and 0.99.

Clade number or taxon	Characters changing and states
Clade-39 (Parastenheliidae, *Parastenhelia*)	**6^{2}**, **8^{2}**, **9^{2}**, 11^{2}, **12^{2}**, **16^{2-1}**, **21^{2}**, **29^{2}**, 34^{4}, **36^{2}**
Clade-38	*4^{4-5}*, 18^{2}
Clade-37	*23^{2}*, *25^{3}*
Clade-36	*7^{2}*, **14^{2}**, *17^{2-3}*, *34^{4-2}*
Clade-35	10^{2-1}
Clade-34	**32^{2}**, *34^{2-3}*
Clade-33	*7^{2-1}*, **31^{2}**
Clade-32	**1^{2-1}**, *3^{3-1}*, 11^{2-1}, **26^{2-1}**
Clade-31	Does not occur in other shortest trees
Clade-30	20^{2}
Clade-29	28^{2}
Clade-28	*35^{3-1}*
Clade-27	*2^{2}*, 13^{2}, *17^{2-3}*, *19^{2}*, 20^{2}, *25^{2}*, 27^{2}
Clade-26	10^{2-1}, 28^{2}
Clade-25 (formally *Karllangia*)	*4^{4-1}*, **5^{2-1}**, *34^{4-5}*
Clade-24	*3^{3-2}*, 20^{2-1}, *33^{3-4}*
Clade-23	*2^{2-1}*, *4^{3}*, **24^{2}**
Clade 22	10^{2-1}

Table 4. Setal formulae for swimming legs of female *Parastenhelia*.
Numbers in brackets indicate the range of possible setal abundances**.**

Swimming legs	Exopod-			Endopod-		
	1	2	3	1	2	3
P2	0–1	1	[1–2].2.3	0–1	1	[0–2].2.1
P3	0–1	1	[2–3].2.3	0–1	1	[0–3].2.1
P4	0–1	1	[2–3].2.3	0–1	1	[0–2].2.1

Table 5. Setal formulae for swimming legs of female *Parastenhelia jenkinsi* sp. nov.

Swimming legs	Exopod-			Endopod-		
	1	2	3	1	2	3
P2	1	1	1.2.3	1	1	1.2.1
P3	1	1	3.2.3	1	1	3.2.1
P4	1	1	3.2.3	1	1	2.2.1

Table 6. Setal formulae for swimming legs of female *Parastenhelia spinosa* (Fischer, 1860)

Swimming legs	Exopod-			Endopod-		
	1	2	3	1	2	3
P2	1	1	1.2.3	1	1	1.2.1
P3	0	1	3.2.3	1	1	2.2.1
P4	0	1	3.2.3	1	1	2.2.1

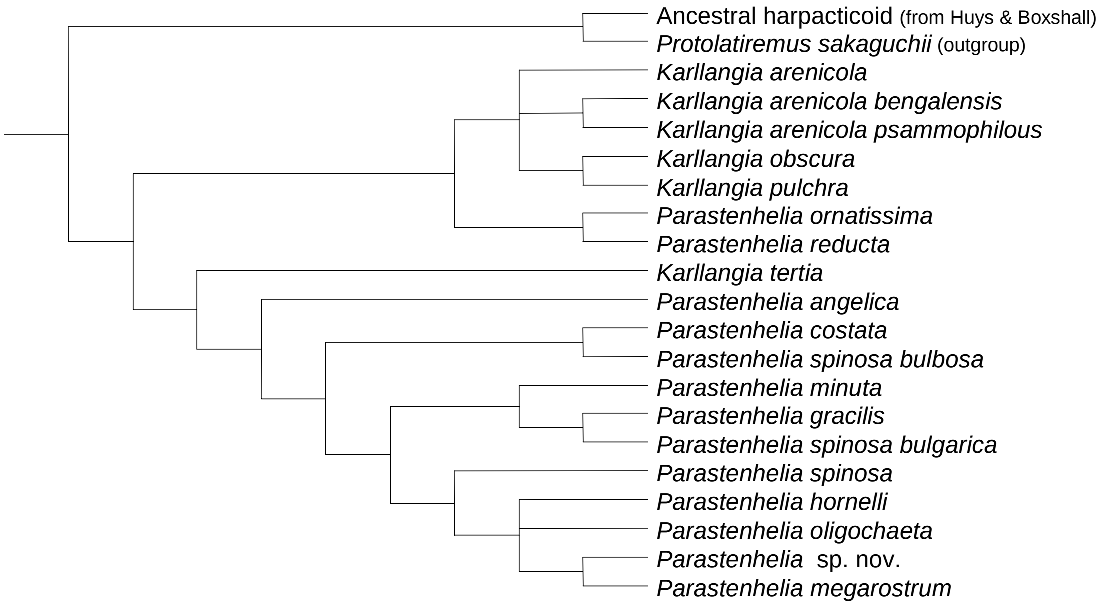
List of figures

Fig. 13. *Parastenhelia spinosa* (Fischer, 1860). Female (NMV J47091): **A**, P1 and intercoxal sclerite; **B**, P2 and intercoxal sclerite. Male (NMV J47090): **C**, P2 endopod. Scale bar = 0.1 mm.

Fig. 14. *Parastenhelia spinosa* (Fischer, 1860). Female (NMV J47091): **A**, P3 and intercoxal sclerite; **B**, P3 exopod-2 of left leg (the normal condition); **D**, P4 and intercoxal sclerite. Male (NMV J47090): **C**, P3 endopod; **E**, P4 endopod. Scale bar = 0.05 mm.

Fig. 15. *Parastenhelia spinosa* (Fischer, 1860). Aberrant female (NMV J47084): **A**, P1; **B**, P2 and intercoxal sclerite; **C**, P3. Scale bar = 0.05 mm.

