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New Ancorabolidae (Copepoda: Harpacticoida) from Korea: two new genera, revisionary notes and updated identification keys

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Two new copepod species of the *Ceratonotus* group in the subfamily Ancorabolinae (Ancorabolidae) are described from the Korean peninsula. ***Dendropsyllus kimi* sp. nov.** differs from its congeners by the one-segmented ♀ P3 endopod, the inner spine on ♀ P5 exopod and the absence of sensillate tubercles on abdominal somites 1 and 2. ***Dimorphipodia* gen. nov.** is proposed to accommodate ***Dimorphipodia changi* sp. nov.** and can be differentiated from its sister taxon, *Arthuricornua*, by the sexual dimorphism in P2–P4 exp-3, the absence of paired laterodorsal processes near the posterior margin of the cephalothorax and the presence of pleural setular tufts on somites bearing P2–P4. *Ancorabolina*, previously placed in the Ancorabolinae, is transferred to the Laophontodinae, whereas *Patagoniaella* is provisionally reassigned to the family Cletodidae. Within *Laophontodes*, the inadequately described *Laophontodes brevis*, *Laophontodes ornatus* and *Laophontodes propinquus* are relegated to *species inquirendae*. ***Laophontodes georgei* sp. nov.** is proposed for the unavailable name *Laophontodes norvegicus*, *Laophontodes multispinatus* is reassigned to *Lobopleura*, and *Laophontodes gracilipes* is fixed as the type of ***Rostrophontodes* gen. nov.**, the potential sister group of *Ancorabolina*. The authenticity of *Laophontodes bicornis* and other dubious ancorabolid records from the Korean peninsula is discussed. Updated keys to genera of both Ancorabolinae and Laophontodinae and to species of *Laophontodes* are provided.

ADDITIONAL KEYWORDS: *Ancorabolina* – copepods – crustaceans – new genera – new species – *Patagoniaella* – taxonomy.

INTRODUCTION

Members of the predominantly deep-water family Ancorabolidae are among the most morphologically distinct and ornate copepods in the Harpacticoida. The family has traditionally been subdivided in two subfamilies (Lang, 1944, 1948) and currently accommodates 83 named species in 23 genera (Table 1). Since Lang's (1948) monograph, the descriptive phase in ancorabolid research stagnated almost entirely for more than five decades, with only few species added to the Laophontodinae (Krishnaswamy, 1957; Božić, 1964; Lang, 1965; Soyer, 1975; Mielke, 1981; Baldari & Cottarelli, 1986; Gee & Fleeger, 1986; Cottarelli & Baldari, 1987; Bodiou & Colomines, 1988; Fiers, 1988; Schizas & Shirley, 1994) and even fewer to the Ancorabolinae (Smirnov, 1946; Soyer, 1965; Drzycimski, 1967; Coull, 1973; George, 1998; George & Schminke, 1998). The last two decades have seen a resurgence in the dynamism of ancorabolid taxonomy, particularly through the efforts of S. Conroy-Dalton (Conroy-Dalton & Huys, 2000; Conroy-Dalton, 2001, 2003a, b, 2004) and K. H. George (George & Schminke, 1998; George, 1998, 2001, 2006a, b, c, 2017, 2018; Arroyo *et al.*, 2003; George & Plum, 2009; George & Tiltack, 2009; Wandeness *et al.*, 2009; Gheerardyn & George, 2010; Schulz & George, 2010; George *et al.*, 2013; George & Müller, 2013; George & Gheerardyn, 2015) and their respective co-workers. This increase in activity resulted in the proposal of several new genera and species, either

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Table 1. Species currently allocated to the two subfamilies of the Ancorabolidae (including *species inquirendae* and *incertae sedis*). The genus *Echinocletodes* Lang, 1936a, with its two valid species, *E. armatus* T. Scott, 1903 (type) and *E. voightae* George & Müller, 2013, is not considered here because morphological evidence corroborating its position in the Ancorabolidae is inconclusive (George & Müller, 2013). The monotypic genus *Patagoniaella* Pallares, 1968 is removed from the Ancorabolidae and transferred to the Cletodidae (see main text).

Ancorabolinae	Laophontodinae
Ancorabolus Norman, 1903	*Laophontodes* T. Scott, 1894
Ancorabolus mirabilis Norman, 1903	*Laophontodes hamatus* (Thomson, 1883) [g]
Ancorabolus confusus Conroy-Dalton & Huys, 2000	*Laophontodes typicus* (T. Scott, 1894) [h]
Ancorabolus inermis Conroy-Dalton & Huys, 2000	*Laophontodes bicornis* A. Scott, 1896
Ancorabolus ilvae George, 2001 [a]	*Laophontodes propinquus* Brady, 1910 [i]
Ancorabolus hendrickxi Gómez & Conroy-Dalton, 2002	*Laophontodes whitsoni* T. Scott, 1912
Ancorabolus chironi Schulz & George, 2010	*Laophontodes antarcticus* Brady, 1918 [j]
	Laophontodes brevis Nicholls, 1944 [k]
Arthropsyllus Sars, 1909	*Laophontodes ornatus* Krishnaswamy, 1957
Arthropsyllus serratus Sars, 1909	*Laophontodes macclintocki* Schizas & Shirley, 1994
	Laophontodes spongiosus Schizas & Shirley, 1994
Ceratonotus Sars, 1909	*Laophontodes mourois* Arroyo, George, Benito &
Ceratonotus pectinatus Sars, 1909	Maldonado, 2003
Ceratonotus coineaui Soyer, 1965	*Laophontodes horstgeorgei* George & Gheerardyn, 2015
Ceratonotus concavus Conroy-Dalton, 2003a	*Laophontodes sabinegeorgeae* George & Gheerardyn,
Ceratonotus thistlei Conroy-Dalton, 2003a	2015
Ceratonotus steiningeri George, 2006a	*Laophontodes gertraudae* George, 2018
Ceratonotus tauroides George, 2006a	*Laophontodes monsmaris* George, 2018
Ceratonotus vareschii George, 2006a	*Laophontodes sarsi* George, 2018
Ceratonotus elongatus Gómez & Díaz, 2017	*Laophontodes scottorum* George, 2018
	Laophontodes georgei* sp. nov. [l]
Echinopsyllus Sars, 1909	
Echinopsyllus normani Sars, 1909	*Paralaophontodes* Lang, 1965
Echinopsyllus brasiliensis Wandeness, George & Santos, 2009	*Paralaophontodes echinatus* (Willey, 1930) [m]
Echinopsyllus grohmannae Wandeness, George & Santos, 2009	*Paralaophontodes armatus* (Lang, 1936c) [n]
Echinopsyllus nogueirae Wandeness, George & Santos, 2009	*Paralophontodes robustus* (Božić, 1964) [o]
	Paralaophontodes hedgpethi (Lang, 1965) [n]
Dorsiceratus Drzycimski, 1967	*Paralaophontodes psammophilus* (Soyer, 1975) [n]
Dorsiceratus octocornis Drzycimski, 1967	*Paralaophontodes elegans* Baldari & Cottarelli, 1986
Dorsiceratus triarticulatus Coull, 1973	*Paralaophontodes exopoditus* Mielke, 1981
Dorsiceratus ursulae George, 2006b	*Paralaophontodes anjae* George, 2017
Dorsiceratus dinah George & Plum, 2009	
Dorsiceratus wilhelminae George & Plum, 2009	*Tapholaophontodes* Soyer, 1975
	Tapholaophontodes rollandi Soyer, 1975
Polyascophorus George, 1998	*Tapholaophontodes remotus* Cottarelli & Baldari, 1987
Polyascophorus gorbunovi (Smirnov, 1946) [b]	
Polyascophorus martinezi George, 1998	*Algensiella* Cottarelli & Baldari, 1987
Polyascophorus monoceratus George, Wandeness & Santos, 2013	*Algensiella boitanii* Cottarelli & Baldari, 1987
	Algensiella laurenceae (Bodiou & Colomines, 1988) [p]
Breviconia Conroy-Dalton & Huys, 2000	
Breviconia australis (George, 1998) [c]	*Prosciphontodes* Fiers, 1988
Breviconia echinata (Brady, 1918) [d]	*Prosciphontodes ptenopostica* Fiers, 1988
	Prosciphontodes stellata Fiers, 1988
Juxtaramia Conroy-Dalton & Huys, 2000	
Juxtaramia polaris Conroy-Dalton & Huys, 2000	*Lobopleura* Conroy-Dalton, 2004
	Lobopleura ambiducti Conroy-Dalton, 2004
Uptionyx Conroy-Dalton & Huys, 2000	*Lobopleura expansa* (Sars, 1908) [q]
Uptionyx verenae Conroy-Dalton & Huys, 2000	**Lobopleura multispinata* (Kornev & Chertoprud, 2008) comb. nov.**

Table 1. Continued

Ancorabolinae	Laophontodinae
Arthuricornua Conroy-Dalton, 2001	*Ancorabolina* George, 2006c
Arthuricornua anendopodia Conroy-Dalton, 2001	*Ancorabolina chimaera* George, 2006c
	Ancorabolina cavernicola George & Tiltack, 2009
Touphapleura Conroy-Dalton, 2001	*Ancorabolina anaximenesi* Gheerardyn & George, 2010
Touphapleura schminkei (George, 1998) [e]	*Ancorabolina belgicae* Gheerardyn & George, 2010
	Ancorabolina divasecunda Gheerardyn & George, 2010
Dendropsyllus Conroy-Dalton, 2003a	*Ancorabolina galeata* Gheerardyn & George, 2010
Dendropsyllus antarcticus (George & Schminke, 1998) [f]	
Dendropsyllus magellanicus (George & Schminke, 1998) [f]	*Calypsophontodes* Gheerardyn & Lee, 2012
Dendropsyllus thomasi Conroy-Dalton, 2003a	*Calypsophontodes latissima* (Brady, 1918) [r]
Dendropsyllus californiensis Gómez & Díaz, 2017	*Calypsophontodes macropodia* (Gee & Fleeger, 1986) [s]
Dendropsyllus kimi sp. nov.	
	Rostrophontodes gen. nov.
Pseudechinopsyllus George, 2006b	**Rostrophontodes gracilipes** (Lang, 1936b) **comb. nov.**
Pseudechinopsyllus sindemarkae George, 2006b	
Dimorphipodia gen. nov.	
Dimorphipodia changi sp. nov.	

[a] Based on copepodid V stage and relegated to *species inquirenda* by Gómez & Conroy-Dalton (2002).

[b] Transferred from *Echinopsyllus* Sars, 1909 by George (1998).

[c] Transferred from *Arthropsyllus* Sars, 1909 by Conroy-Dalton & Huys (2000).

[d] Transferred from *Laophontodes* T. Scott, 1894 and placed *species inquirenda* in *Breviconia* Conroy-Dalton & Huys, 2000 by Conroy-Dalton & Huys (2000).

[e] Transferred from *Polyascophorus* George, 1998 by Conroy-Dalton (2001).

[f] Transferred from *Ceratonotus* Sars, 1909 by Conroy-Dalton (2003a).

[g] Transferred from *Merope* Thomson, 1883 by Gurney (1927).

[h] T. Scott (1894: 249) designated the new species '*Laophontodes typicus*' as the type (by monotypy) for the new subgenus *Laophontodes* in the genus *Laophonte* Philippi, 1840. However, in the description of the accompanying plate (p. 270) he cited the species as '*Laophontodes typicus*, gen. et sp. nov.' attributing instead generic rank to *Laophontodes*. According to ICZN Recommendation 69A.10, when designating the type species for a genus (or subgenus), all other things being equal (i.e. a choice cannot be made on the basis of Recommendations 69A.1–9), an author should give preference to the species (or spelling) cited first in the work, page or line. Huys (2009) followed this position precedence and pointed out that the author and date of the type species of the genus *Laophontodes* should therefore be enclosed in parentheses, reflecting the changed combination currently adopted. The first author to use *Laophontodes* explicitly as a generic name was A. Scott (1896: 148).

[i] Brady's (1910) description is grossly incomplete and probably deficient. No information is available on P2–P3 except that the endopods are one-segmented. Given that the species cannot be identified unequivocally on the basis of the original description, it is here relegated to *species inquirenda* in the genus. It is known from very few specimens from Observatory Bay in the Kerguelen Islands and has never been found again since its discovery.

[j] Relegated to *species incertae sedis* by Lang (1936b); according to Gheerardyn & Lee (2012), it should probably be retained in *Laophontodes* (as shown by the elongate caudal rami and certain characteristics of antennule, P1 and P5), but no firm conclusion can be made because of the lack of detail in the original description.

[k] Lang (1965) claimed that *Laophontodes brevis* agreed well with the last copepodid of *La. bicornis* found in the Gullmarfjord (Sweden) and that both species were probably conspecific; he did not, however, formally synonymize them, although some authors subsequently listed them as such (Bodin, 1997) or no longer regarded *La. brevis* as a valid species (Gee & Fleeger, 1986; Schizas & Shirley, 1994; Wells, 2007; George & Gheerardyn, 2015; George, 2018). The description of the latter is indeed based on a copepodid V, but given the confusion surrounding the identity of Nicholls's (1944) material of the co-occurring *La. bicornis* (cf. George & Gheerardyn, 2015) it seems prudent to maintain *La. brevis* as a *species inquirenda* in the genus.

[l] George (2018: 34) proposed the new name *Laophontodes norvegicus* for the species originally redescribed by Sars (1908: 270) under the name *La. typicus* (T. Scott, 1894). In the absence of extant material, the author refrained from explicitly fixing a holotype, but his course of action effectively makes the new name unavailable (ICZN Art. 16.4). The ovigerous female specimen illustrated by Sars (1908: pl. CLXXXVII) is here designated as the holotype of **Laophontodes georgei sp. nov.** (ICZN Art. 72.5.6). The new species can be differentiated by the characters mentioned and illustrated by Sars (1908: 270–271, pl. CXXXVII) (ICZN Art. 13.1) and summarized by George (2018: 37–38). It is named after Dr Kai Horst George in recognition of his contributions to the systematics and phylogeny of ancorabolid harpacticoids. LSID: urn:lsid:zoobank. org:act:011872B0-D001-40D8-95B5-94B86A11E3E7.

[m] Transferred from *Laophonte* Philippi, 1840 by Lang (1965). Božić (1964) proposed the new replacement name *Laophontodes willeyi* for *Laophontodes echinatus* (Willey, 1930), a junior secondary homonym at the time of *La. echinatus* Brady, 1918. Given that both species are no longer considered congeneric (having been transferred to *Paralaophontodes* Lang, 1965 and *Breviconia*, respectively) a substitute name is not necessary, and the junior secondary synonym is to be reinstated (ICZN Art. 59.4).

[n] Transferred from *Laophontodes* by George (2017). Soyer (1976: 146) listed '*Laophontodes kerguelenensis*' from the Rivière norvégienne, which is the type locality of *Laophontodes psammophilus* Soyer, 1976. It is conceivable that he referred to the latter species, because it was mentioned as one of the two ancorabolid representatives obtained in the Kerguelen samples (Soyer, 1976: 149).

[o] Transferred from *Laophontodes* by Lang (1965). Synonymized with *P. echinatus* by Wells & Rao (1987) but reinstated as a valid species by George (2017).

[p] Transferred from *Tapholaophontodes* Soyer, 1975 by Wells (2007).

[q] Transferred from *Laophontodes* by Conroy-Dalton (2004).

[r] Transferred from *Laophontodes* and placed *species inquirenda* in *Calypsophontodes* Gheerardyn & Lee, 2012 by Gheerardyn & Lee (2012).

[s] Transferred from *Laophontodes* by Gheerardyn & Lee (2012).

discovered in previously unexplored habitats, such as hydrothermal vents (Conroy-Dalton & Huys, 2000), seamounts (George, 2006b, 2018; George & Plum, 2009; Gheerardyn & George, 2010; Schulz & George, 2010) and submarine caves (George & Tiltack, 2009), or recognized on the basis of revisionary systematic studies (Conroy-Dalton & Huys, 2000; Conroy-Dalton, 2003a; George & Gheerardyn, 2015; George, 2017, 2018).

Although some recent studies have advocated a monophyletic Ancorabolidae (George, 2006c), there now exists a general consensus that the relationship between the two subfamilies, Ancorabolinae and Laophontodinae, is not well understood and that at least one of them (e.g. Gheerardyn & George, 2010), if not the entire family (George & Müller, 2013), is paraphyletic. Although the phylogeny of the Ancorabolinae appears largely to be resolved with the recognition of a basal divide into an *Ancorabolus* group (Conroy-Dalton & Huys, 2000) and a *Ceratonotus* group (Conroy-Dalton, 2001), this outcome was disputed to some extent in subsequent work and, unfortunately, created unwarranted animosity (e.g. George, 2006a, b, c). Little progress has been made towards elucidating the phylogenetic interrelationships in the Laophontodinae, but some recently discovered apomorphic character states appear to lend support to its monophyletic status (Gheerardyn & George, 2010; Gheerardyn & Lee, 2012).

Despite their global distribution, representatives of the family Ancorabolidae (subfamily Laophontodinae) have been recorded on only four occasions in East Asia. Zhang & Li (1976) reported *Laophontodes hamatus* (Thomson, 1883) from seaweed washings collected in Yongxing Island (= Woody Island) and the Xisha (= Paracel) Islands in the South China Sea. Baldari & Cottarelli (1986) described *Paralaophontodes elegans* Baldari & Cottarelli, 1986 from a sandy beach on Mindoro Island, Philippines. Recently, Kim (2013) recorded *Laophontodes bicornis* A. Scott, 1896 from Seogwipo on Jeju Island, South Korea, where he recovered a small number of specimens from washings of wood infested by limnoriid isopods and teredinid bivalves and from coralline sand collected at moderate depths. In a later report, Kim (2014) listed *Paralaophontodes psammophila* (Soyer, 1975) and *Algensiella boitanii* Cottarelli & Baldari, 1987 from the same locality and habitat as *La. bicornis*, but both records are highly dubious and should be discarded (see below - Authenticity of *Laophontodes bicornis* in Korea). Members of the Ancorabolinae have remained unrecorded from this part of the world so far. Here, we describe two new deep-water representatives of the latter subfamily, both belonging to the *Ceratonotus* group and collected from fine sandy deposits at 105 m depth off the south coast of the Korean peninsula. This contribution also: (1) addresses the taxonomic position of two genera of uncertain affinity, *Patagoniaella*

Pallares, 1968 and *Ancorabolina* George, 2006c; (2) reviews the status of certain species in *Laophontodes* T. Scott, 1894; and (3) provides updated keys to the species of *Laophontodes* and to the genera of both Ancorabolinae and Laophontodinae.

MATERIAL AND METHODS

Sediment samples were collected by multiple coring (a set of eight cores, each one 10 cm in diameter) during the Korea Institute of Ocean Science and Technology (KIOST) cruise of the research vessel *RV Onnuri* between 31 May and 8 June 2015 in the South Sea of Korea (Fig. 1). The upper 5 cm of sediment cores were transferred to 1-L plastic bottles, to which 7% $MgCl_2$ solution was added; after 5–10 min the samples were fixed in 10% formalin. In the laboratory, specimens were extracted from the sediments by flotation-centrifugation using the Ludox HS-40 colloidal silica polymer (Burgess, 2001) and rinsed and filtered with tap water through a sieve of mesh size 63 µm. Copepods were sorted under a Leica M165C stereomicroscope, transferred to glycerin and then dissected in lactic acid. Whole specimens and appendages were drawn using a camera lucida mounted on a Leica DM2500 microscope equipped with differential interference contrast. After examination, the dissected parts were mounted in glycerin and sealed.

The descriptive terminology is adopted from Huys & Boxshall (1991) and Huys *et al.* (1996). Abbreviations used in the text are as follows: ae, aesthetasc; apo, apophysis; exp, enp and benp for exopod, endopod and baseoendopod, respectively; exp (enp)-1 (-2, -3) to denote the proximal (middle, distal) segments of a ramus; and P1–P6, swimming legs 1–6. The term 'acrothek' denotes the trifid setal structure found primitively on the apical margin of the distal antennulary segment (Huys & Iliffe, 1998). Scale bars in figures are in µm.

Type specimens were deposited in the National Biological Resources Center (NIBR), Incheon, Republic of Korea (NIBRIV registration numbers). Additional material was stored in the Korea Institute of Ocean Science and Technology (KIOST), Busan, Korea (MInRB registration numbers).

TAXONOMY

ORDER HARPACTICOIDA SARS, 1903

FAMILY ANCORABOLIDAE SARS, 1909

SUBFAMILY ANCORABOLINAE SARS, 1909

GENUS *DIMORPHIPODIA* GEN. NOV.

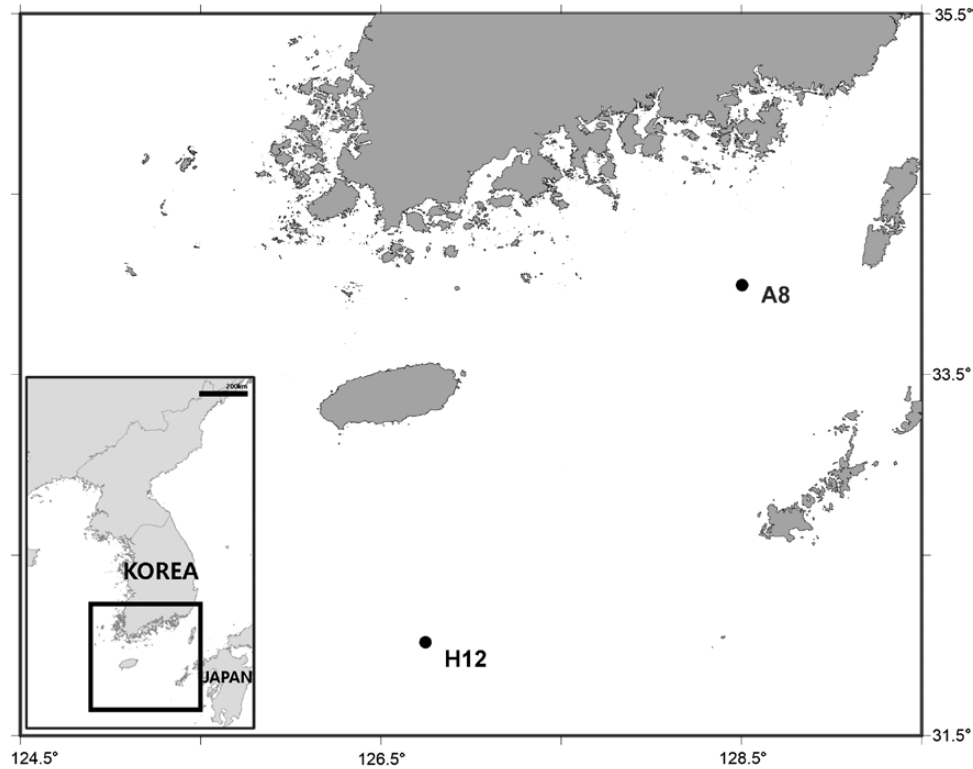urn:lsid:zoobank.org:act:322B971F-B357-4AA4-A6E1-CB4CE2496329

Figure 1. Sampling localities in the South Sea of Korea.

Diagnosis: Ancorabolinae. Body cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome. Urosomites without paired processes or tubercles. Cephalothorax with large, conical frontolateral horns; posterior margin without paired laterodorsal processes; lateroventral margin forming setulose lobate outgrowth. Somites bearing P2–P4, each with paired dorsal processes which are distinctly smaller in ♂; none of the thoracic processes dendroid; pleural areas with setular tufts. Genital somite (anterior half of genital double-somite in ♀) with lateral bulbous projections. Ventral posterior margins of urosomites with very fine setular extensions. Body somites and caudal rami with conspicuous tube-pores dorsally and laterally. Anal operculum with fine setules. Caudal rami elongate and cylindrical, with seven setae; seta III pinnate. Sexual dimorphism in body size, antennule, P2–P4 exopods, P3 endopod, P5, P6, genital segmentation and degree of development of dorsal body processes.

Rostrum small, discernible in dorsal aspect; fused to cephalic shield; with paired plumose sensilla, membranous projections and long distinctive midventral tube-pore subapically. Antennule four-segmented in ♀, six-segmented and with one segment distal to geniculation in ♂; aesthetasc arising from segments 3 and 4 in ♀, segments 5 and 6 in ♂; segment 1 elongate and with long spinules along

anterior margin. Antenna with allobasis showing partial suture halfway along outer margin, abexopodal margin with two setae of equal length; exopod entirely absent; free endopodal segment with three lateral and six distal elements. Mandible with robust coxa; palp one-segmented, uniramous with five setae (three endopodal, one basal and one exopodal). Maxillule with two elements on coxal endite; basis with four elements; exopod and endopod completely incorporated into basis, represented by two and three setae, respectively. Maxillary syncoxa with two well-developed endites, each with three elements; allobasis drawn out into claw with three accessory elements around its base; endopod minute, with two setae. Maxilliped subchelate, slender and elongate; syncoxa with one reduced seta; endopod drawn out into long, narrow, curved claw with one accessory seta.

