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Molecular and morphological evidence for short range endemism in the *Kinnecaris solitaria* complex (Copepoda: Parastenocarididae), with descriptions of seven new species

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Abstract

Recent investigation of one of the larger calcretes in the uppermost reaches of the Carey palaeochannel in the Yilgarn region of Western Australia revealed an unprecedented diversity of copepod crustaceans. Twenty-two different species and subspecies, from six copepod families, represent 70% of the previously recorded copepod α-diversity in the whole region, although the area investigated is less than 3% of its surface. The aims of this study were to explore the diversity of the harpacticoid genus *Kinnecaris* Jakobi, 1972 using both molecular and morphological methods, establish precise species boundaries, find their accurate area of distribution, reconstruct phylogenetic relationships, and explore colonisation pathways. To achieve this we sampled very intensively in the area, as well as in two neighbouring palaeochannels, analysing more than 700 samples from 230 different localities, half of which contained copepods. Seven species are described here as new, five of them from the Yeelirrie palaeochannel (*K. esbe* **sp. nov.**, *K. lined* **sp. nov.**, *K. linel* **sp. nov.**, *K. linesae* **sp. nov.**, and *K. uranusi* **sp. nov.**) and one each from two neighbouring palaeochannels (*K. barrambie* **sp. nov.** and *K. lakewayi* **sp. nov.**). *Parastenocaris jane* Karanovic, 2006 from the Pilbara region, along with a newly described third Australian parastenocaridid genus from the Yilgarn, were used as outgroups in our molecular analysis. The COI fragment was successfully PCR-amplified from 12 parastenocaridid specimens using a nested combination of primers. All analyses supported the presence of at least seven genetically divergent lineages, most supported with very high bootstrap values. Three genera formed three separate clades, and the average pairwise distances between *Kinnecaris* morpho-taxa were found to be very high (8.2-16.8 %), while the highest divergences within morpho-taxa were 0.3%. Some conflict between molecular phylogenies and morphological data was observed when it came to recognizing different groups of species. While morphology indicates that *K. esbe, K. linel,* and *K. uranusi* represent a group of very closely related species, supported by a number of synapomorphies, molecular analyses suggest that *K. linel* and *K. uranusi* are only remotely related. We argue

in favor of morphological data, until more markers can be studied to try to resolve these differences. In Yeelirrie, morphological evidence would suggest a downstream colonisation history in the genus *Kinnecaris*, where the most plesiomorphic form (*K. linesae*) lives in the uppermost reaches of the palaeochannel, and the trend in the caudal rami elongation and denser somite ornamentation is obvious downstream the palaeochannel (*K. uranusi*, *K. linel*, and then *K. esbe*), with the only exception being *K. lined*, which probably represents an independent colonisation event. Parastenocarids are copepods of freshwater origin, and we argure that they can probably disperse downstream during periods of increased rainfall, evolving into separate species in isolated calcrete pockets during periods of increased aridity. Although some of the questions remained unanswered in this study, detailed morphological and molecular observations indicate that we are not dealing with one widely distributed and variable species in the Yilgarn region, but rather with a complex of short range endemics. Areas of distribution for different species range from 30 km to less than 5 km in diameter. Very strong seasonal dynamics in this subterranean community was observed, and this is a novel concept for these ecosystems globally. A key to nine Australian species of *Kinnecaris* is also included.

Key words: Western Australia, Harpacticoida, stygofauna, taxonomy, systematics, barcoding

Introduction

Family overview. The family Parastenocarididae Chappuis, 1940 is a monophyletic group within Harpacticoida, being easily distinguished by the sexual dimorphism in the third pair of swimming legs (Corgosinho et al. 2007). Modification of these legs in males into a grasping organ, that allows them to hold females during copulation (Glatzel 1996), is one of the most important synapomorphies of the group (Martinez Arbizu & Moura 1994), but many other morphological characters make it very easy to instantly recognize its members (Karanovic & Cooper in press). However, a great number of morphological characters are conservative within this family, making generic division a real and long lasting problem (Reid 1995; Galassi & De Laurentiis 2004; Karanovic 2005; Schminke 2010), and the family stayed monogeneric for a long time despite a steady accumulation of new species.

Chappuis (1937) divided its only genus *Parastenocaris* Kessler, 1913 into four groups, which he numbered rather than named, each containing two species. Kunz (1938) added another group. Lang (1948) subdivided the family into eight species-groups for 31 of the 40 species known at that time (nine species were either known only as females or were insufficiently described), accepting the group proposed by Kunz (1938), but rearranging three of those proposed by Chappuis (1937) and naming them after the most characteristic species. For diagnosing all these groups all three authors mostly used characters of the male fourth leg endopod. Despite being chiefly based on a single character, Lang's system was widely accepted and was coping rather well with a subsequent steady influx of newly described species from around the world, culminating in the decade between 1963 and 1972 when 75 new species were added (Schminke 2010). Five new species groups were added subsequently by Noodt (1962, 1963, 1972), mostly for the newly discovered and very diverse South American fauna, but it became apparent that this increasingly more complex system of species groups was not a reflection of true phylogenetic relationships, which were not taken into account in the description of many of the new taxa.

Jakobi (1969) described one of the Noodt's groups as a new genus, and it was Jakobi (1972) who made the first effort to revise the family by splitting it into 26 different genera (although only assigning to them 98 out of the 155 known species). This system was strongly criticised by Schminke (1976), and was ignored for a long time by most subsequent taxonomists working on this group, all of them accepting only two of Jakobi's genera (see Por & Hadel 1986; Dussart & Defaye 1990; Reid 1995; Karanovic & Bobic 1998; Ranga Reddy 2001; Galassi & De Laurentiis 2004; Boxshall & Halsey 2004; Karanovic 2005, 2006; Cottarelli et al. 2006, 2007, 2008; Wells 2007; Ranga Reddy & Defaye 2007, 2009; Huys 2009). Jakobi (1972), for example, divided the *brevipes*-group of Lang (1948) into five different genera, which was shown by Reid (1995) to be a group of very closely related species. She even demonstrated that the type species of one new genus proposed by Jakobi is in fact a junior subjective synonym of the type species of *Parastenocaris.* Nevertheless, new genera were proposed for some unusual new members from South America (Dussart 1979; Reid 1994), Europe (Galassi & De Laurentiis 2004), Africa (Schminke 2009), Asia (Cottarelli et al. 2010), and Australia (Karanovic & Cooper in press), and two more groups of species were proposed by Berera & Cottarelli (2003) and Galassi & De Laurentiis (2004). Recently, some researchers (Corgosinho & Martinez Arbizu 2005; Schminke 2008; Corgosinho et al. 2010) started to revalidate and redefine some genera originally proposed by Jakobi (1972), as most of them remained valid and available names under the rules of the ICZN (1999), while at the same time synonymising some others.

Genus overview. Schminke (2008) redefined the genus *Kinnecaris* Jakobi, 1972 to include 17 species from Africa, Madagascar, Papua New Guinea, and Australia, basing his generic diagnosis chiefly on characters recognized as phylogenetically informative by Karanovic (2004, 2005), who suggested ten of those species to be relatively closely related. Ranga Reddy & Schminke (2009) added one more species from India. Only two of those 18 species were originally placed in the genus by Jakobi (1972), who designated *Parastenocaris forficulata* Chappuis, 1952 as the type species, and included additionally *P. arenicola* Chappuis, 1954 and *P. marlieri* Chappuis, 1955, although noting that "kann *P. marlieri* als möglicher Grundtyp eines neuen Genus sufgefasst warden". Schminke (2008) does not mention *P. marlieri* anywhere in his paper, but Schminke (2010) lists this species as *incertae sedis* in *Parastenocaris.* Schminke (2008), however, includes in the redefined genus *Kinnecaris* three species from the genus *Cafferocaris* Jakobi, 1972: *C. caffer* (Chappuis, 1935), *C. muscicola* (Chappuis, 1935), and *C. variolata* (Chappuis, 1952). Three other members of *Cafferocaris* were relegated as *incertae sedis* by Schminke (2008), and because *C. caffer* was designated as the type species of this genus by Jakobi (1972), *Cafferocaris* became a junior subjective synonym of *Kinnecaris*. Besides the above mentioned six species of *Kinnecaris* and *Cafferocaris*, Schminke (2008) included the following 11 species in the newly revised genus *Kinnecaris*: *K. aethiopica* (Cottarelli & Bruno, 1995), *K. arenosa* (Fryer, 1956) [Note: incorrectly spelled as *arenosus* both by Fryer (1956) and Schminke (2008)], *K. cornuta* (Chappuis, 1955) [Note: this species was placed in the genus *Macacocaris* Jakobi, 1972 by Jakobi (1972)], *K. eberhardi* (Karanovic, 2005), *K. fluviatilis* (Wells, 1964), *K. giselae* Schminke, 2008, *K. impervia* (Cottarelli & Bruno, 1995), *K. lyncaea* (Cottarelli & Bruno, 1994), *K. madagascarensis* (Chappuis, 1952), *K. quollensis* (Cottarelli & Bruno, 1995), *K. sinoiaica* (Wells, 1964), and *K. solitaria* (Karanovic, 2004). Finally, Ranga Reddy & Schminke (2009) added *K. godavari* Ranga Reddy & Schminke, 2009 to the list. In this paper we describe seven new species in this genus, all from the Yilgarn region of Western Australia.

The latest family revision. Schminke (2010) listed all 258 species described until then in the family Parastenocarididae, provisionally accepted 27 genera as valid (accepting most of those described by Jakobi, although mainly listing just their type species as valid members), and subdivided the family into two subfamilies. As a result of the Principle of Coordination, Parastenocaridinae Chappuis, 1940 has already (potentially) existed since 1940, with *Parastenocaris* as its type genus. In that respect, "Parastenocaridinae nov.", Schminke's (2010) most frequent way to refer to the taxon, is an error. Schminke does, however, correctly call it "Parastenocaridinae Chappuis, 1940" in three places in his paper. On the other hand, he seems reluctant to call these two groups subfamilies, putting the word "subfamily" in quotes in the abstract and noting that such subgroups as he is proposing are "traditionally called subfamilies" (p. 344). Besides these instances, he does not use the term subfamily in the diagnosis section (pp. 361-362) or anywhere else. Still, the above quoted notation on p. 344, together with the frequent notation "nov.", is enough to show that he is intentionally proposing a new taxon (Fontinalicaridinae) of subfamily rank (i.e., it is not some sort of informal or "provisional" or Phylocode-type unavailable taxon), and he explicitly designates its type genus. Therefore, we think, he has (barely) met the requirements for availability of new names. Due mostly to incomplete descriptions or absence of males, he was able to classify only 112 species of Parastenocarididae to the genus level, leaving a majority of them in the genus *Parastenocaris.* Division of the genus *Parastenocaris* into *Parastenocaris s. str.* and *Parastenocaris s. l.*, as first proposed by Galassi & De Laurentiis (2004) and adopted with a different meaning by Schminke (2010), has neither nomenclatural bearing nor phylogenetic justification, as *s. str.* by definition must be part of *s. l.*

Zoogeography of Parastenocarididae. Members of this family are highly specialized for life in continental groundwater, and almost exclusively restricted to this habitat (Galassi and De Laurentiis 2004). They are, however, distributed on all continents except Antarctica and New Zealand (Karanovic 2004), which is remarkable considering that stygofauna (aquatic subterranean fauna) has a limited active dispersal potential and lacks resting stages that could be dispersed passively (Schram 2008; Culver & Pipan 2009). Because parastenocarids have no marine relatives or modern pathways between different continents (Boxshall & Jaume 2000), it has been postulated that they have a Pangaean origin (Karanovic 2006). In Australia, for example, Karanovic (2004) speculated that they started colonising subterranean waters just after the Permo-Carboniferous glaciation, which spread throughout much of what will subsequently become Gondwana supercontinent and covered the entire Australian plate (Frakes 1999; Playford 2003). This makes it likely that present distributions of most parastenocarids are a result of continental drift (Boxshall & Jaume 2000), and thus an ideal group to study vicariance models in zoogeography. Unfortunately, no research has been done on their phylogeography so far to test this hypothesis. The present study offers the first insight into phylogenetic relationships of parastenocaridid copepods using modern molecular tools, even though

only for species from the Australian continent. One of the aims was to stimulate similar research on other continental plates, which will help us to better understand the evolution and historical zoogeography of this interesting group of copepods.

Parastenocarididae in Australia. Compared to other continents, the diversity of parastenocaridid copepods is surprisingly low in Australia (Karanovic 2004, 2006), which is probably a result of prolonged aridity with increased salinity in many inland aquifers on this continent (Karanovic 2005). It was Schminke (1981) who first reported a discovery of "four species belonging to three genera" of parastenocarids from here, but unfortunately they all remain as yet undescribed.

The first described species, *Parastenocaris solitaria* Karanovic, 2004, was reported from the Yilgarn region of Western Australia by Karanovic (2004), and only from three females collected from three different bore holes in Depot Springs pastoral station, some 65 km west of Leinster. Several damaged specimens were later on discovered in the Yilgarn region and provisionally identified as *P. cf. solitaria* (Karanovic unpublished), but when more specimens became available from the Lake Way and Barrambie areas (which inspired the start of this study) it became clear that we were dealing with a complex of closely related species rather than with one widely distributed and highly variable species (see below). Karanovic (2005) described another two species from Western Australia: one from a cave near Margaret River (*Parastenocaris eberhardi* Karanovic, 2005), and the other from a bore in the Argyle Diamond Mine in the Kimberley region (*P. kimberleyensis* Karanovic, 2005). The former species was later collected also from several caves in the Yanchep National Park and near Ellenbrook by Tang & Knott (2009). Both species were described from males and females. Because females of *P. eberhardi* are very similar to those of previously described *P. solitaria*, both species were confidently assigned to the *minuta*-group of Lang (1948) by Karanovic (2005). Schminke (2008) moved them both into the redefined genus *Kinnecaris* Jakobi, 1972 (see above). *Parastenocaris kimberleyensis*, on the other hand, is a member of the *brevipes*-group of Lang (1948), which was considered by Galassi & De Laurentiis (2004) and Schminke (2010) as *Parastenocaris s. str.*, because the group contains the type species of this genus. Finally, Karanovic (2006) described both sexes of one new species from the Pilbara region in Western Australia: *Parastenocaris jane* Karanovic, 2006. This species also belongs to the *brevipes*-group.