Fig. 16. *Parastenhelia spinosa* (Fischer, 1860). Male (NMV J47090): **A**, urosome, dorsal view; **B**, urosome, ventral view; **D**, P5. Female (NMV J47088): **C**, genital double-somite, ventral view. Female (NMV J47091): **E**, P5. Scale bars = 0.05 mm.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Karllangia obscura
Karllangia pulchra
Parastenhelia ornatissima
Parastenhelia reducta
Karllangia tertia
Parastenhelia angelica
Parastenhelia costata
Parastenhelia spinosa bulbosa
Parastenhelia minuta
Parastenhelia gracilis
Parastenhelia spinosa bulgarica
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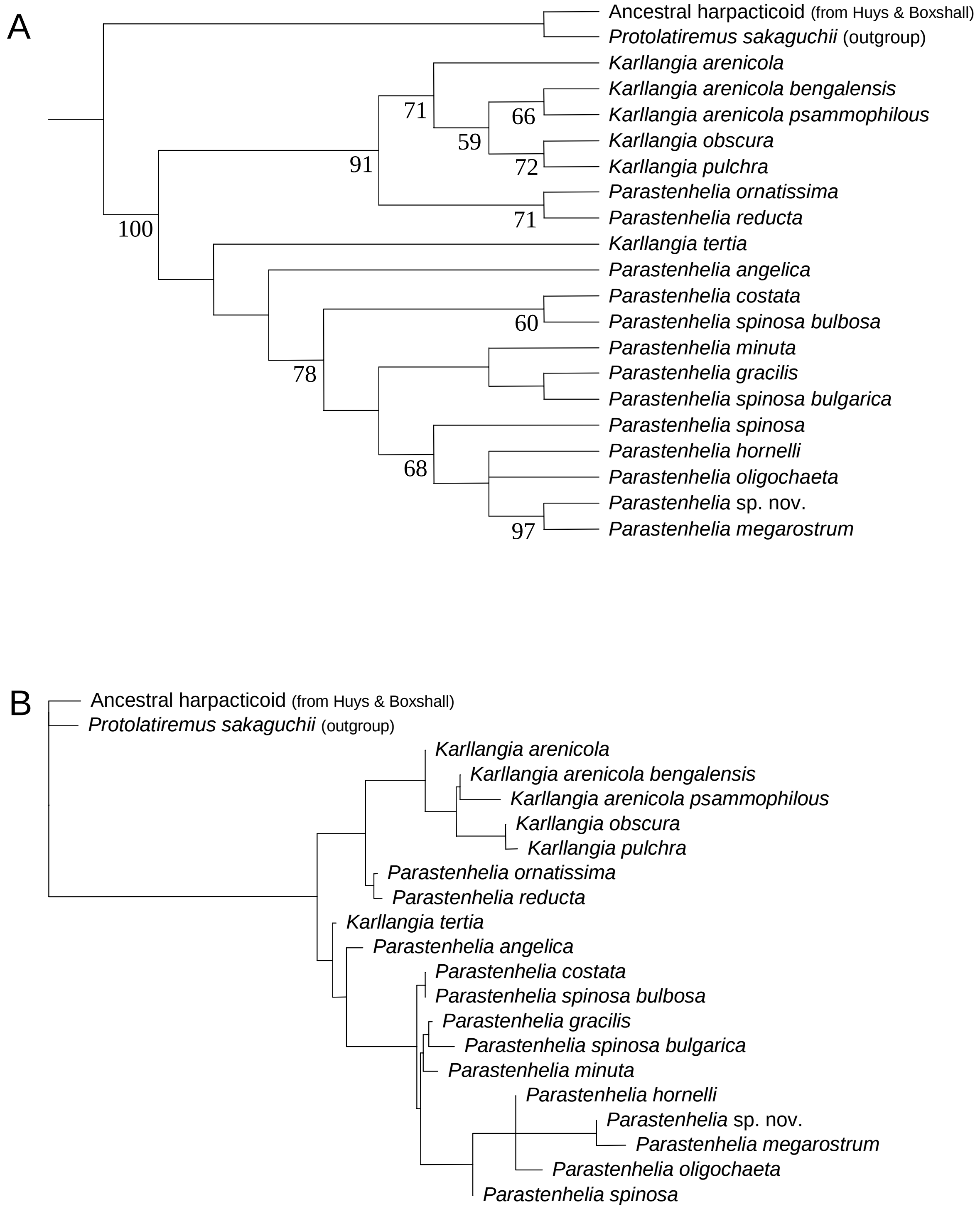
Parastenhelia sp. nov.
Parastenhelia megarostrum

FIGURE 1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Karllangia obscura
Karllangia pulchra
Parastenhelia ornatissima
Parastenhelia reducta
Karllangia tertia
Parastenhelia angelica
Parastenhelia costata
Parastenhelia spinosa bulbosa
Parastenhelia minuta
Parastenhelia gracilis
Parastenhelia spinosa bulgarica
Parastenhelia spinosa
Parastenhelia hornelli
Parastenhelia oligochaeta
Parastenhelia sp. nov.
Parastenhelia megarostrum
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B
Ancestral harpacticoid (from Huys & Boxshall)
Protolatiremus sakaguchii (outgroup)
Karllangia arenicola
Karllangia arenicola bengalensis
Karllangia arenicola psammophilous
Karllangia obscura
Karllangia pulchra
Parastenhelia ornatissima
Parastenhelia reducta
Karllangia tertia
Parastenhelia angelica
Parastenhelia costata
Parastenhelia spinosa bulbosa
Parastenhelia gracilis
Parastenhelia spinosa bulgarica
Parastenhelia minuta
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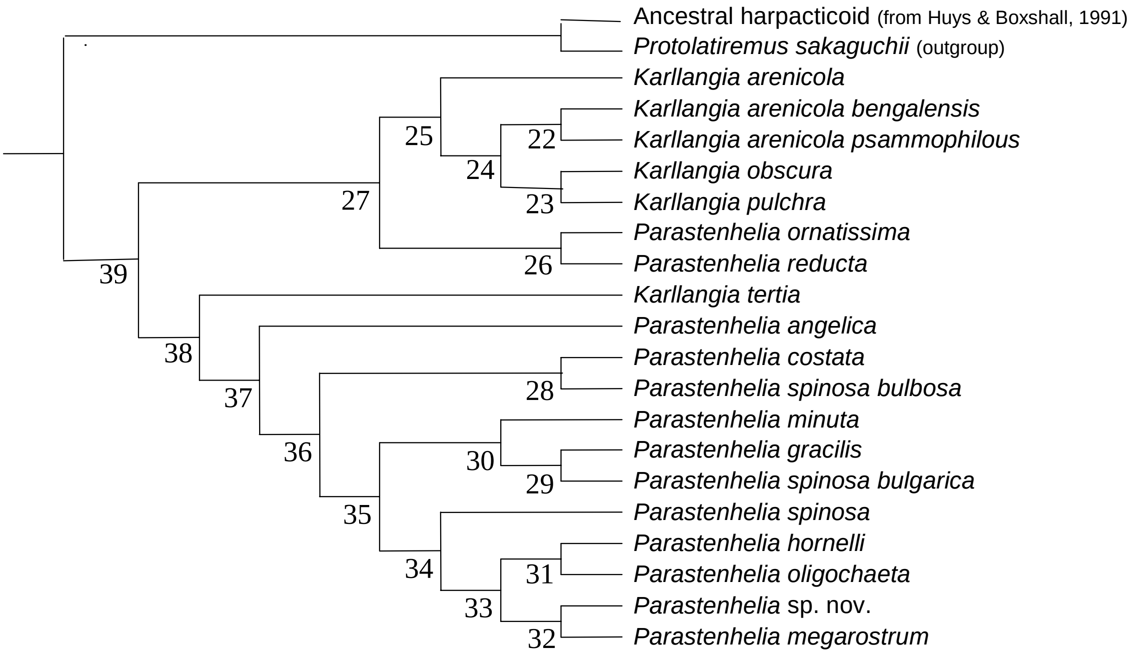
Parastenhelia sp. nov.
Parastenhelia megarostrum
Parastenhelia oligochaeta
Parastenhelia spinosa

FIGURE 2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Karllangia arenicola bengalensis
Karllangia arenicola psammophilous
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Parastenhelia spinosa
Parastenhelia hornelli
Parastenhelia oligochaeta
Parastenhelia sp. nov.
Parastenhelia megarostrum
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FIGURE 3