P1–P4: Intercoxal sclerites wide and narrow; praecoxae well developed; coxae small, trapezoid; bases extremely transversely elongate. P1 endopod absent, original position indicated by slightly membranous area with small nodule; exopod two-segmented, exp-2 with four geniculate setae and one outer bipinnate seta. P2–P4 ♀ with three-segmented exopods; endopods absent (P2) or two-segmented (P3–P4); without inner setae on exp-1 and endopodal segments; exp-3 with only two outer spines. P2–P4 exp-2 ♂ inner seta much

longer than in ♀. Exp-3 ♂ with one (P2, P4) or two (P3) inner setae; apical elements longer than in ♀. P3 endopod ♂ three-segmented; enp-2 elongate, anterior surface produced distally into recurved apophysis; enp-3 with two apical setae. Armature formula as follows:

	Exopod	Endopod
P2	0.1.022 [♂: 0.1.122]	absent
P3	0.1.022 [♂: 0.1.222]	0.020 [♂: 0.apo.020]
P4	0.1.022 [♂: 0.1.122]	0.020

P5 uniramous in both sexes; basal setophore reduced to short cylindrical outgrowth; endopodal lobe vestigial, represented by two minute setae and one (♀) or two (♂) conspicuous tube-pores; exopod elongate, with one inner, one apical and three outer elements (middle outer spine shortest and displaced to posterior surface), fused with baseoendopod in ♀, distinct in ♂. Female genital field located anteriorly, with moderately large copulatory pore; gonopores covered by common genital operculum derived from medially fused P6 with one naked seta on either side. Male P6 asymmetrical; without armature; functional member represented by small membranous flap.

Type and only species: Dimorphipodia changi gen. et sp. nov.

Etymology: The generic name is derived from the Greek δις (*dis*, twice), μορφή (*morphe*, form) and πους (*pous*, foot) and refers to the sexual dimorphism expressed on the exopods of each of the swimming legs (P2–P4). Gender: feminine.

DIMORPHIPODIA CHANGI SP. NOV.
(FIGS 2–8)

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Type locality: South Korea, south coast, Stn A8 (33°59.851′N, 128°30.413′E); fine sand with high silt content; depth 105.7 m (Fig. 1).

Type material: Holotype ♀ dissected on ten slides (reg. no. NIBRIV0000829704), allotype ♂ dissected on nine slides (reg. no. NIBRIV0000829705), remaining paratypes (three ♀♀, two ♂♂) preserved in formalin (reg. no. NIBRIV0000829706); all type specimens

collected on 8 June 2015 from type locality.

Description of female: Body length measured from anterior margin of rostrum to posterior margin of caudal rami 611–664 µm (mean = 641 µm; $N = 4$; holotype = 642 µm). Body (Fig. 2A) cylindrical, without clear demarcation between prosome and urosome; urosome slightly narrower than prosome, maximal width (128 µm) measured at P3-bearing somite. Integument moderately chitinized. Cephalothorax with marked bilateral constrictions separating posterior third from anterior two-thirds; with paired elongate frontolateral horns immediately posterior to insertion sites of antennules at anterior outer corners (Fig. 2A); each horn ending in long sensillum and bearing minute denticles and few proximal setules (see inset in Fig. 2A); dorsal surface of cephalothorax with three pairs of conspicuous tube-pores; frontal margin concave, bearing small median rostrum; lateroventral margin forming setulose lobate outgrowth (not figured). Posterior processes absent. Most sensilla on cephalic shield branched.

*Rostrum (*Fig. 2B*):* Fused to cephalic shield; small, trapezoid in shape; dorsal surface with paired plumose sensilla subapically; ventral surface with paired, pointed, membranous projections subapically and long median tube-pore.

*Somites bearing legs 2–5 (*Fig. 2A*):* With well-developed pleurotergites forming distinct lateral expansions so that somites are clearly demarcated in dorsal aspect; separated by distinct membranous zones; hyaline frills plain. Somites bearing legs 2–4 with paired, slightly backwardly produced processes dorsally and paired setular tufts lateroventrally (Fig. 2C); processes relatively short, covered with small denticles and bearing apical sensillum; somites with paired tube-pores dorsolaterally and median tube-pore dorsally.

Original segmentation of genital double-somite indicated by lateral bulbous projections in anterior half and pairwise pattern of tube-pores and sensilla (Fig. 2A, D); projections ornamented with few spinules and bearing conspicuous apical sensillum; second pair of smaller lateral projections present in posterior half, with apical sensillum; posterior margin with continuous row of setular extensions and pair of closely set tube-pores midventrally (Fig. 2A, D). Genital field (Fig. 2D) with medially fused gonopores, opening via common midventral slit covered by genital operculum derived from fused vestigial sixth legs; each leg 6 with one naked seta. Copulatory pore moderately large, flanked by paired tube-pore triplet, immediately posterior to each gonopore.
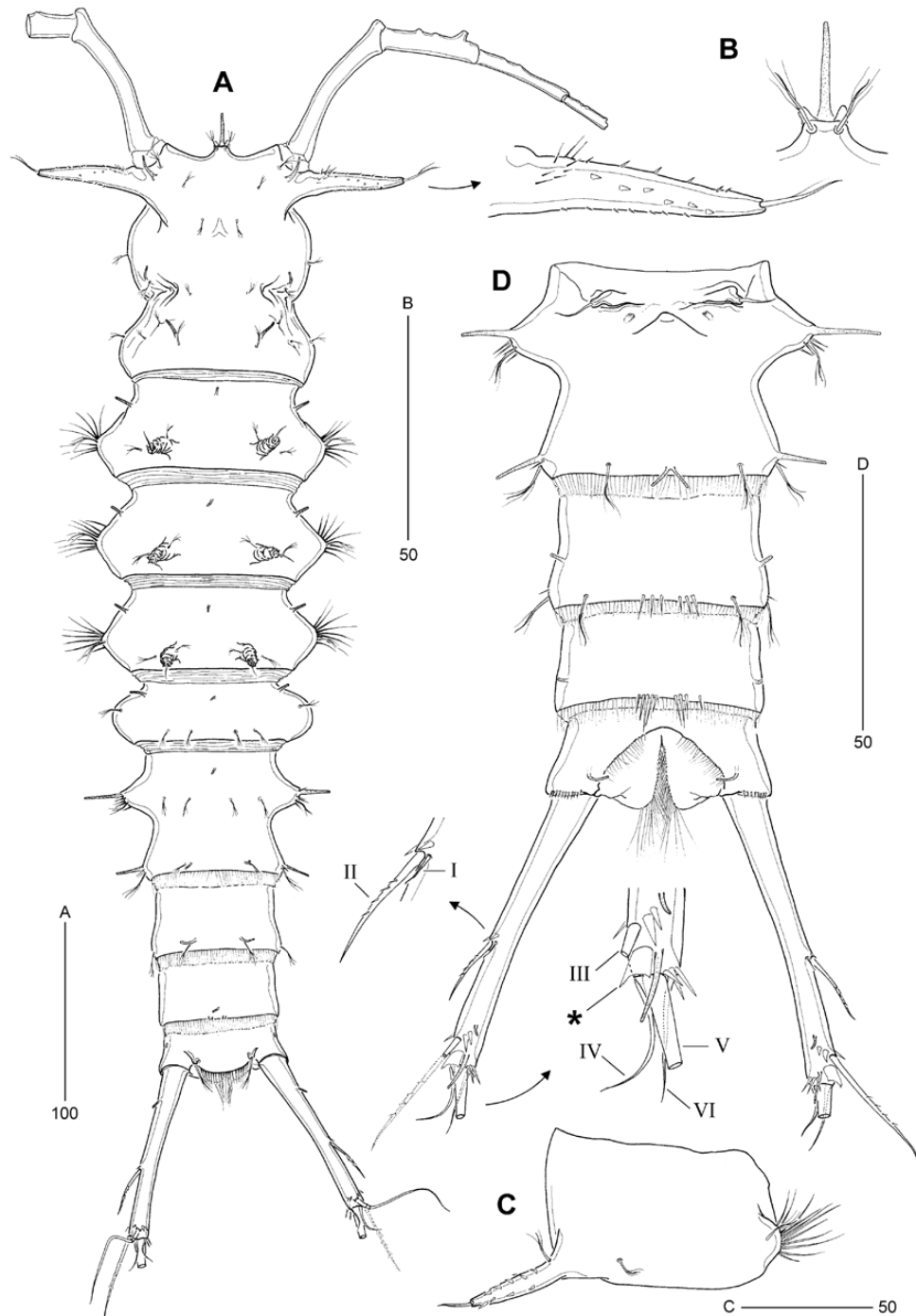
Figure 2. *Dimorphipodia changi* (♀). A, habitus, dorsal (inset showing detail of right frontolateral horn). B, rostrum, dorsal. C, leg 2-bearing somite, lateral. D, urosome (excluding leg 5-bearing somite), ventral (details of insertion sites of caudal ramus setae I–II and III–VI shown in left and right insets, respectively; large tube-pore indicated by *).

Second and third abdominal somites: With few spinules midventrally near posterior margin (Fig. 2D); both somites with paired tube-pores ventrolaterally and with a continuous row of fine setular extensions around hind margin; dorsal surface of second somite with paired tube-pores, that of third somite with single tube-pore and few spinules medially (Fig. 2A). Anal somite partly cleft medially (Fig. 2D); with paired tube-pores dorsolaterally and long sensilla arising from socles either side of anal operculum; paired tube-pores
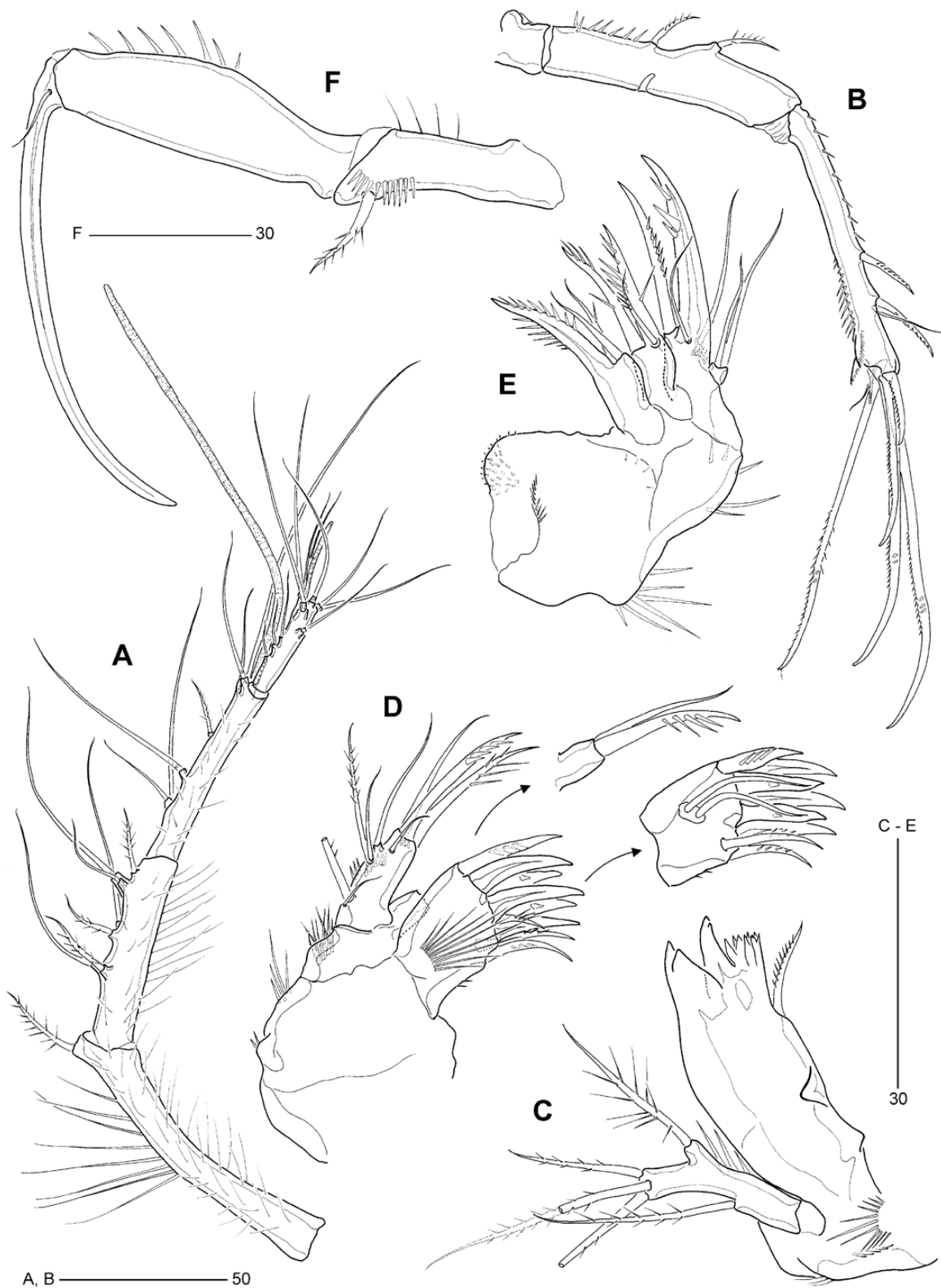
Figure 3. *Dimorphipodia changi* (♀). A, antennule, dorsal. B, antenna. C, mandible. D, maxillule, posterior (insets showing armature of coxal endite and anterior view of praecoxal arthrite, respectively). E, maxilla. F, maxilliped.
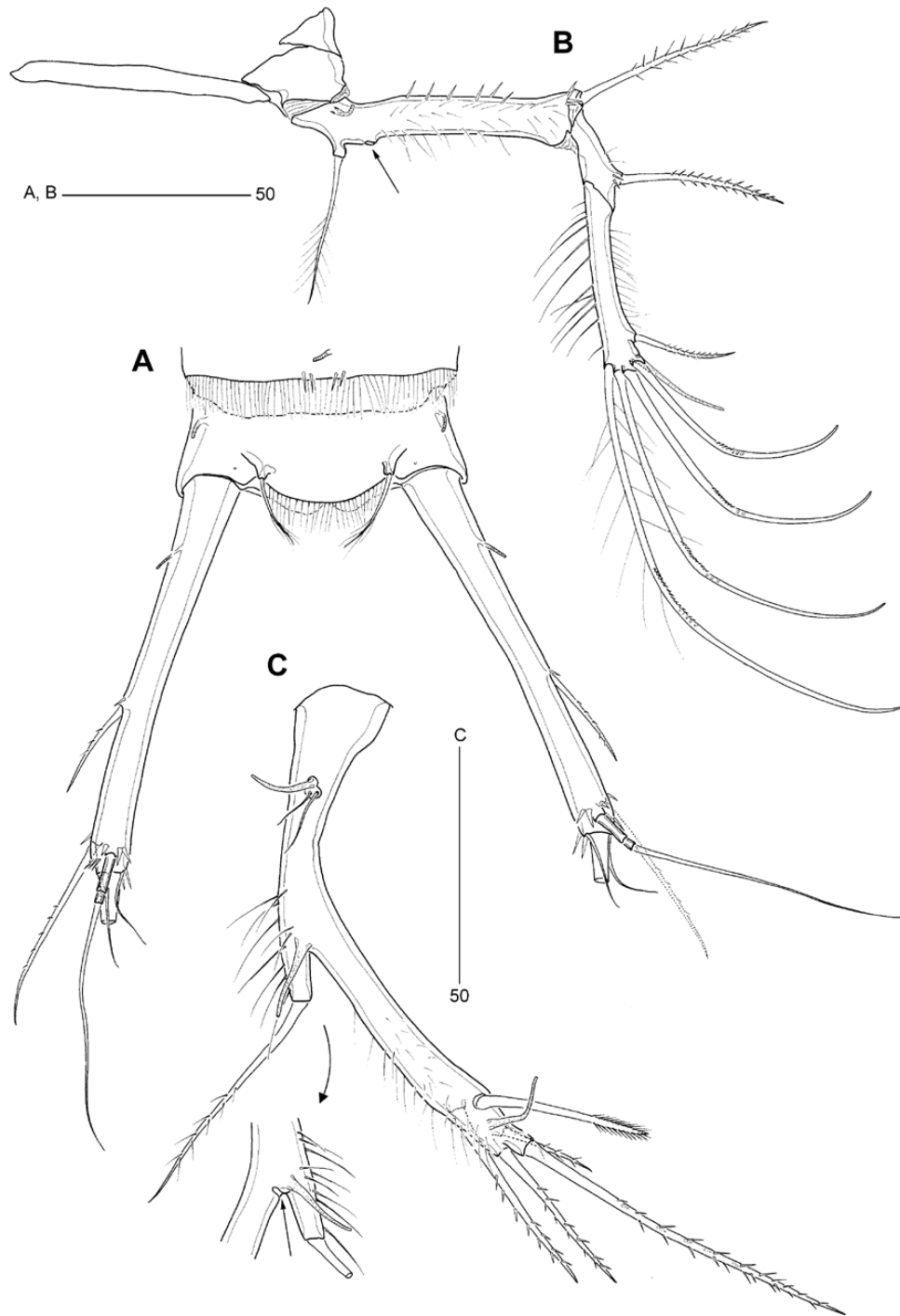
Figure 4. *Dimorphipodia changi* (♀). A, anal somite and caudal rami, dorsal. B, leg 1, anterior (arrow indicating original position of endopod). C, leg 5, anterior (inset showing membranous area (arrowed) distal to tube-pore, marking original segment boundary between baseoendopod and exopod).

and small spinules present around ventral hind margin near bases of caudal rami; anal operculum rounded, furnished with long, fine setules; anal frill deeply incised, forming long setular extensions (Figs 2A, D, 4A). All sensilla on urosomites sparsely plumose, often giving them a branched appearance.

Caudal rami: Elongate, divergent and slightly bent inwards, cylindrical, slightly shorter than last three
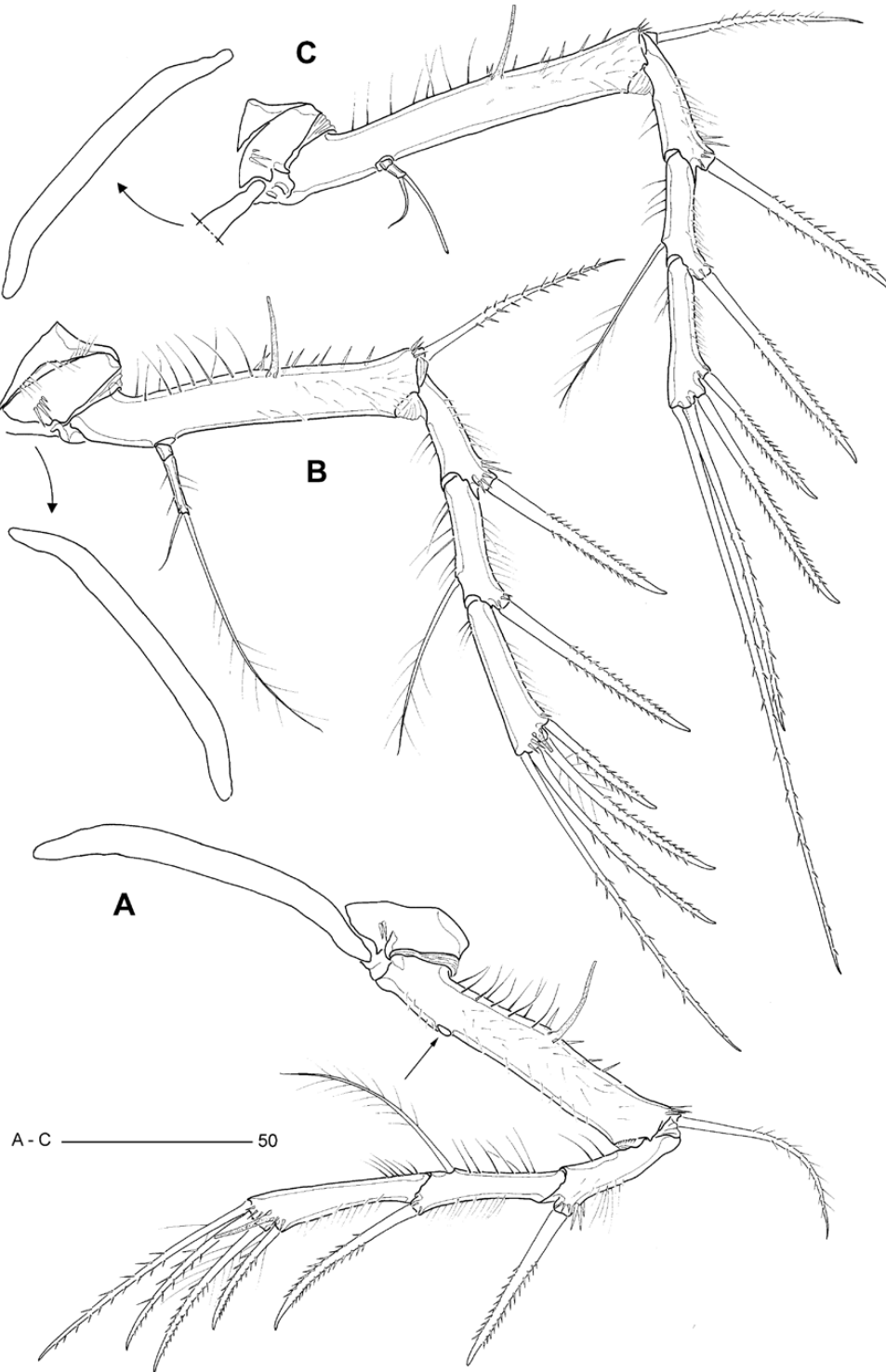
Figure 5. *Dimorphipodia changi* (♀). A, leg 2, anterior (arrow indicating original position of endopod). B, leg 3, anterior. C, leg 4, anterior. Intercoxal sclerites disarticulated in B, C.

urosomites combined (Figs 2D, 4A); with few spinules around insertion sites of setae I–III (Fig. 2D), VI and VII (Fig. 4A); with four tube-pores and seven setae.