Given the size of the regions surveyed by Karanovic (2004, 2006), it is clear that parastenocarids are indeed very rare in Australia. However, there is an interesting zoogeographical pattern emerging, with members of the genus *Parastenocaris* being present in the northern part of Western Australia (Pilbara and Kimberley regions) and *Kinnecaris* in the southern part of Western Australia (Yilgarn region and south-western Western Australia). Recent discoveries of new species (Karanovic in preparation; Karanovic & Cooper in press; and this study) only confirm this subdivision. Two new species from the Pilbara region are awaiting description (Karanovic in preparation) and both are closely related to *Parastenocaris jane*, while all seven short range endemics from the Yilgarn region described in this paper are extremely similar to *Kinnecaris solitaria*, and can only be distinguished confidently morphologically from each other by details in urosomal ornamentation and caudal rami shape.

Australian stygofaunal regions. Although one has to assume that the zoogeography of some of the most ancient landscapes on earth would be very complex, what does not cease to amaze are the regional differences in stygofauna assemblages in Australia, and especially those between the neighbouring Pilbara and Yilgarn regions of Western Australia (see also Karanovic 2006, 2008). These two regions show remarkable differences in most major groups of stygofauna that were well studied. For example, diving beetles are completely absent from the Pilbara region (Watts & Humphreys 2006; Leys & Watts 2008), ostracods show differences at the tribus level (Karanovic 2007), and copepods are mostly different at the genus level (Karanovic 2006), with no shared stygobitic species whatsoever (Humphreys 2008). Even those few shared copepod genera show significant phylogenetic divergences between the two regions, with currently known members being only remotely related (Karanovic 2010; Karanovic et al. 2011). The discovery that Australian regions have different relationships to other Gondwanan areas was already anticipated by Weston and Crisp (1994). Giribet and Edgecombe (2006) showed the importance of looking at small-scale patterns when inferring Gondwanan biogeography for terrestrial invertebrates. Karanovic (2006) proposed a "pulsating desert hypothesis" as a novel dynamic model that may explain some of the differences observed between these two neighbouring regions. Other, published (Karanovic and Hancock 2009; Karanovic 2010; Karanovic et al. 2011) and unpublished research (Karanovic in preparation), conducted recently on subterranean waters in eastern Australia showed a similar dividing line between the stygofaunas of Queensland and New South Wales. Although it is not quite clear yet where this border lies precisely, phylogenies show that copepods

found in Queensland are more closely related to those from the Western Australian Pilbara region, than the neighbouring New South Wales, and a strong connection between the Pilbara region, tropical Queensland, and New Zealand was observed, which may even predate Gondwanan regionalism (Karanovic et al. 2011).

The calcretes of Western Australia. Subterranean waters of Western Australia are becoming known as a significant hot-spot for faunal diversity on a global scale (Humphreys 2008, Guzik et al. 2011). Arid Western Australia is famous for numerous isolated calcrete aquifers that lie along palaeodrainage channels (Timms 1992), and range in diameter from tens of kilometres to hundreds of meters (Humphreys 2001, 2006). Highly porous and carbonate rich sediments here represent an ideal habitat for various groups of stygofauna, including dytiscid beetles (Watts & Humphreys, 2006), amphipods (Finston et al. 2007), isopods (Wilson 2008), bathynellids (Cho et al. 2006 a, b), ostracods (Karanovic 2007), and copepods (Karanovic 2004, 2006). Previous genetic and morphological studies suggested that individual calcretes are equivalent to closed island habitats, which have been isolated for millions of years (Cooper et al 2008). The majority of stygobitic species evolved within individual calcretes following independent colonisation by epigean ancestors (Leys et al. 2003; Cooper et al. 2002, 2007, 2008; Guzik et al. 2008; Leys & Watts 2008). Phylogeographic studies of dytiscid beetles (Cooper et al. 2002; Leys et al. 2003), amphipods (Cooper et al. 2007; Bradford et al. 2010), isopods (Cooper et al. 2008), bathynellids (Guzik et al. 2008), and copepods (Bradford et al. 2010) have confirmed the presence of monophyletic groups restricted to single calcretes. The diversity of stygofauna is mostly dependent on the size of the calcrete, and typically includes one to three species from each major group, most of them endemic to that site (Karanovic 2004, 2006, 2007; Finston et al. 2007; Leys & Watts 2008). An example of a typical Yilgarn calcrete is that at Sturt Meadows, where multiple studies from a very dense grid of bores (115 bore holes in an area of 3.5 km^2) revealed only two copepod species, one cyclopoid and one harpacticoid (Allford et al. 2008, Bradford et al. 2010).

Recent investigations of one of the larger calcretes (about 40 km long) near Yeelirrie pastoral station, in the uppermost reaches of the Carey Palaeochannel in the Yilgarn region, revealed an unprecedented diversity of copepod crustaceans. Using morphological methods we were able to distinguish 22 different species and subspecies, from six copepod families, 21 of them stygobionts. This represents 70% of previously recorded copepod α-diversity in the whole Yilgarn region, and this region was relatively well surveyed (Karanovic 2004). Especially diverse in this newly explored calcrete was the harpacticoid genus *Kinnecaris* Jakobi, 1975, which is the subject of this study. This very high diversity posed a couple of challenges in regard to species delineation and discovering their precise distributions. To solve this we sampled very intensively in the area, as well as in two neighbouring palaeochannels, and employed molecular techniques, in addition to traditional morphological ones, to aid in species delineation and reconstruction of their phlylogenetic relationships. Recently, DNA-based species identification methods, referred to as "DNA barcoding", have been widely employed to estimate levels of species diversity, with the 5'end of the mitochondrial cytochrome C oxidase subunit 1 gene (COI) proposed as the "barcode" for all animal species (Hebert et al. 2003). The advantage of the COI gene is that it often shows low levels of genetic variation within species, but high levels of divergence between species (for a wide range of examples in crustaceans see Lefébure et al. 2006). The availability of so-called "universal" primers developed by Folmer et al. (1994) for the PCR-amplification of COI also greatly facilitates the use of this marker to investigate species boundaries in animals, and these primers have previously been employed successfully to PCR-amplify copepod DNA (Adamowicz et al. 2007; Bradford et al. 2010; Sakaguchi & Ueda 2010).

Material and methods

Material. All specimens studied here were collected from subterranean waters by private environmental consulting agencies (Subterranean Ecology Pty Ltd, Outback Ecology Pty Ltd, and Bennelongia Pty Ltd) and entrusted to the senior author for morphological identification. They resulted from various impact assessment and monitoring projects, primarily done for the mining industry. Most specimens were collected from or near proposed or existing mining sites, but due to the sensitivity of such data no further information about mining operations or plans will be given here. Locality data and number of specimens are listed for every species separately and all types are deposited in the Western Australian Museum (WAM), Perth. Some specimens were kept as vouchers by consulting agencies, but will be ultimately also deposited in the WAM. One recently described new genus and species of *Parastenocarididae* Chappuis, 1940 came from the Yeelirrie palaochannel (Karanovic & Cooper in press), as do

five new species of *Kinnecaris* Jakobi, 1972 described here: *K. esbe* **sp. nov.**, *K. linel* **sp. nov.**, *K. lined* **sp. nov.**, *K. uranusi* **sp. nov.**, and *K. linesae* **sp. nov.** One new species was collected in a calcrete near Lake Way (*Kinnecaris lakewayi* **sp. nov.**), which lies in a palaochannel parallel to Yellirrie, and the two join some 100 km south-east to from the Carey palaeochannel (Timms 1992). The seventh new species described in this paper (*Kinnecaris barrambie* **sp. nov.**) was collected near Barrambie, on the other side of the Yeelirrie palaochannel, in the uppermost reaches of the extensive Nowthanna/Lake Annean palaeodrainage system. *Parastenocaris jane* Karanovic, 2006 was collected from several bores near Newman in the Pilbara region of Western Australia, and was intended as an outgroup for our molecular phylogenies, together with the new genus.

Sampling methods. More than 700 samples were collected from 230 different localities in the Yeelirrie area, around Lake Way, and at Barrambie, about half of them containing copepods. Samples were collected with haul-nets (mesh size 50 or 150 μm) or a groundwater sampling pump from bores. Bores are holes mainly made by mining companies or agricultural enterprises for the purpose of water monitoring and abstraction or mineral exploration. They are usually 50 to 200 mm in diameter and may be lined entirely, or in part, by PVC tubing (the casing). This tubing may be open only at the bottom, or it may be pierced at one or more levels by holes of various sizes ("slots"). The top may be securely capped or entirely open to the elements. Some bores record the water pressure at a given level in the aquifer (piezometers), while others, together with hand dug wells (ca. 1 x 1.5 m) equipped with windmills, provide water for pastoral use. Many of these features are derelict. Haul-nets are actually simple plankton nets of a different size suitable for the bore; collar can range from 30 to 150 mm in diameter and is made of stainless steel. Weighed nets (using simple fishing leads, or more complicated brass intermediate collars) were lowered down into the bore with a bottle screwed on its distal part and then hauled through the water column, usually a number of times. Samples were preserved in the field in 100% ethanol, sorted in a laboratory under a dissecting microscope, and assigned a field number. Every consulting agency has a different system of field and/or lab numbers, and they are also given with every sample in addition to other locality data (as an example oeLN7122 stands for Outback Ecology Lab Number 7122, but some others are not so intuitive and we were not provided with any explanation). Many bores established for hydrogeological work, mineral exploration and water monitoring have prefixes or suffixes of relevance only to that drilling program. These codes are cited in the material examined for each species to aid specification of the location, although precise coordinates are also provided for each sample.

Morphological methods. Specimens were dissected and mounted on microscope slides in Faure's medium, which was prepared following the procedure discussed by Stock & von Vaupel Klein (1996), and dissected appendages were then covered by a coverslip. For the slides containing the urosome or the entire animal, two human hairs were mounted between the slide and coverslip, so the parts would not be compressed. By manipulating the coverslip carefully by hand, the whole animal or a particular appendage could be positioned in different viewing plans, making possible the observation of morphological details. Water slowly evaporates during the examination, and appendages eventually remained in a completely dry Faure's medium, ready for long-term depositing. All line drawings were prepared using a drawing tube attached to a Leica MB2500 phase-interference compound microscope, with N-PLAN (5x, 10x, 20x, 40x & 63x) or PL FLUOTAR (100x) objectives. Specimens that were not drawn were examined in propylene glycol ($CH_3CH(OH)CH_2OH$) and, after examination, were again preserved in 100% ethanol. Photographs of whole specimens were taken in propylene glycol with a Leica DFC420 micro-camera attached to a Leica M205C dissecting microscope. The software package Leica Application Suite (LAS), Version 3.5.0, was used to create a multifocal montage image. Specimens for the scanning electron microscopy were dehydrated in progressive ethanol concentrations, critical-point dried, coated with carbon and observed under a LEO 1525 microscope on the in-lens detector, with working distances between 5.9 and 6.1 mm and accelerating voltages of 5 or 10 kV. Hundreds of SEM photographs were taken, but they are not all presented here to avoid unnecessary repetition, especially for structures that show no morphological differences in different species. Most descriptions were also shortened by making them comparative, and only the first species is described in full.

Morphological terminology follows Huys & Boxshall (1991), except for caudal ramus setae numbering (major reasons being that they did not study caudal rami of parastenocaridid copepods, and nobody so far has provided any conclusive evidence on the homology of different caudal armature elements in different copepod orders), and small differences in the spelling of some appendages (antennula, mandibula, maxillula instead of antennule, mandible, maxillule), latter as an attempt to standardise the terminology for homologous appendages in different crustacean groups. Biospeleological terminology follows Humphreys (2000).

PCR-amplification methods. Specimens for molecular analysis were examined without dissecting under a compound microscope (objective 63x dry) in propylene glycol for identification to morpho-species. After examination they were returned in 100% ethanol. DNA was extracted using the GENTRA method (Puregene) according to the manufacturer's protocol for fresh tissues. PCR amplifications of a 623-bp fragment from the mitochondrial COI gene were generally carried out with the "universal" primers LCOI490 and HCO2198 (Folmer et al. 1994). The use of these primers, however, proved problematic in many cases and hence additional 'nested' primers were designed by Ms. Kathleen Saint (South Australian Museum) from preliminary copepod COI sequence data and used in combination with the Folmer et al. (1994) primers to improve the PCR-amplification efficiency (Table 1). An initial PCR-amplification used the combination LCOI490/HCO2198, then 1 µl of product was used to seed nested PCRs in the following combinations: M1323/ HCO2198 or M1321/M1322 (see Table 1 for codes). PCR-amplifications were carried out in 25 µl volumes containing 4 mM $MgCl_2$, 0.20 mM dNTPs, 1× PCR buffer (Applied Biosystems), 6 pmol of each primer and 0.5 U of AmpliTaq Gold (Applied Biosystems). PCR amplification was performed under the following conditions: 94 °C 9 min, then 34 cycles of 94 °C 45 s; annealing 48 °C 45 s; 72 °C, 60 s; with a final elongation step at 72 °C for 6 min. PCR products were purified using a vacuum plate method and sequencing was undertaken using the ABI prism Big Dye Terminator Cycle sequencing kit (PE Applied Biosystems, Foster City, CA). Sequencing was carried out on an ABI 3700 DNA analyser and sequences were edited and manually aligned in SeqEd version 1.0.3 (Applied Biosystems). For this study DNA was extracted and the COI fragment successfully PCR-amplified from 12 copepod specimens (Table 2).

TABLE 1. Oligonucleotide primers used to PCR-amplify the 5' end of COI. Note: three additional primers were also developed but were unsuccessful in PCR-amplifications of COI.

Primer code	Primer sequence (5'-3')	Designed by
LCOI490 (M414)	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (2004)
HCO2198 (M423)	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. (2004)
M1321	TRRNGAYGAYCARRTTTATAATGT	K. Saint
M1322	TCAAAATARRTGYTGRTAWARHAC	K. Saint
M1323	GAYGAYCARRTTTATAATGT	K. Saint

TABLE 2. List of copepod specimens studied in this paper for which the COI fragment was successfully amplified; see text for generic names and authors of the specific names.