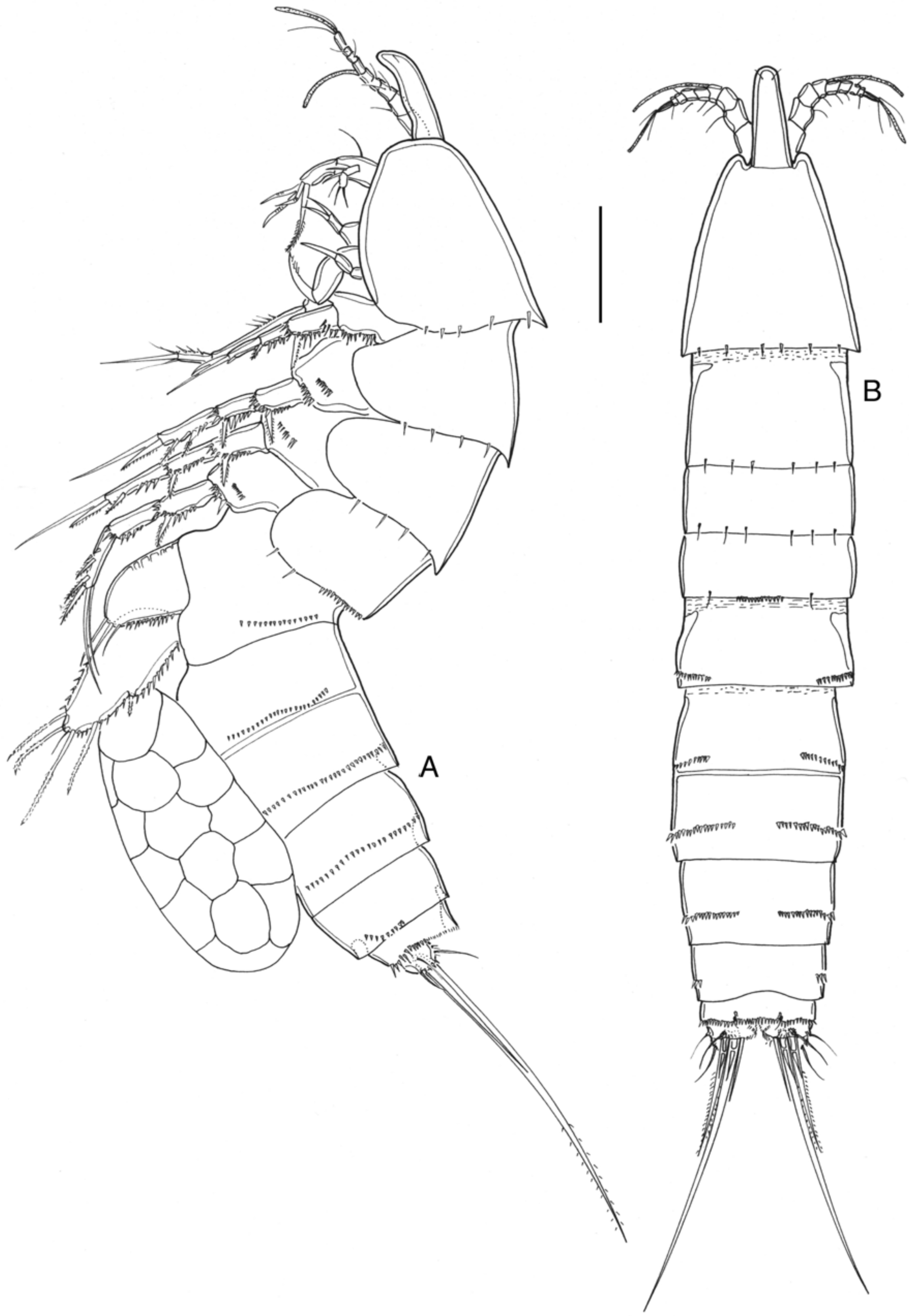


FIG. 4.

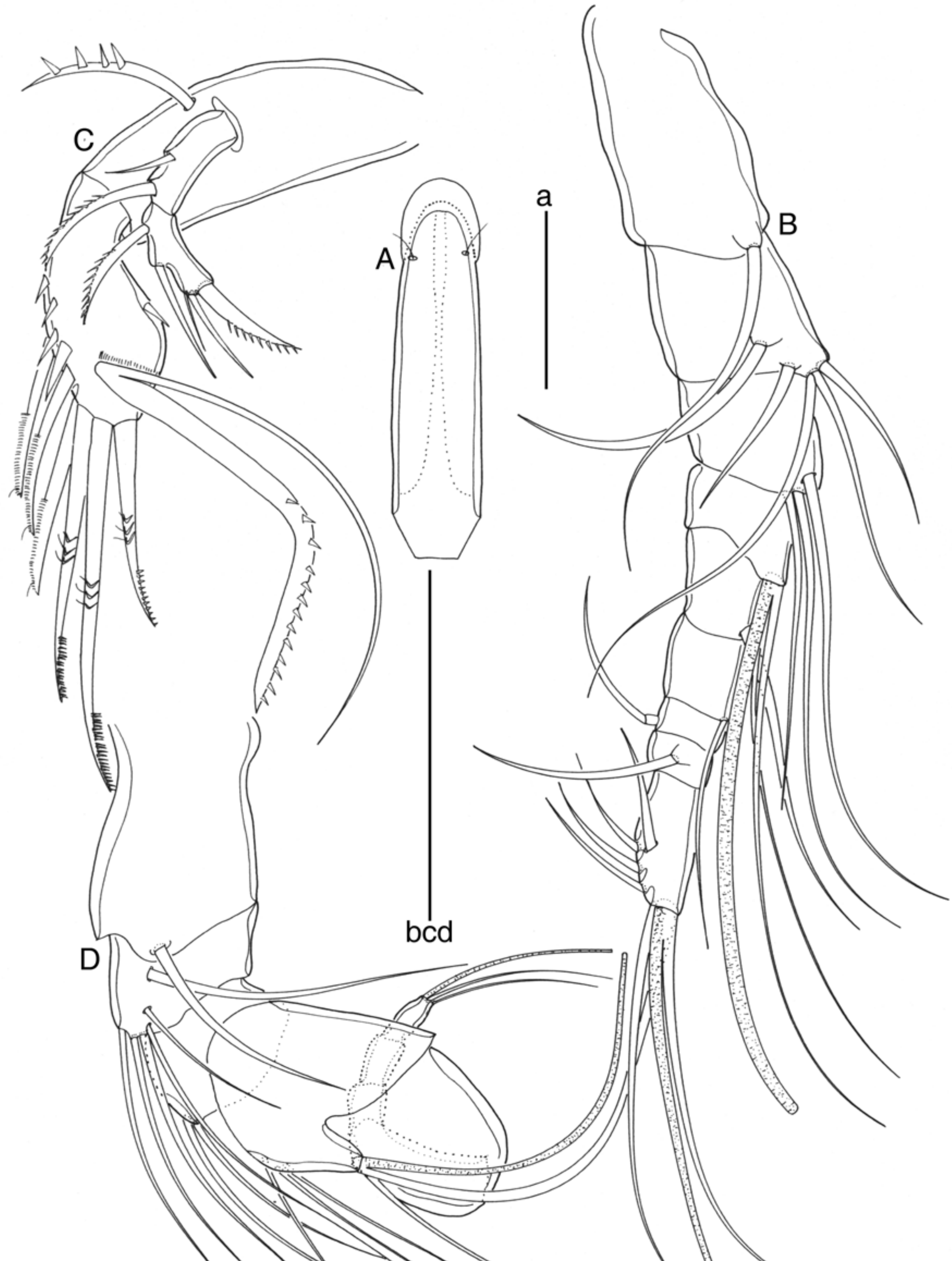
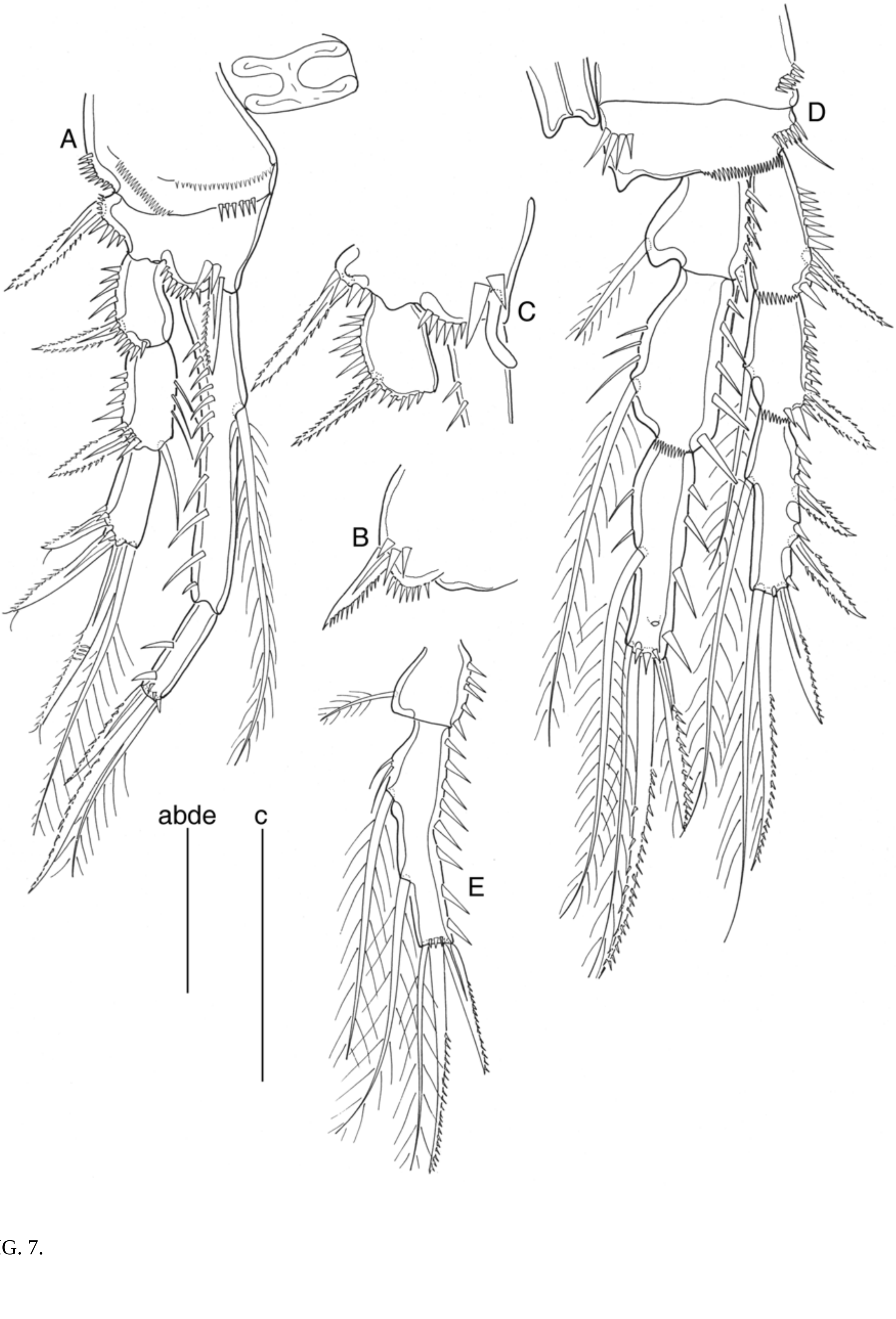