Setae III–VII arranged around posterior margin of ramus; seta I minute, positioned ventral to seta II (see right inset of Fig. 2D); setae II–III unipinnate; setae IV
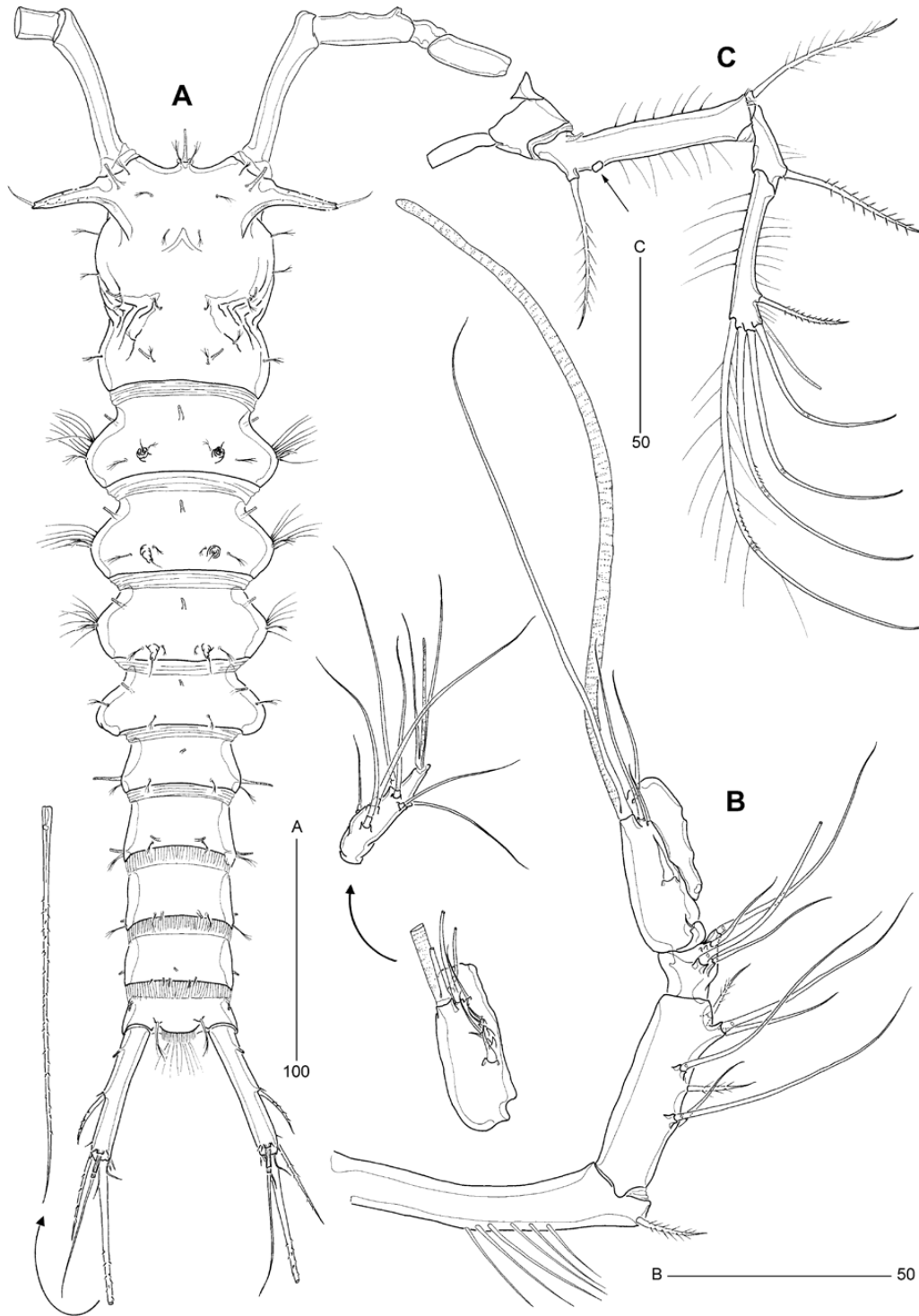
Figure 6. *Dimorphipodia changi* (♂). A, habitus, dorsal (inset showing caudal ramus seta V at full length). B, antennule, ventral (armature of segments 5 and 6 shown in insets). C, leg 1, anterior (arrow indicating original position of endopod).

and VI naked; seta V well developed, ornamentation unconfirmed; seta VII tri-articulate at base and arising from minute dorsal pedestal. Dorsolateral tube-pore positioned in proximal quarter of ramus; remaining three tube-pores arising near ventral posterior margin, outer one much wider than inner ones and represented by flaccid scale-like extension (indicated by * in Fig. 2D).
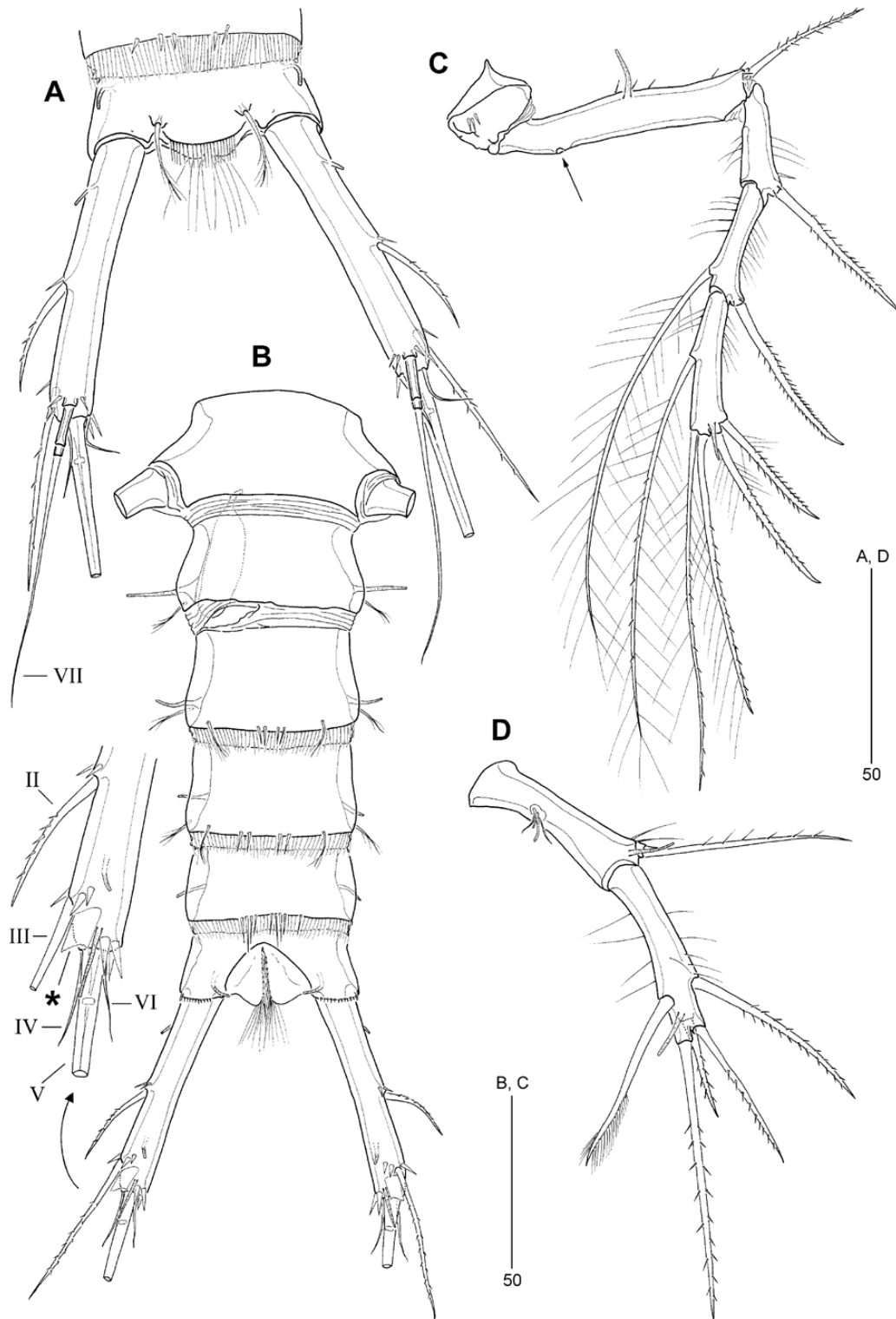
Figure 7. *Dimorphipodia changi* (♂). A, anal somite and caudal rami, dorsal. B, urosome, ventral (inset showing armature of distal half of right caudal ramus, ventral; large tube-pore indicated by *). C, leg 2, anterior (arrow indicating original position of endopod). D, leg 5, anterior.
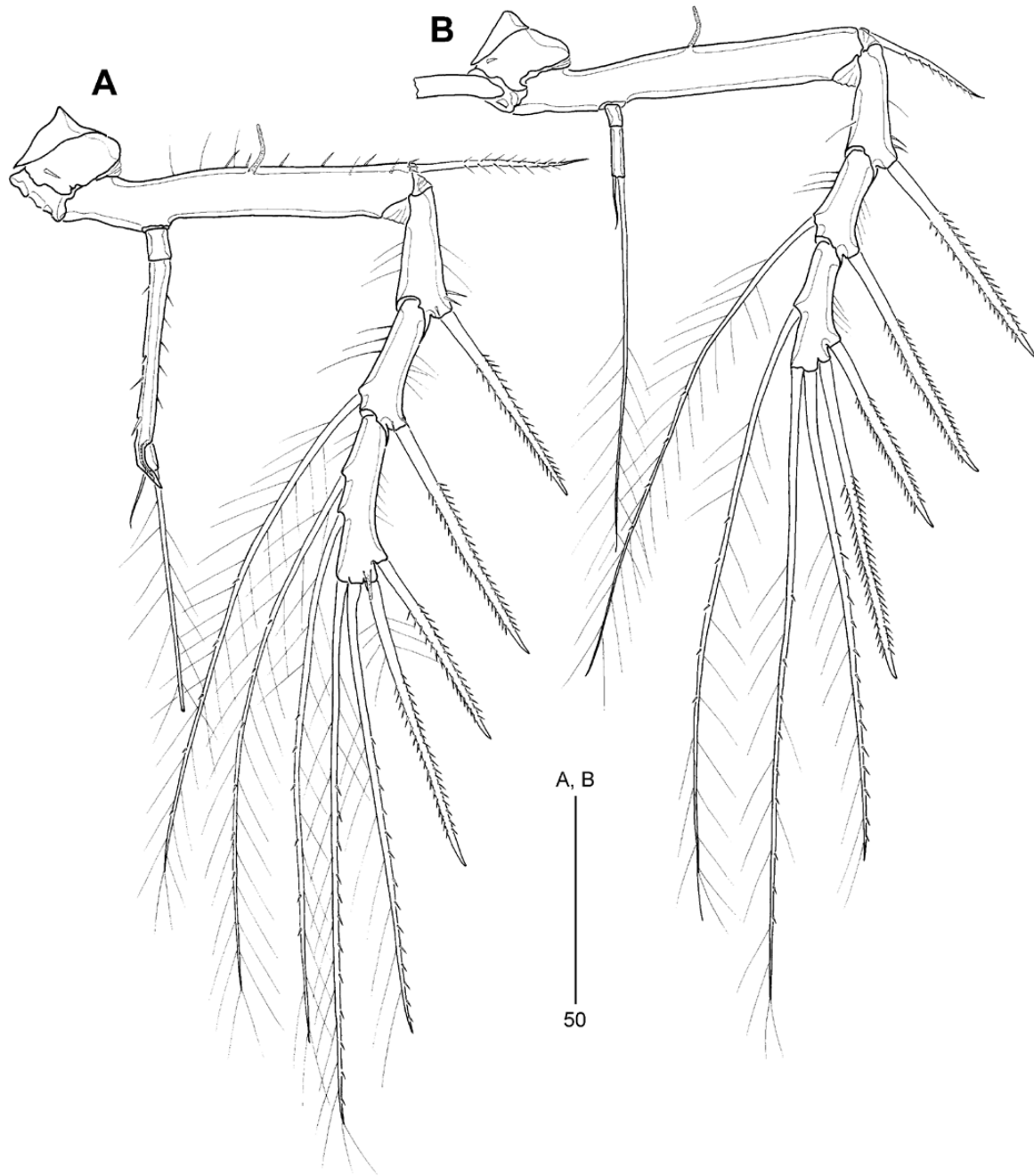
Figure 8. *Dimorphipodia changi* (♂). A, leg 3, anterior. B, leg 4, anterior.

*Antennule (*Fig. 3A*):* Four-segmented. Dorsal surface of segments 1–3 covered with fine setules. Segment 1 longest, with long, fine spinules along distal half of anterior margin; with bipinnate seta sub-apically. Segment 3 second longest, with aesthetasc (length 135 μm). Segment 4 with apical acrothek consisting of short aesthetasc (length 25 μm) and two slender setae. Armature formula: 1-[1 pinnate], 2-[4 + 3 pinnate], 3-[5 + 1 pinnate + (1 + ae)], 4-[9 + acrothek].

*Antenna (*Fig. 3B*):* Slender and elongate. Coxa represented by well-developed sclerite. Basis and proximal endopod segment fused, forming allobasis; membranous insert halfway along outer margin marking original position of exopod; exopod completely absent; abexopodal margin with few spinules in basal half; with two short, pinnate setae. Free endopodal segment with two distal surface frills and spinule row along distal outer and proximal medial margins;

lateral armature consisting of two unipinnate spines and one bare seta; distal armature consisting of two unipinnate spines and three geniculate setae with pinnules around geniculation; outermost geniculate seta with one spinule distally and fused basally to vestigial seta and with tube-pore arising from its base.

*Mandible (*Fig. 3C*):* Coxa robust, with several spinule rows proximally; gnathobase with two multicuspidate teeth and series of thin incised blades; with one unipinnate seta at dorsal corner. Palp well developed, one-segmented; with one bipinnate seta along inner margin (representing basal element), three apical setae (representing incorporated endopod) and one bipinnate seta along outer margin (representing exopod); inner margin with few strong spinules.

*Maxillule (*Fig. 3D*):* Praecoxal arthrite subrectangular, with two setae on anterior surface and spinule row on posterior surface; distal armature consisting of three pinnate setae and six spines (outermost one unipinnate, others naked); outer margin of praecoxa with few spinules as indicated. Coxa with spinules round outer margin; endite with one unipinnate spine and one bare seta. Basis with three spinule rows; basal endites indistinguishable, represented by one short and one long naked seta and two unipinnate spiniform elements. Rami completely incorporated into basis; exopod represented by one short and one long seta; endopod represented by one bipinnate and two naked setae.

*Maxilla (*Fig. 3E*):* Syncoxa with two groups of strong spinules along outer margin and additonal patches of small spinules as figured; with two endites arising from membranous area; proximal endite with one strong bipinnate spine fused at base to endite and two setae; distal endite with two pinnate spines (distal one fused at base to endite) and one small, unipinnate seta. Allobasis drawn out into claw bearing few strong spinules subdistally; accessory armature consisting of two bare setae and one unipinnate spine. Endopod one-segmented, minute, with two naked setae.

*Maxilliped (*Fig. 3F*):* Subchelate, slender and elongate. Syncoxa with one bipinnate seta surrounded by spinules around its base; with few setules around outer margin. Basis with strong spinules along outer margin, unarmed. Endopod drawn out into long narrow, curved claw; claw smooth with one accessory seta at base.

*P1 (*Fig. 4B*):* Intercoxal sclerite wide and narrow; without ornamentation. Praecoxa represented by well-developed sclerite. Coxa small, trapezoid. Basis transversely elongate, with conspicuous anterior tube-pore near articulation with coxa; anterior surface covered by setules and spinules as figured; with bipinnate outer spine and plumose inner seta. Exopod two-segmented. Exp-1 shortest, with few

spinules/setules along outer margin; outer spine long and bipinnate, but shorter than exp-2. Exp-2 with fine setules along outer and inner margins; with four geniculate setae (the innermost one plumose) and one pinnate outer spine; outer distal corner with very long tube-pore. Endopod absent; original position indicated by slightly membranous area (arrowed in Fig. 4B).

*P2–P4 (*Fig. 5A–C*):* Intercoxal sclerites wide and narrow, lacking surface ornamentation. Praecoxae represented by well-developed sclerites (not figured for P2), with fine setules in P3 (Fig. 5B). Coxae trapezoid, with few spinules anteriorly. Bases transversely elongate; outer margin with long setules in proximal half, spinules in distal half and large, basally reinforced, anterior tube-pore; additional patches of fine setules on anterior surface; outer distal seta bipinnate, arising from a tiny, posteriorly displaced setophore. Exopods three-segmented; outer and inner margins with fine setules as figured; outer spines elongate and bipinnate. P2 endopod absent, position indicated by slightly membranous area (arrowed in Fig. 5A). P3–P4 endopod (Fig. 5B, C) reduced, two-segmented; enp-1 tiny, unarmed; enp-2 longer with two apical setae, with few setules along inner and outer margins in P3. Armature formula of P2–P4 as in the generic diagnosis.

*P5 (*Fig. 4C*):* One-segmented; original segment boundary between baseoendopod and exopod marked by minute membranous area (arrowed in inset of Fig. 4C). Baseoendopod with long setules along outer margin and large subdistal tube-pore; setophore reduced, fused to baseoendopod, bearing pinnate outer basal seta. Endopodal lobe absorbed into basis, represented by one conspicuous tube-pore and two tiny naked setae. Exopodal lobe long and slender; with fine setules and one subapical tube-pore on anterior surface; inner spine finely serrated; with one bipinnate seta distally and three bipinnate outer setae (proximal and middle ones displaced posteriorly).

Description of male: Distinctly smaller and more slender than ♀. Body length measured from anterior margin of rostrum to posterior margin of caudal rami 373–453 µm (mean = 417 µm; *N* = 3; dissected paratype = 453 µm). Sexual dimorphism in body size, degree of development of body processes, antennule, P2–P6, urosomal segmentation and caudal ramus length.

Frontolateral horns and body processes on somites bearing P2–P4 relatively smaller than in ♀ (Fig. 6A). Ornamentation pattern of processes and sensilla essentially as in ♀. Urosome (Figs 6A, 7B) slender; genital somite without pleural extensions; ornamentation of abdominal somites as in ♀.

*Caudal rami (*Fig. 7A, B*):* Slightly shorter than in ♀; armature and ornamentation as in ♀, including appearance of flaccid scale-like outer tube-pore (indicated by * in inset of Fig. 7B).

*Antennule (*Fig. 6B*):* Six-segmented, geniculation between segments 5 and 6; aesthetasc present on segment 5 (length 160 µm) and as part of apical acrothek on segment 6. Segment 1 longest, with few long spinules along anterior margin. Segment 4 represented by a U-shaped sclerite. Segment 5 not markedly swollen. Armature formula: 1-[1 bipinnate], 2-[2 bipinnate + 5], 3-[4 + 2 vestigial], 4-[1 vestigial], 5-[7 + 1 spine + (1 + ae)], 6-[7 + acrothek]. Apical acrothek consisting of two setae and aesthetasc (length 29 µm).

*P1 (*Fig. 6C*):* As in ♀.

*P2–P4 (*Figs 7C, 8A, B*):* Inner seta of exp-2 much longer than in ♀. Exp-3 with one (P2, P4) or two (P3) plumose inner setae; apical elements longer than in ♀. P3 endopod (Fig. 8A) three-segmented; enp-1 slightly longer than wide; enp-2 elongate, with sparse spinules along inner and outer margins, anterior distal surface produced into small recurved spinous apophysis; enp-3 with two apical setae, outermost seta proportionally longer than in ♀. Armature formula of P2–P4 as follows:

	Exopod	Endopod
P2	0.1.122	absent
P3	0.1.222	0.apo.020
P4	0.1.122	0.020

*P5 (*Fig. 7D*):* Two-segmented: Baseoendopod with large distal tube-pore; setophore reduced, fused to baseoendopod, bearing pinnate outer basal seta. Endopodal lobe absorbed, represented by two conspicuous tube-pores and two minute setae. Exopod completely defined at base, elongate; with fine setules on anterior surface; with finely serrated spine and long subdistal tube-pore along inner margin, one bipinnate spine apically, and three pinnate setae along outer margin (middle one shortest and displaced posteriorly).

*P6 (*Fig. 7B*):* Sixth pair of legs asymmetrical, with only one functional member, represented by reduced membranous flap; other member fused to somite; without armature.

*Spermatophore (*Fig. 7B*):* Ovoid, 40 µm.

Etymology: The species is dedicated to Professor Cheon Young Chang (Daegu University), mentor of the senior author, in recognition of his major contributions to copepod systematics and taxonomy.

Remarks: Conroy-Dalton (2001) proposed the *Ceratonotus* group for five genera in the subfamily Ancorabolinae, i.e. *Ceratonotus* Sars, 1909,

Dorsiceratus Drzycimski, 1967, *Polyascophorus* George, 1998, *Arthuricornua* Conroy-Dalton, 2001 and *Touphapleura* Conroy-Dalton, 2001. The group was defined by the following suite of synapomorphies: (1) body somites virtually cylindrical; (2) somites bearing P2–P4 with paired backwardly produced (latero)dorsal processes; (3) rostrum small, without apical elongation anterior to insertion point of sensillae; no sexual dimorphism where males are known; (4) antennulary segment 1 elongate (fused to segment 2 in *Ceratonotus*, but equivalent portion also elongate); (5) P1–P4 endopods reduced, with armature elements always arranged around apex of terminal segment; (6) P3 male with three-segmented endopod; apophysis arising from middle segment; and (7) P5 endopodal lobe in both sexes absorbed into protopod; with reduced armature, represented by at most two setae (Conroy-Dalton, 2001). The *Ceratonotus* group saw the addition of *Dendropsyllus* Conroy-Dalton, 2003a, a new genus proposed for two species previously allocated to *Ceratonotus*, i.e. *Ceratonotus antarcticus* George & Schminke, 1998 and *Ceratonotus magellanicus* George & Schminke, 1998 (Conroy-Dalton, 2003a). Finally, George (2006b) added both *Echinopsyllus* Sars, 1909 and *Pseudechinopsyllus* George, 2006b, a course of action subsequently corroborated by a phylogenetic analysis (Wandeness *et al.*, 2009), although synapomorphies supporting the common ancestry of the remaining members of the *Ceratonotus* group could not be identified, and the evidence underpinning the sister-group relationship between *Echinopsyllus* and *Pseudechinopsyllus* does not appear to be particularly robust.

In their revision of the *Ancorabolus* group, Conroy-Dalton & Huys (2000) noted a remarkable overall consistency in the number of cephalothoracic sensillae, whereas the number, size and shape of spinous processes on the cephalothorax varied considerably between genera. Analysis of this variation against the background of a conserved sensillar reference pattern unequivocally determined the homology of processes between genera. Likewise, the position, shape and number of horns and processes on the cephalothorax (and the trunk) can be radically divergent between genera of the *Ceratonotus* group (Fig. 9). Failure to understand the homology between these processes has resulted in erroneous interpretations of their morphology and/or confusion surrounding the relationships of certain genera. In its most elaborate form (discounting the *Echinopsyllus* condition from the discussion below), the cephalothorax displays four pairs of outgrowths: (1) frontolateral horns (FLH); (2) posterior laterodorsal processes (CLDP); (3) posterior lateroventral processes (CLVPp); and (4) anterior lateroventral processes (CLVPa). This pattern is fully expressed in *Dendropsyllus*, *Pseudechinopsyllus*

and at least some members of *Ceratonotus* and *Polyascophorus*, whereas in other genera one or more pairs are absent.

Frontolateral horns (FLH) originate from the anterolateral corners of the cephalothorax and invariably bear a sensillum at the apex and typically one or two sensilla and a tube-pore at the base. They can be considered the positional homologues of the first pair of lateral cephalothoracic processes (L1) in the terminology of Wandeness *et al.* (2009). Horns are moderately developed in *Pseudechinopsyllus*, completely absent in both *Dorsiceratus* and *Touphapleura*, and represented by long processes in the remaining genera of the *Ceratonotus* group (Fig. 9). In *Arthuricornua*, *Polyascophorus* and *Dimorphipodia*, the frontolateral horns are practically straight and directed at a virtually right angle to the longitudinal body axis, whereas in *Ceratonotus* and *Dendropsyllus* they are typically curved and backwardly directed. In some species of *Ceratonotus*, a pair of small, pointed or conical projections arise from the frontal margin of the cephalothorax (as in *Ceratonotus concavus* Conroy-Dalton, 2003a, *Ceratonotus steiningeri* George, 2006a, *Ceratonotus tauroides* George, 2006a and *Ceratonotus vareschii* George, 2006a). These projections (= anterior horn-like processes sensu Gómez & Díaz, 2017) carry the sensilla typically found on either side of the frontal tube-pore and are therefore rostral in origin. Their presence appears to be associated with species whose rostral margin has secondarily become distinctly concave. Similar sensillate tubercles are present in some *Dendropsyllus* species (e.g. *Dendropsyllus californiensis* Gómez & Díaz, 2017; Gómez & Díaz, 2017: fig. 8C).

Most members of the *Ceratonotus* group exhibit a pair of laterodorsal processes (CLDP) arising from the posterior half of the cephalothorax. Exceptions include the genera *Touphapleura* and *Dimorphipodia* and two species in the genus *Polyascophorus* [*Po. gorbunovi* (Smirnov, 1946) and *Po. martinezi* George, 1998]. In some species, such as *Dendropsyllus thomasi* Conroy-Dalton, 2003a, *Dendropsyllus kimi* and *Pseudechinopsyllus sindemarki* George, 2006b, the processes assume a slightly more dorsal position (Conroy-Dalton 2003a: fig. 9A; George 2006b: fig. 19A; fig. 10A herein). They are relatively short and lack ornamentation in *Ps. sindemarki*, spinulose along their entire length in members of *Dorsiceratus* and *Arthuricornua* and dendroid in representatives of *Ceratonotus* and *Dendropsyllus*. Conroy-Dalton (2001) postulated that the processes have migrated from their ancestral laterodorsal position to a lateroventral location in the two Arctic *Polyascophorus* species (*Polyascophorus gorbunovi* and *Polyascophorus martinezi*). It was assumed that during this process they had also become apically bifurcate, forming a

short anterior and a long posterior branch, and had undergone excessive development, becoming the largest pair of body processes. The recent discovery of *Polyascophorus monoceratus* George, Wandeness & Santos, 2013 has proved this scenario to be incorrect, because both laterodorsal and bifurcate lateroventral processes are expressed in this species (George *et al.*, 2013). The posterior pair of (latero)dorsal processes are the positional homologues of the second pair of dorsal cephalothoracic processes (DII) in the system devised by Wandeness *et al.* (2009).

A pair of posterior lateroventral processes (CLVPp), each bearing an apical sensillum, is expressed in *Ceratonotus*, *Dendropsyllus*, *Pseudechinopsyllus* and *Polyascophorus*, but only in the last genus are they bifurcate. In *Dendropsyllus*, the processes are very large, being smooth [*Dendropsyllus antarcticus* (George & Schminke, 1998)] or more commonly dentate (remaining species), whereas in *Ceratonotus* their size and form vary considerably between species. In *Ceratonotus pectinatus* Sars, 1909, *Ceratonotus thistlei* Conroy-Dalton, 2003 and *Ceratonotus vareschii*, the lateroventral processes are small and conical (Conroy-Dalton, 2003a: figs 1C, 5B; George, 2006a: fig. 16). Conversely, in *C. concavus* (Conroy-Dalton, 2003a: fig. 7C), *C. tauroides* (George, 2006a: fig. 2A) and *Ceratonotus elongatus* Gómez & Díaz, 2017 (Gómez & Díaz, 2017: fig. 2A), the conical processes are much larger and clearly discernible in dorsal aspect. In *C. steiningeri*, the processes are elongate and dentate (George, 2006a: fig. 10A, C), resembling the typical *Dendropsyllus* condition. The posterior lateroventral processes correspond to the third pair of lateral cephalothoracic processes (LIII) in the terminology of Wandeness *et al.* (2009). Their claim that the presence of these processes is a synapomorphy for *Echinopsyllus* + *Pseudechinopsyllus* is therefore incorrect.