Species	Code	Region	Bore line	Bore number	Date	GenBank
K. lined	100401a	Yilgarn	D	D-trog	23 Sep 2010	JN091677
K. lined	100401b	Yilgarn	D	D-trog	23 Sep 2010	JN091678
K. linel	7315	Yilgarn	L	L-UNK1	14 Nov 2009	JN039162
K. linel	8310	Yilgarn	L	Snake Well	18 Mar 2010	JN039167
K. linesae	100387a	Yilgarn	E	YYHC0103B	22 Sep 2010	JN091681
K. linesae	100379c	Yilgarn	E	YYHC0118A	22 Sep 2010	JN091680
K. sp.	100411b	Yilgarn	P	YYHC0133A	22 Sep 2010	JN091679
K. uranusi	8496	Yilgarn	1	YYD22	15 Mar 2010	JN039169
K. uranusi	8536	Yilgarn	F	YU2	17 Mar 2010	JN039171
K. uranusi	8563	Yilgarn	H	TPB33	18 Mar 2010	JN039172
New Genus	8405	Yilgarn	P	YYHC0133A	20 Mar 2010	JN039168
P. jane	7101	Pilbara	-	FMGSM1386	24 Jan 2010	JN039164

Outgroups. Our choice of outgroup taxa was limited by the amount of sequences available on GenBank (none as yet for COI from this family) and the accessibility of freshly collected parastenocaridid material. We considered members of the genus *Parastenocaris* Kessler, 1913 as very suitable candidates. They are morphologically quite distant from *Kinnecaris* Jakobi, 1972 *sensu* Schminke (2008), but both belong to the same nominotypical subfam-

ily (Schminke 2010). Our first outgroup for the molecular analysis, *Parastenocaris jane*, was collected from subterranean waters near Newman in the Pilbara region. The second outgroup was a newly discovered parastenocaridid genus, which was collected sympatrically with members of the genus *Kinnecaris* on three bore lines (P, E, A; see Fig. 24) in the Yeelirrie area of the Yilgarn region (Karanovic & Cooper in press).

Phylogenetic methods. Phylogenetic analyses of the COI sequence data were conducted with outgroup taxa, and using a combination of different approaches to assess the robustness of the tree topology. A distance approach, using Neighbour Joining (NJ), and a Maximum Parsimony (MP) methods were conducted with the program PAUP* version 4.0b10 (PC program, Swofford 2002). A Maximum Likelihood (ML) approach was conducted using the maximum likelihood program RAxML and the WEB-based RAxML "black box" (http://phylobench.vital-it.ch/raxml-bb/; Stamatakis et al., 2008) provided by the Vital-IT Unit of the Swiss Institute of Bioinformatics, or using MEGA v 5.0.3 (Tamura et al. in press) and an HKY+G model of evolution (selected using a Bayesian Information Criterion as being the optimal model). An HKY-85 (Hasegawa et al. 1985) distance model was used for the NJ analyses. MP analyses were conducted using a heuristic search option and default options (TBR branch swapping, ACCTRAN character state optimisation), with the exception of using random stepwise addition repeated 100 times. NJ and MP bootstrap analyses (Felsenstein 1985) were carried out using 500 bootstrap pseudoreplicates, employing a heuristic search option as above with random input of taxa and "max trees" set to 100 for the MP bootstrap analysis. The ML analyses were conducted applying a General Time Reversible model and unequal variation at sites modeled using a Gamma distribution. Support for branches was estimated using the bootstrap option in RAxML, using 100 bootstrap pseudoreplicates.

Average DNA sequence divergence within groups (morpho-taxa) and between groups was estimated using the program MEGA v. 4 (Tamura et al. 2007; Kumar et al. 2008), with a composite likelihood distance applied under a HKY-85 model of DNA sequence evolution.

Taxonomic results

Subphylum Crustacea Brünnich, 1772
Class Maxillopoda Dahl, 1956
Subclass Copepoda H. Milne Edwards, 1840
Order Harpacticoida G.O. Sars, 1903
Family Parastenocarididae Chappuis, 1940
Subfamily Parastenocaridinae Chappuis, 1940
Genus *Kinnecaris* Jakobi, 1972 *sensu* Schminke (2008)

Kinnecaris lakewayi sp. nov.

(Figs. 1–4)

Type locality. Australia, Western Australia, Yilgarn region, Lake Way borefield, bore SB32-1, 26.873739°S 120.202798°E.

Type material. Holotype male dissected on one slide (WAM C45369); allotype female dissected on one slide (WAM C47178); other paratypes: one male, five females, and two copepodids in alcohol (WAM C47179), one female on one SEM stub *in toto* coated with carbon (WAM C47180), and one male and one female dissected on one slide each (WAM C47181 and C47182); all collected at type locality, leg. V. Campagna & E. Thomas, 21 November 2009, oeLN7122. Additional paratype: one female in alcohol (WAM C45500), collected at type locality, leg. V. Campagna & E. Thomas, 16 August 2010, oeLN0719.

Other material examined. One male in alcohol (WAM C45499), Australia, Western Australia, Yilgarn region, Lake Way borefield, bore P70, 26.650792°S 120.152298°E, leg. V. Campagna & E. Thomas, 15 August 2010, oeLN0736.

One damaged male in alcohol (WAM C45504), Australia, Western Australia, Yilgarn region, Lake Way borefield, bore LakeOES41, 26.704722°S 120.338611°E, leg. V. Campagna & E. Thomas, 16 August 2010, oeLN0724. One male and one copepodid in alcohol (WAM C45368), Australia, Western Australia, Yilgarn region, Lake Way

borefield, bore SB26-1, 26.888636°S 120.132299°E, leg. V. Campagna & E. Thomas, 20 November 2009, oeLN0367.

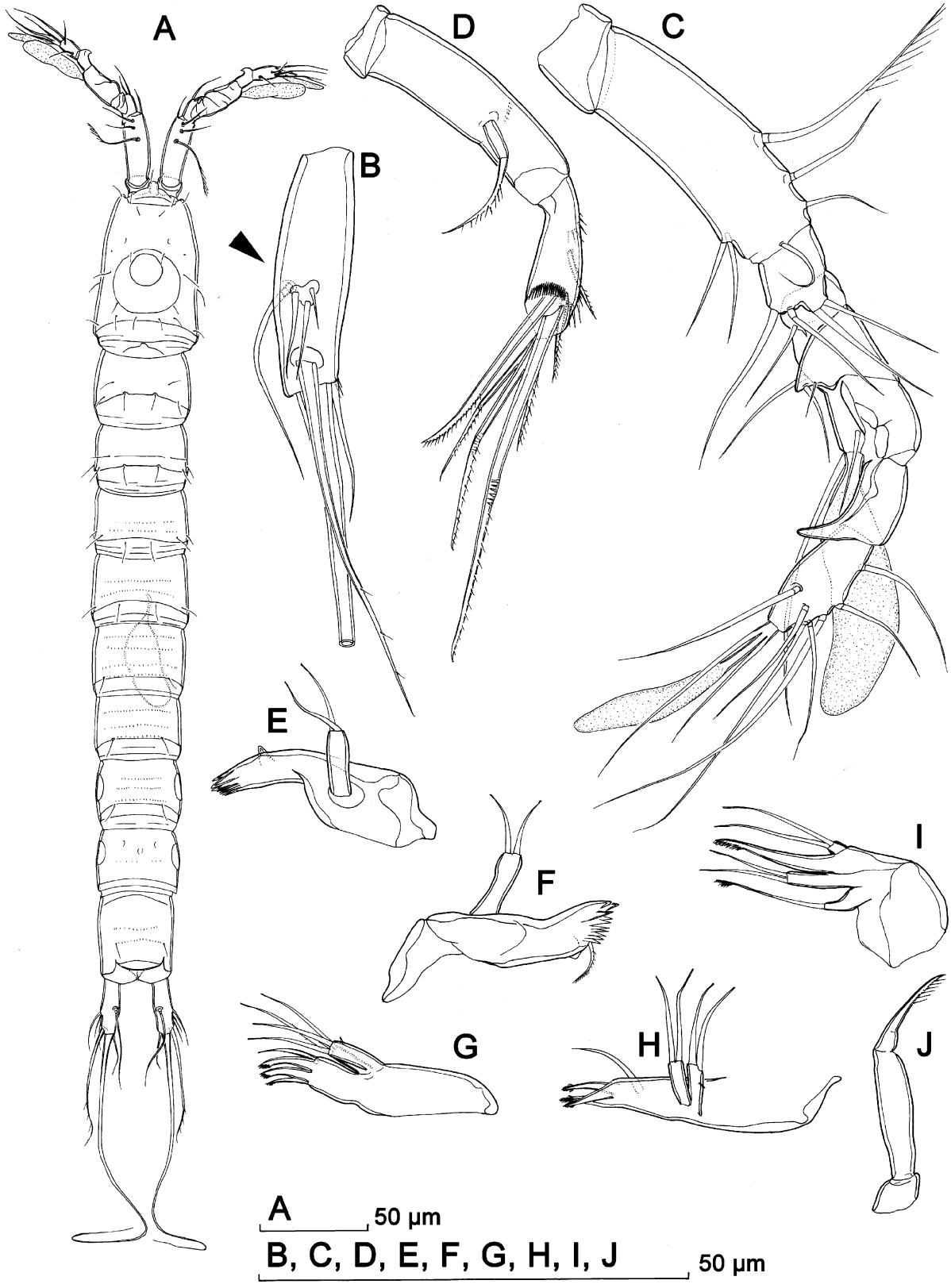

FIGURE 1. *Kinnecaris lakewayi* **sp. nov.**, holotype male: A, habitus, dorsal view; B, right caudal ramus, lateral view; C, antennula, antero-dorsal view; D, antenna, outer view; E, mandibula, ventral view; F, mandibula, anterior view; G, maxillula, anterior view; H, maxillula, squashed from ventral side; I, maxilla, anterior view; J, maxilliped, anterior view. Arrow pointing short and inflated caudal rami in lateral view.

Description. Male (based on holotype and two paratypes). Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 397 to 402 µm (400 µm in holotype). Preserved specimens colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites; first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus (Fig. 1A) cylindrical and very slender, without any demarcation between prosome and urosome; prosome/urosome ratio 0.8; greatest width from dorsal view at posterior end of cephalothorax. Body length/width ratio about eight; cephalothorax 1.15 times as wide as genital somite. Free pedigerous somites without any lateral or dorsal expansions, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and hard to distinguish from arthroidal membranes, especially dorsally, except in preanal somite (fifth urosomite) where hyaline fringe more pronounced. Integument relatively weakly sclerotized, without cuticular pits, but ornamented with several rows of minute spinules on all urosomites (especially dorsally) and some additional larger spinules on fourth and fifth (preanal) urosomites ventrally, as well as large sensilla on all somites except preanal one; cephalothorax with clearly visible (Fig. 1A) double dorsal cuticular window (smaller window with thinner integument inside bigger one) posteriorly; fourth and fifth urosomites each with pair of lateral circular windows. Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view (not covered by pleuras). Rostrum (Fig. 1A) small, membraneous, not demarcated at base , linguiform, almost reaching distal margin of first antennular segment, about as long as wide ornamented with two large dorsal sensilla; area around rostrum with much thinner cuticle, clearly demarcated dorsally, without any surface ornamentation.

Cephalothorax (Fig. 1A) about 1.6 times as long as wide in dorsal view; representing almost 20% of total body length. Surface of cephalic shield with 10 large sensilla in posterior half (posterior to cuticular window, corresponding to fused first pedigerous somite; six dorsal and two lateral on each side), and 16 sensilla in anterior half (six dorsal, two lateral on each side, and three on each side near ventral margin of pleuras); single cuticular pore laterally on each side of anterior half.

Tergites and pleuras of second and third pedigerous somites (Fig. 1A) with two pairs of dorsal sensilla (pair at 2/3 more widely spaced than posterior pair), one pair of dorso-lateral posterior sensilla, and one pair of lateral sensilla (one sensillum on each side); anterior pair of dorsal sensilla more widely spaced on third pedigerous somite. Fourth pedigerous somite with sensilla only on posterior margin, six in total; with two additional dorsal rows of minute spinules.

Fifth pedigerous somite (Fig. 1A) with three pairs of sensilla on posterior margin (one dorsal, one dorso-lateral, and one ventro-lateral), pair of very small cuticular pores in anterior part ventro-laterally, at base of fifth legs, and two dorsal rows of minute spinules.

Genital somite (Fig. 1A) with three pairs of sensilla on posterior margin (one dorsal, one dorso-lateral, and one ventro-lateral), one pair of very small cuticular pores in anterior part ventro-laterally, and four dorsal rows of minute spinules; about 1.3 times as wide as long, with single, large, completely formed and longitudinally placed spermatophore visible inside; spermatophore about 1.2 times as long as genital somite and placed more on right side. Third and fourth urosomites (Fig. 1A) also with six posterior sensilla (two dorsal, two ventral, and one lateral on each side), several rows of minute spinules dorsally, and few shorter rows of minute spinules ventrally and laterally. Fourth urosomite with four additional groups of 3-4 large spinules midventrally. Similar spinules on fifth (preanal) urosomite, but no sensilla or pores.

Anal somite (Figs. 1A, 2A) with pair of large dorsal sensilla at base of anal operculum, pair of large cuticular pores laterally (one pore on each side) in anterior half, two pairs of minute cuticular pores laterally closer to posterior margin, and pair of slightly larger cuticular pores ventrally, at base of caudal rami, in addition to several short rows of minute spinules dorsally and laterally. Anal operculum (Figs. 1A, 2A) well-developed, outer surface unornamented,, row of spinules on inner surface, convex and smooth distal margin, not reaching posterior end of anal somite, representing 66% of somite's width. Anal sinus widely opened, with two diagonal rows of slender spinules on ventral side and transverse row of spinules on dorsal side (below anal operculum).

Caudal rami (Figs. 1A, B, 2A) about 2.9 times as long as greatest width (dorsal view) and 0.6 times as long as anal somite, nearly cylindrical but slightly inflated at midlength (arrowed in Figs 1B, 2A), with inner margin slightly convex in dorsal view and base about as wide as rest of ramus; rami nearly parallel, with space between them almost 1.7 times one ramus' width; with seven armature elements (three lateral, one dorsal, and three apical). Dorsal distal margin protruding in lateral view (Fig. 1B) and with characteristic dorsal posterior saddle in lateral view. Ornamentation consists of large cuticular pore ventro-laterally close to posterior margin (between two princi-

pal apical setae), and row of spinules along posterior margin ventro-medially. Dorsal seta slender and smooth, inserted somewhat closer to inner margin at about midlength, almost 1.4 times as long as caudal ramus, triarticulate basally, and sparsely pinnate distally. Lateral setae thin and smooth, inserted close to each other (two proximal and one distal) in one depression at 3/5 of ramus' length; proximal seta close to dorsal surface strongest and longest, about 0.7 times as long as ramus, 1.7 times as long as proximal seta closer to ventral side, and about 1.3 times as long as distal lateral seta. Inner apical seta smooth and slender, inserted closer to ventral side, about 0.7 times as long as ramus. Middle apical seta strongest, inserted distally, without breaking plane, smooth, with strongly curled tip, about 2.6 times as long as outer apical seta and 0.35 times as long as whole body. Outer apical seta strong and without breaking plane, unipinnate distally and inserted closer to ventral side, about twice as long as ramus.