FIG. 5.

FIG. 6.



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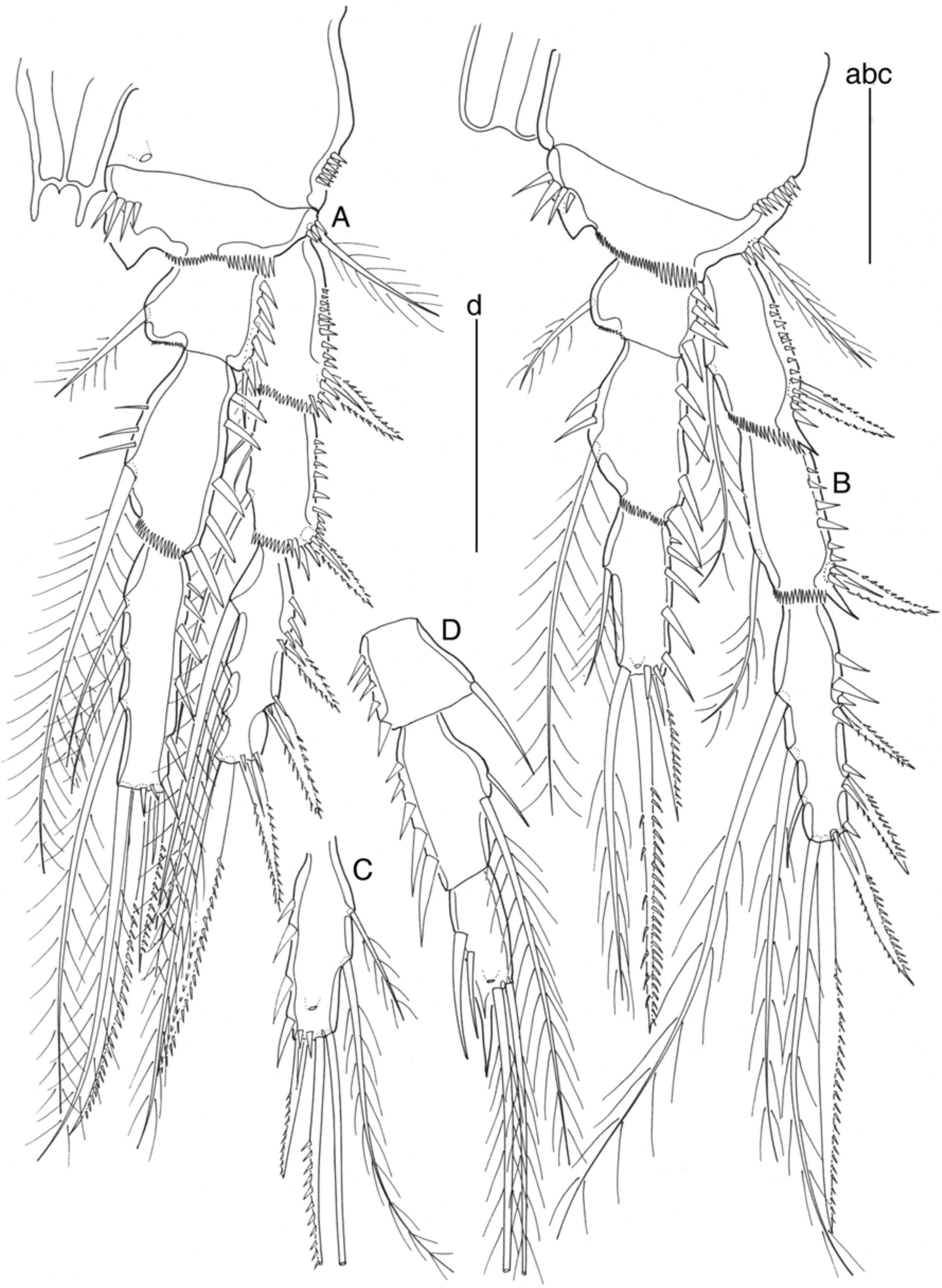