Some members of the *Ceratonotus* group have a propensity for developing a second extension of the free lateroventral pleural margins of the cephalothorax, usually in the area around the base of the antenna. In *Arthuricornua*, *Dorsiceratus* and *Dimorphipodia*, this is represented by a lobate expansion, which typically bears a tuft of setules (Conroy-Dalton, 2001; this study); the condition in *Touphapleura* is yet to be confirmed. Further extension has resulted in the formation of small, conical protuberances, here referred to as the anterior lateroventral processes (CLVPa). Each conical process has an apical sensillum and two sensilla plus a tube-pore at its base and is often found in close proximity to the posterior lateroventral processes. The presence of such processes is not uniformly distributed throughout the genera *Ceratonotus*, *Dendropsyllus* and *Polyascophorus*. The genus *Ceratonotus* contains members that clearly lack them, such as *C. pectinatus* and *C. thistlei* (Conroy-Dalton, 2003a: figs 1C, 5B),
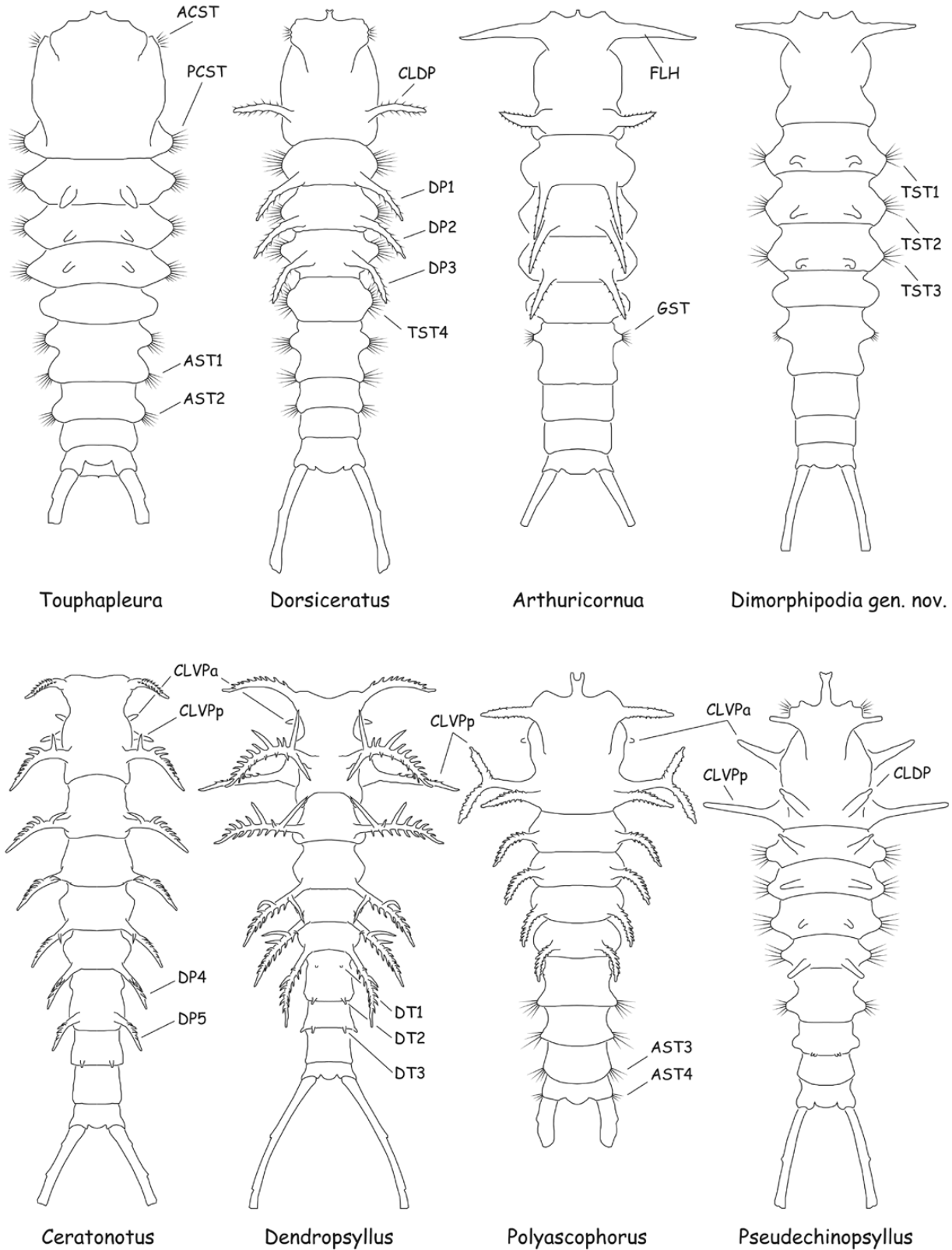
Figure 9. Generalized dorsal habitus views of members of the *Ceratonotus* group (females only; *Echinopsyllus* excluded). Abbreviations: ACST, anterior cephalothoracic setulose/spinulose tuft; AST1–3, lateral setulose/spinulose tufts on

and others that display them, such as *C. concavus* (Conroy-Dalton, 2003a: fig. 7C) and *Ceratonotus vareschii* George, 2006a (George, 2006a: fig. 16). Within *Dendropsyllus*, anterior lateroventral processes appear to be absent in *De. antarcticus* but are either minute, as in *De. thomasi* (Conroy-Dalton, 2003a: Fig. 9B), or moderately developed, as in *Dendropsyllus magellanicus* (George & Schminke, 1998: fig. 1; George, 2006a: fig. 21A), *De. californiensis* (Gómez & Díaz, 2017: fig. 7A) and *De. kimi* (present study: Fig. 10). Within *Polyascophorus*, they have been documented only for *Polyascophorus martinezi* (George, 1998: fig. 1A). In *Pseudechinopsyllus*, the processes have undergone extreme development, resulting in the displacement of the basal tube-pore onto the process. The anterior lateroventral processes can be considered the positional homologues of the second pair of lateral cephalothoracic processes (LII) in the scheme of Wandeness *et al.* (2009). This weakens their claim that the presence of these processes is a synapomorphy supporting the sister-group relationship between *Echinopsyllus* and *Pseudechinopsyllus*.

The new genus *Dimorphipodia* belongs to a lineage of genera that lacks paired dorsal processes on the urosome and both anterior and posterior lateroventral processes on the cephalothorax, including *Touphapleura*, *Dorsiceratus* and *Arthuricornua*, which all have dorsal extensions on the pedigerous somites bearing P2–P4 (Fig. 9). Within this lineage, it is morphologically similar to *Arthuricornua*, which was proposed for its type and only species, *Arthuricornua anendopodia*, collected in the San Diego Trough in the northeastern Pacific (Conroy-Dalton, 2001). Both genera can be considered sister taxa in the *Ceratonotus* group, because they share: (1) a cephalothorax, which is bilaterally constricted in its posterior half [other genera that show a similar constriction display it in the anterior half of the cephalothorax, such as *Ceratonotus*, *Dendropsyllus* and *Pseudechinopsyllus*]; (2) paired elongate, frontolateral horns, which are directed at virtually a right angle to the longitudinal body axis [absent in *Touphapleura* and *Dorsiceratus*; both genera have anterior cephalothoracic setulose/spinulose tufts (ACST) at the anterior corners, which are lacking in *Arthuricornua* and *Dimorphipodia*]; (3) paired lateral,

rounded protuberances (with spinules/setules) (GST) on the anterior half of genital double-somite ♀ [similar setulose/spinulose tufts are found on the urosome in *Touphapleura* and *Dorsiceratus,* but the pattern differs (cf. AST1–2; Fig. 9)]; (4) the complete absence of endopods on P1–P2; (5) an elongate P5 exopod, which is fused to the baseoendopod in the ♀, but free in the ♂ and bears five elements, of which the middle outer spine is reduced and displaced to the posterior surface; and (6) a rounded anal operculum furnished with long, fine spinules.

Dimorphipodia can be differentiated from *Arthuricornua* by the following characters: (1) cephalothorax without paired laterodorsal processes near posterior margin (vs. present); (2) P2–P4 exp-3 with sexually dimorphic armature, showing no inner setae in the female (022), but with one inner seta in the male on P2 and P4 (122) and two inner setae on P3 (222) (the male condition is therefore identical to that of both sexes in *Arthuricornua anendopodia*; Table 2); (3) pedigerous somites bearing P2–P4, with setular tufts on the expanded pleural areas (vs. without); and (4) pedigerous somites bearing P2–P4, with moderately developed dorsal processes (vs. well developed and backwardly directed).

GENUS *DENDROPSYLLUS* CONROY-DALTON, 2003A

DENDROPSYLLUS KIMI SP. NOV.

(FIGS 10–14)

urn:lsid:zoobank.org:act:EC684AC7-0375-49D6-ABF1-B3AA538FB953

Type locality: South coast of Korea; Stn A8 (33°59.851′N, 128°30.413′E); fine sand with high silt content; depth 105.7 m (Fig. 1).

Type material: Holotype ♀ dissected on 12 slides (reg. no. NIBRIV0000829701), allotypic paratype ♂ dissected on ten slides (reg. no. NIBRIV0000829702), remaining paratypes (two ♀♀, one ♂) preserved in formalin (reg. no. NIBRIV0000829703); all type specimens collected on 8 June 2015 from type locality.

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abdominal somites 1–3; AST4, lateral setulose/spinulose tuft on anal somite; CLDP, cephalothoracic laterodorsal process; CLVPa, cephalothoracic lateroventral process (anterior pair); CLVPp, cephalothoracic lateroventral process (posterior pair); DT1, dorsal sensillate tubercle on genital somite (anterior half of genital double-somite); DT2, dorsal sensillate tubercle on abdominal somite 1 (posterior half of genital double-somite); DT3, dorsal sensillate tubercle on abdominal somite 2; DP1–4, dorsal processes on somites bearing P2–P5; DP5, dorsal process on first abdominal somite (posterior half of genital double-somite); FLH, frontolateral horn on cephalothorax; GST, lateral setulose/spinulose tuft on genital somite (anterior half of genital double-somite); PCST, posterior cephalothoracic setulose/spinulose tuft; TST1–4, lateral setulose/spinulose tufts on thoracic somites 3–6 (somites bearing P2–P5). Habitus drawings adapted from Conroy-Dalton (2001, 2003a), George (1998, 2006a, b), George *et al.* (2013) and present study.

Table 2. Female armature formulae in known species of Ancorabolinae. The genus *Ancorabolina* George, 2006c was placed in the Ancorabolinae by Gheerardyn & George (2010), but this has been questioned since by Gheerardyn & Lee (2012); it is here removed to the subfamily Laophontodinae (see main text). Formulae in square brackets denote male condition (setation pattern of male P3 endopod omitted). Abbreviations: G, geniculate setae; S, sexes described.

	S	P1		P2		P3		P4	
		exp	enp	exp	enp	exp	enp	exp	enp
Ceratonotus group									
Arthuricornua									
Ar. anendopodia*	♀♂	0.4G+1	Absent	0.1.122	Absent	0.1.222	0.020	0.1.122	0.020
Ceratonotus									
C. coineaui	♂	0.3G+2 [a]	0.2G	0.1.122	0.020	0.1.222	Unknown	0.1.122	Unknown [010]
C. concavus	♂	0.3G+2	0.2G	0.1.122	0.020	0.1.222	Unknown	0.1.122	Unknown [0.020]
C. elongatus	♀	0.3G+2	0.2G	0.1.122	0.020	0.1.222	0.020	0.1.122	0.010
C. pectinatus*	♀♂	0.3G+2	0.2G	0.1.122	020	0.1.222	020	0.1.122	010 [b]
C. steiningeri	♀♂	0.3G+2	0.2G	0.1.122	Absent	0.1.222	0.010	0.1.122	0.010 [0.020]
C. tauroides	♀♂	0.3G+2 [c]	0.2G	0.1.122	0.010	0.1.222	0.020	0.1[d].122	0.010 [0.020]
C. thistlei	♀	0.3G+2	0.2G	0.1.122	0.020	0.1.222	0.020	0.1.122	0.010
C. vareschii	♂	0.3G+2	0.2G	0.1.122	0.010	0.1.222	Unknown	0.1.122	Unknown [0.020]
Dendropsyllus									
De. antarcticus	♀	0.4G+1	0.010	0.1.122	Absent	Unknown	0.020	0.1.022	010
De. magellanicus	♀♂	0.4G+1	0.010	0.1.122	Absent	0.1.122	0.020	0.1.022	0.010
De. thomasi*	♀	0.4G+1	0.010	0.1.122	Absent	0.1.122	0.020	0.1.022	0.010
De. californiensis	♀	0.4G+1	0.010	0.1.122	Absent	0.1.122	0.021	0.1.022	0.010
De. kimi sp. nov.	♀♂	0.4G+1	0.010	0.1.122	Absent	0.1.122	020	0.1.022	010
Dimorphipodia gen. nov.									
Di. changi sp. nov.*	♀♂	0.4G+1	Absent	0.1.022 [0.1.122]	Absent	0.1.022 [0.1.222]	0.020	0.1.022 [0.1.122]	0.020
Dorsiceratus									
Do. dinah	♀	0.4G+1	0.020	0.1.122	0.010	0.1.222	0.020	0.1.122	0.020
Do. octocornis*	♀♂	0.4G+1	0.020	0.1.122	0.010	0.1.222	0.020	0.1.122	0.020 [0.021]
Do. triarticulatus	♀♂	0.0.4G [e]	0.020	0.1.122	0.010	0.1.222	0.020	1.1.122	0.020 [0.021]
Do. ursulae	♀	0.4G+1	0.020	0.1.122	0.010	0.1.222	0.020	0.1.122	0.020
Do. wilhelminae [f]	♀	0.4G+1	Unknown	0.1.122	Unknown	0.1.222	Unknown	0.1.122	Unknown
Echinopsyllus									
E. brasiliensis	♂	0.0.4G	Absent	0.0.022	Absent	0.0.022	Unknown	0.0.022	Unknown [0.020]
E. grohmannae	♀	0.0.4G	Absent	0.0.022	Absent	0.0.022	020	0.0.022	020
E. nogueirae	♀	0.0.3G+1	Absent	0.0.022	Absent	0.0.022	020	0.0.022	010
E. normani*	♀♂	0.0.3G+1	Absent	0.1.022	Absent	0.1.022	0.020	0.1.022	010
Polyascophorus									
Po. gorbunovi	♀	0.4G+1	0.010	0.1.122	010	0.1.222	010	0.1.122	010
Po. martinezi*	♀♂	0.4G+1	0.010	0.1.122	Absent	0.1.222	0.020	0.1.122	0.010 [0.020]
Po. monoceratus	♀♂	0.4G+1 [0.5G]	0.010 [absent]	0.1.122	Absent	0.1.222	0.020	0.1.122	0.010 [0.021]
Pseudechinopsyllus									
Ps. sindemarkae*	♀	0.4G+1	Absent	0.1.122	Absent	0.1.222	010	0.1.122	010
Touphapleura									
T. schminkei*	♀♂	0.3G+2	0.G+1	0.1.122	0.020	0.1.222	0.021	0.1.122	0.020
Ancorabolus group									
Ancorabolus									
An. chironi	♀♂	0.3G+2	0.2G+1	0.1.022	0.020	0.1.022	0.021	0.1.022	0.021
An. confusus	♀♂	0.3G+2	0.2G+1	0.1.022	0.120	0.1.022	0.021	0.1.022	0.021
An. hendrickxi	♀	0.3G+2	0.2G+1	0.1.022	0.120	0.1.022	0.021	0.1.022	0.021

Table 2. *Continued*

	S	P1		P2		P3		P4	
		exp	enp	exp	enp	exp	enp	exp	enp
An. ilvae [g]	♀	0.3G+2	0.2G+1	0.123	0.020	0.123	0.021	0.123	0.021
An. inermis	♀♂	0.3G+2	0.2G+1	0.1.022	0.020	0.1.022	0.021	0.1.022	0.021
*An. mirabilis** [h]	♀	0.3G+2	0.2G+1	—————————————— Unknown ——————————————					
Arthropsyllus									
*A. serratus**	♀♂	0.2G+3	0.2G+1	0.1.022	0.120	0.1.022	0.121	0.1.022	0.121 [0.021]
Breviconia									
*B. australis**	♀	0.3G+2	0.2G+1	0.1.022	0.120	0.1.022	0.121	0.1.022	0.121
B. echinata	♀	————————— Unknown —————————				0.1.022	0.121	——— Unknown ———	
Juxtaramia									
*J. polaris**	♀♂	0.4G+1	0.2G+1	0.1.022	0.020	0.1.022	0.021	0.1.022	0.021
Uptionyx									
*U. verenae**	♀	0.3G+2	0.2G+1	0.1.022	0.120	0.1.022	0.121	0.1.022	0.121

*Type species.
[a] Soyer (1965: fig. 4A) illustrates only four elements on enp-2 but mentions five in the text (albeit erroneously on the proximal segment; p. 335).
[b] Although the adult male has been reported twice in the literature (Lang, 1948; Drzycimski, 1969), its swimming leg armature has not been described in any detail.
[c] George (2006a: 89) describes P1 exp-2 as '…with 2 outer bipinnate spines, terminally with 3 bare geniculate setae'. His proposed emendation (on p. 118) ['P1 exp2 with 2–3 geniculate setae and 2 outer spines (cf. *C. tauroides* sp. nov.)'] of Conroy-Dalton's (2003a) generic diagnosis is therefore unjustified and was probably based on his illustration (fig. 4B), which shows only two geniculate setae, with the third one apparently being dislodged as indicated by the dashed lines.
[d] This seta was absent in the holotype (George, 2006a: fig. 6A).
[e] Contrary to Coull's (1973) original description, the suture between exp-2 and -3 is incomplete (George, 2006b: fig. 17A).
[f] Based on damaged specimen, no information available on endopodal armature of P1–P4 (George & Plum, 2009).
[g] Based on ♀ copepodid V stage.
[h] Norman's (1911) description was based on a composite of two species, making it impossible to decide which of the figured appendages belong to the lectotype illustrated in his habitus drawing (Conroy-Dalton & Huys, 2000).

Other material examined: Three ♂♂ (reg. no. MInRB-Hr38-L001) preserved in formalin; south coast of Korea; Stn H12 (32°01.081′N, 126°44.812′E) (Fig. 1); fine sand with high silt content; depth 110 m; collected on 2 June 2015.

Description of female: Body length measured from anterior outer corner of cephalothorax to posterior margin of caudal rami 463–539 μm (mean = 505 μm; N = 3; holotype = 539 μm). Body (Fig. 10A, B) cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome; integument well chitinized. Somatic hyaline frills weakly developed, plain. Cephalothorax (Fig. 10A) bilaterally constricted in anterior half; anterior half of dorsal surface with irregular pattern of fine surface wrinkles, as in ♂ (cf. Fig. 14A); anterior corners with sensory triplet consisting of three sensilla and closely associated tube-pore (Fig. 11A) and a pair of strongly dentate, backwardly recurved frontolateral horns (Fig. 10A, B); posterior half with a pair of large laterodorsal dendroid processes; lateroventral margins with strongly dentate, upwardly recurved, conical process (CLVPp) and smaller bifid process (CLVPa) proximal to the latter; all processes sensillate, with sensilla positioned apically.

Rostrum: Absorbed into concave anteroventral surface of cephalothorax; with paired widely separated sensilla and midventral tube-pore (Fig. 11A).

Somites bearing P2–P5: Each with paired laterodorsal dendroid processes decreasing in size posteriorly (Fig. 10A); processes of somites bearing P2–P4 with anterior sensillum halfway along length of process; all somites with middorsal tube-pore.

Original segmentation of genital double-somite (Figs 10A, B, 13B) indicated by bilateral constriction, dorsal transverse surface ridge and sensillar pattern (Fig. 10A, B); genital half with two pairs of sensilla and middorsal tube-pore, abdominal half with three pairs of sensilla and two pairs of tube-pores; all sensilla arising from minute tubercles; posterior margin with continuous row of setular extensions. Genital field (Fig. 13B) positioned far anteriorly, with fused gonopores opening via common midventral slit covered by genital operculum derived from vestigial sixth legs. P6 unarmed. Copulatory pore flanked by paired tube-pores, immediately posterior to each gonopore.

Second and third abdominal somites (Figs 10A, B, 13B): With continuous row of setular extensions
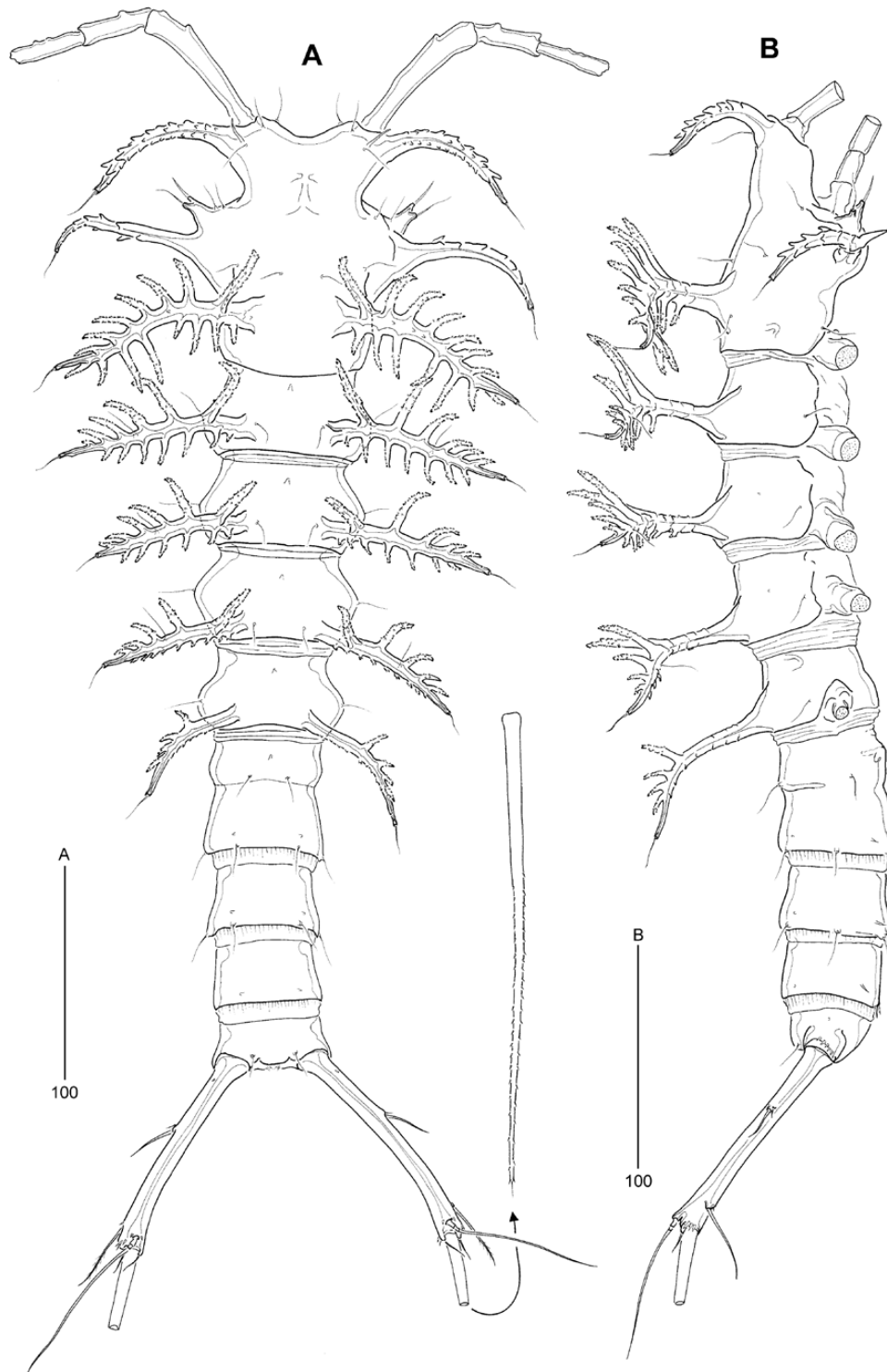
Figure 10. *Dendropsyllus kimi* (♀). A, habitus, dorsal (inset showing caudal ramus seta V at full length). B, habitus, lateral (swimming legs omitted).