Antennula (Fig. 1A, C) slightly longer than cephalothorax, prehensile and strongly digeniculate, unornamented, seven-segmented but third and fourth segments somewhat subdivided with surface sutures on inner and ventral sides. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment protruding as large, apically bifid, spiniform process; a second smaller spiniform process present basally on fourth segment, two processes making powerful pincers. Broad aesthetasc on fourth segment reaching slightly beyond tip of appendage, fused basally to slightly longer seta. Slightly shorter and much more slender apical aesthetasc on seventh segment, fused basally to two setae. Setal formula: 0.6.5.6.0.1.9. All setae slender and almost all with pore on tip; proximalmost seta on second segment uniplumose distally, all other setae smooth. Seta on sixth segment minute and partly hidden behind spiniform process. Largest seta on second segment, one seta on third segment, and four setae on seventh segment biarticulate basally, but some other setae showing some trace of ancestral biarticulation.

Antenna (Fig. 1D) relatively stout and long, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unarmed and unornamented. Allobasis about 3.6 times as long as wide, unarmed, ornamented with single short, transverse row of minute spinules on anterior surface. Endopod about 3.1 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal somewhat shorter) and apically with five strong and unipinnate elements (two geniculate). Exopod minute, cylindrical, about 2.6 times as long as wide, unornamented, armed with single unipinnate apical seta, which about 2.6 times as long as segment.

Labrum strong and large, with convex and smooth anterior surface, and narrow cutting edge; cutting edge ornamented apically with row of slender and apically bifid spinules, and with some stronger, simple spinules on outer corners; posterior surface with many rows of minute slender spinules.

Paragnaths fused into strong plate, densely ornamented with short spinules near distal margin and on anterior surface; posterior surface ornamented with one transverse row of eight long spinules and two diagonal rows of five or six smaller spinules; lateral surface smooth except for large cuticular pore proximally.

Mandibula (Fig. 1F, G) with narrow cutting edge on elongated coxa, which positioned between labrum and paragnaths, armed with tricuspidate complex tooth ventrally, unipinnate seta dorsally, and several smaller teeth and/or spinules in between. Palp one-segmented, cylindrical, about three times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on tip.

Maxillula (Fig. 1G, H) with relatively small praecoxa, arthrite rectangular, about 1.5 times as long as wide from lateral view, unornamented, armed with four apical elements (probably three spines and one strong seta; spines each with tuft of basally fused spinules at distal end, forming little scoops; seta with pore on tip). Coxal endite slightly shorter than praecoxal arthrite, armed with two slender setae apically, both with pore on tip; dorsal seta unipinate along dorsal surface (although hardly visible), other setae smooth. Basis slightly longer than coxal endite, armed with one subapical minute seta (or perhaps tubular pore?) and two long smooth apical setae of about same length; all three elements with pore on tip. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 1I) composed of syncoxa, basis, and one-segmented endopod; ornamented only with large cuticular pore on syncoxal posterior surface proximally, with closely shut and horizontally placed opening. Syncoxa with two endites; proximal one conical and bent dorsally, armed apically with single distally unipinnate seta; distal endite longer than proximal one, cylindrical, armed apically with two smooth setae with pore on tip. Basis drawn out into strong claw, without seta at base, with tuft of basally fused spinules distally, forming small scoop, and single pore on ventral surface close to base of scoop (pore not visible with light microscope and in anterior view). Endopod represented by minute but distinct segment, armed with two smooth subequal apical setae, both with pore on tip.

Maxilliped (Fig. 1J) three-segmented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa short, unarmed and unornamented. Basis slender, almost four times as long as wide and 3.4 times as long as syncoxa, unornamented and unarmed. Endopod represented by short curved claw, about 0.8 times as long as basis, swollen at base as indication of ancestral one-segmented endopod, ornamented with row of long and slender spinules along concave side distally.

First swimming leg (Fig. 2B) with small, trapezoidal and smooth intercoxal sclerite with distal margin slightly concave. Leg composed of praecoxa, coxa, basis, three-segmented exopod and two-segmented endopod. Praecoxa triangular, unarmed, ornamented with diagonal row of minute spinules on both anterior and posterior surfaces. Coxa large, quadriform, unarmed, ornamented with several short rows of minute spinules on anterior and posterior surfaces. Basis smaller than coxa, more or less pentagonal, armed with single slender seta on outer margin, ornamented with few large spinules along inner margin at midlength, transverse row of minute spinules at base of outer seta, and few minute spinules along distal margin on anterior surface, between exopod and endopod. Exopod armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments; inner distal corners of first and second segments smooth (no frills). Endopod slightly longer than exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about 3.4 times as long as wide, unarmed, ornamented with two short rows of large spinules along outer margin and one long on inner margin; second segment armed apically with long geniculate seta and much shorter spine; geniculate seta 1.7 times as long as entire endopod and 1.2 times as long as larger geniculate exopodal seta.. All armature elements on ultimate endopodal and exopodal segments strongly unipinnate along outer concave margin.

Second swimming leg (Fig. 2C) with smooth and large intercoxal sclerite, which more than twice as wide as long, quadriform, with concave distal margin. Leg composed of praecoxa, coxa, basis, three-segmented exopod, and one-segmented endopod. Praecoxa, coxa, and basis unarmed, with integument of different thickness forming distinct plates; praecoxa and coxa unornamented; basis with several minute spinules on outer margin. Exopod slightly curved inwards, ornamented with large spinules along outer margin, and with distal inner hyaline frills on each segment ; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about 1.4 times as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and slender, about seven times as long as wide, reaching 2/3 of first exopodal segment in length, ornamented with several small spinules along apical margin; armed apically with one smooth seta, about 0.7 times as long as segment, slightly curved inwards.

Third swimming leg (Fig. 2D, G, H) with smooth praecoxa, coxa, and intercoxal sclerite. Intercoxal sclerite large, trapezoidal, unornamented, and with slightly concave distal margin. Praecoxa larger than in second leg. Basis robust, armed with long, slender, smooth outer seta, ornamented with short longitudinal row of small spinules along inner margin at base of endopod, and several spinules on posterior surface proximally. Endopod minute but distinct segment (probably with fused apical armature element), about four as long as largest spinules on inner margin, unornamented; similar to smooth minute seta. Exopod with both segments fused; ancestral proximal segment curved, about 5.7 times as long as wide, with fairly smooth and slightly concave inner margin, ornamented with one longitudinal row of spinules along outer margin distally, armed subapically with strong, smooth and curved element (thumb), 1.5 times as long as apophysis, with distal part curved inwards, and middle part with distinct inner hump; ancestral distal segment (apophysis) short, slightly curved and inflated distally, bifid apically (arrowed in Fig. 2D), slightly curved outward, unornamented and unarmed; apophysis and thumb forming complex three-dimensional structure.

Fourth swimming leg (Fig. 2E) with smooth praecoxa, coxa, and intercoxal sclerite. Intercoxal sclerite smaller than in second or third legs, and with more deeply concave distal margin. Praecoxa relatively large, while coxa smaller than in second or third leg. Basis large, semicircular, armed with slender and smooth outer seta, ornamented with five large spinules at base of endopod, and several minute spinules along outer margin. Exopod curved inwards, three-segmented, ornamented with few large spinules along outer margin on all segments, and with distal inner hyaline frills; first segment with slightly concave inner margin, armed with outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta 1.4 times as long as entire exopod and four times as long as outer spine. Endopod one-segmented, about 0.6 times as long as first exopodal segment, claw-like, curved inwards, armed with single unipinnate apical element, fused basally to segment and ornamented with row of small spinules along outer margin.

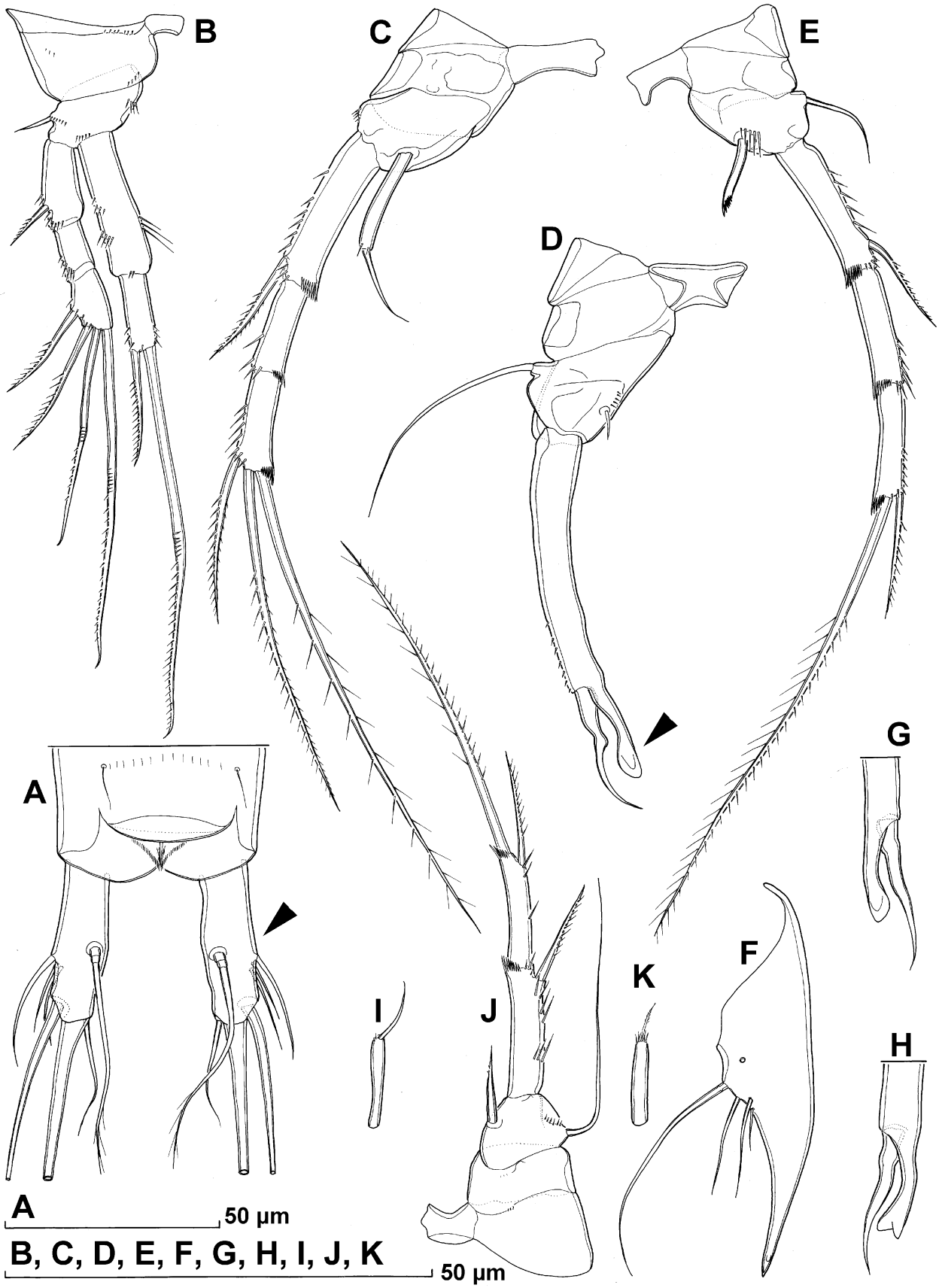

FIGURE 2. *Kinnecaris lakewayi* **sp. nov.**, A–F, holotype male; G & H, paratype male; I-K, allotype female: A, anal somite and caudal rami, dorsal view; B, first swimming leg, anterior view; C, second swimming leg, anterior view; D, third swimming leg, posterior view; E, fourth swimming leg, anterior view; F, fifth leg, anterior view; G & H, distal part of third swimming leg, posterior view; I, endopod of second swimming leg, anterior view; J, third swimming leg, anterior view; K, endopod of fourth swimming leg, anterior view. Arrows pointing characteristic shapes of caudal rami (A) and apophysis of third swimming leg (D).

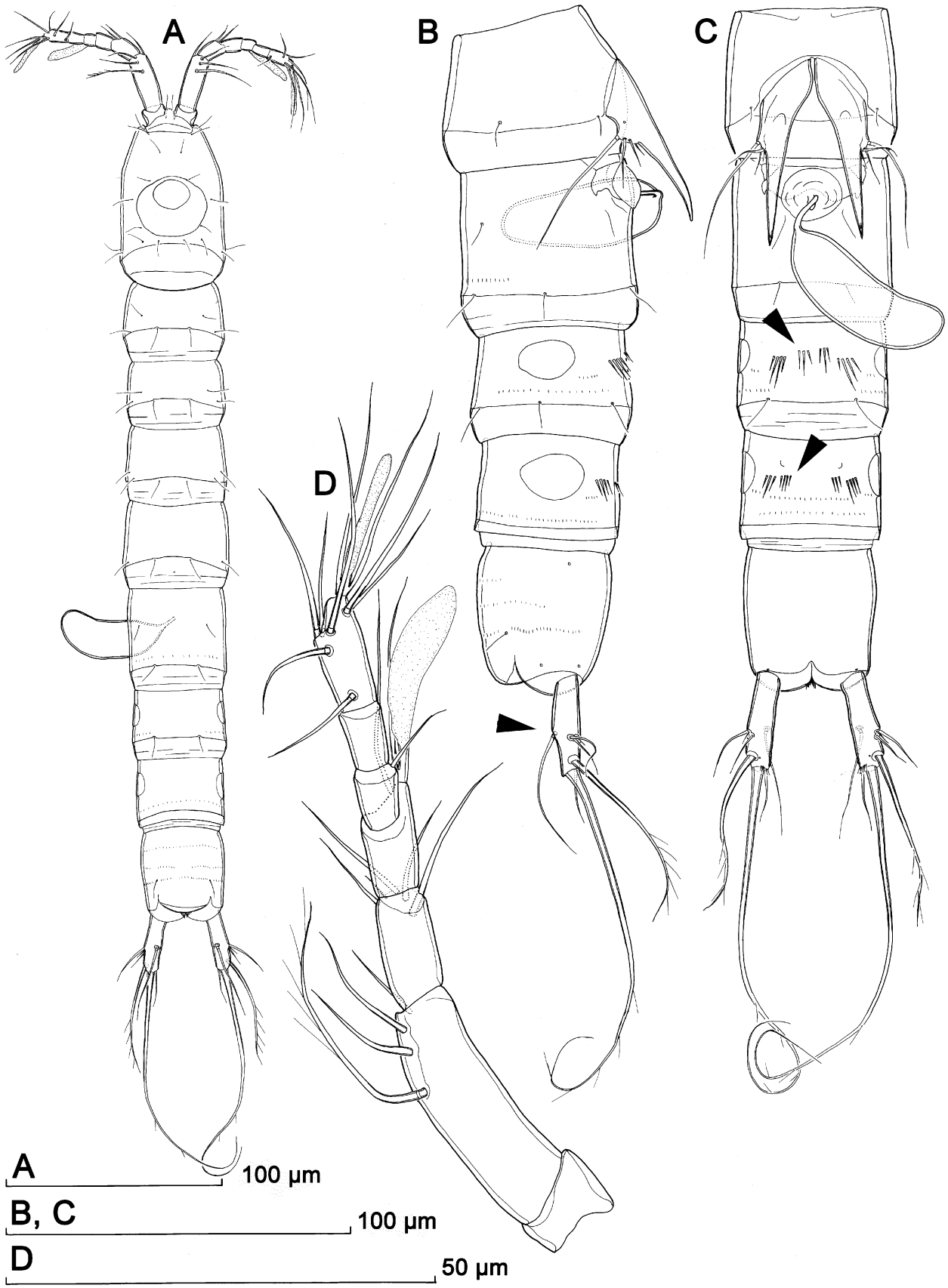

FIGURE 3. *Kinnecaris lakewayi* **sp. nov.**, allotype female: A, habitus, dorsal view; B, urosome, lateral view; C, urosome, ventral view; D, antennula, antero-dorsal view. Arrows pointing characteristic shape of caudal rami in lateral view (B) and additional rows of large spinules on urosome (C).