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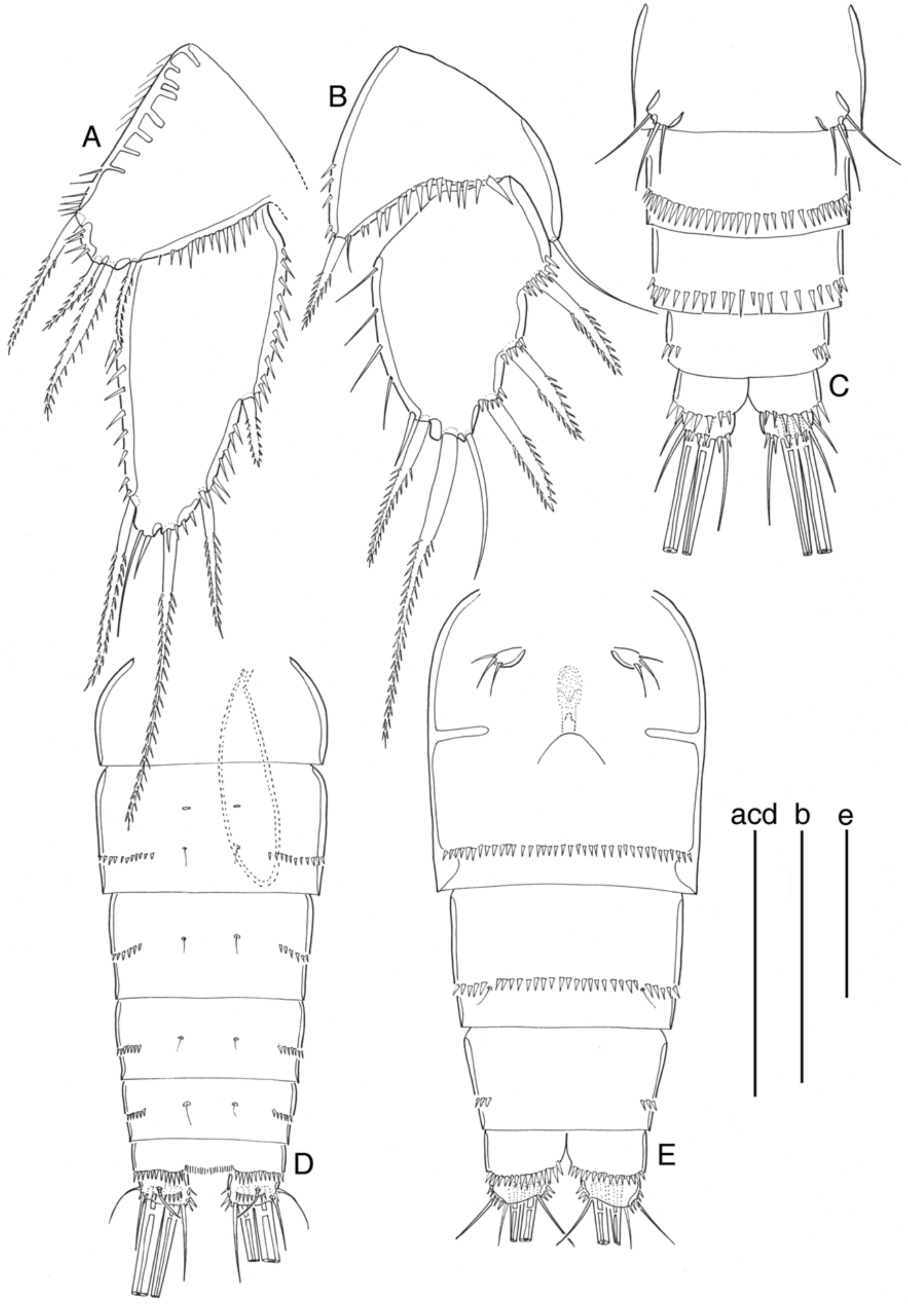


FIG. 9.

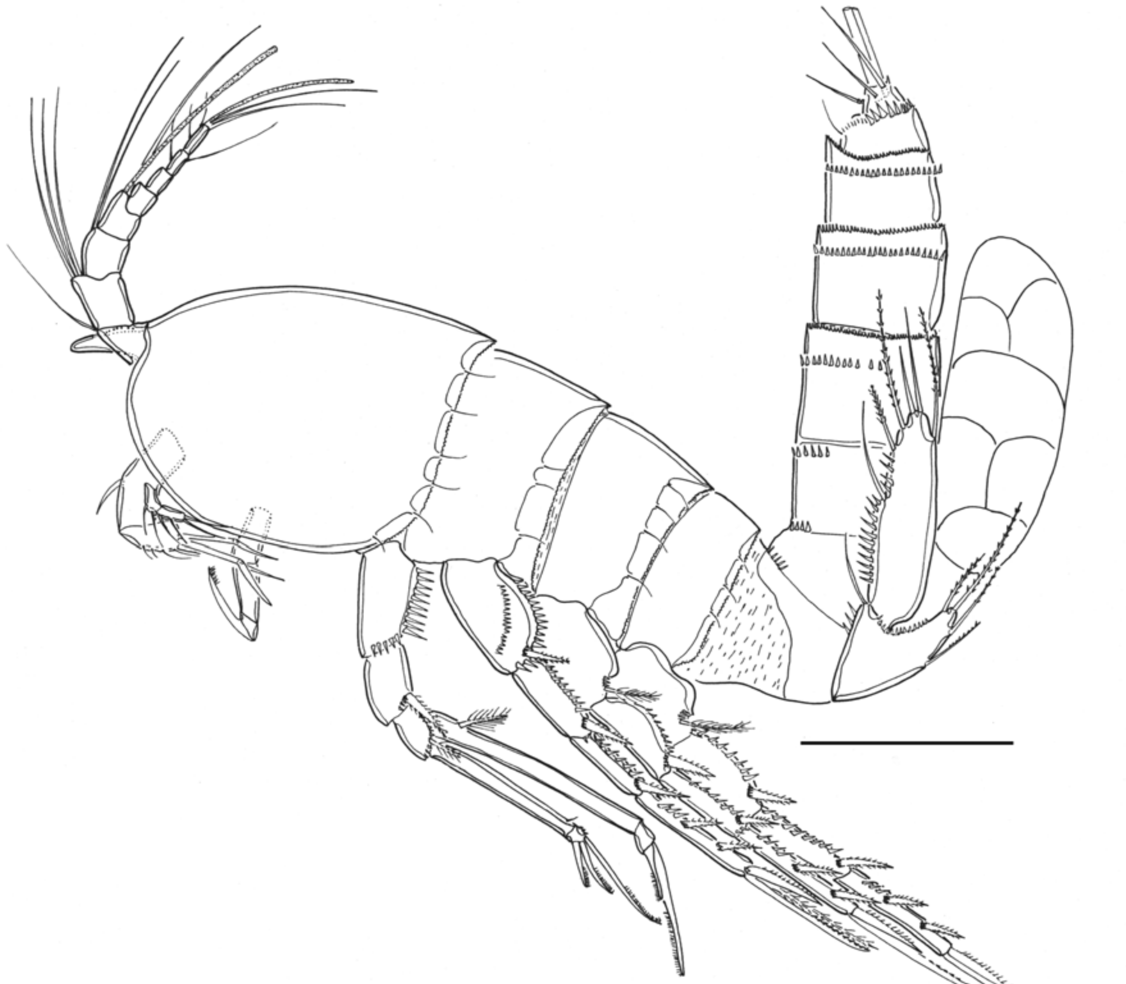


FIG. 10.