around posterior margin; with midventral spinule row near hind margin and paired tube-pores ventrally (Fig. 13B) and dorsally (Fig. 10A). Anal somite partly cleft midventrally (Fig. 13B); with few small spinules around ventrolateral hind margin; anal operculum rounded, smooth (Fig. 13A); paired dorsal sensilla
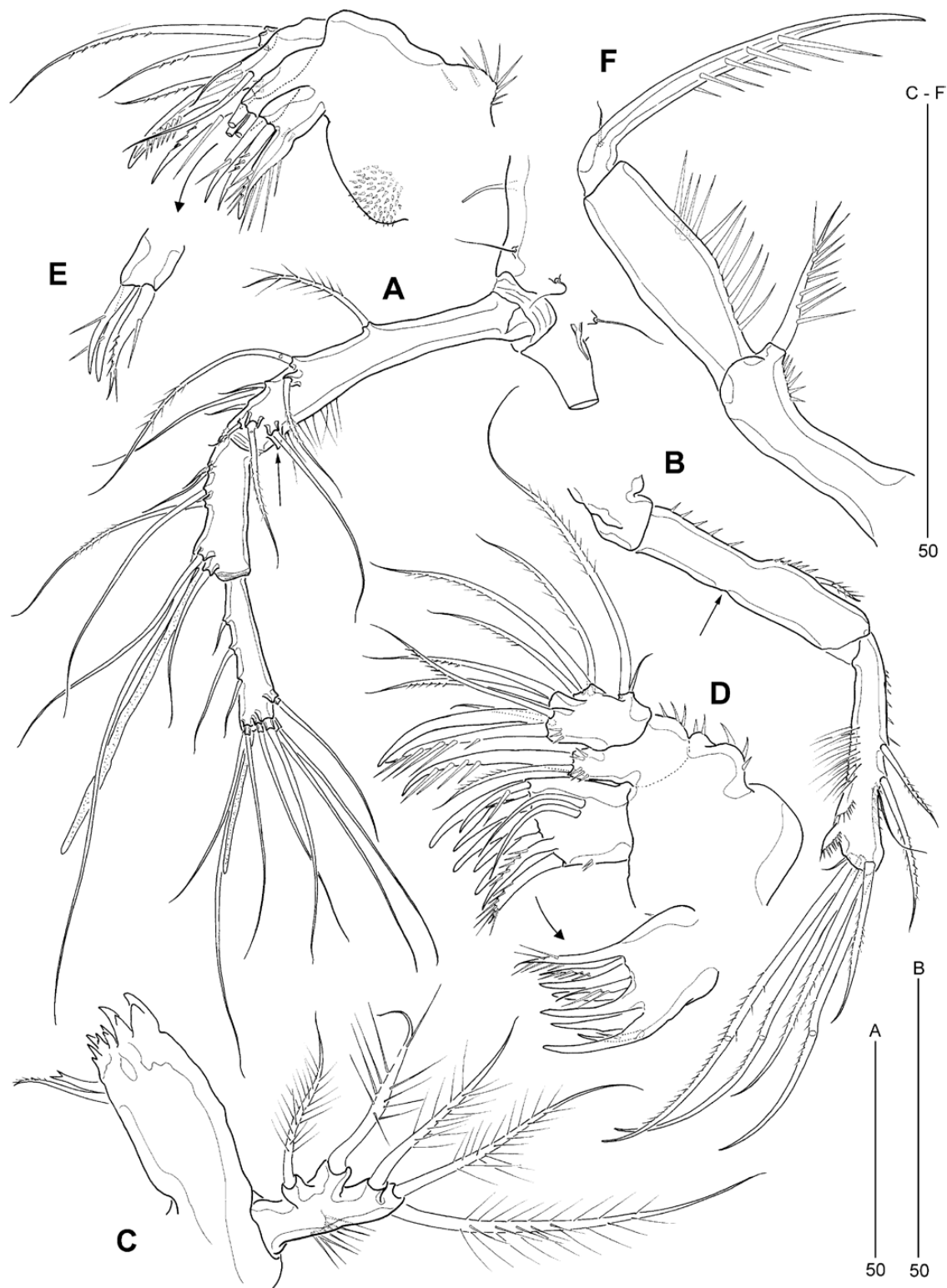
Figure 11. *Dendropsyllus kimi* (♀). A, antennule and rostrum, dorsal (dorsal spinous projection arrowed). B, antenna (membranous insert marking original position of exopod arrowed). C, mandible. D, maxillule, anterior (inset showing posterior view of praecoxal arthrite). E, maxilla (inset showing detail of distal coxal endite). F, maxilliped.
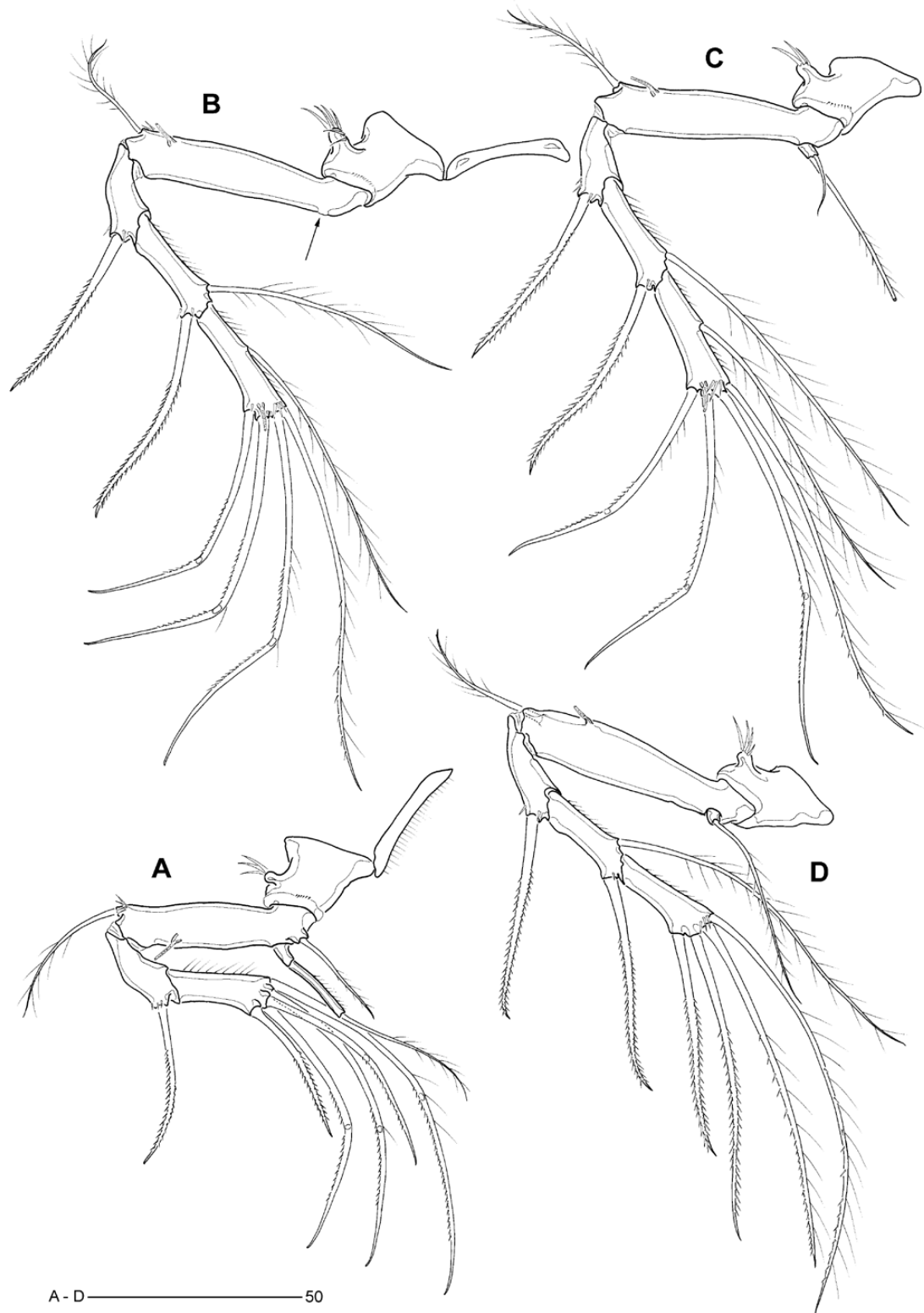
Figure 12. *Dendropsyllus kimi* (♀). A, leg 1, anterior. B, leg 2, anterior (membranous insert indicating original position of endopod arrowed). C, leg 3, anterior (intercoxal sclerite omitted). D, leg 4, anterior (intercoxal sclerite omitted).
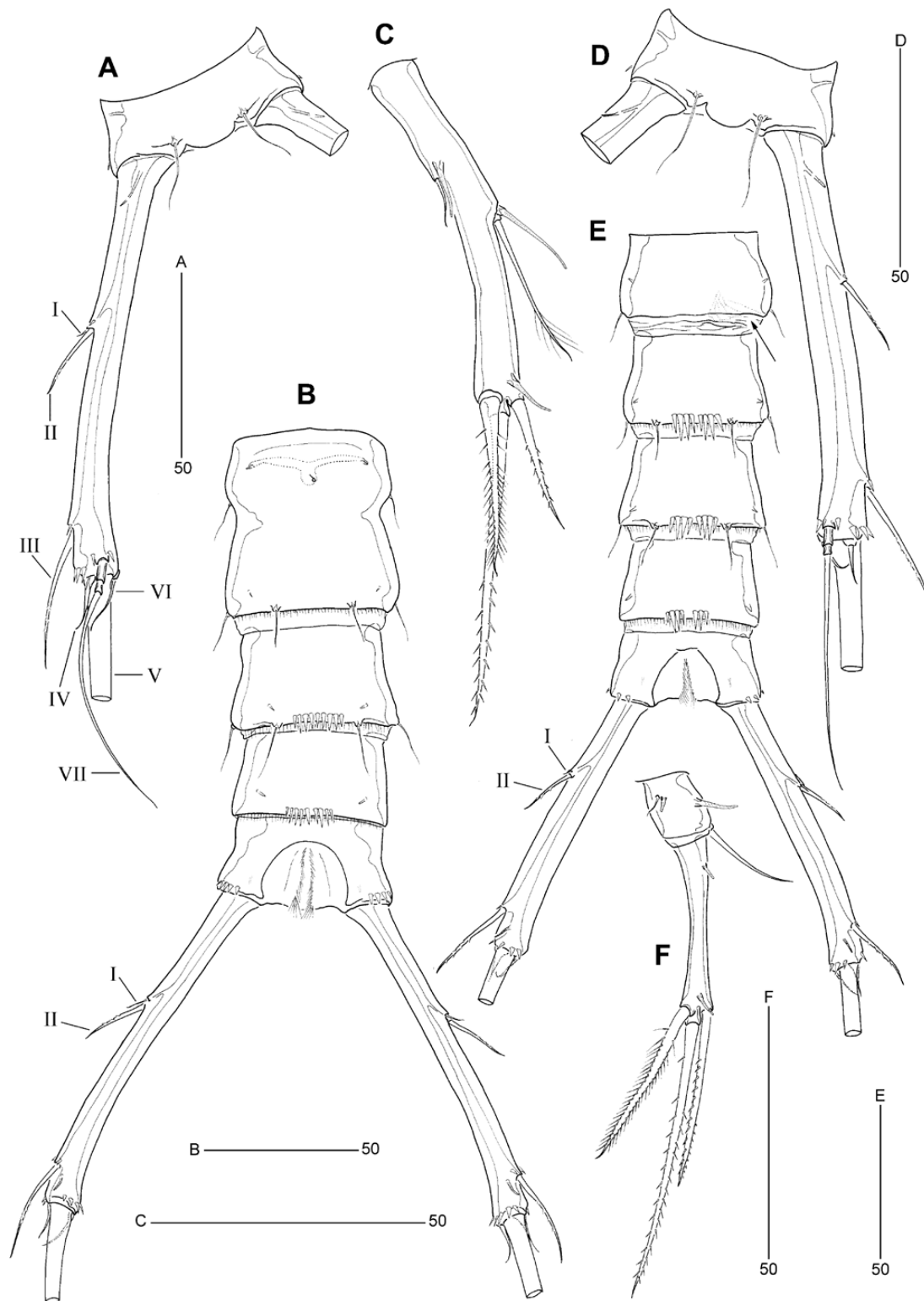
Figure 13. *Dendropsyllus kimi*. A, anal somite and left caudal ramus, dorsal (♀). B, urosome (excluding leg 5-bearing somite), ventral (♀). C, leg 5, anterior (♀). D, anal somite and right caudal ramus, dorsal (♂). E, urosome (excluding leg 5-bearing somite), ventral (♂) (membranous P6 indicated by arrow; functional gonopore indicated by dotted line). F, leg 5, anterior (♂).
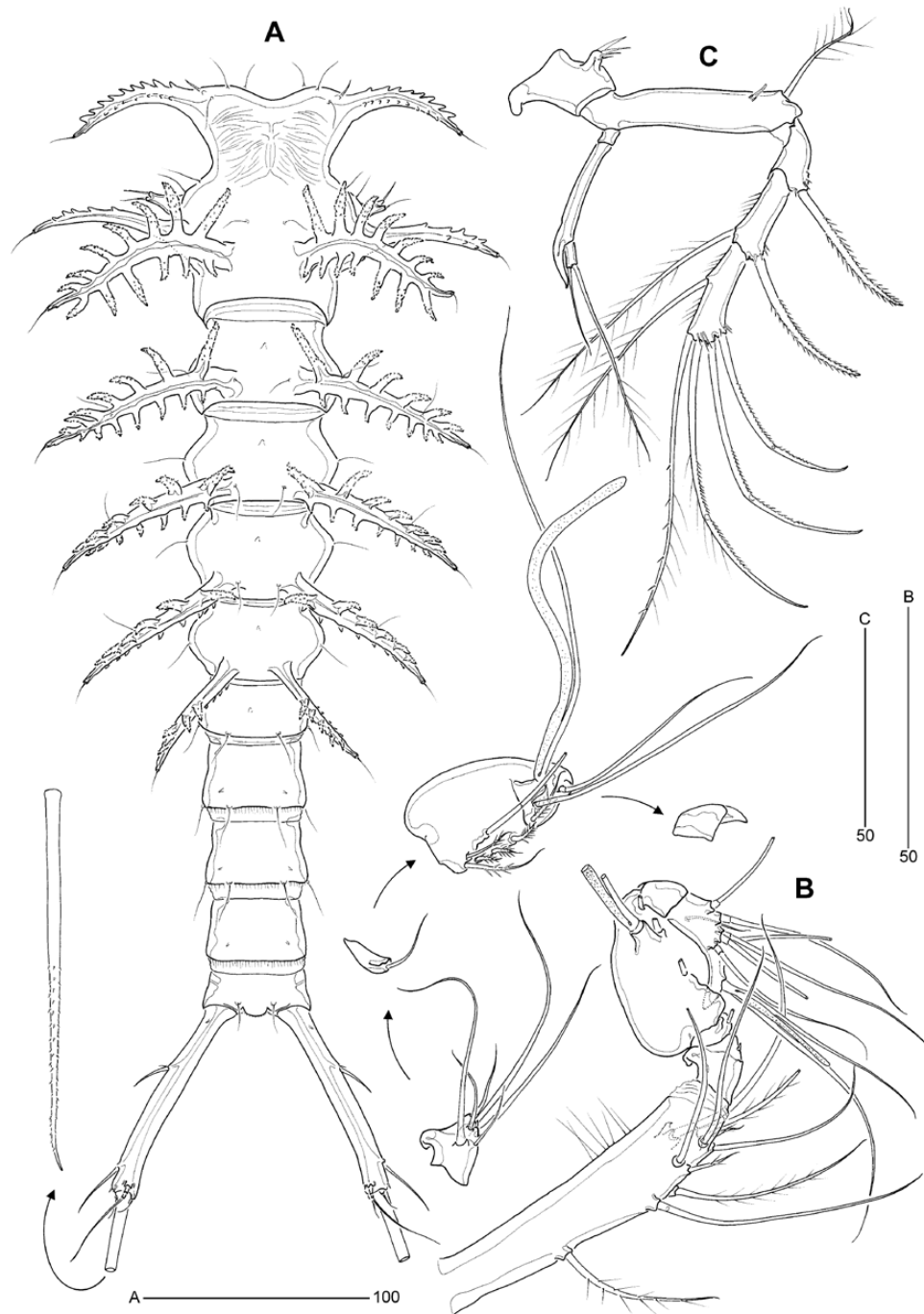
Figure 14. *Dendropsyllus kimi* (♂). A, habitus (inset showing caudal ramus seta V at full length), dorsal. B, antennule, ventral (disarticulated segments 2–5 shown in inset). C, leg 3, anterior.

arising from minute tubercles; with ventral pore either side of anal opening.

*Caudal rami (*Fig. 13A, B*):* Divergent and slightly bent inwards, cylindrical; 13 times as long as wide (width measured at insertion point of seta II); with dorsal tube-pore in proximal one-ninth of ramus and ventral tube-pore near seta III; spinules present around ventral hind margin and at base of seta VII; with seven setae. Seta I minute, positioned ventral to seta II; setae II and III minutely pinnate; seta V well developed, spiniform, bipinnate, ~43% of body length (Fig. 10A); setae IV and VI short and naked; seta VII tri-articulate at base and arising from minute dorsal pedestal, near posterior margin.

*Antennule (*Fig. 11A*):* Three-segmented. Segment 1 compound, longest; posterior margin with long setules in distal third; one dorsal subapical seta arising from spinous projection (arrowed in Fig. 11A). Segment 2 with aesthetasc (length 73 μm) fused at base to long seta. Segment 3 with apical acrothek consisting of aesthetasc (length 32 μm) and two slender setae. Armature formula: 1-[4 + 5 pinnate], 2-[5 + 1 pinnate + (1 + ae)], 3-[9 + acrothek].

*Antenna (*Fig. 11B*):* Coxa represented by well-developed sclerite. Basis and proximal endopod segment fused, forming allobasis; exopod completely absent; membranous insert along outer margin marking original position of exopod (arrowed in Fig. 11B); abexopodal margin with two spinule rows, with one short bipinnate seta in endopodal half. Surface of free endopod with patch of long setules and two distal surface frills; with spinules along medial margin; lateral armature consisting of two bipinnate setae and fine, hair-like seta; distal armature consisting of two pinnate spines and three geniculate setae, longest one fused basally to vestigial seta.

*Mandible (*Fig. 11C*):* Coxa robust, expanding distally to gnathobase bearing two bicuspidate teeth, several incised blades, and one bifid spine plus a pinnate seta at dorsal corner. Palp well developed, one-segmented; with two plumose setae along inner margin (representing basal elements) and three apical plumose setae (representing incorporated endopod); outer margin without armature but with a row of long spinules.

*Maxillule (*Fig. 11D*):* Praecoxal arthrite subrectangular, with two setae on anterior surface; distal armature consisting of five bare and four pinnate spines. Coxal endite with one unipinnate spine and one unipinnate seta; with few spinules around bases of armature elements. Basis with two closely set endites; proximal endite with one naked spine, and one bare and two unipinnate setae; distal endite with two unipinnate setae. Rami completely incorporated into basis; endopod represented by three unipinnate setae; exopod represented by one bipinnate seta and one tiny seta.

*Maxilla (*Fig. 11E*):* Syncoxa with spinule patches as figured; with two coxal endites; proximal endite with one strong bipinnate spine fused basally to endite and two articulating unipinnate spines; distal endite with three spinulose spines. Allobasis drawn out into unipinnate claw; accessory armature consisting of one unipinnate and two naked setae in addition to one spinulose spine. Endopod tiny, one-segmented, with two unipinnate setae.

*Maxilliped (*Fig. 11F*):* Subchelate, slender. Syncoxa with one strong unipinnate seta; with few spinules along medial margin. Basis with robust, long spinules along palmar margin. Endopod drawn out into long, narrow, curved claw; claw bipinnate with anterior and posterior row of strong pinnules, and with one minute accessory seta at base.

*P1 (*Fig. 12A*):* Intercoxal sclerite moderately wide and narrow; with fine setular extensions along free margin. Praecoxa weakly developed (not shown). Coxa trapezoid, with small, spinulose lobate process on outer margin. Basis transversely elongate, with conspicuous anterior tube-pore near distal margin between rami; both outer and inner element setiform and plumose. Both rami two-segmented; exp-1 outer spine bipinnate; exp-2 with fine spinules along inner margin, with four geniculate setae (two of them with few spinules) and one bipinnate outer seta. Enp-1 small, unarmed; enp-2 3.75 times as long as enp-1, with one plumose seta apically.

*P2–P4 (*Fig. 12B*–*D*):* With moderately wide intercoxal sclerites without ornamentation (as shown for P2; see Fig. 12B). Praecoxae weakly developed (not shown). Coxae trapezoid, with small, spinulose lobate process on outer margin. Bases transversely elongate; with anterior tube-pore near distal outer margin; outer distal seta plumose. Exopods three-segmented, outer spines elongate; P2–P3 exp-3 with anterior tube-pore near distal margin; outer and outer distal setae of P2–P3 exp-3 with defined flexure zone. Endopods absent (P2) or reduced and one-segmented (P3–P4); original position of P2 endopod marked by membranous insert (arrowed in Fig. 12B). Armature formula as follows:

	Exopod	Endopod
P2	0:1:122	Absent
P3	0:1:122	020
P4	0:1:022	010

*P5 (*Fig. 13C*):* Baseoendopod and exopod fused, without membranous area marking original segmentation; outer basal seta plumose and arising from short setophore, with long tube-pore at base. Endopodal lobe absorbed, represented by tiny pedestal with one minute seta and conspicuous tube-pore at its base. Exopod slender and elongate; with one outer, one apical and one inner pinnate seta; subdistal outer margin with tube-pore.

Description of male: Body length, measured from outer anterior corner of cephalothorax to posterior margin of caudal rami, 474–505 μm (mean = 489 μm; *N* = 2; dissected paratype = 505 μm). Sexual dimorphism in antennule, P3 endopod, P5, P6, urosomal segmentation and caudal ramus length.

Pattern of dendroid processes, sensilla and pores essentially as in ♀ (Fig. 14A); cephalothorax with irregular pattern of fine surface wrinkles in anterior half.

*Urosome (*Fig. 13E*):* Slender, six-segmented; sensillar pattern and ornamentation of somites as in ♀ except for additional midventral spinule row on first abdominal somite.

*Caudal rami (*Fig. 13D, E*):* Divergent and slightly bent inwards; shorter and less slender than in ♀; nine times as long as wide (width measured at insertion point of seta II). Armature and ornamentation essentially as in ♀ except for seta V being relatively shorter (~35% of body length).

*Antennule (*Fig. 14B*):* Six-segmented and subchirocer, geniculation between segments 4 and 5; aesthetasc present on segment 4 (length 75 µm) and as part of apical acrothek on segment 6. Segment 1 compound, longest; posterior margin with few long setules in distal half; one dorsal subapical seta arising from spinous projection as in ♀. Segment 3 represented by a U-shaped sclerite. Segment 4 swollen. Segment 5 with spinous outgrowth representing modified element. Armature formula: 1-[5 + 5 pinnate], 2-[6 + 1 vestigial spine], 3-[1], 4-[3 + 6 pinnate + (1 + ae)], 5-[1 spinous process], 6-[7 + acrothek]. Apical acrothek consisting of two setae and aesthetasc (length 28 µm).

*P3 (*Fig. 14C*):* Protopod and exopod as in ♀. Endopod three-segmented; enp-1 minute, as long as wide, unarmed; enp-2 elongate, anterior distal surface produced into small, recurved spinous apophysis reaching beyond distal margin of enp-3; enp-3 minute, slightly longer than wide, with two apical setae, one of them plumose.

*P5 (*Fig. 13F*):* Baseoendopod and exopod completely separated. Baseoendopod ~1.4 times as long as maximal width; outer basal seta naked and arising from short setophore; outer margin with tube-pore. Endopodal lobe completely absorbed, represented by tiny seta accompanied by tube-pore. Exopod slender and elongate; with one outer, one apical and one inner bipinnate seta; with anterior tube-pores in proximal and distal quarters.

Sixth pair of legs: Asymmetrical (Fig. 13E), represented by membranous flap (arrowed) covering single functional genital aperture (indicated by dotted line); P6 without armature.

Etymology: The species is named after Professor Il-Hoi Kim (Gangneung-Wonju National University), in recognition of his massive contribution to our knowledge of the Korean copepod fauna.