Fifth leg (Fig. 2F) triangular cuticular plate, with inner-distal corner produced into long and curved spiniform process, ornamented with large cuticular pore on anterior surface basally, and another pore near tip of spiniform process that opens also on anterior surface; armed with four smooth setae along outer margin; outermost seta (probably ancestral basal) longest, reaching beyond tip of appendage, twice as long as second and third seta from outer side and nearly five times as long as innermost seta. Third seta inserted more on anterior surface, while other three setae inserted on outer margin. Fifth legs distinct at base, with very small space between them, with distal tips pointing outwards.

Sixth legs very disproportionate in size, right one almost completely reduced, left one enlarged, forming single, smooth, large operculum covering gonopore, which represents 60% of genital somite's width; no ornamentation or armature.

Female (based on allotype and several paratypes). Body length, excluding caudal setae, from 396 to 404 µm (400 µm in allotype). Habitus (Fig. 3A), ornamentation of prosomites, pigmentation, and nauplius eye similar to those in male, except genital and first abdominal somite fused into double-somite and middle part of body slightly less slender. Prosome/urosome ratio 0.85; greatest body width in dorsal view hard to establish; body length/width ratio 8.17; cephalothorax as wide as genital double-somite.

Genital double-somite (Fig. 3A, B, C) about as long as wide, without any trace of subdivision except for pair of ancestral dorso-lateral sensilla at middle; additionally ornamented with six posterior sensilla (two dorsal, two ventral, and two lateral), and one dorso-lateral row of minute spinules. Genital complex (Figs 3B, C, 4C) occupying anterior ventral half of genital double-somite; single genital aperture covered by fused vestigial sixth legs; median copulatory pore located medially at 2/5 of double-somite length and also covered by sixth legs; seminal receptacles small, hard to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotized; allotype female with single attached spermatophore (Fig. 3B, C), its neck inserted between and under sixth legs and heavily cemented over best part of sixth legs.

Third, fourth (preanal), and fifth (anal) urosomites similar to those in male (Fig. 3B, C), also with four groups of large spinules ventrally on third and fourth urosomites (arrowed in Fig. 3C).

Caudal rami (Figs 3A, B, C) similar to those in male but slightly shorter in proportion to anal somite and slightly wider at middle from lateral view (arrowed in Fig. 3B); ornamentation and armature similar to those in male, except that smallest lateral seta even smaller and main apical seta unipinnate.

Antennula (Figs. 3D, 4D) seven-segmented, unornamented, slightly shorter than cephalothorax, with broad aesthetasc on fourth segment almost reaching tip of appendage, and more slender apical aesthetasc on seventh segment, fused basally to two apical setae; both aesthetascs more slender than in male; setal formula: 0.4.5.2.1.1.8. Only largest seta on second segment uniplumose, all other setae smooth and most of them with pore on tip. Largest seta on second segment and four setae on seventh segment biarticulated basally. Seta on sixth segment inserted apically and leaning against seventh segment for its entire length, so very hard to observe without SEM (Fig. 4D). Length ratio of antennular segments, from proximal end, 1 : 2.8 : 1.4 : 1 : 0.8 : 0.8 : 1.5.

Antenna (Fig. 4A), labrum (Fig. 4A), paragnaths (Fig. 4B), mandibula (Fig. 4A), maxillula (Fig. 4B), maxilla (Fig. 4A, B), maxilliped (Fig. 4A), first swimming leg (Fig. 4A), second swimming leg (Fig. 2I), and exopod of fourth swimming leg very similar to those of male. Endopod of second swimming leg (Fig. 2I) only slightly shorter than in male.

Third swimming leg (Fig. 2J) with smaller intercoxal sclerite than in male, smooth and with concave distal margin. Leg composed of praecoxa, coxa, basis, two-segmented exopod and one-segmented endopod. Praecoxa large, unarmed, ornamented with few minute spinules. Coxa similar in size to male and also unarmed, but ornamented with several rows of minute spinules. Basis armed with very long and smooth outer seta, about as long as first exopodal segment, ornamented with row of large spinules near outer margin. Exopod ornamented with large spinules along outer margin, and both segments with distal inner hyaline frills; first segment with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, hardly reaching 3/5 of first exopodal segment in length, straight and spiniform, armed apically with single element, fused basally to segment and unipinnate along inner margin.

Fourth swimming leg without spiniform processes on basis. Endopod (Fig. 2K) one-segmented, cylindrical, about five times as long as wide and half as long as first exopodal segment, with single apical slender and bipinnate seta with four spinules at base of apical seta.Fifth leg (Figs 3B, C, 4C) very similar to that of male, but slightly more elongated, with narrower distal part; armature and ornamentation as in male.

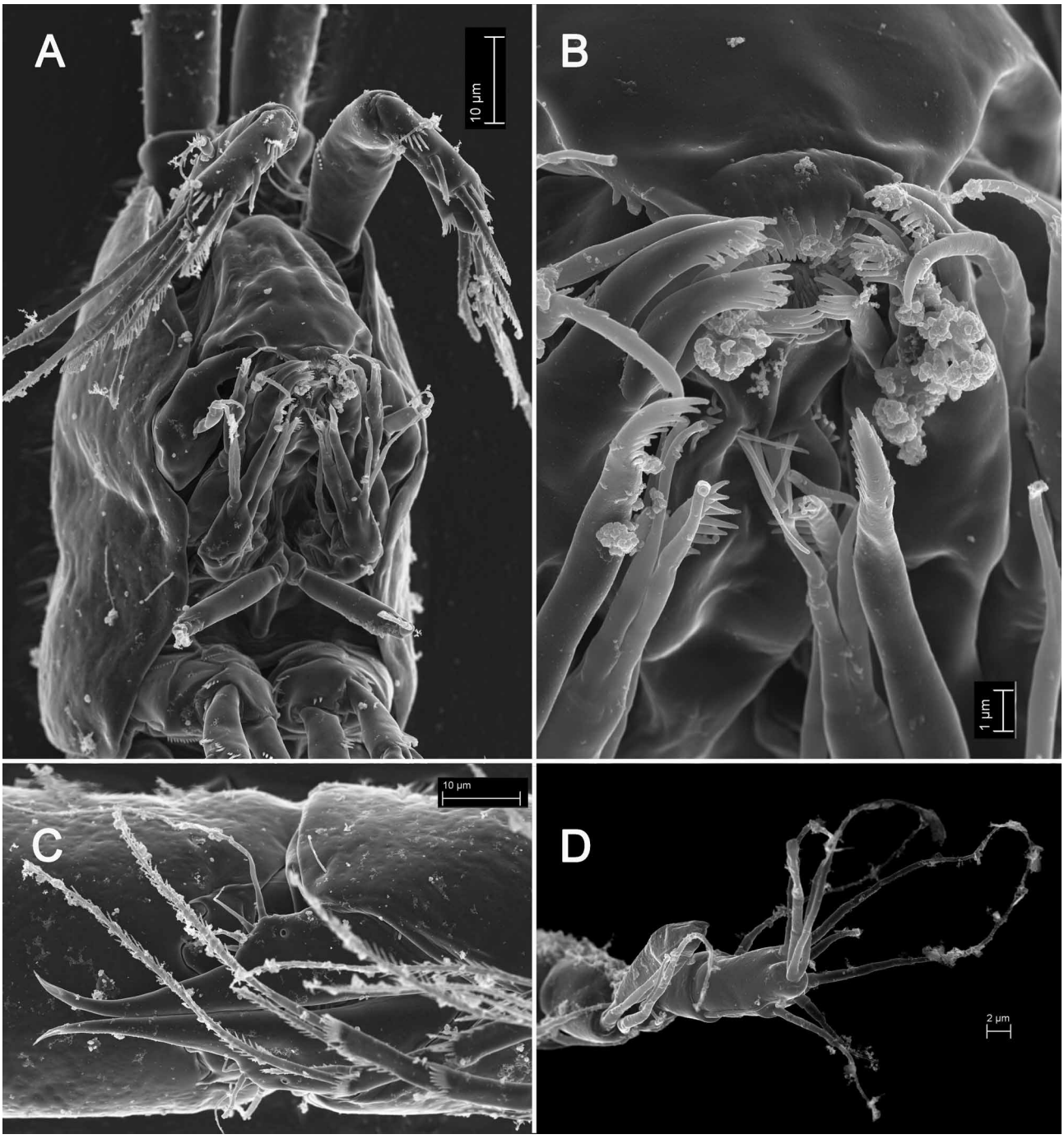

FIGURE 4. *Kinnecaris lakewayi* **sp. nov.**, SEM photographs, paratype female: A, cephalothorax, ventral view; B, distal part of mouth appendages and labrum, ventral view; C, fifth legs and genital double-somite, ventral view; D, distal part of antennula, ventral view.

Sixth legs (Fig. 4C) vestigial, fused into simple bilobate cuticular plate, covering gonopore, unornamented and unarmed; outer distal corners produced into sharp processes.

Etymology. The species name comes from its type locality (Lake Way), but should be treated as comprising an arbitrary combination of letters that can be treated as a Latin word and may be conceived as a noun in apposition to the generic name.

Variability. Body length of males ranges from 397 to 402 µm (399 µm average; n = 5), while in females it ranges from 396 to 404 µm (400 µm average; n = 8). The shape of the apophysis of the third leg in male varies slightly depending on the angle of observation (Fig. 2D, G, H), because it is a complex tridimensional structure, but it is actually quite constant. The number and exact position of minute spinules on urosomites varies slightly, but the number and position of larger spinules is constant (Fig. 3C).

Remarks. This species differs from all other eight Australian congeners by the shape of the caudal rami, which are short, widely spaced, and with a characteristic dorsal posterior saddle in lateral view (arrowed in Fig. 3B). Another unique character of *K. lakewayi* **sp. nov.** are the large spinules on the penultimate (preanal) somite (arrowed in Fig. 3C), which are also not reported for any other member of the genus. *Kinnecaris lakewayi* seems to be most similar to *K. barrambie* **sp. nov.** (see below), with which it shares four ventral rows of large spinules on the fourth urosomite (third in female) (arrowed in Fig. 3C), relatively similar caudal rami shape, and presence of posterior spinules on the caudal rami ventrally, although some of these may be plesiomorphic character states, and if so not indicative of a close phylogenetic relationship. They differ chiefly in the ornamentation of the genital double-somite (arrowed in Fig. 6C), preanal somite (arrowed in Fig. 6B), and proportions of the caudal rami (arrowed in Figs 1B, 2A, 6C). The only other Australian *Kinnecaris* with posterior spinules on the caudal rami is *K. linesae* **sp. nov.** (see below), but this species differs from *K. lakewayi* by a number of characters, including smooth cuticule, absence of any urosomal spinules in female, heavier ornamentation of the fourth leg basis and exopod in male, as well as a different shape of the third leg apophysis in male. Finally, we should mention generally similar caudal rami shape in *K. eberhardi* (Karanovic, 2005), a species that lives nearly 800 km SSW from any other Australian congener, in the Margaret River area, although the caudal rami have an inflated look in this species and are shorter in proportion to the anal somite. The two species, however, differ in many characters and the general similarity in the caudal rami shape almost certainly indicates that this is a plesiomorphic character (or a group of characters). Another support for this hypothesis is that relatively similar caudal rami (although more slender) can be found in the Madagascan *K. forficulata* (Chappuis, 1952) and *K. madagascarensis* (Chappuis, 1952), and even to some extent in the Indian *K. godavari* Ranga Reddy & Schminke (2009) and Papua New Guinean *K. giselae* Schminke, 2008, although all these species differ from *K. lakewayi* in many other morphological characters (see Chappuis 1952; Schminke 2008; Ranga Reddy & Schminke 2009).

***Kinnecaris barrambie* sp. nov.**
(Figs. 5 & 6)

Type locality. Australia, Western Australia, Yilgarn region, Barambie, bore B3M, 27.213178°S 118.919514°E.

Type material. Holotype male and allotype female on one SEM stub *in toto* coated with carbon (WAM C47183), both collected at type locality, leg. E. Thomas & V. Campagna, 26 November 2008, oeRBV055. Paratype: one female dissected on one slide (WAM C47184), Australia, Western Australia, Yilgarn region, Barambie, bore B14M, 26.832544°S 118.886097°E, leg. E. Thomas & V. Campagna, 26 November 2008, oeRBV0585.

Description. Male (based on holotype). Total body length, measured in the same way as in *Kinnecaris lakewayi* (see above), 328 µm. Surface of integument of all somites with sparse and shallow cuticular pits. Colour, naupliar eye, rostrum, body segmentation, and pore and sensilla pattern of all somites as in *K. lakewayi*. Habitus (Fig. 5A) cylindrical and very slender, without any dorsal demarcation between prosome and urosome, but urosome wider in lateral view; prosome/urosome ratio about 0.7; greatest width from dorsal view at posterior end of cephalothorax. Body length/width ratio about 7.5; cephalothorax 1.1 times as wide as genital somite. Integument relatively weakly sclerotized, ornamented with several very short dorsal and lateral rows of minute spinules on all urosomites, and some additional larger spinules ventrally or laterally on second (genital), third and fourth urosomites (Fig. 5A, B). Cephalothorax with clearly visible (Fig. 5A) posterior double dorsal cuticular window ; fourth and fifth urosomites with pair of lateral circular windows each, although these harder to distinguish than in *K. lakewayi*.