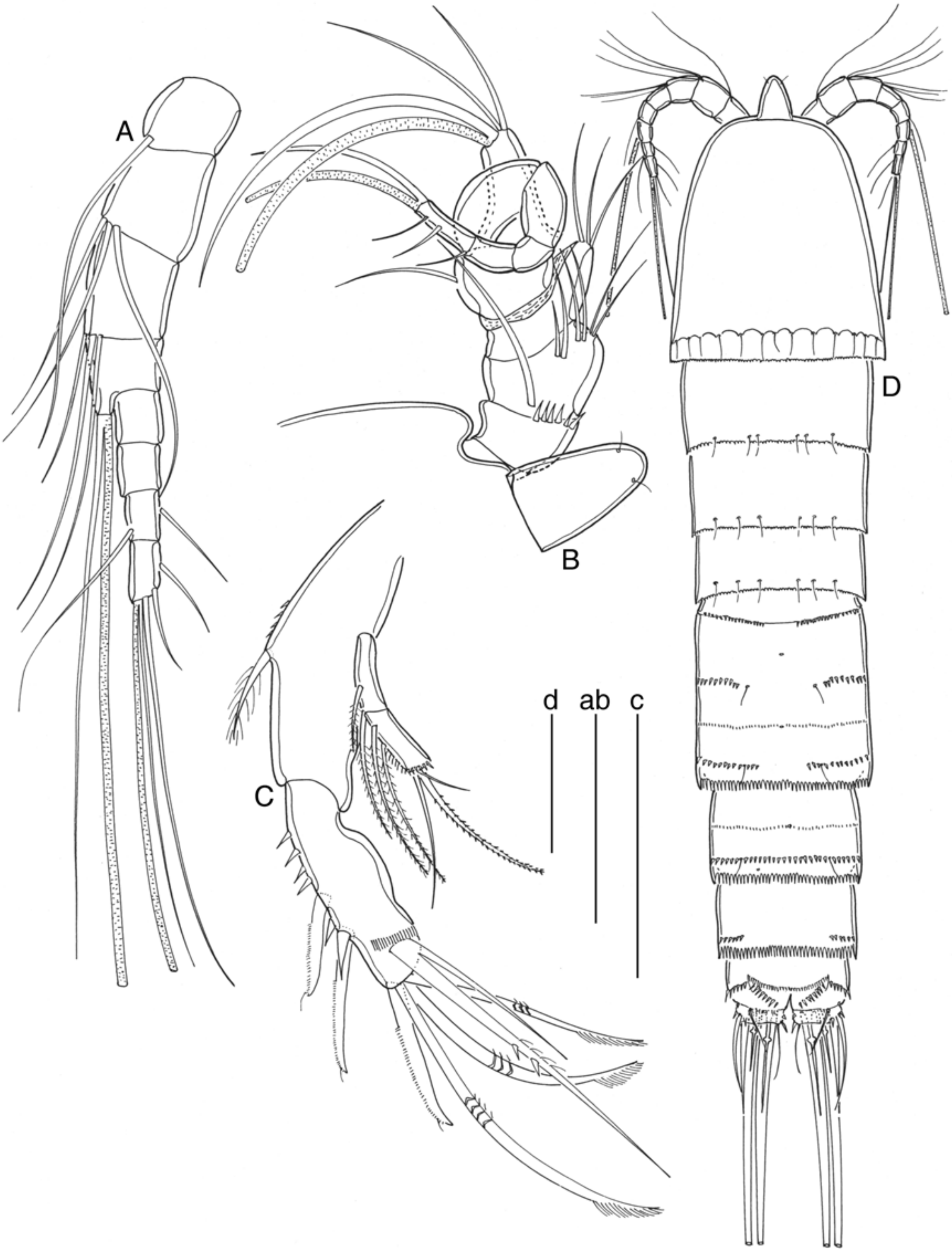
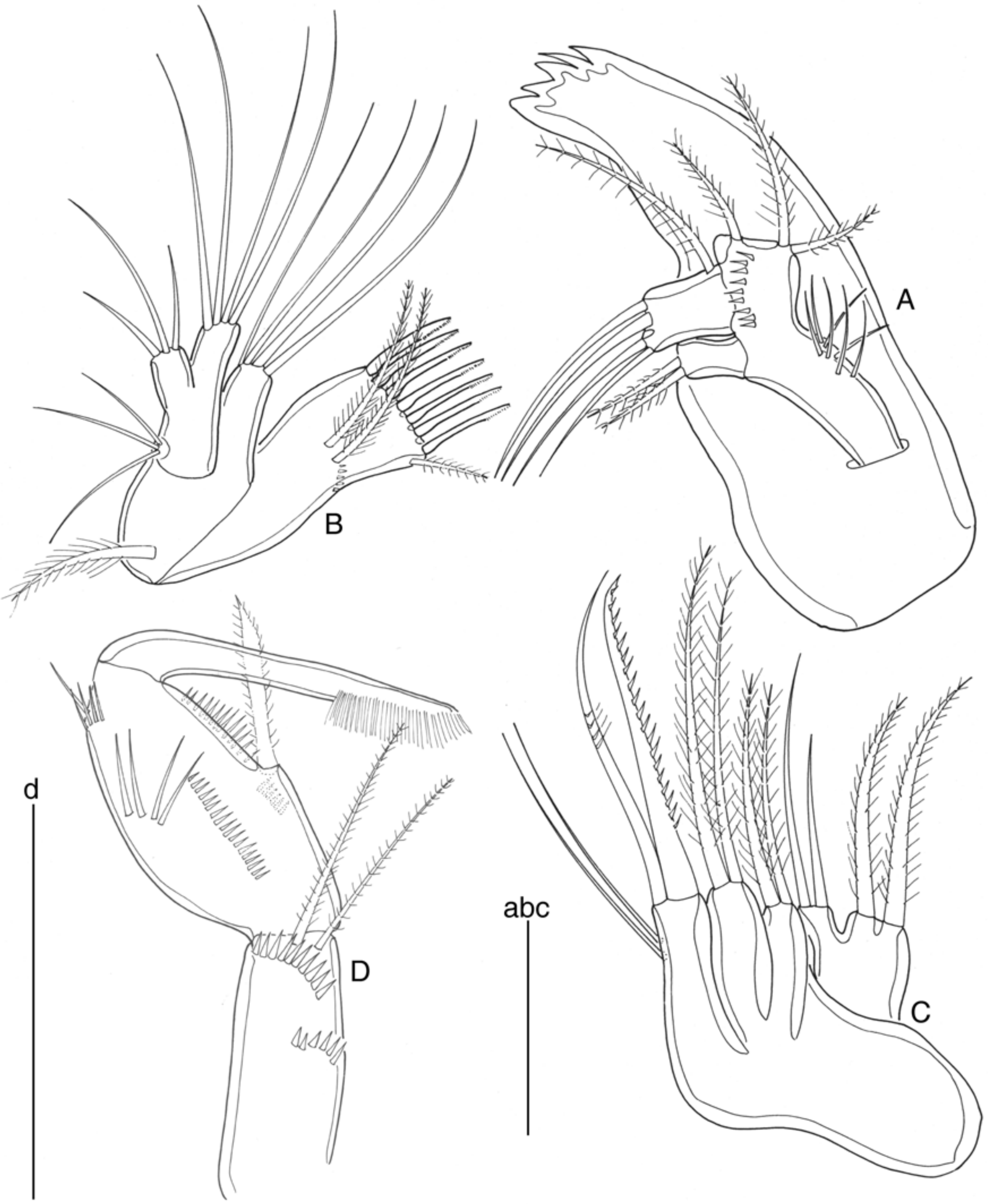


FIG. 11.