Remarks: Conroy-Dalton (2003a) proposed the genus *Dendropsyllus* to accommodate a species, *De. thomasi*, described from the San Diego Trough, northeastern Pacific. The genus was characterized by the distinctive pattern of dendroid body processes (lacking on abdominal somites), the presence of a well-developed conical process on the lateroventral margins of the cephalothorax, P1 exp-2 with four geniculate setae, P1 enp-2 with one apical seta, the complete absence of P2 endopod, P3 exp-3 with one inner seta and the loss of the inner seta on P4 exp-3. She transferred the Southern Hemisphere species *Ceratonotus magellanicus* George & Schminke, 1998 (Straits of Magellan, Chile) and *Ce. antarcticus* George & Schminke, 1998 (Halley Bay, Weddell Sea, Antarctic) to *Dendropsyllus*, because they deviate significantly from her revised diagnosis for *Ceratonotus*. George (2006a) re-examined *De. magellanicus* (George & Schminke, 1998) based on new material from the Chilean Pacific continental slope off Chiloé Island and provided the first description of a male in the genus. Gómez & Díaz (2017) recently added a fourth species, *De. californiensis*, from the Southern Trough of the Guaymas Basin in the Gulf of California.

The morphology of *De. kimi* is in complete accordance with the characters summarized in Conroy-Dalton's (2003a) generic diagnosis. It exhibits a number of unique characters not found in any of its congeners (Table 3): (1) dorsal sensillate tubercles on abdominal somites 1–2 absent (but note that the condition in *De. antarcticus* is unclear); (2) P3 endopod ♀ one-segmented with armature formula 020 instead of two-segmented with formula 0.020 or 0.021; and (3) inner spine on P5 exopod ♀ longer than outer seta (ratio 0.75) instead of being shorter. The female antennule of the new species also displays a first segment that is more elongate than in most of its congeners, being 1.1 times the length of segments 2 and 3 combined (measured along the posterior margin). The one-segmented condition of the P4 endopod in the female is shared with *De. antarcticus*.

Males of *Dendropsyllus* spp. appear to be very rare. George (2006a) reported a single one of *De. magellanicus*, and *De. kimi* is the first species to be known from more than one male. Comparison of male characters will therefore have to be confined to these two species. *Dendropsyllus kimi* shows sexual dimorphism in the ventral spinule patterns on the abdominal somites, with the male exhibiting an additional transverse row near the posterior margin of the first abdominal somite (absent on the genital double-somite of the female; Fig. 13B, E). Unfortunately, George (2006a) figured the male of *De. magellanicus* only in dorsal aspect and did not mention any sex-related differences in abdominal spinulation in the text; the potential significance of this character at generic level therefore remains unconfirmed. George (2006a) reported slight sexual dimorphism in the size of the P4 endopod in *De. magellanicus*, but this was not observed in the new species. Relative differences in caudal ramus length have been discerned between sexes of both species. In *De. magellanicus*, the caudal ramus is longer in the female (length:width ratio 16.0) than in the male (10.5); likewise, in *De. kimi* it is shorter in the male (9.1) than in the female (13.7). Males of both species show an identical modification of the P3 endopod, being three-segmented with an apophysis arising from the middle

Table 3. Morphological comparison between *Dendropsyllus* species. Width of caudal ramus measured just posterior to insertion site of seta II.

Character	*De. antarcticus*	*De. magellanicus*	*De. thomasi*	*De. californiensis*	*De. kimi*
♀ Body length (mean) (μm)	635	530	550–690 (620)	670	463–539 (505)
♂ Body length (mean) (μm)	?	460	?	?	474–505 (489)
Lateroventral processes on cephalothorax	Not dendroid	Dendroid	Dendroid	Dendroid	Dendroid
Dorsal tubercles on abdominal somites 1–2	Not conclusive*	Present	Present	Present	Absent
Antennule ♀ (length of segment 1:length of segments 2–3)	1.00	0.93	1.05	0.85	1.10
Maxilliped basis palmar margin	Without spinules	Long spinules	Long spinules	Long spinules	Long spinules
P3 endopod armature ♀	0.020	0.020	0.020	0.021	020
P4 endopod armature ♀	010	0.010	0.010	0.010	010
P5 exopod condition ♀	Free	Fused to benp	Partly fused	Fused to benp	Fused to benp
P5 exopod condition ♂	Unknown	Free	Unknown	Unknown	Free
P5 exopod (length of outer seta: length of inner spine) ♀	Unknown†	1.75	1.45	1.50	0.75
P5 exopod (length of outer seta: length of inner spine) ♂	Unknown	1.75	Unknown	Unknown	1.00
Caudal ramus (length:width ratio) ♀	15.2	10.5	28.4	16.4	13.7
Caudal ramus (length:width ratio) ♂	Unknown	16.0	Unknown	Unknown	9.1

*George & Schminke (1998) mention the presence of 'sensilla raised on small knobs', but it is unclear how they compare with the sensillate tubercles reported in other members of the genus.
†Outer seta broken in the only available female. Abbreviation: benp, baseoendopod.

segment and displaying two apical setae on the terminal segment. Females of both species exhibit two apical setae on the (only or) distal endopodal segment of P3 (Table 3) and lack an outer spine/seta as in most members of the *Ceratonotus* group (Table 2). Recently, Gómez & Díaz (2017) reported an outer spine-like element on the female P3 enp-2 of *De. californiensis*, a condition observed so far only in *Touphapleura schminkei* (George, 1998). Despite the male being unknown, they considered this element as novel and autapomorphic for *De. californiensis* and not homologous to the inner apophysis observed for the male of *De. magellanicus*. This supposition is unlikely, because in every species of the Ancorabolinae that shows this seta in the female, it is suppressed in the male (*T. schminkei* and all species of the *Ancorabolus* group) and takes part in the formation of the apophysis. Unlike the great majority of species in the Laophontidae and related families, where an apophysis becomes expressed in the male only when an outer spine is present in the female (Huys, 1990), the presence of such a spine is not necessarily required for the formation of an apophysis in the Ancorabolinae, suggesting different ontogenetic pathways in males and females.

Based on the records published so far, the genus essentially assumes a Pacific distribution, with *De. antarcticus* the only, albeit neighbouring, outlier from the Weddell Sea in the Southern Ocean.

DISCUSSION

TAXONOMIC POSITION OF *PATAGONIAELLA* PALLARES, 1968 AND *ANCORABOLINA* GEORGE, 2006C

ANCORABOLINA GEORGE, 2006C

George (2006c) established the genus *Ancorabolina* for *Ancorabolina chimaera* from the Southern Atlantic deep sea, which displayed a combination of ancorabolinid apomorphies (absence of the antennary exopod, transverse elongation of P1 basis) and laophontodinid plesiomorphic character states (antennule ♀ five-segmented; P2–P4 exp-3 with three outer spines). A number of additional apomorphic character states shared between *Ancorabolina chimaera* and subsets of ancorabolinid taxa were also identified, such as: (1) cephalothorax and/or body somites with dorsal cuticular processes (as in all other Ancorabolinae); (2) cephalothorax with paired lateral processes near the distal margin (as in *Echinopsyllus*, *Polyascophorus* and *Pseudechinopsyllus*); (3) pedigerous somites bearing P2–P5 with middorsal tube-pore (as in all other Ancorabolinae); (4) rostrum small and constricted (as in *Dorsiceratus*, *Polyascophorus*, *Arthuricornua* and *Touphapleura*) and with frontal part forming a 'peak' (as in all other Ancorabolinae); (5) segment 1 of antennule elongate and with long spinules along anterior margin (as in the *Ceratonotus* group); (6) anal somite shorter than

wide, trapezoid in shape (as in the *Ceratonotus* group); and (7) caudal rami elongate and divergent, originating from the outer distal corners of the anal somite and directed upwards (as in the *Ceratonotus* group). George (2006c) placed *Ancorabolina* in the Ancorabolinae, solely because it shared only symplesiomorphies with the Laophontodinae, but he did not discuss its relationships with other genera in the subfamily.

In an attempt to refute Huys' (1990) claim that there is no close relationship between Laophontoidea and Ancorabolidae, George (2006c) proposed a hypothetical scenario of leg 1 evolution in these taxa, in which the condition displayed by *Ancorabolina* was construed as a missing link in the ancorabolinid lineage. The weakness in this hypothesis lies in the fact that it hinges heavily on the supposed monophyly of the Ancorabolidae, for which there is no tangible evidence. It also requires the removal of genera such as *Tapholaophontodes* Soyer, 1975 and *Algensiella* Cottarelli & Baldari, 1987 to a basal position in the ancorabolid tree, pre-dating the split of the two subfamilies.

Gheerardyn & George (2010) added four new species to the genus and re-evaluated its phylogenetic position, narrowing down the number of ancorabolinid autapomorphies from ten (cf. George, 2006c) to only two, i.e. the loss of the antennary exopod, and the frontal part of cephalothorax forming a 'peak' (sensu George, 2006b). They also recognized three, previously overlooked, synapomorphies of the Laophontodinae that are shared by *Ancorabolina*, but are absent in the remaining Ancorabolinae: (1) segment 2 of antennule with outer bump bearing long spinules in both sexes; (2) P1 coxa elongate, produced along the dorsoventral (proximodistal) axis; and (3) outer seta of P1 exp-2 geniculate (note that this element becomes the proximalmost along the outer margin of exp-2 in species that have a two-segmented exopod (*Tapholaophontodes remotus* Cottarelli & Baldari, 1987 and some species of *Ancorabolina* and *Paralaophontodes* Lang, 1965; see Table 4). In spite of this evidence in support of laophontodinid affinity, Gheerardyn & George (2010) decided to maintain *Ancorabolina* in Ancorabolinae. Gheerardyn & Lee (2012) reiterated the phylogenetic significance of two of those characters (geniculation of the outer seta on exp-2 of P1 and the presence of an outer bump with long spinules on the second antennulary segment) and proposed them as potential synapomorphies of the Laophontodinae (+ *Ancorabolina*). Despite the fact that some of the proposed apomorphies (transverse elongation of P1 basis, elongation of segment 1 of antennule) display a gradual development in *Ancorabolina*, George & Müller (2013) continued to maintain the genus in an otherwise monophyletic Ancorabolinae.

Previous attempts to shoehorn *Ancorabolina* into the Ancorabolinae were partly based on an incorrect assessment of the morphology of leg 1. In *Ancorabolina chimaera*, the basis has not only elongated along the proximodistal axis distad from the coxa-basis joint, but its distal half has also expanded transversely, forming cylindrical pedestals for the exopod and, in particular, the endopod. The presence of a basal pedestal for the endopod is a diagnostic (and potentially apomorphic) character for all members of the Laophontodinae and may be seen as new evidence lending further credence to the position of *Ancorabolina* in the Laophontodinae. Conversely, in members of the Ancorabolinae, transverse elongation of the basis is not restricted to its distal half, but starts immediately posterior to the coxa-basis joint and involves allometric growth of the entire protopodal segment, even in the most primitive genus *Arthropsyllus* (cf. Conroy-Dalton & Huys, 2000: figs 13D, 16B, F). Moreover, although most species in this subfamily display a prehensile endopod, none of them possesses a pedestal supporting it. The modifications of leg 1 in *Ancorabolina* and the remaining Ancorabolinae cannot therefore be considered as homologous and, consequently, the former genus is here reassigned to the Laophontodinae (despite its unfortunate name). Four apomorphic character states lend support to a potential sister-group relationship between *Laophontodes gracilipes* Lang, 1936b and *Ancorabolina* (see below - Taxonomic notes on *Laophontodes* T. Scott, 1894).

PATAGONIAELLA PALLARES, 1968

Pallares (1968) proposed the genus *Patagoniaella* for a new species, *Patagoniaella vervoorti*, from two localities in the vicinity of Puerto Deseado in Patagonia, Argentina, and placed it in the Laophontodinae (which included only *Laophontodes* T. Scott, 1894 and *Paralaophontodes* at the time) based on the morphology of the basis in leg 1 and the exopods in legs 2–4 (presence of three outer spines on P2–P4 exp-3). Although Pallares did not explicitly state the reason for assigning *Patagoniaella vervoorti* to a new genus, her comparative table suggested that it was based on the different pattern of endopodal segmentation of P2–P4. *Patagoniaella vervoorti* has not been recorded again since its original description, and discussions about its relationships to other members of the Laophontodinae have remained vague. Cottarelli & Baldari (1987) recognized a certain affinity between *Patagoniaella* and both *Tapholaophontodes* and *Algensiella*, because members of all three genera have reduced swimming legs, displaying a simplified chaetotaxy, and also share a similar ecology, because all are found in marine interstitial waters of the Southern Hemisphere. The latter part of this claim is, strictly speaking, incorrect, because *Patagoniaella vervoorti* was found abundantly in muddy sapropelic deposits, consisting chiefly

Table 4. Female armature formulae in known species of Laophontodinae. Formulae in brackets denote male condition (setation pattern of male P3 endopod omitted).

	S	P1		P2		P3		P4	
		exp	enp	exp	enp	exp	enp	exp	enp
Algensiella									
*Al. boitanii**	♀	0.0.4G	0.G+C+1	0.0.023	Absent	0.0.023	020	0.0.023	020
Al. laurenceae	♀♂	0.0.4G	0.G+C+1	0.0.023	Absent	0.0.023	020	0.0.023	020
Ancorabolina									
An. anaximenesi	♀♂	0.5G	0.G+c+1	0.1.123	0.020	0.1.123	0.120	0.1.123	0.120 [0.121]
An. belgicae	♀	0.5G	0.G+c	0.1.123	0.020	0.1.123	0.120	0.1.123	0.120
An. cavernicola	♀♂	0.5G	0.c+2	0.0.123	0.020	0.0.123	0.020	0.1.123	0.020 [0.021]
*An. chimaera**[a]	♀♂	0.5G	0.3	0.1.123	0.020	0.1.123	0.020	0.1.123	0.020 [0.021]
An. divasecunda	♀♂	0.0.4G	0.2G+1	0.1.123	0.020	0.1.123	0.120	0.1.123	0.120 [0.121]
An. galeata	♀♂	0.0.4G	0.G+c+2	0.1.123	0.020	0.1.123	0.120	0.1.123	0.120 [0.121]
Calypsophontodes									
C. latissima	♀	0.0.4G	0.G+C+1	—— Unknown ——		0.0.023	011[b]	—— Unknown ——	
*C. macropodia**	♀♂	0.0.4G	0.G+C+1	0.0.023	0.020	0.0.023	0.121	0.0.023	0.121 [0.021]
Laophontodes									
La. antarcticus	♀	0.0.4G	0.C	—— Unknown ——		0.0.123	121	—— Unknown ——	
La. bicornis	♀♂	0.0.4G	0.G+C+1	0.1.123	0.020	0.1.223	0.021	0.1.223	0.121
La. brevis	CopV♀	0.0.4G	0.G+C	0.1.123	020	0.1.223	020	0.1.223	0.120
La. gertraudae	♀♂	0.0.4G	0.G+C+1	0.0.023	0.020	0.0.023	0.020	0.0.023	0.020
La. hamatus	♀♂	0.0.4G	0.G+C+1	0.1.123	0.020	0.1.223	0.020	0.1.223	0.121
La. horstgeorgei	♀♂	0.0.4G	0.G+C+1	0.1.123	0.020	0.1.223	0.020	0.1.223	0.121
La. macclintocki	♀♂	0.0.4G	0.G+C+1	0.1.123	0.020	0.1.123	0.020	0.1.123	0.121
La. monsmaris	♀♂	0.0.4G	0.G+C+1	0.1.123	0.020	0.1.223	0.020	0.1.223	0.120 [0.121]
La. mourois	♀♂	0.0.4G	0.G+C+1	0.0.123	0.020	0.0.123	0.120	0.0.123	0.020
La. georgei sp. nov.	♀♂	0.0.4G	0.G+C	0.0.023	0.020	0.0.023	0.120	0.0.023	120
La. ornatus	♀	0.0.G+2 [c]	0.G+C	0.0.123	020 [d]	————Unknown[d]————			120 [d]
La. propinquus	♀♂	0.0.4G	0.G+C+1	————————Unknown————————				0.0.023	010
La. sabinegeorgeae	♀♂	0.0.4G	0.G+C+1	0.1.123	0.020	0.1.223	0.020	0.1.223	0.121
La. sarsi	♀	0.0.4G	0.G+C+1	0.0.023	0.020	0.0.023	0.120	0.1.023	0.120
La. scottorum	♀	0.0.4G	0.G+C	0.0.023	Unknown [e]	0.0.123	0.120	0.0.023	0.120
La. spongiosus	♀	0.0.4G	0.G+C+1	0.0.023	0.020	0.0.023	0.020	0.0.123	0.020
*La. typicus**	♀♂	0.0.4G	0.G+C+1	0.0.123	0.020	0.0.123	0.120	0.0.123	0.120
La. whitsoni	♀♂	0.0.4G	0.G+C+1	0.1.123	0.020	0.1.223	0.020	0.1.223	0.121[f]
La. bicornis sensu Kim (2013)	♀♂	0.0.4G	0.G+C+1	0.1.123	020	0.1.123	020	0.1.123	121
Lobopleura									
*Lo. ambiducti**	♀♂	0.0.4G	0.G+C+2	0.0.023	Absent	0.0.023	0.020	0.0.023	0.010
Lo. expansa [g]	♀	0.0.4G	0.G+C+?	0.0.023	020	0.0.023	020	0.0.023	010
Lo. multispinata	♀♂	0.0.4G	0.G+C+1	0.0.023	Absent	0.0.023	0.020	0.0.023	0.010
Paralaophontodes									
Pa. anjae	♀	0.5G	0.C+1	0.0.023	Absent	0.0.023	Absent	0.0.023	Absent
Pa. armatus	♀♂	0.0.4G	0.G+C+1	0.0.023	Absent	0.0.023	0.020	0.0.023	0.020 [0.120]
*Pa. echinatus**	♀♂	0.4G	0.C+1	0.0.023	Absent	0.0.023	010	0.0.023	Absent
Pa. elegans	♀	0.4G	0.C+1	0.0.023	Absent	0.0.023	1	0.0.023	Absent
Pa. exopoditus	♀♂	0.5G	0.C+1	0.0.023	Absent	0.0.023	1	0.0.023	Absent
Pa. hedgpethi	♀♂	0.0.4G	0.G+C+1	0.1.123	0.020	0.1.123	0.020	0.1.123	0.020 [0120]
Pa. psammophilus	♀	0.0.4G	0.G+C+1	0.0.023	0.020	0.0.023 [g]	0.020	0.0.023 [h]	0.020
Pa. robustus	♀	0.4G	0. C+1	0.0.023	Absent	0.0.023	Absent	0.0.023	Absent

Probosciphontodes

Table 4. *Continued*

	S	P1		P2		P3		P4	
		exp	enp	exp	enp	exp	enp	exp	enp
Pr. ptenopostica	♀♂	0.0.4G	0.G+C+1	0.0.022	Absent	0.0.022	Absent	0.0.022	Absent
*Pr. stellata**	♀♂	0.0.4G	0.G+C+1	0.0.022	Absent	0.0.022	Absent	0.0.022	Absent
Rostrophontodes									
*R. gracilipes**	♀♂	0.0.4G	0.G+c+1	0.1.123	0.010	0.1.123	0.010	0.1.123	0.010
Tapholaophontodes									
*T. rollandi**	♀♂	0.0.4G	0.G+C+1	0.0.022	Absent	0.0.022	010	0.0.022	Absent
T. remotus	♀♂	0.5G	0.G+C+1[i]	0.0.022	Absent	0.0.022	0.010	0.0.022	Absent

*Type species.

[a] George's (2006c: 164) original armature formula was corrected by Gheerardyn and George (2010).

[b] Although Gheerardyn & Lee (2012) considered the armature pattern of P3 enp sufficient evidence to rule out conspecificity with *C. macropodia* Gee & Fleeger, 1986, it is conceivable that Brady's (1918) illustration is incorrect in showing only two elements and depicting the ramus as one-segmented.

[c] Krishnaswamy (1957) illustrates three elements on exp-3 but states in the text that '… the third [segment] bears one outer spine and three apical setae'.

[d] Krishnaswamy (1957) states 'Third and the fourth legs resemble the second one, the endopod of fourth leg however differs in having one apical and two inner setae' but illustrates only P4 enp. It is questionable whether his observation of a one-segmented endopod in P2–P4 is correct, because within the genus this condition has so far been recorded only for P2–P3 in *La. brevis* Gurney, 1944 (which was based on a juvenile; see Table 1). Pending a thorough redescription of the species and contrary to George & Gheerardyn's (2015: 93) proposition, this character should not be used to differentiate *La. ornatus* from *La. bicornis* A. Scott, 1896 and/or *La. horstgeorgei* George & Gheerardyn, 2015. Likewise, Arroyo *et al.* (2003) used it as a discriminant between *La. ornatus* and *La. mourois* Arroyo, George, Benito & Maldonado, 2003. Given the contradictions between the text and illustrations and the deficiencies in the original description, it is recommended here to rank *La. ornatus* as *species inquirenda* in the genus.

[e] P2 endopod not discernible ('missing or broken') according to George (2018: 15).

[f] George & Gheerardyn (2015) recorded intraspecific variability in the presence/absence of the outer element, whereas Pallares (1975) observed specimens that lacked the inner element.

[g] Sars (1908) probably overlooked the rudimentary seta(e) on P1 enp-2 and misinterpreted the endopodal segmentation of P2–P4 (cf. Conroy-Dalton 2004: 28).

[h] Soyer (1975) figured a short seta along the distal inner margin of exp-3; comparison with Mielke's (1981) detailed description of *Pa. exspoditus* shows that these 'elements' on P3–P4 are, in reality, long tube-pores (see his Abb. 59c–d). The presence of these setae was wrongly assumed by George (2017) in his phylogenetic analysis of *Paralaophontodes*.

[i] Cottarelli & Baldari (1987: fig. 2F) show a long spinule at the inner distal corner, which they erroneously interpreted as a 'short, latero-distal seta'.

of decomposed organic matter formed in stagnant conditions. Concurring with Cottarelli & Baldari (1987), Fiers (1988) also claimed a close relationship between these genera, because they differ from *Laophontodes* and *Paralaophontodes* by the absence of ornamentation on the dorsal surfaces of the body somites and by the much smaller bases in P2–P4. The first author to doubt the currently accepted taxonomic position of *Patagoniaella* was George (2006c: 169), who stated in a footnote that its type species '…presents several features making its affiliation to Ancorabolidae questionable'.

The major stumbling block to inclusion of *Patagoniaella vervoorti* in the Laophontodinae in particular appears to be the divergent morphology of its non-prehensile leg 1, an observation reiterated repeatedly in the recent literature (Gheerardyn & George, 2010; Gheerardyn & Lee, 2012; George & Müller, 2013). In members of this subfamily, the outer spine of P1 exp-2 (or the proximalmost outer spine of exp-2 when the exopod is two-segmented; i.e. some species of *Paralaophontodes*, *Tapholaopontodes* and *Ancorabolina* George, 2006c) is invariably modified into a geniculate seta, whereas in *Patagoniaella vervoorti* exp-2 has retained its bipinnate spine, which represents the plesiomorphic condition (Gheerardyn & Lee, 2012). Likewise, in laophontodinids the P1 coxa has typically undergone secondary elongation along the proximodistal axis, but this apomorphic

condition is not revealed in Pallares' (1968) description (note also that as in most past descriptions, the coxa was only partly figured). Gheerardyn & George (2010) also identified a third apomorphy for the Laophontodinae that is not displayed by *Patagoniaella*, i.e. the presence of a spinular protuberance on the posterior margin of segment 2 of the antennule in both sexes. Finally, the leg 1 basis of *Patagoniaella vervoorti* shows moderate transverse elongation in the distal half but lacks the basal pedestal for the endopod, which, in combination with the three previous characters, precludes the species from being assigned to the Laophontodinae (see above).

The alternative option of transferring *Patagoniaella* to the Ancorabolinae is not justifiable because it would dramatically alter the diagnosis of the subfamily as evidenced by the following characters displayed by *Patagoniaella vervoorti*: (1) cephalothorax and free body somites without spinous projections (vs. present); (2) rostrum triangular, with apex not forming a 'peak' (vs. 'peak' present); (3) antennule ♀ five-segmented (vs. segments 3 and 4 fused to form a compound segment); (4) transverse elongation of P1 basis restricted to basal half only (vs. elongation involves allometric growth of the entire protopodal segment); and (5) P2–P4 exp-3 with three outer spines (vs. two outer spines). The quality of Pallares' (1968) illustrations does not allow assessment of other characters, such as the presence of

a middorsal tube-pore on pedigerous somites bearing P2–P5, which is found in all Ancorabolinae. However, it is obvious from the above that the genus *Patagoniaella* cannot be accommodated in this subfamily either and should therefore be excluded from Ancorabolidae.

Although a thorough analysis, at least at generic level, would be required to assess its position with more confidence, several morphological similarities suggest that *Patagoniaella* is related to members of Cletodidae. The short, five-segmented ♀ antennule, the moderate elongation of the bases and the segmentation/shape of the endopods of P1–P4, and the morphology of leg 5, with the long setophore carrying the outer basal seta, all indicate cletodid affinity. Pallares' (1968: pl. 1, fig. 10) illustration of leg 1 of *Patagoniaella vervoorti* suggests the presence of setae with a brush-like tip on the endopod and exopod. Such penicillate setae have previously been reported in a number of cletodid genera (e.g. *Stylicletodes* Lang, 1936a; *Schizacron* Gee & Huys, 1996; *Strongylacron* Gee & Huys, 1996; *Triathrix* Gee & Burgess, 1997; *Spinapecruris* Gee, 2001) and in some species of *Enhydrosoma* Boeck, 1873 (cf. Gee, 1994, 2001; Gee & Huys, 1996; Fiers, 1997; Gee & Burgess, 1997; Gómez, 2000, 2003). Based on this circumstantial evidence, *Patagoniaella* is here provisionally assigned to the Cletodidae.