Cephalothorax (Fig. 5A) about 1.5 times as long as wide in dorsal view; representing about 18% of total body length. Surface of cephalic shield, tergites and pleuras of free pedigerous somites ornamented as in *K. lakewayi*, except for presence of sparse and shallow cuticular pits and fewer minute spinules on fifth pedigerous (first urosomal) somite (Fig. 5A, B).

Genital somite (Fig. 5A, B) with three short lateral rows of spinules (from five to seven) at midlength, three pairs of sensilla on posterior margin (one dorsal, one dorso-lateral, and one ventro-lateral), one pair of very small cuticular pores in anterior part ventro-laterally, and several dorsal and lateral rows of minute spinules (pore and sensilla pattern being same as in *K. lakewayi*); spermatophore not visible inside.

Third urosomite (Fig. 5A) with dorso-lateral large spinules (two parallel short rows of eight spinules each), ventro-lateral rows of large spinules, six posterior sensilla, and several dorsal rows of minute spinules.

Fourth urosomite (Fig. 5A) ornamented with two or three large spinules laterally (covered with dirt in Fig. 5A), and four midventral groups of four large spinules; lateral oval cuticular window not easy to observe (more visible with light compound microscope).

Fifth (preanal) urosomite (Fig. 5A) with similar windows to those observed in fourth urosomite but without any large spinules, sensilla or pores; only other ornamentation sparse and shallow cuticular pits.

Anal somite (Fig. 5A, C) ornamented with pair of large dorsal sensilla at base of anal operculum, pair of large cuticular pores laterally (one pore on each side) in anterior half, two pairs of minute cuticular pores laterally closer to posterior margin, and pair of slightly larger cuticular pores ventrally, at base of caudal rami, in addition to hardly visible cuticular pits; spinules absent. Anal operculum well developed, unornamented on outer surface, ornamented with row of slender spinules on inner surface, with convex and smooth distal margin, not reaching posterior end of anal somite, representing 60% of somite's width. Anal sinus widely opened, with two diagonal rows of slender spinules on ventral side and transverse row of spinules on dorsal side (below anal operculum).

Caudal rami (Fig. 5C) about 3.5 times as long as greatest width (dorsal view) and 0.8 times as long as anal somite, nearly cylindrical in dorsal and ventral view, but clearly inflated at midlength in lateral view, with proximal part of inner margin slightly convex in dorsal (or ventral) view and base much narrower than rest of ramus, nearly parallel, with space between them about 1.2 times ramus width. Armature and ornamentation as in *K. lakewayi,* but lateral setae inserted slightly more posteriorly (or proximal part of caudal rami longer).

Antennula (Fig. 5A), antenna (Fig. 5A), mouth appendages (Fig. 5A), and first two pairs of swimming legs (Fig. 5A) as in *K. lakewayi*.

Third swimming leg (Fig. 5D) also very similar to that in *K. lakewayi* but apophysis with much sharper tip; ornamentation same as in *K. lakewayi*, including longitudinal row of large spinules on outer margin of first exopodal segment distally; exopodal spine also 1.5 times as long as apophysis.

Fourth swimming leg (Fig. 5D) similar to that in *K lakewayi*, i.e. with five relatively large spinules on basis at base of endopod, and endopod spiniform with spinules only along outer margin. Apical seta on third exopodal segment 1.2 times as long as entire exopod and 3.2 times as long as outer spine.

Fifth leg (Fig. 5B) without any difference from that in *K. lakewayi*, except for several shallow cuticular pits on anterior surface in proximal part, and weak outline of cuticular window similar to that in *K. eberhardi* (Karanovic, 2005), but not so clearly visible.

Sixth legs (Fig. 5B) as in *K. lakewayi*.

Female (based on allotype and one paratype from bore B14M). Body length 405 µm in allotype and 425 µm in paratype. Habitus (Fig. 6A), ornamentation of prosomites, colour and nauplius eye similar to those in male, except genital and first abdominal somites fused into double-somite and middle part slightly less slender. Prosome/urosome ratio 0.78; greatest width from dorsal view hard to establish; body length/width ratio about 8.2; cephalothorax less than 1.1 times as wide as genital double-somite.

Genital double-somite (Fig. 6A, B, C) only slightly longer than wide in dorsal view, without any trace of subdivision except for pair of ancestral dorso-lateral sensilla in anterior half; additionally ornamented with six posterior sensilla, many short rows of minute spinules, and two parallel short rows of large spinules (five and each spinules respectively); latter similar to that in *K. esbe* but not overlapping (arrowed in Fig. 6C). Genital complex (Figs. 6B) as in *K. lakewayi*, sixth legs also with large spiniform processes.

Third urosomite (Fig. 6B, C) similar to that in male, with four rows of four large spinules ventro-laterally, one row of three large spinules dorsolaterally (arrowed in Fig. 6C), and clearly visible lateral cuticular windows.

Fourth (preanal), and fifth (anal) urosomites also very similar to those in male (Fig. 6B, C), without any large spinules, except those in anal sinus.

Caudal rami (Figs 5C, 6A, B, C) similar to those in male but slightly more divergent.

Antennula (Fig. 6D) very similar to that in *K. lakewayi*, with only slightly shorter proximal aesthetascs (arrowed in Fig. 6D).

Antenna (Fig. 6E), mouth appendages (Fig. 6F), first swimming leg, second swimming leg (Fig. 6G), and exopod of fourth swimming leg very similar to those in male and almost without any difference from those in *K. lakewayi*.

Endopod of second swimming leg (Fig. 6G) 5.6 times as long as wide, its apical seta 0.9 times as long as segment.

Third swimming leg (Fig. 6H, I) similar to *K. lakewayi*, with only slightly proportionately longer apical seta on second segment and more strongly scletotised cuticular plates on praecoxa and coxa.

Endopod of fourth swimming leg (Fig. 6J) about 7.8 times as long as wide, half as long as first exopodal segment, armed with single robust bipinnate element apically, ornamented with four spinules along distal margin, at base of apical element. Exopod similar to that in male.

Fifth leg (Fig. 6B, C) similar to that in male, but slightly more elongated, with narrower distal part and cuticular window on anterior surface better defined (although not easily visible with light microscope).

Sixth legs (Fig. 6K) vestigial, fused into simple bilobate cuticular plate, covering gonopore, unornamented and unarmed; outer distal corners produced into sharp processes like in previous species, longer than inner lobes.

Etymology. The species name comes from its type locality (Barrambie), but should be treated as comprising an arbitrary combination of letters that can be treated as a Latin word and may be conceived as a noun in apposition to the generic name.

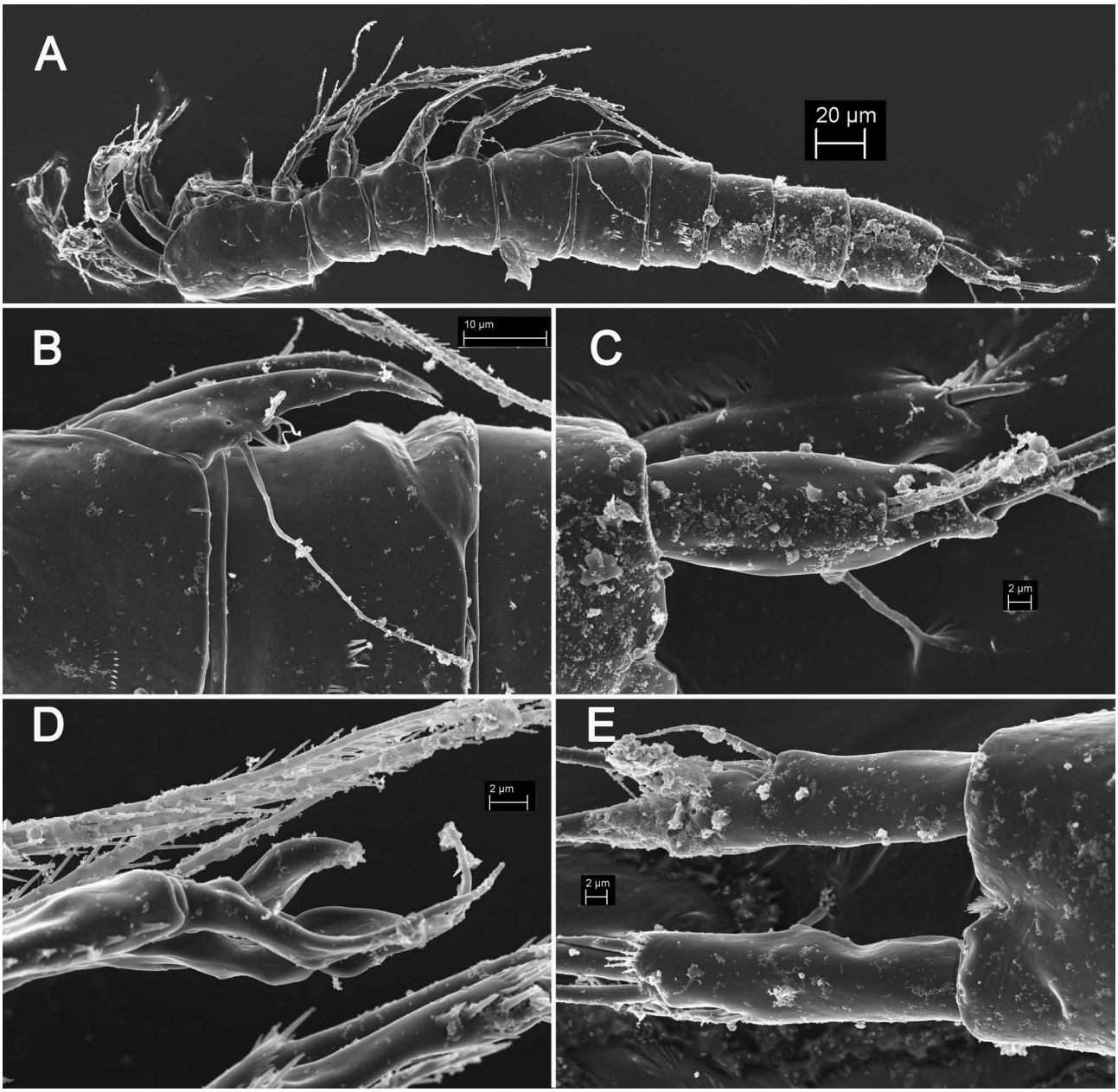

FIGURE 5. *Kinnecaris barrambie* **sp. nov.**, SEM photographs, A-D, holotype male; E, allotype female: A, habitus lateral view; B, fifth and sixth legs, lateral view; C, anal somite and caudal rami, lateral view; D, distal part of third swimming legs, lateral view; E, anal somite and caudal rami, ventral view.

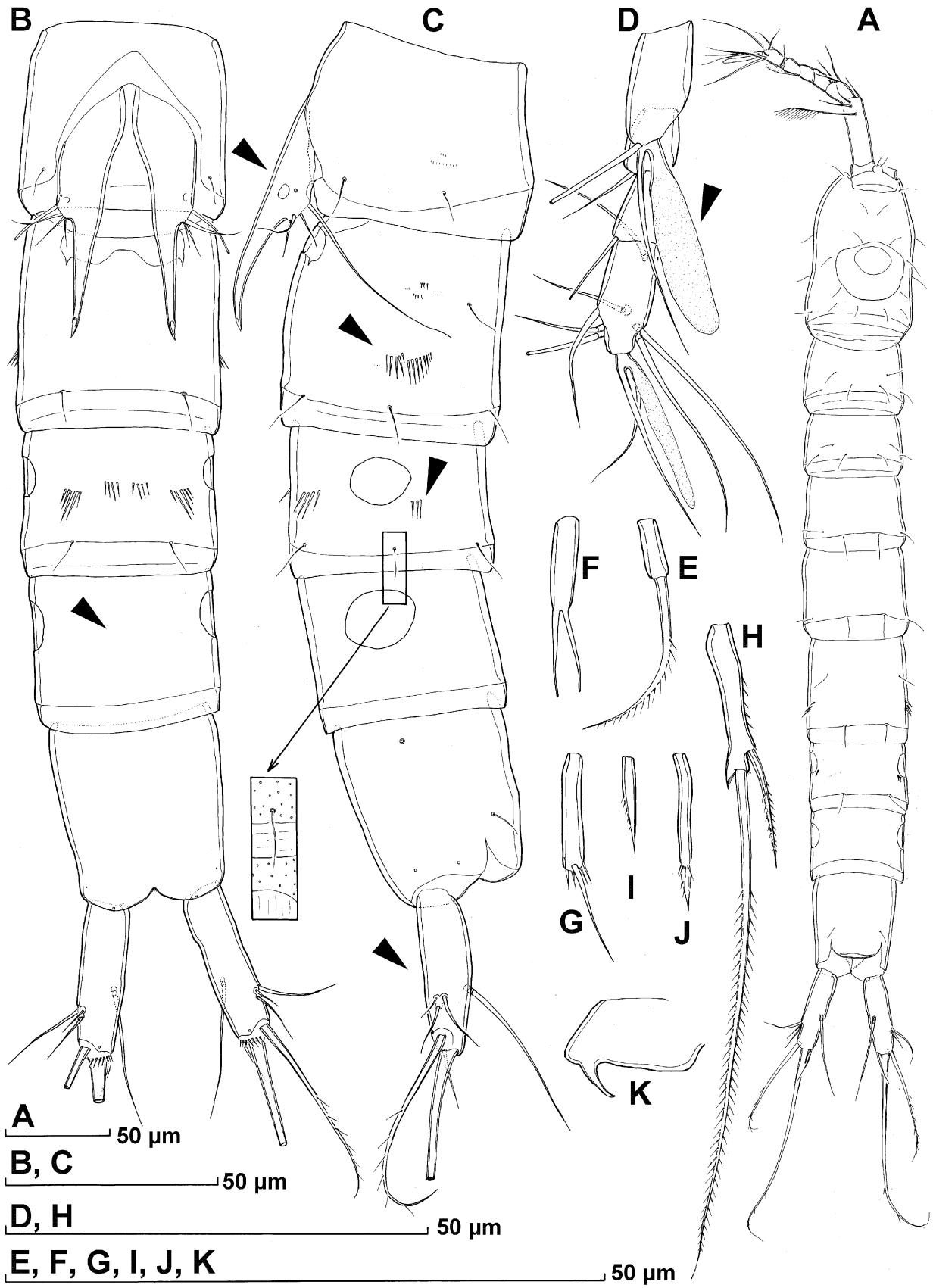

FIGURE 6. *Kinnecaris barrambie* **sp. nov.**, paratype female from bore B14M: A, habitus, dorsal view; B, urosome, ventral view; C, urosome, lateral view; D, distal part of antennula, ventral view; E, exopod of antenna, outer view; F, mandibular palp, posterior view; G, endopod of second swimming leg, posterior view; H, second exopodal segment of third swimming leg, posterior view; I, endopod of third swimming leg, posterior view; J, endopod of fourth swimming leg, anterior view; K, sixth leg, ventro-lateral view. Inset showing cuticular pits and fine ornamentation of urosome. Arrows pointing major morphological differences from other species.