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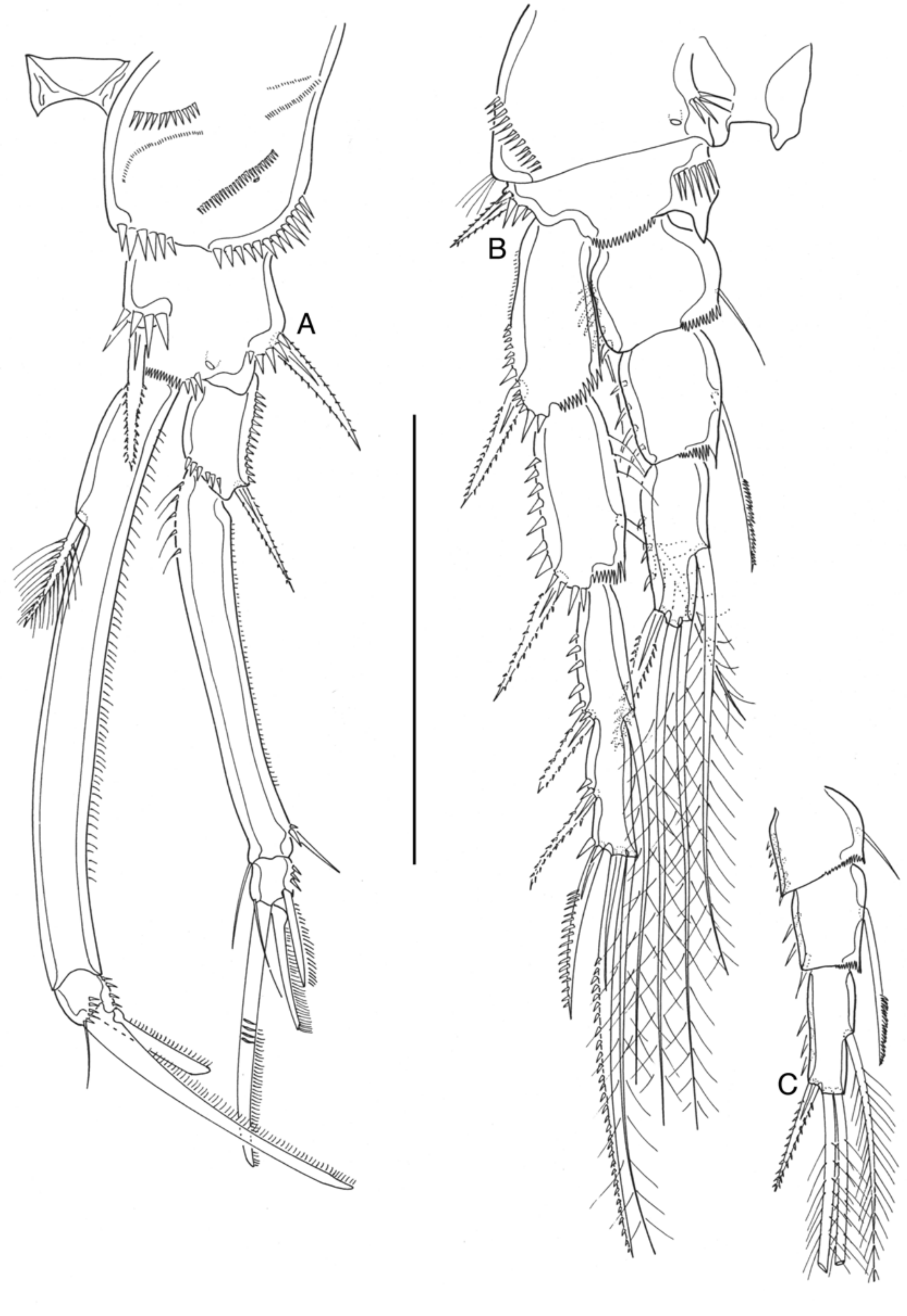

FIG. 13.

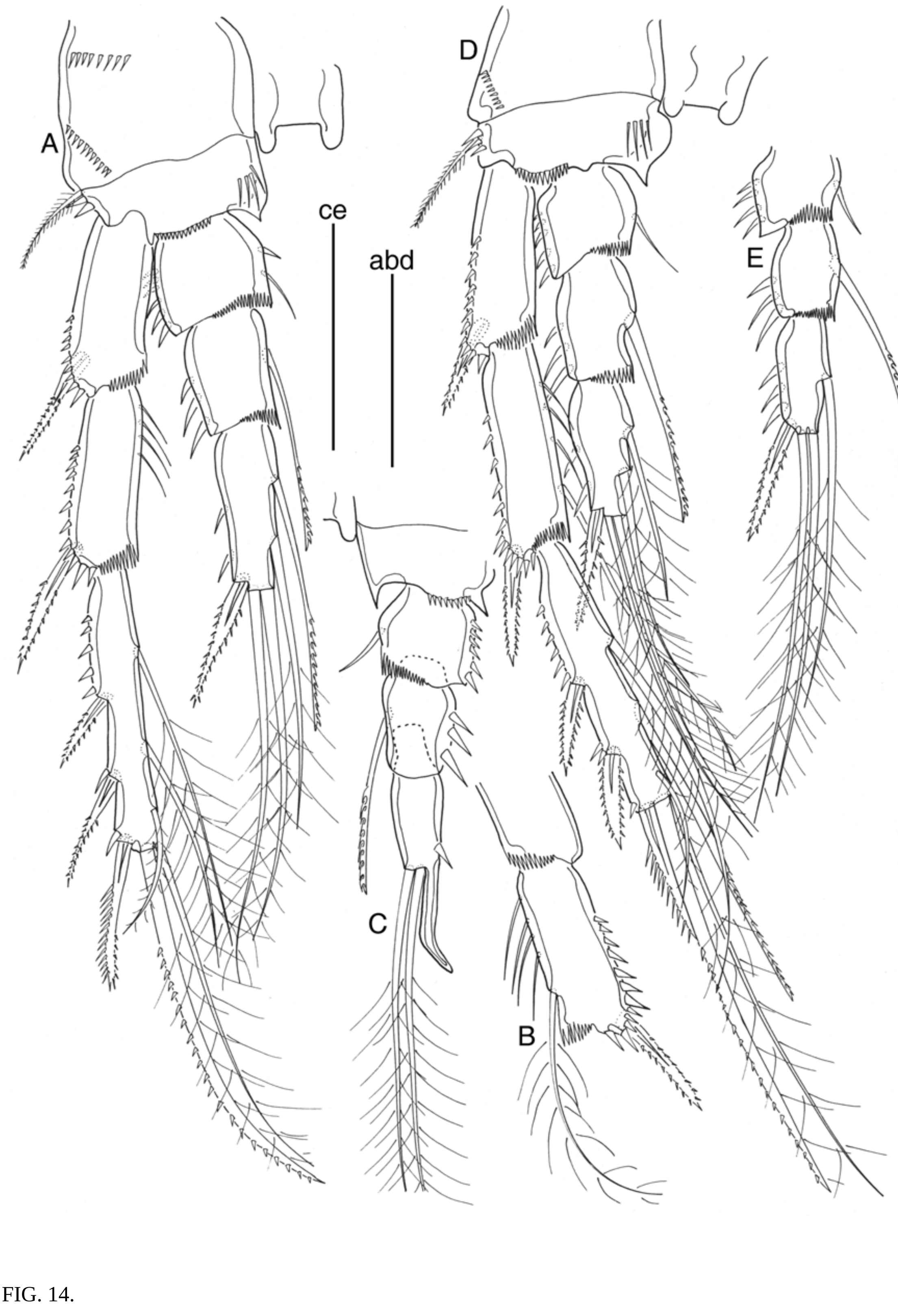

FIG. 14.