TAXONOMIC NOTES ON *LAOPHONTODES* T. SCOTT, 1894

The taxonomic concept of *Laophontodes* has changed significantly since Schizas & Shirley (1994) listed 14 valid species in the genus. Lang (1965) had previously removed *Laophontodes robustus* Božić, 1964 to *Paralaophontodes*, and this course of action was repeated by George (2017), who moved *Laophontodes armatus* Lang, 1936c, *Laophontodes hedgpethi* Lang, 1965 and *Laophontodes psammophilus* Soyer, 1975 to the same genus. Conroy-Dalton & Huys (2000) transferred the inadequately described *Laophontodes echinatus* Brady, 1918 as *species inquirenda* to *Breviconia* Conroy-Dalton & Huys, 2000. *Laophontodes expansus* Sars, 1908 was subsequently placed in the new genus *Lobopleura* by Conroy-Dalton (2004), and Gheerardyn & Lee (2012) proposed *Calypsophontodes* to accommodate two (sub-Antarctic) species, *Laophontodes macropodia* Gee & Fleeger, 1986 and *Laophontodes latissimus* Brady, 1918 (the latter as *species inquirenda*). Although the genus *Laophontodes* saw the addition of eight new species in recent years (Arroyo *et al.*, 2003; Kornev & Chertoprud, 2008; George & Gheerardyn, 2015; George, 2018) it is known that other as yet unidentified or undescribed species have been recorded from the Thames estuary in England (Attrill, 1998), Galicia in Spain (Miranda *et al.*, 1999), Pulia (Moscatello & Belmonte, 2007) and Sardinia (Noli *et al.*, 2018) in Italy, the Great Meteor

Seamount in the subptropical North Atlantic (George & Schminke, 2002), Zanzibar (Gheerardyn *et al.*, 2008), the Clarion-Clipperton zone in the tropical Eastern Pacific (Amon *et al.*, 2017), New Zealand (Hicks, 1977), the South Shetland Islands (Hong *et al.*, 2011; Bick & Arlt, 2013), South Georgia (Dartnall, 2005), the Straits of Magellan (George, 2005) and Washington State (Toft *et al.*, 2010). Although George & Gheerardyn (2015) provided an updated generic diagnosis for *Laophontodes*, they cursorily expressed their dissatisfaction about the current inclusion of a number of species. Below, we provide justification for the exclusion of two of them, *Laophontodes gracilipes* Lang, 1936b and *Laophontodes multispinatus* Kornev & Chertoprud, 2008.

LAOPHONTODES GRACILIPES LANG, 1936B

Lang (1936b) described both sexes succinctly based on material collected from muddy sediments at 50–100 m depth in the Gullmar Fjord, Sweden. Illustrations were confined to the rostrum, caudal ramus, maxilliped, P1 and female P5. Although the species did not appear to be rare at the type locality, occurring all year round (Lang, 1948), it has been recorded from only two other localities since its original description, i.e. at 30–90 m depth in the Kandalaksha Gulf of the White Sea (Kornev *et al.*, 2004; Kornev & Chertoprud, 2008) and at 1259 m depth on the Anaximenes Seamount in the eastern Mediterranean Sea (George *et al.*, 2018). Kornev & Chertoprud (2008) provided a detailed redescription of both sexes, which forms the basis for the argumentation below.

For more than a century, *Laophontodes* has served as a taxonomic repository for ancorabolids that possess a rostrum, a three-segmented P1 exopod and a prehensile, two-segmented P1 endopod with enp-1 being longer than the exopod. Although Lang (1936b) did not explicitly state his reasons, it was probably on the basis of the last combination of characters that he assumed that the appropriate generic placement of *La. gracilipes* was also in *Laophontodes.* Neither Lang (1936b, 1948) nor any subsequent workers commented on its relationships with other congeners. Gheerardyn & George (2010: 51) labelled *La. gracilipes* as a 'typical' *Laophontodes*, but in a subsequent paper (George & Gheerardyn, 2015: 86) briefly hinted at the possibility of excluding it from this genus. Their amended diagnosis of *Laophontodes* contains two characters that are not displayed by *La. gracilipes*: (1) rostrum small; and (2) P1 enp-2 with one claw and one longer geniculate seta (and occasionally one minute accessory seta). Comparative morphological analysis reveals that the species exhibits a suite of mostly autapomorphic characters preventing its inclusion in *Laophontodes*:

(1) Rostrum very large, about two-thirds the length of the cephalic shield, sharply pointed towards the apex and markedly recurved ventrally. Large rostra have been reported in other Laophontodinae, such as *Calypsophontodes macropodia* (Gee & Fleeger, 1986), both known species of *Probosciphontodes* Fiers, 1988 and some members of *Ancorabolina,* but they are typically of a different size, shape and orientation (cf. Fiers, 1988; George & Tiltack, 2009; Gheerardyn & George, 2010; Gheerardyn & Lee, 2012).

(2) Cephalic shield, pedigerous somites and anterior half of genital double-somite (genital somite in ♂) with reticulate surface ornamentation. Some species of *Laophontodes*, such as *Laophontodes typicus* T. Scott, 1894, *Laophontodes whitsoni* T. Scott, 1912, *Laophontodes sabinegeorgeae* George & Gheerardyn, 2015 and *Laophontodes scottorum* George, 2018, show dorsal striations near the posterior margin of the body somites (but not the cephalic shield), but their pattern, distribution and nature are different (cf. George & Gheerardyn, 2015; George, 2018).

(3) Dorsal surface of P5-bearing somite, genital double-somite (anteriorly and posteriorly) and first free abdominal somite with paired, backwardly directed, spinous projections. Comparable projections are found only in *Ancorabolina* spp. (see below); members of *Paralaophontodes* typically have paired, dorsal, sensillate processes on all somites (except the anal one), but these conspicuous protuberances are not homologous with the spiniform structures found in *La. gracilipes* (cf. Lang, 1965; Mielke, 1981; Fiers, 1988, George, 2017).

(4) Endopodal claw of maxilliped with long pinnules along the distal half of the inner margin. Some *Laophontodes* spp., such as *La. whitsoni*, *Laophontodes macclintocki* Schizas & Shirley, 1994, *Laophontodes mourois* Arroyo et al., 2003 and *Laophontodes horstgeorgei* George & Gheerardyn, 2015, exhibit small spinules on the maxillipedal claw, but in most members of the genus the claw is naked (cf. Schizas & Shirley, 1994; Arroyo et al., 2003; George & Gheerardyn, 2015). Minute spinules have also been recorded in some species of *Calypsophontodes* and *Tapholaophontodes* (cf. Cottarelli & Baldari, 1987; Gheerardyn & Lee, 2012), but in all other members of the Laophontodinae the endopodal claw lacks ornamentation.

(5) P1 basis transversely prolonged in distal half, causing rami to be widely separated by its concave distal margin. In members of *Laophontodes*, the endopod is positioned closely and adjacent to the exopod, typically being originating from a cylindrical pedestal formed by the inner distal portion of the basis.

(6) P1 enp-2 with elongate slender claw, being almost as long as adjacent geniculate seta. Except for *La. whitsoni* (cf. George & Gheerardyn, 2015: fig. 21D), all species of *Laophontodes* have a robust, acutely curved claw that is distinctly shorter than the accompanying geniculate seta.

(7) Armature of P2–P4 enp-2 reduced to a single, extremely long apical seta.

(8) Caudal ramus seta II (and probably also seta I) positioned in proximal third of ramus. Both Lang (1936b) and Kornev & Chertoprud (2008) show only a single seta (II) along the proximal outer margin, but it is highly likely that seta I was concealed by it. In *Laophontodes* spp., all caudal setae typically arise from the distal half (*Laophontodes georgei* sp. nov., *Laophontodes gertraudae* George, 2018, *La. mourois*, *Laophontodes sarsi* George, 2018, *La. scottorum*, *La. typicus* and *La. whitsoni*) or even quarter (*Laophontodes bicornis* A. Scott, 1896, *La. horstgeorgei*, *La. macclintocki*, *La. sabinegeorgeae* and *Laophontodes spongiosus* Schizas & Shirley, 1994). The only exception is the recently described *Laophontodes monsmaris* George, 2018, in which setae I and II originate from the middle third of the outer margin (cf. George, 2018: fig. 16B). Being unique within the Ancorabolinae, the proximal displacement of setae I and II is here regarded as an autapomorphy for *La. gracilipes*, because in all other species of the subfamily all caudal setae arise from the distal half of the ramus, even in species of *Algensiella*, *Calypsophontodes* and *Tapholaophontodes*, all of which exhibit short to very short rami (cf. Soyer, 1975; Mielke, 1985; Cottarelli & Baldari, 1987; Bodiou & Colomines, 1988).

Based on the suite of autapomorphies (1–2, 4, 7–8) outlined above, *La. gracilipes* is here excluded from *Laophontodes* and fixed as the type species of a new genus to be diagnosed as follows.

GENUS *ROSTROPHONTODES* GEN. NOV.

urn:lsid:zoobank.org:act:A7BEFC7B-3430-4470-AB6B-F17E7CA1F89A

Diagnosis: Laophontodinae. Body subcylindrical; body somites strongly chitinized, separated from each other by pronounced constrictions. Cephalothorax wider than remainder of prosome; with lobate extensions bilaterally. Cephalic shield and somites bearing P2–P6 (genital half of double-somite in ♀), with reticulated integument dorsally and laterally. Dorsal surface of P5-bearing somite, genital double-somite (anteriorly and posteriorly)

in ♀ (or genital somite and first abdominal somite in ♂) and second abdominal somite with paired, backwardly directed, spinous projections around posterior margin. Anal somite with strongly protruding, round anal operculum. Caudal rami much longer than wide (about six times in the type species), slightly constricted in the middle; with seven setae; setae I and II originating from proximal third of outer margin, setae III–VII positioned around or near posterior margin.

Sexual dimorphism in antennule, P3 endopod, P5, P6 and segmentation of urosome.

Rostrum very large, about two-thirds of the length of cephalic shield, sharply pointed towards apex, and markedly recurved ventrally. Antennule five-segmented in ♀, with aesthetascs on segments 3 and 5; six-segmented and chirocer in ♂, with one segment distal to geniculation and aesthetascs on segments 5 and 6; posterior margin of segments 2 and 3 reportedly without spinules. Antenna with incompletely fused allobasis lacking abexopodal seta; exopod represented by minute segment with one seta. Mandibular palp one-segmented, with one outer, two apical and two inner setae. Maxilliped subchelate; syncoxa with one pinnate seta; endopod drawn out into curved claw with long pinnules in distal half, bearing one accessory seta at its base.

P1 with well-developed praecoxa and coxa; basis transversely prolonged in distal half, causing rami to be widely separated by its concave distal margin; outer and inner basal setae long and bipinnate. Exopod three-segmented; exp-1 with unipinnate spine bearing long pinnules; exp-2 with one outer, geniculate seta; exp-3 with four geniculate setae. Endopod two-segmented and prehensile; enp-1 very long, more than three times as long as exopod, with setules/spinules on both inner and outer margins; enp-2 short, with one small inner seta and an elongate slender claw apically, being almost as long as adjacent geniculate seta.

P2–P4 with well-developed praecoxae and coxae; bases transversely elongate, becoming progressively longer from P2 to P4. Exopods three-segmented; exp-1 without inner seta, exp-2 with inner seta, exp-3 with one inner seta, two apical setae and three outer spines; outer spines of all segments long and bipinnate. Endopods two-segmented in ♀; enp-1 minute, without armature; enp-2 elongate (becoming progressively shorter from P2 to P4), with one extremely long seta apically. P3 endopod three-segmented in ♂; enp-1 minute and unarmed; enp-2 with short apophysis; enp-3 very short, not extending beyond apophysis, with one very long apical seta.

P5 one-segmented in both sexes; outer basal seta arising from long, demarcated setophore; exopod represented by one outer and three apical elements;

endopodal setae absent. Female genital field positioned anteriorly, with median copulatory pore; P6 represented by small cuticular plates, each with one minute seta. Male P6 unconfirmed.

Type and only species: Laophontodes gracilipes Lang, 1936b = *Rostrophontodes gracilipes* (Lang, 1936b), comb. nov.

Etymology: The generic name is derived from the Latin *rostrum*, meaning beak, and the suffix *-phontodes*, commonly used in the formation of generic names in subfamily Laophontodinae. It refers to the excessively large curved rostrum. Gender: feminine.

Remarks: According to Kornev & Chertoprud's (2008) illustrations of the female and male antennules (their fig. 5.192B, И) segments 2 and 3 do not exhibit any spinules along their respective posterior margins. This observation requires confirmation, because the presence of spinules, usually on a rounded, bump-like expansion, on segment 2 is considered a potential synapomorphy for the Laophontodinae (Gheerardyn & George, 2010; Gheerardyn & Lee, 2012; George, 2017).

Four character states lend support to a potential sister-group relationship between *Rostrophontodes* and *Ancorabolina*:

(1) Maxillipedal claw with ornamentation along distal half of inner margin. All known species of *Ancorabolina* display small spinules on the endopodal claw (e.g. Gheerardyn & George, 2010: figs 3F, 9D, 18C, 27D). In *Rostrophontodes*, the positional homologues of these ornamentation elements are secondarily enlarged, forming long pinnules along the distal inner margin. Spinular ornamentation has been reported in a few other members of the Laophontodinae (see above), but its presence does not appear to be strictly diagnostic for these genera (i.e. *Calypsophontodes*, *Laophontodes* and *Tapholaophontodes*).

(2) P1 basis transversely elongate. In both *Rostrophontodes* and *Ancorabolina*, the distal half of the basis is bilaterally expanded, being at least twice as wide as the proximal margin and forming a distinct cylindrical pedestal for the endopod and a similar expansion for the exopod. The origins of both rami are typically widely separated by the concave distal margin of the basis. Some species show secondary modifications such as in *Ancorabolina cavernicola* George & Tiltack, 2009, where the endopodal pedestal has undergone

extreme elongation along the dorsoventral axis, reaching to about the distal end of the exopod (cf. George & Tiltack, 2009: fig. 6A). In *Ancorabolina galeata* Gheerardyn & George, 2010, the outer distal portion of the basis shows a similar elongation along the transverse axis (cf. Gheerardyn & George, 2010: fig. 18A), causing a disproportionate displacement of the exopod. Transverse elongation of the basis has not been reported in other genera of the Laophontodinae.

(3) Claw of P1 enp-2 replaced by a slender element. In *R. gracilipes*, it is represented by a curved spine being almost as long as the adjacent geniculate seta. In *Ancorabolina* spp., the distal endopod segment typically has one anterior claw-like seta and one posterior geniculate seta, with the former being slightly shorter than the latter (e.g. Gheerardyn & George, 2010: figs 4A, 9E). Although this condition is regarded here as the ancestral pattern in the genus, some secondary deviations have been observed in certain species, such as the presence of two non-geniculate setae in *Ancorabolina chimaerae* George, 2016c, two geniculate setae in *Ancorabolina divasecunda* Gheerardyn & George, 2010 (cf. George, 2006c: fig. 7A; Gheerardyn & George, 2010: fig. 28A) and extreme reduction of the posterior geniculate seta in *A. cavernicola* (cf. George & Tiltack, 2009: fig. 6A'). Except for *La. whitsoni*, which shares the same condition with *R. gracilipes* (cf. George & Gheerardyn, 2015: fig. 21D), all other members of the Laophontodinae display a robust claw, being invariably and distinctly shorter than the geniculate seta.

(4) Body somites with dorsal spinous processes. In *R. gracilipes*, the dorsal surface of the P5-bearing somite, genital double-somite (both genital and first abdominal somite) and first free (second) abdominal somite exhibit paired, backwardly directed, spinous projections. Members of *Ancorabolina* have a propensity to develop similar tooth-like processes, but their distribution pattern differs between species (ranging from the cephalothorax to the penultimate somite). Hence, the significance of this character must be treated with caution when used in a phylogenetic context.

LAOPHONTODES MULTISPINATUS KORNEV & CHERTOPRUD, 2008

Conroy-Dalton (2004) proposed the genus *Lobopleura* to accommodate a new species *Lobopleura ambiducti* Conroy-Dalton, 2004 and *Laophontodes expansus*, and provided compelling evidence for its sister-group

relationship with *Probosciphontodes*. Kornev & Chertoprud (2008) described *Laophontodes multispinatus* from specimens collected at 10 m depth in the Kandalaksha Gulf of the White Sea. Apparently unaware of Conroy-Dalton's (2004) work, they considered their new species to be most closely related to *La. expansus* based on the shared similarity in body shape and ornamentation and in P1 morphology. They separated both species on the degree of dorsoventral flattening of the body, the relative length of the first antennulary segment in the female, the shape of the outer element of P1 exp-2, the morphology of the P2 endopod and the elongation of the bases of P2–P4.

Gheerardyn & Lee (2012: 263) had previously announced the imminent removal of *La. multispinatus* to *Lobopleura*. It is here formally transferred to this genus as *Lobopleura multispinata* (Kornev & Chertoprud, 2008) comb. nov. based on the following combination of characters: dorsoventrally depressed body shape; somites with laterally produced lobate processes; wide, bell-shaped cephalothorax; rostral shape and morphology of antennule, antenna, mouthparts and P1–P5. It also shares three of the four autapomorphies of the genus (cf. Conroy-Dalton, 2004: 35): (1) paired genital system in both sexes (Kornev & Chertoprud do not discuss the condition of the male reproductive system, but their fig. 5.194a clearly shows the presence of paired spermatophores); (2) P4 endopod with only one apical seta; and (3) P5 baseoendopodal armature reduced to one vestigial seta. The fourth autapomorphy identified by Conroy-Dalton (2004) (i.e. male P3 endopod-2 not secondarily subdivided) cannot be confirmed for *Lo. multispinata* because according to Kornev & Chertoprud (2008) no sexual dimorphism is displayed on the swimming legs. This is likely to be based on an observational error, because all members of the Laophontodinae exhibit a sexually dimorphic P3 endopod (except for the two species of *Probosciphontodes*, which lack this ramus in both sexes).

Lobopleura multispinata is morphologically very close to the type species *Lo. ambiducti*. It is maintained as a distinct species based on the following characters: (1) the shape of the cephalothorax in both sexes, being broader and tapering more gradually towards the anterior end in *Lo. ambiducti* (particularly in the female); (2) shape of the rostrum (broader at base and with straight lateral margins in *Lo. multispinata*, with concave lateral margins in *Lo. ambiducti*); (3) lateral spinulate processes on somites bearing P2–P5 and genital (double-)somite distinctly more produced in *Lo. ambiducti*; (4) body ornamentation consisting of numerous spinules in *Lo. multispinata* vs. smooth in *Lo. ambiducti*; (5) caudal rami distinctly longer in the

male in *Lo. ambiducti*; (6) second antennulary segment in female relatively shorter in *Lo. multispinata*; (7) bases of P2–P4 more transversely elongate in *Lo. ambiducti*; (8) P2 endopod represented by relatively larger unarmed protuberance in *Lo. multispinata*; (9) P3 enp-2 relatively longer in *Lo. multispinata* and its inner distal seta being plumose and about as long as the outer distal one vs. naked and less than half the length of the outer distal seta; and (10) P4 enp-2 slightly longer in *Lo. multispinata*, but its apical seta distinctly shorter than in *Lo. ambiducti*. Other potential differences, such as the armature of the mandibular palp (six setae vs. five in *Lo. multispinata*) and the number of accessory setae on P1 enp-2 (one long + two minute in *Lo. ambiducti* vs. one long + one minute in *Lo. multispinata*), require confirmation. Differences based on observational errors in Kornev & Chertoprud's (2008) description include the alleged absence of: (1) the vestigial antennary exopod; (2) the inner basal seta on P1; (3) the outer basal seta on P4; and (4) sexual dimorphism on the P3 endopod (no apophysis in male).

The genus *Lobopleura* assumes, so far, a northern Atlantic–Arctic distribution. The type species *Lo. ambiducti* is known from the Dalkey region (Co. Dublin) in Ireland (Roe, 1958: as *Laophontodes* sp.), the Gullmar Fjord in Sweden (Lang, 1948: as *Laophontodes expansus*) and the Isle of Iona in Scotland (Conroy-Dalton, 2004). *Lobopleura expansa* was originally described from the Saltenfjord (Skjærstadfjord) in Norway (Sars, 1908). Steinarsdóttir & Ingólfsson (2004) reported it (as *Lo. expansus*) from the eulittoral *Ascophyllum nodosum* (L.) Le Jol. zone in Hvassahraun in southwestern Iceland. Willems *et al.* (2009) collected the species in the Singlefjord, Sandviken along the Swedish west coast (Koster area), and Gheerardyn *et al.* (2009) (see also Buhl-Mortensen *et al.*, 2010: fig. 10) recorded it from the coral degradation zone in the Porcupine Seabight (NE Atlantic). The species provisionally identified by Cuvelier *et al.* (2014) as '*Lobopleura* cf. *expansa*' [and by Sarrazin *et al.* (2015) as *Lobopleura* and by Plum *et al.* (2017) as *L. expansa*] from the Eiffel Tower edifice (Lucky Strike vent field) at 1700 m depth on the Mid-Atlantic Ridge south of the Azores probably refers to a different taxon. *Lobopleura multispinata* is, so far, known only from its type locality in the White Sea.

AUTHENTICITY OF *LAOPHONTODES BICORNIS* IN KOREA

The original description of *La. bicornis* was based on a single female dredged off Port Erin, Isle of Man, in the Irish Sea (A. Scott, 1896). The male was first reported, but not described, in dredgings from Kilbrennan Sound, Firth of Clyde in Scotland

(T. Scott, 1896). It has subsequently been recorded from several localities in northwestern Europe, including Norway (Sars, 1908), Sweden (Lang, 1948), Ireland (Farran, 1913; Roe, 1958, 1960; Sloane *et al.*, 1961; Holmes, 1983), Northern Ireland (Wells, 1963), England (Norman & Scott, 1906; Wells, 1961; Ventham, 2011) and France (Monard, 1935: as *L. hamatus* var. *reflexus*; Bodin & Le Guellec, 1992). Mediterranean records include those from France (Monard, 1928; Bodin, 1964; Soyer, 1971; Mascart *et al.*, 2015), Italy (Pesta, 1959), Croatia (Brian, 1923), Greece (Brian, 1928a, b), Turkey (Noodt, 1955), Egypt (Gurney, 1927) and Israel (Por, 1964), whereas Griga (1964) reported it from the Crimea in the Black Sea. Additional records outside Europe were added from the Suez Canal by Por & Marcus (1973) and from the Red Sea by Nicholls (1944) and Por (1967).

George & Gheerardyn (2015) redescribed both sexes of *La. bicornis* in detail based on material from Kopervik (Western Norway, collected by G. O. Sars) and the Gullmar Fjord (Sweden, collected by K. Lang) and concluded that its allegedly wide distribution documented in the literature is probably unfounded. The only records of the species they considered as authenticated are those from the type locality (A. Scott, 1896), Norway (Sars, 1908) and Sweden (Lang, 1948).

Within the genus *Laophontodes*, there is a well-delimited group of species characterized by the presence of: (1) paired posterolateral, backwardly directed, corniform processes on the cephalothorax; and (2) crenulate posterior margins on the body somites. This *bicornis* group includes *La. bicornis*, *La. hamatus*, *Laophontodes brevis* Nicholls, 1944, *Laophontodes ornatus* Krishnaswamy, 1957 and *La. horstgeorgei* George & Gheerardyn, 2015, but it is likely that other closely related species await discovery or have previously been confounded with described members of this group. The underlying reason for this unsatisfactory state of affairs is twofold.