Variability. Only one male and two females were examined and no variability or asymmetry was observed, except in their body length. Note that the male is significantly smaller than females (328 µm *vs.* 405 µm and 425 µm), but that is probably a consequence of a small sample size rather than a specific character.

Remarks. This species differs from other eight Australian congeners in the shape of the caudal rami (which have much narrower base than the rest of the ramus and are inflated in lateral view; arrowed in Fig. 6C), armature of the genital double-somite in female (arrowed in Fig. 6C), as well as in the presence of some large spinules on the third urosomite in female dorso-laterally (arrowed in Fig. 6C). Similarities and differences between *K. barrambie* **sp. nov.** and *K. lakewayi* **sp. nov.** are discussed in the remarks section for the latter species (see above), as the two seem to share the greatest number of morphological characters. The only other Australian *Kinnecaris* Jakobi, 1972 with two rows of large spinules on the genital double-somite laterally is *K. esbe* **sp. nov.** (see below), but this species has much longer caudal rami, more ornamentation on most somites, as well as a very different shape of the third leg apophysis in male. Besides, the rows of large spinules are much closer to each other and clearly parallel in *K. esbe* (compare Fig. 6C and Fig. 9B), which makes us to question their homology (or at least one of them). These structures have not been reported for any other member of the genus *Kinnecaris*, but it is fair to say that fine urosomal ornamentation did not always receive full attention in early descriptions.

Kinnecaris esbe sp. nov.

(Figs. 7–10)

Type locality. Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore SB14-1, 27.344283˚S 120.307708˚E (south-eastern corner on Fig. 24).

Type material. Holotype male, allotype female, and one paratype female on one SEM stub *in toto* coated with carbon (WAM C47185); one paratype male dissected on one slide (WAM C47186); one paratype female dissected on one slide (WAM C47187); one paratype female destroyed for DNA sequence (amplification unsuccessful); 13 paratypes (one male + seven females + five copepodids) in alcohol; all collected at type locality, leg. T. Karanovic & S. Callan, 18 March 2010, seLN8180. Other paratypes: One female destroyed for DNA sequence (amplification unsuccessful); one male + three females + five copepodids in alcohol; all collected at type locality, leg. T. Karanovic & G. Perina, 16 March 2010, seLN8517.

Description. Male (based on holotype and several paratypes). Total body length from 374 to 425 µm (374 µm in holotype). Surface of integument of all somites with relatively dense and shallow cuticular pits, and all somites after cephalothorax with numerous short rows of minute spinules; third and fourth urosomites with some additional larger spinules ventrally and/or laterally (Figs. 7A, C, 8A). Colour, nauplius eye, rostrum, body segmentation, and pore and sensilla pattern of all somites as in *Kinnecaris lakewayi* (see above). Habitus (Fig. 7A) cylindrical and very slender, without any demarcation between prosome and urosome dorsally, but with urosome wider in lateral view; prosome/urosome ratio about 0.6; greatest width from dorsal view at posterior end of cephalothorax, but very hard to establish. Body length/width ratio about 8.9; cephalothorax only slightly wider than genital somite in dorsal view. Integument more strongly sclerotized than in previous two species, and with relatively deep and irregular depressions on all somites but especially on cephalothoracic shield and pleuras and tergites of three free prosomites (Fig. 7A, B). Cephalothorax with clearly visible (Fig. 7A) double dorsal cuticular window posteriorly; fourth and fifth urosomites each with pair of lateral circular windows, both clearly visible and that on fifth urosomite slightly larger (Figs. 7A, 8A).

Cephalothorax (Fig. 7A) about 1.5 times as long as wide in dorsal view; representing about 17% of total body length. Surface of cephalic shield, tergites and pleuras of free pedigerous somites ornamented as in *K. lakewayi*, except for presence of sparse and shallow cuticular pits and many more minute spinules on free pedigerous somites (Fig. 7A, C); many of short rows of minute spinules arched, especially on lateral sides (Fig. 7C), while those on ventral side of urosomites tend to be straight, parallel, and sometimes join into longer rows (Fig. 8A).

Genital somite (Fig. 7A, C) ornamented with more than forty dorso-lateral short rows of spinules (each from three to nine spinules), in addition to three pairs of sensilla on posterior margin (one dorsal, one dorso-lateral, and one ventro-lateral), and one ventro-lateral pair of very small cuticular pores in anterior part (i.e., pore and sensilla pattern as in *K. lakewayi*); no large spinules on this somite; spermatophore visible inside and similar in size to that in *K. lakewayi*.

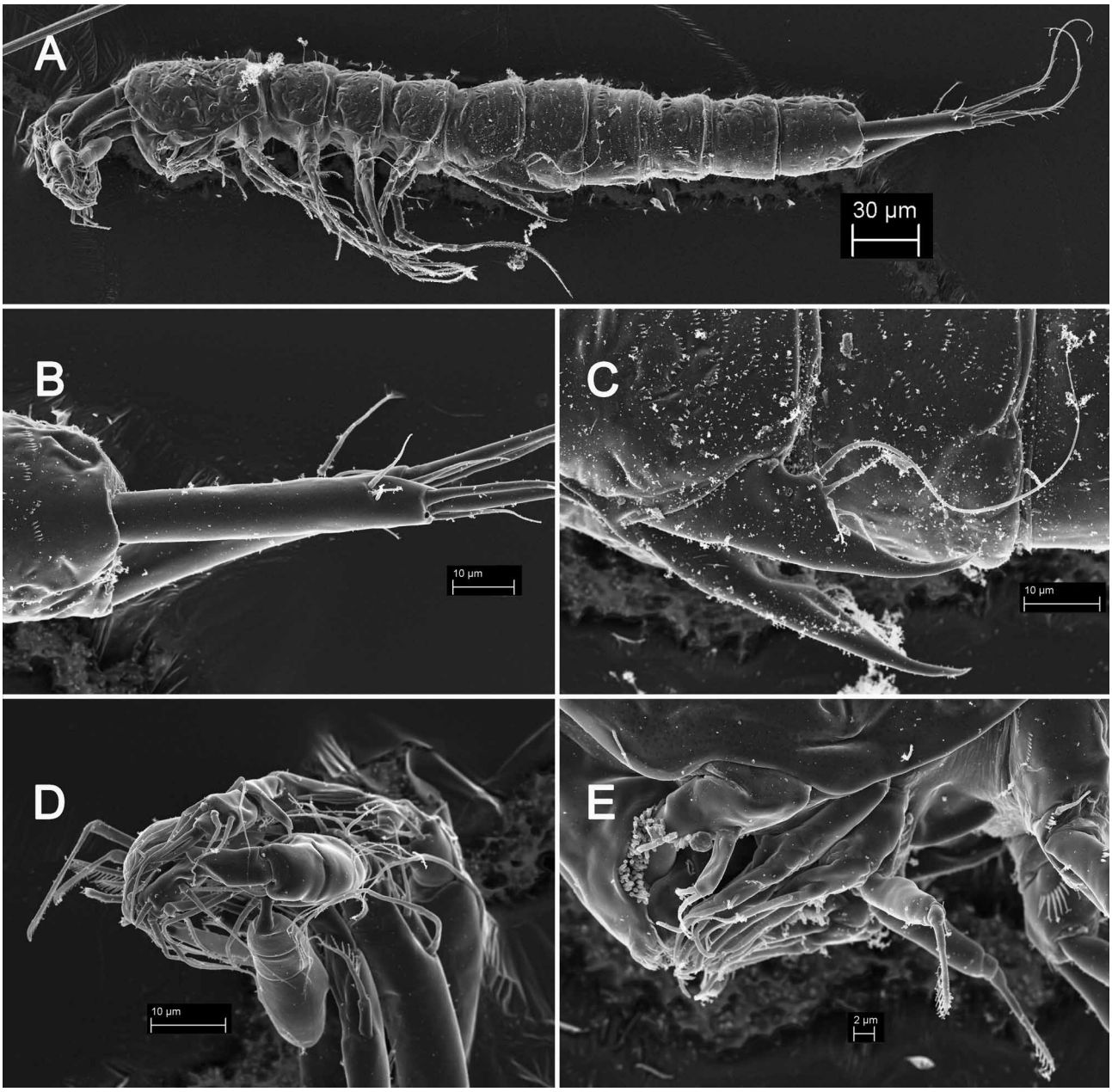

FIGURE 7. *Kinnecaris esbe* **sp. nov.**, SEM photographs, holotype male: A, habitus, lateral view; B, anal somite and caudal rami, lateral view; C, fifth and sixth legs, lateral view; D, antennulae, latero-apical view; D, mouth appendages, lateral view.

Third urosomite (Fig. 7A) with four rows of large spinules in anterior half (two ventro-laterally and two dorso-laterally; each with five to six spinules and central ones largest), in addition to six posterior sensilla, and many rows of minute spinules.

Fourth urosomite (Fig. 7A) ornamented with two or three ventro-lateral large spinules ventrally of large and slightly swollen lateral cuticular window; additional ornamentation represented by six posterior sensilla and numerous minute spinules.

Fifth (preanal) urosomite (Figs. 7A, 8A) with larger and more more swollen windows but without any large spinules, sensilla or pores; only ornamentation sparse and shallow cuticular pits and numerous minute spinules, forming nearly continuous row along hyaline fringe.

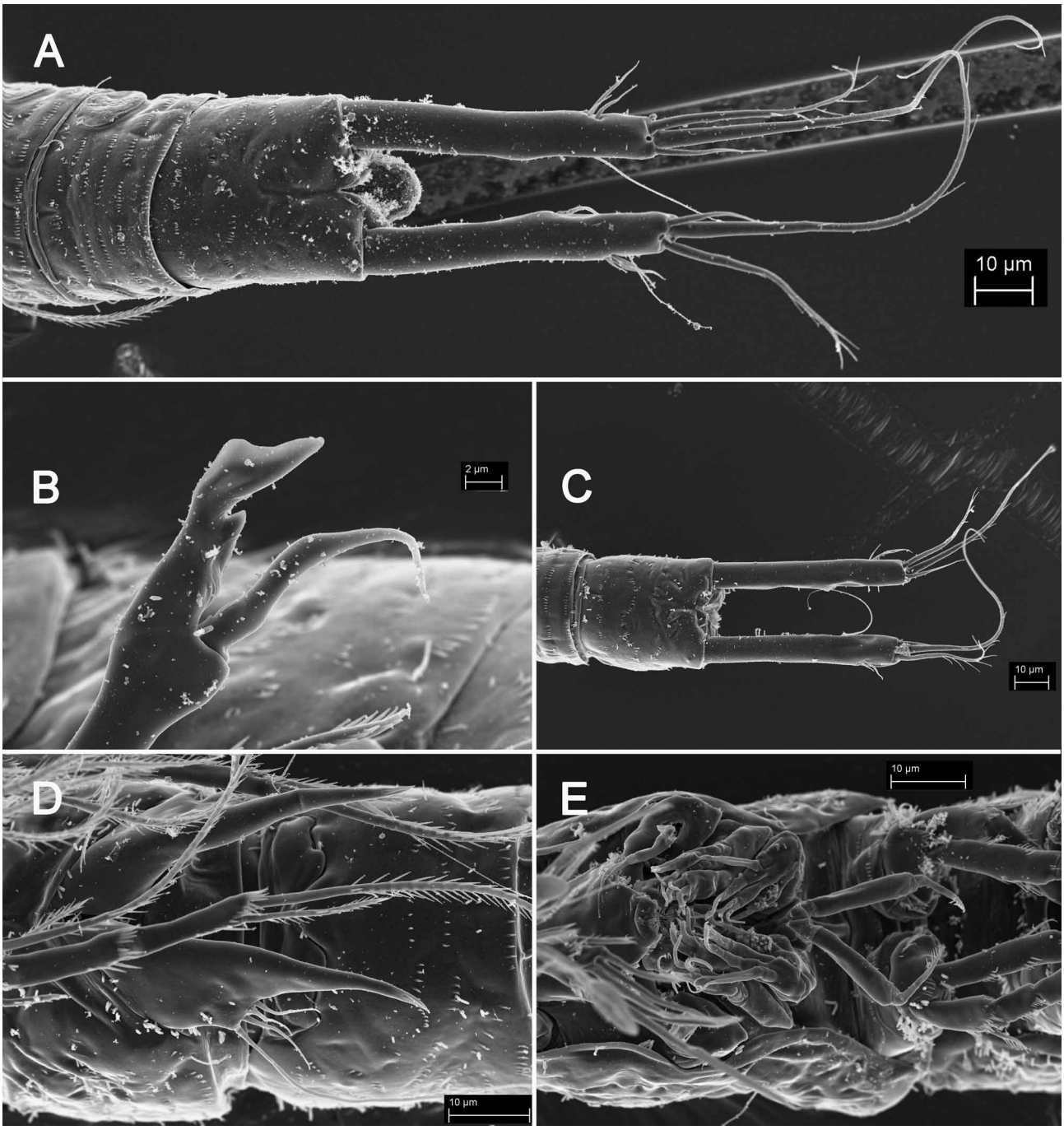

FIGURE 8. *Kinnecaris esbe* **sp. nov.**, SEM photographs, A & B, paratype male; C-E, allotype female I: A, last three urosomites and caudal rami, ventral view; B, distal part of third swimming leg, anterior view; C, abal somite and caudal rami, ventral view; D, fifth legs and genital double-somite, ventral view; E, mouth appendages, ventral view.

Anal somite (Figs. 7A, B, 8A) ornamented with pair of large dorsal sensilla at base of anal operculum, pair of lateral large cuticular pores (one pore on each side) in anterior half, two pairs of minute cuticular pores laterally close to posterior margin, and pair of slightly larger ventral cuticular pores at base of caudal rami, in addition to hardly visible cuticular pits and many rows of minute spinules. Anal operculum less developed than in *K. lakewayi* and bent slightly towards ventral side, unornamented on outer surface, with row of slender spinules on inner surface, convex and smooth distal margin, almost reaching posterior end of anal somite, representing 68% of somite width. Anal sinus less widely opened than in *K. lakewayi*, with two diagonal rows of slender spinules on ventral side and transverse row of spinules on dorsal side (below anal operculum).