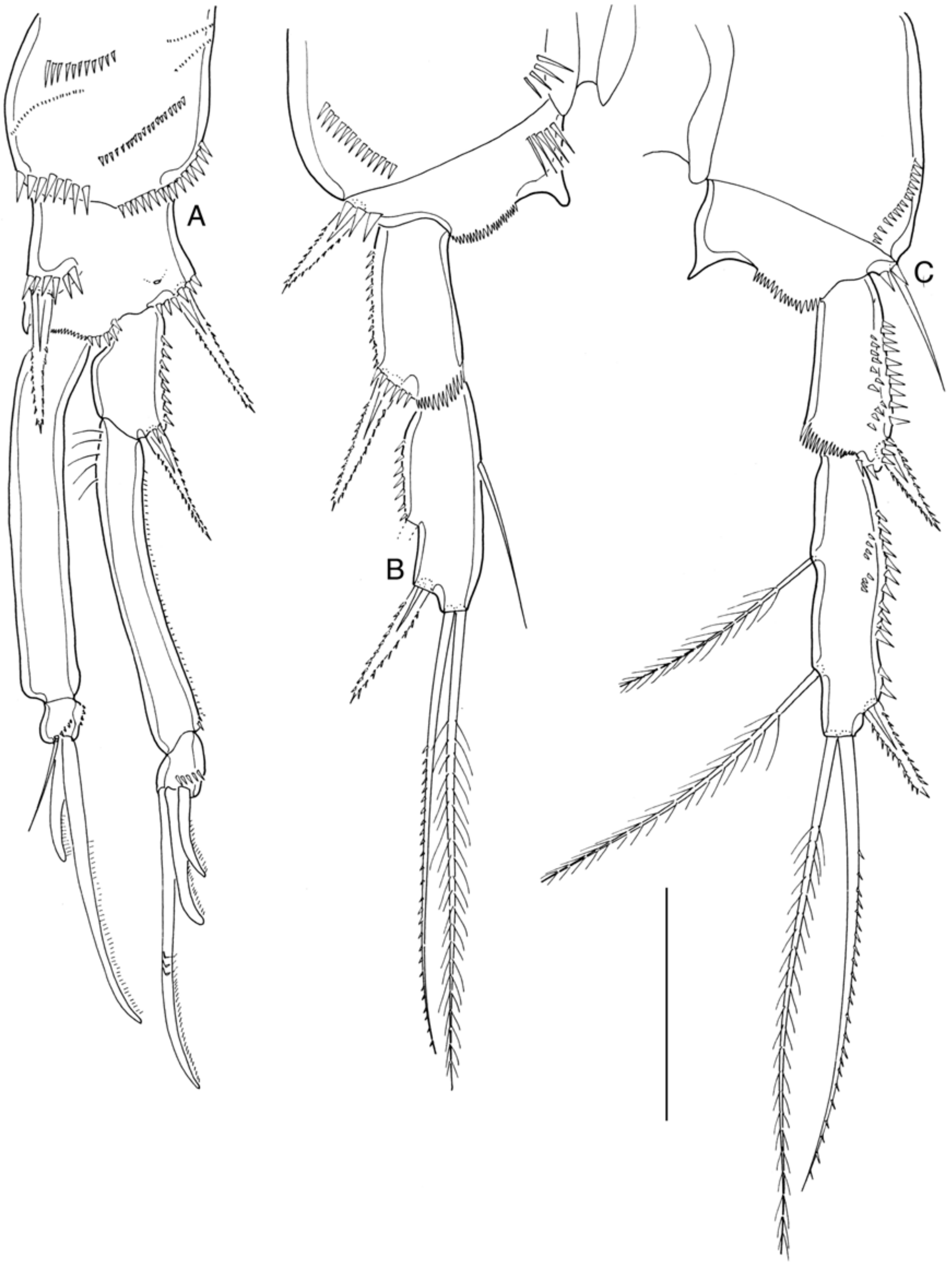

FIG. 15.

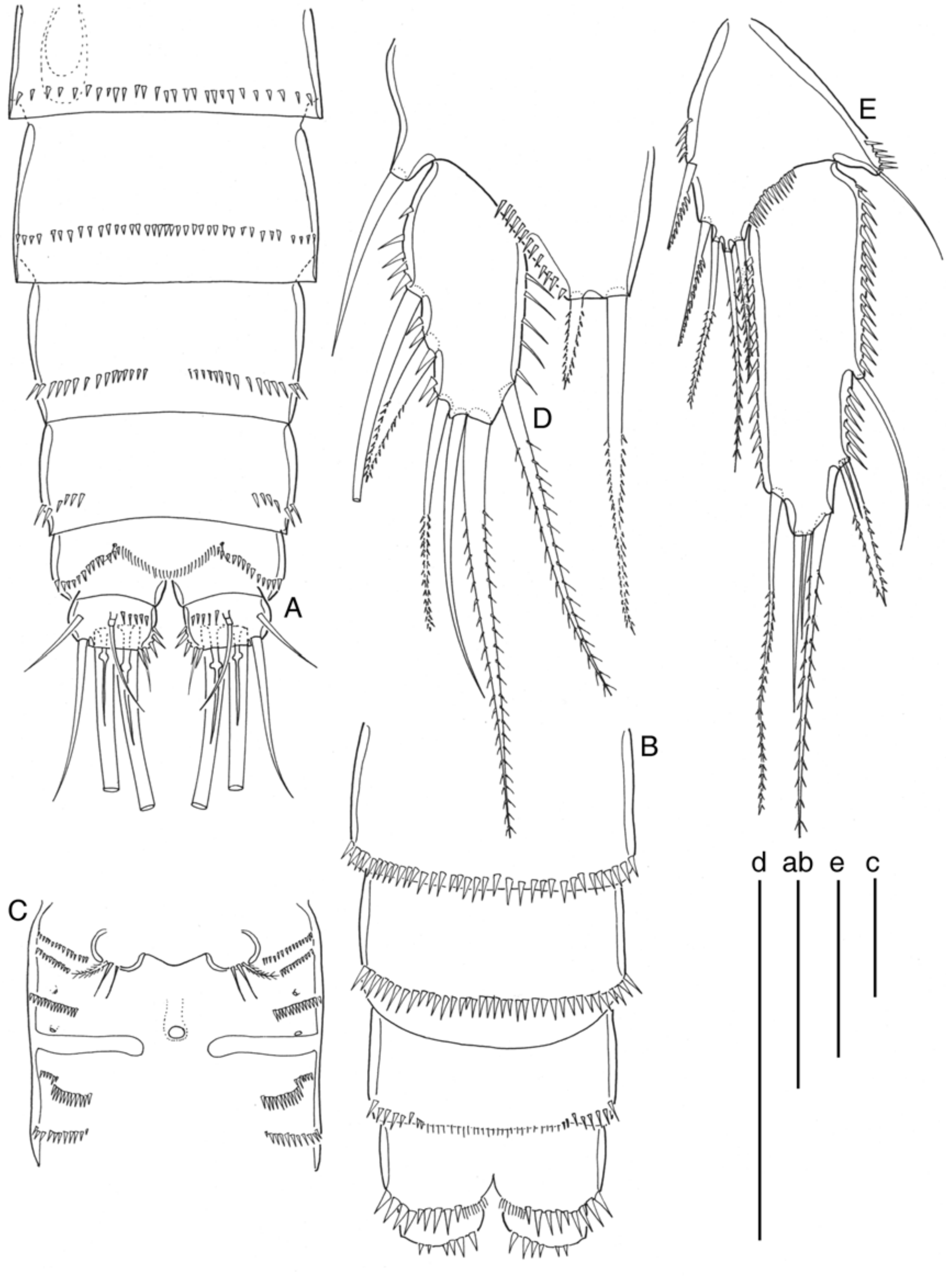

FIG. 16.