Firstly, the available descriptions of *La. hamatus*, *La. brevis*, *La. ornatus* and, until recently, *La. bicornis*, are inadequate for unequivocal identification, and this has led to considerable confusion in the past. Thomson (1883) described the genus and species *Merope hamata*, on the basis of a single female from Dunedin Harbour in New Zealand. Gurney (1927) considered the species conspecific with *La. bicornis*, whose binomen loses in priority to *M. hamata*. However, since *Merope* Thomson, 1883 is preoccupied, being a junior homonym of *Merope* Newman, 1838 (Mecoptera), *Merope* Adams & Adams, 1856 (Mollusca) and *Merope* Albers, 1860 (Mollusca), he proposed *Laophontodes hamata* (Thomson, 1883) as the new combination. Lang (1934) reinstated Thomson's species with the corrected spelling, *Laophontodes hamatus*, and provided a

partial redescription based on material from Campbell Island and Stewart Island (New Zealand). Monard (1935) proposed a new variety, *La. hamatus* var. *reflexus*, based on differences in colour, rostrum size and shape of the somites observed in specimens from the Roscoff area, but its validity was subsequently refuted by Lang (1936b), who considered it a variety of and subsequently (Lang, 1948: 1455) synonymous with *La. bicornis*. *Laophontodes brevis* was described by Nicholls (1944) based on six specimens from Ghardaqa, Egypt in the Red Sea. Nicholls (1944) did not disclose the sex of his individuals, but Lang (1965) recognized a similarity between *La. brevis* and the copepodid V stage of *La. bicornis*, believing that both species were probably conspecific. Contrary to certain authorities, who list *La. brevis* as a junior synonym of *La. bicornis* (e.g. Bodin, 1997) or omit it altogether (Gee & Fleeger, 1986; Schizas & Shirley, 1994; Wells, 2007; George & Gheerardyn, 2015; George, 2018), Lang (1965) did not formally synonymize it with the latter, hence the species must remain as valid until forthcoming evidence proves otherwise. Krishnaswamy (1957) described *La. ornatus* from four females dredged off the coast of Chennai (Madras), Tamil Nadu (India). Although the species is clearly a member of the *bicornis* group, its description is grossly inadequate, and various authors (e.g. Lang, 1965) have pointed out discrepancies between the text and accompanying illustrations. It should be noted that Gee & Fleeger (1986) erroneously listed the species under the name *L. armatus* in their table 2 (p. 158).

Secondly, Gheerardyn & George (2010) pointed out the superficial resemblance between *La. bicornis* and members of the genus *Ancorabolina*. Given that both share the paired corniform processes on the cephalothorax, George & Gheerardyn (2015) argued strongly that some earlier records of the former in reality were based on as yet undescribed species of the latter. This claim has been confirmed for Büntzow's (2011) *La.* var. *bicornis* from the Seine seamount in the subtropical NE Atlantic (George, 2013) and extrapolated to the entire area where *Ancorabolina* spp. have been sighted so far, including the Mediterranean basin, where *La. bicornis* has allegedly been reported on numerous occasions (see above). Likewise, the authenticity of the records from the Black Sea and the Red Sea must remain unconfirmed, particularly those of Nicholls (1944), who reported two co-existing morphs of *La. bicornis* alongside *La. brevis*.

The records of Nicholls (1944) and Por (1967) from the Red Sea and the recent discovery of *La. horstgeorgei* from the Fiji Islands indicate that the *bicornis* group probably assumes a distribution throughout the Indo-Pacific. This is further corroborated by Kim's (2013) report of *La. bicornis* from Seogwipo on Jeju Island,

South Korea, where it was found in washings of wood infested by limnoriid isopods and teredinid bivalves and of coralline sand collected at moderate depths. Kim's (2013) report consists of a text description of both sexes and three accompanying photographs illustrating the habitus, cephalothorax and urosome (all in dorsal aspect) of the female. However, the Korean material (six ♀♀, four ♂♂) differs from George & Gheerardyn's (2015) redescription of *La. bicornis* in several significant aspects: (1) the lateral corniform processes on the cephalothorax are much shorter and blunt in appearance; (2) the pleural areas of the body somites are much more produced, so that the constrictions between individual somites appear more pronounced in dorsal aspect; (3) P3 and P4 exp-3 bears one inner seta instead of two; (4) P2–P4 endopod is one-segmented instead of two-segmented; (5) P3 endopod without outer seta instead of 0.021 pattern in *La. bicornis*; (6) the caudal rami are relatively shorter; and (7) from Kim's (2013) text description, it can be inferred that the male antennule shows two segments (instead of one) distal to the geniculation (cf. 'Antennule 6-segmented …; fourth segment swollen, with aesthetasc arising from process near distal margin; sixth segment with an aesthetasc'). Within the *bicornis* group, Kim's (2013) material is unique in the presence of only one inner seta on P3 and P4 exp-3, indicating that it deserves distinct specific status. In accordance with ICZN (1999) Articles 16.4 and 72.5.6, we would have selected the female specimen illustrated by Kim (2013) in his fig. 19 as the holotype of a new species, but this would be premature. Huys & Lee (2018) pointed out that Kim (2013) copied the original text description of *Folioquinpes mangalis* Fiers & Rutledge, 1990 virtually verbatim, explaining the many discrepancies between the text and some of his illustrations of what appeared to be the new species *Folioquinpes pseudomangalis* Huys & Lee, 2018. Upon closer inspection this practice of unorthodox copying and pasting text blocks turns out to be rampant in his two reports of the Korean marine harpacticoid fauna (Kim, 2013, 2014), casting serious doubts on the scientific integrity of the work. For example, his 2014 text description (totally lacking in illustrations) of "*Laophontodes psammophilus*" – a species in reality belonging to another genus (George, 2017) – is repeated in exactly the same words (and typographical errors) as were used originally in his 2013 description of "*L. bicornis*". In addition, the same text (except for body length measurements) was reproduced verbatim for the description of *Algensiella boitanii* (Kim, 2014: 88–89) which differs radically from members of *Laophontodes*. Clearly the taxonomic mess created by Kim (2013, 2014) in his two reports can only be cleared up by thorough re-examination of the original material and clearly demonstrates the pitfalls of publications that have not been subjected to peer-review.

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KEY TO SPECIES OF *LAOPHONTODES* T. SCOTT, 1894

The genus currently accommodates 15 valid species ([Tables 1](#) and [4](#)). *L. propinquus* Brady, 1910 (*species incertae sedis*), *L. antarcticus* Brady, 1918 and *L. ornatus* Krishnaswamy, 1957 (both *species inquirendae*; cf. [Table 4](#)) are excluded from the key below, which is applicable to both sexes (except for couplet 4).

1. Cephalothorax with paired posterolateral, backwardly directed, corniform processes; posterior margins of body somites crenulate ………………*bicornis* group .... 2.

–   Cephalothorax without paired posterolateral, backwardly directed, corniform processes; posterior margins of body somites not crenulate .... 6.

2. P3–P4 exp-3 without inner seta ………………………………… *L. bicornis* A. Scott, 1896 sensu [Kim (2013)](#).

–   P3–P4 exp-3 with inner seta ....3.

3. P3 enp-2 ♀ with outer spine ………………………………………………………*L. bicornis* A. Scott, 1896.

–   P3 enp-2 ♀ without outer spine ....4.

4. P4 enp-2 with outer spine/seta ....5.

–   P4 endopod with armature pattern 0.120 or 120 ……………………………………*L. brevis* Nicholls, 1944.

5. P5 ♂ with total of six setae/spines ……………………………*L. horstgeorgei* George & Gheerardyn, 2015*.

–   P5 ♂ with total of five setae/spines ……………………………………………*L. hamatus* (Thomson, 1883)*.

6. P3 exp-2 with inner seta ....7.

–   P3 exp-2 without inner seta ....10.

7. P3–P4 exp-3 with one inner seta ……………………………………*L. macclintocki* Schizas & Shirley, 1994.

–   P3–P4 exp-3 with two inner setae ....8.

8. P4 enp-2 ♀ without outer spine/seta (present in ♂); penultimate somite forming dorsal pseudoperculum covering most of anal somite ……………………………………………………*L. monsmaris* George, 2018.

–   P4 enp-2 typically with outer spine/seta in both sexes (but note that [George & Gheerardyn (2015)](#) recorded intraspecific variability in the presence/absence of the outer element in *L. whitsoni*); no such pseudoperculum present ....9.

9. Rostrum with setular tuft along anterior margin; P1 enp-2 claw robust, unipinnate and about half as long as adjacent geniculate seta; all caudal setae (I–VII) located in distal quarter of ramus; outer spine of P1 exp-1 unipinnate with long pinnules along outer margin; P5 exopodal lobe with five elements in ♀ and three in ♂ ………………………………………………………*L. sabinegeorgeae* George & Gheerardyn, 2015.

–   Rostrum without setular tuft; P1 enp-2 claw slender, naked and almost as long as adjacent geniculate seta; all caudal setae (I–VII) located in distal half of ramus; outer spine of P1 exp-1 bipinnate with short pinnules; P5 exopodal lobe with four elements in both sexes …………………*L. whitsoni* T. Scott, 1912.

10. P2 exp-3 with inner seta ....11.

–   P2 exp-3 without inner seta ....12.

11. P4 enp-2 with inner seta; inner seta of P3 exp-3 naked and not extending beyond distal margin of segment; distal (pseudo-)segment of P3 endopod ♂ short, not extending beyond apophysis ……………………………… …………………………………………………………………………………………… *L. typicus* T. Scott, 1894.

–   P4 enp-2 without inner seta†; inner seta of P3 exp-3 pinnate/plumose and extending far beyond distal margin of segment; distal (pseudo-)segment of P3 endopod ♂ elongate, clearly extending beyond apophysis ……………………………………………………*L. mourois* Arroyo, George, Benito & Maldonado, 2003.

12. P3 exp-3 with inner seta; body dorsoventrally depressed …………………………*L. scottorum* George, 2018.

–   P3 exp-3 without inner seta; body not markedly depressed ....13.

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13. P3 enp-2 (♀) and P4 enp-2 (or enp-1 when endopod one-segmented) with armature pattern 120 (with inner seta) .... 14.

– P3 enp-2 (♀) and P4 enp-2 with armature pattern 020 (without inner seta) .... 15.

14. P4 exp-2 with inner seta; P4 endopod two-segmented ....*L. sarsi* George, 2018.

– P4 exp-2 without inner seta; P4 endopod one-segmented ....**L. georgei** sp. nov.

15. P4 exp-3 with inner seta; P5 baseoendopod ♀ represented by one seta; P5 ♂ with four elements on exopodal lobe ....*L. spongiosus* Schizas & Shirley, 1994.

– P4 exp-3 without inner seta; P5 baseoendopod ♀ represented by two setae; P5 ♂ with three elements on exopodal lobe ....*L. gertraudae* George, 2018.

* Both Southern Hemisphere species are extremely similar in the shape of the cephalothorax, armature patterns of P2–P5 in the female and caudal ramus morphology. Provided Lang's (1934) redescription of *L. hamatus* is correct, they can be differentiated only by the number of elements on the male P5. Slight differences can be detected in the relative length of the caudal rami, but these are probably insignificant as interspecific discriminants. Surprisingly, George & Gheerardyn (2015) did not compare *L. horstgeorgei* with *L. hamatus*, restricting the comparison instead to *L. bicornis* and *L. ornatus*. Having been synonymized previously with *L. bicornis* (cf. Gurney, 1927), Lang (1934) maintained *L. hamatus* as a distinct species based on differences in the shape of the rostrum and the last two abdominal somites, neither of which characters are useful to distinguish it from *L. horstgeorgei*. Given the geographical proximity of their respective type localities, it is conceivable that *L. hamatus* (New Zealand) and *L. horstgeorgei* (Fiji Islands) are conspecific.

† Note that Arroyo *et al*.'s (2003) illustration of leg 4 (their fig. 3b) was poorly reproduced by the publishers; the largest spinule shown along the inner margin of enp-2 agrees in position and size with the inner seta on this segment in *L. typicus* (cf. George 2018: fig. 5D), casting doubt on its reported absence in *L. mourois*.

KEY TO GENERA OF ANCORABOLINAE

Various authors (Gee & Fleeger, 1986; Conroy-Dalton, 2004; George, 2006c; Gheerardyn & George, 2010; Gheerardyn & Lee, 2012) have commented on the heterogeneity of the family Ancorabolidae, with the two recognized subfamilies, Ancorabolinae and Laophontodinae, forming a well-defined division based on differences in female antennulary segmentation, leg 1 morphology and the number of outer spines on the third exopodal segment of legs 2–4 (Lang, 1948). Conroy-Dalton & Huys (2000) recognized an *Ancorabolus* group in the Ancorabolinae, whereas Conroy-Dalton (2001) allocated *Ceratonotus*, *Dorsiceratus*, *Polyascophorus*, *Arthuricornua* and *Touphapleura* to a newly defined *Ceratonotus* group. Conroy-Dalton (2003a) added *Dendropsyllus* to the latter, which was subsequently redefined by George (2006b) to encompass also *Echinopsyllus* and *Pseudechinopsyllus*. The latest keys to genera (Boxshall & Halsey, 2004; Wells, 2007) are outdated. The subfamily currently accommodates 40 species (two *species inquirendae*) in 14 genera (Tables 1 and 2).

1. Body somites virtually cylindrical; somites bearing P2–P4 with backwardly produced (latero)dorsal processes; antennulary segment 1 (or equivalent portion of compound segment in three-segmented antennule of *Ceratonotus* and *Dendropsyllus*) distinctly elongate; P1 endopod two-segmented (with enp-1 markedly shorter than enp-2) or entirely absent; P2–P4 endopods reduced, with armature typically arranged around apex of (terminal) segment; P3 endopod ♂ three-segmented, with apophysis arising from middle segment; P5 endopodal lobe of both sexes at least partially absorbed into protopod, with at most two setae ....*Ceratonotus* group .... 2.

– Body dorsoventrally depressed; all somites except last two (three in *Ancorabolus* males) abdominal ones; with lateral wing-like processes; antennulary segments 1–2 fused (incompletely in *Juxtaramia*), resulting in three-segmented and seven-segmented condition in ♀ and ♂, respectively; P1 endopod two-segmented with enp-1 markedly longer than enp-2, often prehensile; P3 endopod ♂ two-segmented, with apophysis arising from apical segment; P5 ♀ endopodal lobe well developed and rectangular (smaller in ♂), with four and two elements in ♀ and ♂, respectively; P5 exopod with five elements in both sexes, inner element represented by serrate spine ....*Ancorabolus* group .... 10.

2. Cephalothorax with large, conical frontolateral horns and with paired bifurcate, laterally displaced processes at posterior margin* .... *Polyascophorus* George, 1998.

– Cephalothorax with different pattern of processes; when present, posterolateral processes never bifurcate .... 3.

3. P1 endopod absent in both sexes .... 4.

– P1 endopod present in both sexes .... 7.

4. Dorsal surface of cephalothorax with two pairs of backwardly directed processes (one in anterior half and one in posterior half) separated by middorsal bulbous projection; first (distal half of genital double-somite in ♀) and second abdominal somites with basally fused pair of divergent conical processes on dorsal surface; P5 exopod ♀ discrete, with four elements ....*Echinopsyllus* Sars, 1909.

– Dorsal surface of cephalothorax without anterodorsal processes, posterodorsal processes sometimes present but middorsal bulbous projection absent; abdominal somites without conical processes; P5 exopod ♀ fused to baseoendopod, with five elements .... 5.

5. Rostrum elongate and protruding; cephalothorax with small paired frontolateral processes, each accompanied at base by anterior setular tuft; P5-bearing somite with paired conical processes on dorsal surface; P3–P4 endopods one-segmented with armature pattern 010 ....*Pseudechinopsyllus* George, 2006b.

– Rostrum small or completely incorporated in anterior margin of cephalic shield; frontolateral cephalic processes very large and directed at virtually right angle to longitudinal body axis, without setular tufts at base; P5-bearing somite without processes on dorsal surface; P3–P4 endopods two-segmented with armature pattern 0.020 .... 6.

6. Cephalothorax with pair of laterodorsal processes near posterior margin; somites bearing P2–P4 without setular tufts on pleural areas; P2–P4 exp-3 armature pattern 122, 222 and 122, respectively, in both sexes .... *Arthuricornua* Conroy-Dalton, 2001.

– Cephalothorax without laterodorsal processes near posterior margin; somites bearing P2–P4 with setular tufts on pleural areas; armature of P2–P4 exp-3 sexually dimorphic [022(P2–P4) in ♀; 122(P2, P4) or 222(P3) in ♂] ....**Dimorphipodia** gen. nov.

7. Cephalothorax with paired frontolateral horns and paired ventrolateral processes†; posterior half of cephalothorax and somites bearing P2–P5 with large, paired dendroid processes on dorsal surface; pleural areas of free body somites (except anal somite) without any conspicuous ornamentation; antennule ♀ three-segmented .... 8.

– Cephalothorax without paired frontolateral horns or ventrolateral processes; dorsal processes on posterior half of cephalothorax (when present) and somites bearing P2–P4 either multipinnate or naked; dorsal processes absent on P5-bearing somite; pleural areas of free body somites (except anal somite) with setular tufts; antennule ♀ four-segmented... 9.

8. First abdominal somite (posterior half of genital double-somite in ♀) with paired dendroid processes on dorsal surface; P1 exp-2 with two non-geniculate and three geniculate setae; P1 enp-2 with two geniculate setae; P3–P4 exp-3 with two and one inner seta(e), respectively ....*Ceratonotus* Sars, 1909.

– First abdominal somite (posterior half of genital double-somite in ♀) without paired dendroid processes on dorsal surface; P1 exp-2 with one non-geniculate and four geniculate setae; P1 enp-2 with one bipinnate seta; P3–P4 exp-3 with one and no inner seta, respectively .... *Dendropsyllus* Conroy-Dalton, 2003a.

9. Cephalothorax with pair of dorsal multipinnate processes in posterior half, posterolateral corners without setular tufts; dorsal processes on somites bearing P2–P4 large (usually smaller in ♂) and multipinnate; rostrum bifurcate and protruding, without ornamentation; P1 exp-2 with four geniculate setae and one spine (when three-segmented exp-3 with four geniculate setae); P1 enp-2 with two non-geniculate setae ... . *Dorsiceratus* Drzycimski, 1967.

– Cephalothorax without dorsal processes in posterior half, posterolateral corners lobate, bearing setular tufts; dorsal processes on somites bearing P2–P4 small, conical and naked; rostrum small, with spinules around frontal margin; P1 exp-2 with three geniculate setae and two non-geniculate elements; P1 enp-2 with one geniculate and one non-geniculate seta ....*Touphapleura* Conroy-Dalton, 2001.

10. P1 exp-2 with one spine and four geniculate setae; P1 enp-1 much longer than enp-2; caudal rami juxtaposed and closely set together; somites bearing P2–P5 with two pairs (one laterodorsal, one dorsolateral) of processes in ♀; anterior and posterior halves of genital double-somite and second abdominal somite with paired laterodorsal processes in ♀; rostrum subrectangular with clear basal constriction; antennule indistinctly four-segmented in ♀, with partial suture between segments 1 and 2; antennary allobasis unarmed ....*Juxtaramia* Conroy-Dalton & Huys, 2000.

– P1 exp-2 with two spines and three geniculate setae; P1 enp-1 slightly longer than enp-2; body somites ♀ without distinct laterodorsal or dorsolateral processes; caudal rami not closely set together; rostrum broadly triangular, with lateral margins forming rectilinear contour with anterolateral portions of cephalic shield; antennule three-segmented in ♀; antennary allobasis with two abexopodal setae ....*Arthropsyllus* Sars, 1909.

– P1 exp-2 with three spines and two geniculate setae; P1 enp-1 at least twice as long as enp-2 but typically much longer; somites bearing P2–P5 with two pairs (one laterodorsal, one dorsolateral) of processes in ♀; anterior and posterior halves of genital double-somite and second abdominal somite with paired laterodorsal processes in ♀; caudal rami not closely set together; rostrum subrectangular with clear basal constriction; antennule three-segmented in ♀; antennary allobasis with two abexopodal setae ....11.

11. Paired simple processes at anterior corners of cephalothorax long and recurved; lateral processes (three pairs) on cephalic shield long and antler-like; P3–P4 enp-2 without inner seta ....*Ancorabolus* Norman, 1903.

– Processes at anterior corners of cephalothorax short and simple; lateral processes (three pairs) on cephalic shield relatively short and simple; P3–P4 enp-2 with inner seta ....12.

12. Cephalothoracic processes bulbous; pedigerous somites (P2–P4) without dorsal processes; mandibular palp with six setae (including two basal); P1 enp-1 much longer than enp-2; outer spine of P2–P4 exp-2 strongly serrated; caudal rami with spinular patch along proximal medial margin ....*Uptionyx* Conroy-Dalton & Huys, 2000.

– Cephalothoracic processes conical or thorn-like; pedigerous somites (P2–P4) with small, paired dorsal processes; mandibular palp with five setae (including one basal); P1 enp-1 about twice as long as enp-2; outer spine of P2–P4 exp-2 bipinnate; caudal rami without spinular patch along proximal medial margin ....*Breviconia* Conroy-Dalton & Huys, 2000.

*Occasionally with additional pair of dorsal (non-bifurcate) processes near posterior margin (cf. *P. monoceratus* George, Wandeness & Santos, 2013; George *et al*. 2013).
†In some *Ceratonotus* species, the ventrolateral processes can be small (as in *C. pectinatus* Sars, 1909; *C. vareschii* George, 2006a; and *C. elongatus* Gómez & Díaz, 2017).

KEY TO GENERA OF LAOPHONTODINAE

In Laophontodinae, swimming leg armature patterns are not very useful for identification, because considerable variation exists within genera (Table 4). For most couplets, we have opted to use combinations of characters in order to provide sufficient data to separate the genera with confidence. The subfamily currently accommodates 44 species (two *species inquirendae*, one *species incertae sedis*) in nine genera (Tables 1 and 4).

1. Cephalothorax with dorsomedian ridge extending into two posteriorly directed blunt, conical elevations and usually covered by setular tuft in anterior half; somites bearing P2–P5 dorsally with sclerotized sensillate processes; first to penultimate abdominal somites with pair of dorsal, transversely connected processes ....*Paralaophontodes* Lang, 1965.

– Cephalothorax and free body somites without such ornamentation ....2.

2. P2–P3 exp-3 with armature pattern 002; endopods of P2 and P4 absent ....3.

– These characters not combined ....4.

3. Body dorsoventrally depressed; pleural areas of cephalothorax and most body somites with long lateral extensions; antennule ♀ four-segmented; P3 endopod absent in both sexes; anal operculum smooth .... *Probosciphontodes* Fiers, 1988.

– Body cylindrical; pleural areas of cephalothorax and body somites without long lateral extensions; antennule ♀ five-segmented; P3 endopod present in both sexes; anal operculum serrate ....*Tapholaophontodes* Soyer, 1975.

4. Rostrum very large, about two-thirds of length of cephalic shield, sharply pointed towards the apex, and curved ventrally; cephalic shield, pedigerous somites and anterior half of genital double-somite (genital somite in ♂) with reticulate surface ornamentation; P1 enp-2 with elongate slender claw, being almost as long as adjacent geniculate seta; armature of P2–P4 enp-2 reduced to a single, extremely long apical seta; caudal ramus seta II (and probably also seta I) positioned in proximal third of ramus .... ***Rostrophontodes* gen. nov.**

– These characters not combined ....5.

5. Cephalothorax with paired lateral spinous processes near posterior corners; distal half of P1 basis bilaterally expanded, being at least twice as wide as the proximal margin and forming widely separated pedestals for both endopod and exopod; P1 enp-2 typically with long anterior claw-like seta and posterior geniculate seta, or occasionally with two geniculate or non-geniculate setae, in addition to minute seta; P4 endopod sexually dimorphic, with additional outer element on enp-2 ♂ ....*Ancorabolina* George, 2006c.

– These characters not combined; claw-like seta on P1 enp-2 typically replaced by short robust claw (except *Laophontodes whitsoni*) ....6.

6. Body dorsoventrally depressed; thoracic somites and first two abdominal somites with well-developed lateral, lobate processes, furnished with spinules; antennule ♀ four-segmented; reproductive system ♂ paired .... *Lobopleura* Conroy-Dalton, 2004.

– Body not dorsoventrally depressed; thoracic somites and first two abdominal somites without conspicuous lateral, lobate processes; antennule ♀ five-segmented; reproductive system ♂ unpaired, with dextral or sinistral configurations ....7.

7. P2 endopod absent ....*Algensiella* Cottarelli & Baldari, 1987.

– P2 one- or two-segmented ....8.

8. P3 enp-2 with four elements (121) in ♀; P4 enp-2 with inner seta in ♀, this seta absent in ♂; P3–P4 exopods ♂ more strongly developed than in ♀; P5 ♀ robust and broad, with a protruding endopodal lobe; anal operculum serrate ....*Calypsophontodes* Gheerardyn & Lee, 2012.

– P3 enp-2 ♀ with at most three elements (120, 021 or 020)*; presence/absence of inner seta on P4 enp-2 and shape of P3–P4 exopods not sexually dimorphic; P5 of a different morphology with endopodal lobe not protruding; anal operculum with fine spinules or setules ....*Laophontodes* T. Scott, 1894.

*Brady (1910: table 11, fig. 16) figured four elements on the one-segmented P3 endopod of *La. antarcticus*, but this species is inadequately diagnosed and considered a *species incertae sedis* (Lang, 1936b). According to Nicholls (1944: fig. 8), the P3 endopod in *La. brevis* is one-segmented (020), but his description indicated that the species was based on a copepodid V stage.

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