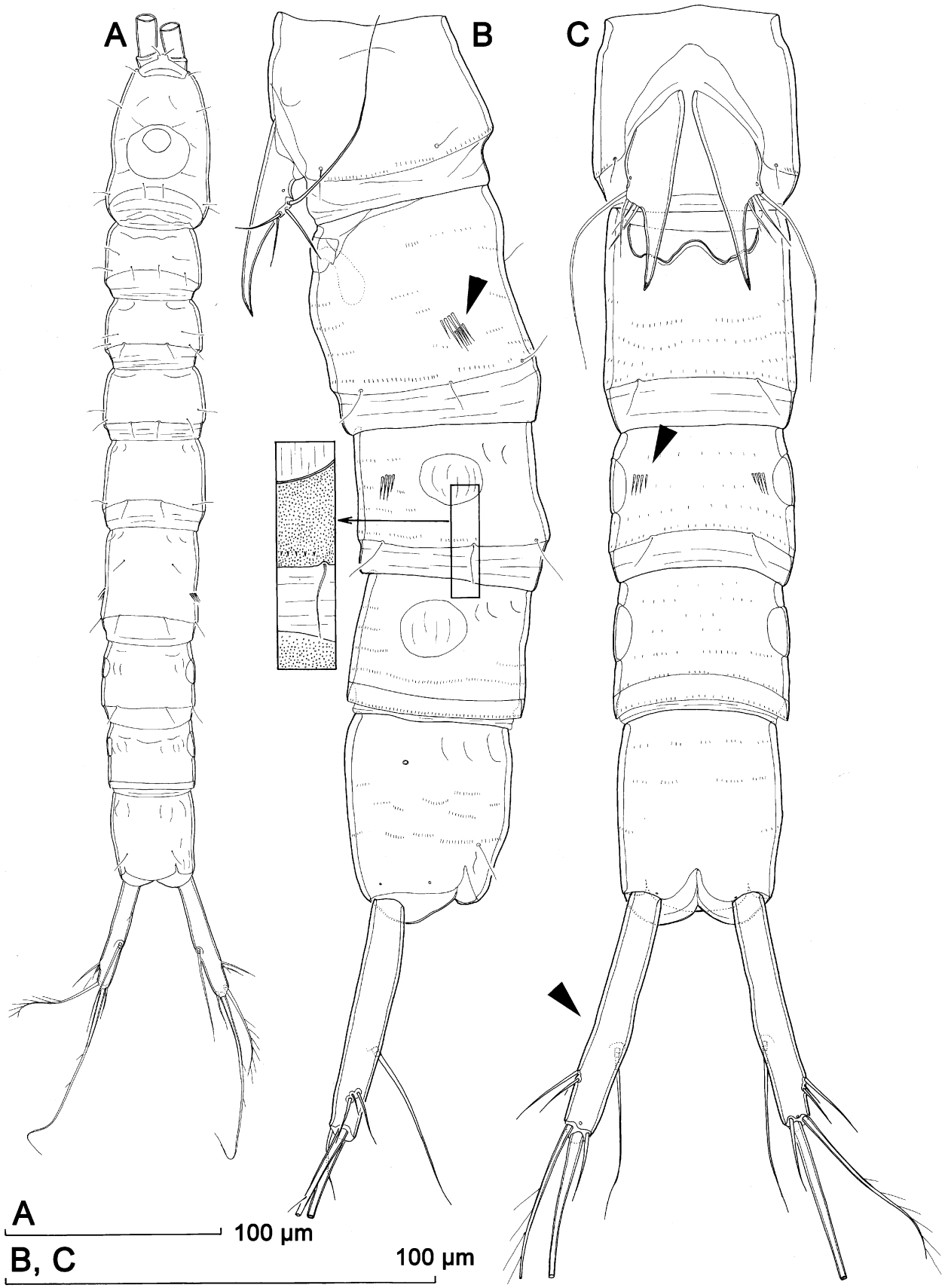

FIGURE 9. *Kinnecaris esbe* **sp. nov.**, paratype female: A, habitus, dorsal view; B, urosome, lateral view; C, urosome, ventral view. Inset showing cuticular pits and fine ornamentation of urosome. Arrows pointing additional rows of large spinules on genital double-somite (B), extremely elongated caudal rami, and fewer large spinules on abdominal somites when compared to previous species (C).

Caudal rami (Figs. 7B, 8A) almost 6.3 times as long as greatest width (dorsal view) and 1.3 times as long as anal somite, cylindrical in all views, nearly parallel, with space between them about 1.5 times one ramus' width. Armature and ornamentation as in *K. lakewayi*, but due to the extreme elongation of the rami, the position of dorsal and lateral setae and their relative lengths differs. Dorsal seta slender and smooth, inserted slightly closer to inner margin at about 2/3 of ramus length, only 0.7 times as long as caudal ramus, triarticulate at base. Lateral setae thin and smooth, inserted close to each other at 5/6 of ramus' length, in one depression with two positioned proximally and one distally; proximal seta which inserted more dorsally strongest and longest of three, but only about 0.2 times as long as ramus, 2.3 times as long as proximal seta wich inserted closer to ventral side, and about 1.3 times as long distal lateral seta. Inner apical seta smooth and slender, inserted closer to ventral surface, about 0.35 times as long as ramus. Middle apical seta strongest, inserted distally, without breaking plane, unipinnate, with slightly curled tip, about 1.6 times as long as outer apical seta and 0.2 times as long as whole body. Outer apical seta also strong, without breaking plane, unipinnate distally, but inserted closer to ventral side than middle apical seta, about 0.75 times as long as ramus.

Antennula (Fig. 7D), antenna (Fig. 7A), mouth appendages (Fig. 7E), and first two pairs of swimming legs (Fig. 7A) as in *K. lakewayi*.

Third swimming leg (Fig. 8B) also very similar to that in *K. lakewayi* but apophysis nearly flat, with narrow notch on outer side and shallow notch on distal margin, making distal part into blade-like structure; ornamentation same as in *K. lakewayi*, but longitudinal row of large spinules on outer margin missing; exopodal spine also 1.5 times as long as apophysis, but with less pronounced inner hump in proximal part.

Fourth swimming leg very similar to next two species (see below), with five small spinules on basis at base of endopod (but not as close to endopod as in *K. lakewayi*), and endopod with seven (on right leg) or eight (on left leg) large spinules arranged into scoop-like structure. Apical seta on third exopodal segment 1.3 times as long as entire exopod and three times as long as outer spine.

Fifth leg (Fig. 7C) without any difference from that in *K. lakewayi*, except for several shallow cuticular pits on anterior surface in proximal part, and very weak outline of cuticular window in some specimens.

Sixth legs (Fig. 7C) as in *K. lakewayi*.

Female (based on allotype and several paratypes). Body length from 383 to 438 µm (402 µm in allotype). Habitus (Fig. 9A), ornamentation of prosomites, colour, and nauplius eye similar to those in male, except genital and first abdominal somite fused into double-somite and middle part slightly less slender. Prosome/urosome ratio 0.7; greatest width from dorsal view hard to establish; body length/width ratio 8.8; cephalothorax only slightly wider than genital double-somite.

Genital double-somite (Figs. 8D, 9B, C) about 1.2 times as long as wide in dorsal view, without any trace of subdivision except for pair of ancestral dorso-lateral sensilla at middle; additionally ornamented with six posterior sensilla (two dorsal, two ventral and two lateral), numerous transverse rows of minute spinules, and two parallel short rows of four large spinules in posterior half laterally (arrowed in Fig. 9B). Genital complex (Figs. 8D, 9B, C) as in *K. lakewayi*, except outer distal corners of genital operculum not produced into spinifom processes.

Third urosomite (Fig. 9B, C) similar to that in male, with two groups of four large spinules ventrally (arrowed in Fig. 9C); lateral cuticular windows well developed and highly visible.

Fourth (preanal), and fifth (anal) urosomites also very similar to those in male (Fig. 9B, C), without any large spinules except those inside anal sinus.

Caudal rami (Figs. 8C, 9A, B, C) similar to those in male, but slightly inflated at middle in ventral view (arrowed in Fig. 9C) and more divergent.

Antennula (Fig. 10A) very similar to that in *K. lakewayi*, with slightly more robust aesthetascs.

Antenna (Fig. 10B), mouth appendages (Fig. 8E), first swimming leg (Fig. 8E), second swimming leg (Fig. 10C), and exopod of fourth swimming leg (Fig. 10E) very similar to those in male and without any difference from those in *K. lakewayi*.

Endopod of second swimming leg (Fig. 10C) 6.7 times as long as wide, its apical seta 0.7 times as long as segment.

Third swimming leg (Fig. 10D) similar to *K. lakewayi*, but with more strongly developed cuticular plates on praecoxa and coxa (arrowed in Fig. 10D), and with proportionately longer apical seta on second segment and shorter endopod.

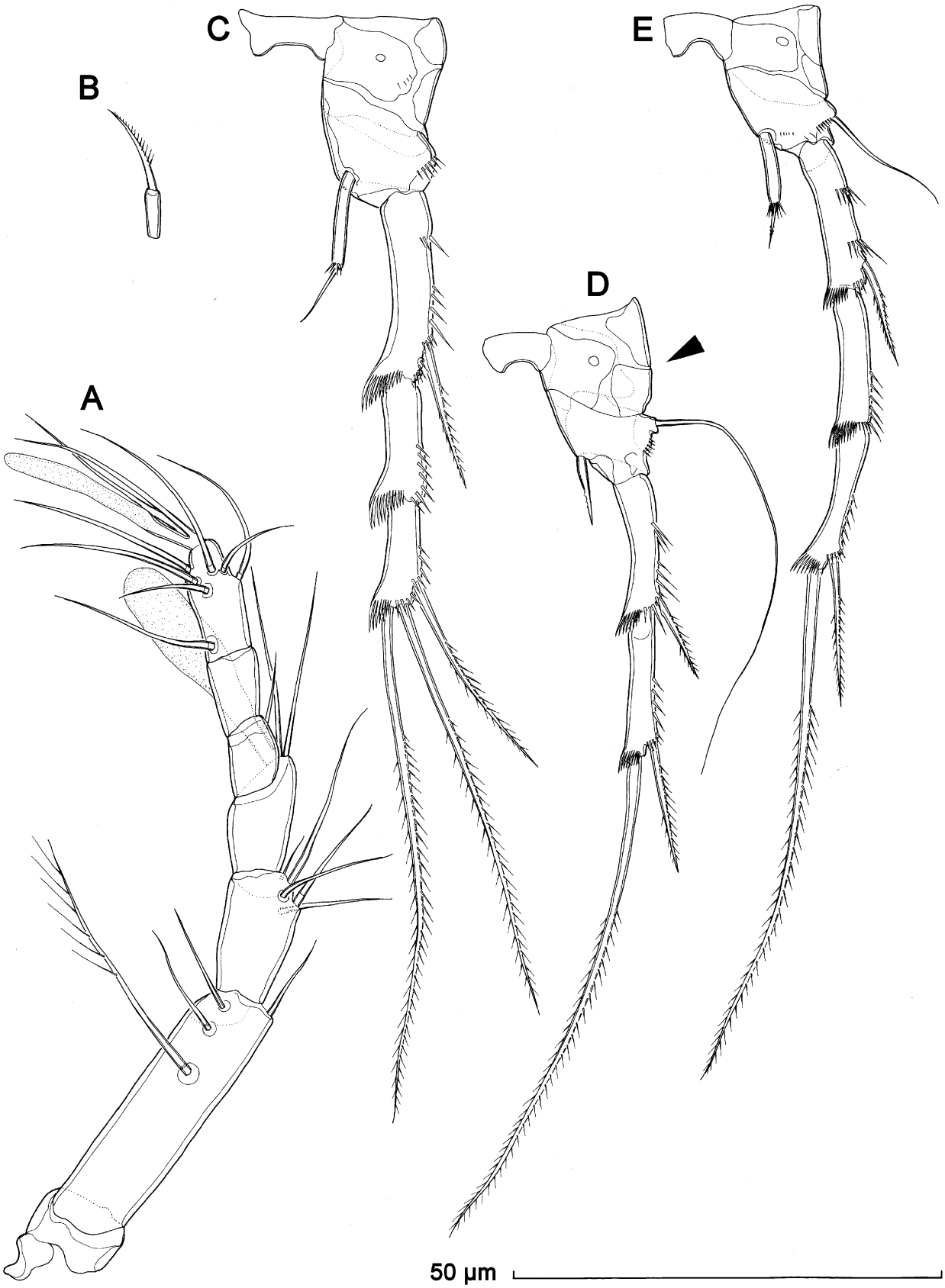

FIGURE 10. *Kinnecaris esbe* **sp. nov.**, paratype female: A, antennula, dorsal view; B, exopod of antenna, lateral view; C, second swimming leg, anterior view; D, third swimming leg, anterior view; E, fourth swimming leg, anterior view. Scale 50 µm for all figures. Arrow pointing smaller praecoxa and coxa of third swimming leg when compared to previous species.

Endopod of fourth swimming leg (Fig. 10E) about five times as long as wide, half as long as first exopodal segment, armed with single slender bipinnate seta apically; ornamented with six slender spinules along distal margin, at base of apical seta. Exopod similar to that of male.

Fifth leg (Figs. 8D, 9B) very similar to that of male, only slightly more elongated, with narrower distal part and cuticular window on anterior surface better defined, but not observable under light microscope.

Sixth leg (Figs. 8D, 9C) vestigial, both fused into simple bilobate cuticular plate, covering gonopore, unornamented and unarmed; outer distal corners not produced into sharp processes, but well rounded and shorter than inner lobes.

Etymology. The species name comes from its type locality (bore SB spelled in English), but should be treated as comprising an arbitrary combination of letters that can be treated as a Latin word and may be conceived as a noun in apposition to the generic name.

Variability. Body length in males ranges from 374 to 425 µm (395 µm average; n = 4), and from 383 to 438 µm in females (405 µm average; n = 15). Note that males are slightly smaller than females, but that may be a consequence of a low number (four) of the male specimens collected and examined. The endopods of the male fourth leg have always seven spinules on the right leg and nine on the left one, which is an unusual asymmetry, but it seems to be a character present also in the next two species (described below). The shape of the apophysis of the third leg in male is not variable, and it is a very good morphological character, as are the groups of large spinules on the urosome of females. The very low morphological variability recorded in this species is not surprising, considering that the species was collected from a single bore, which was the only access at the time of sampling to a small calcrete body in south-east of the Yeelirrie area (see Fig. 24).

Remarks. *Kinnecaris esbe* **sp. nov.** has the longest and most slender caudal rami of all the Australian congeners, which are also among the most slender recorded for the family. In every other aspect, this is a typical member of the genus *Kinnecaris* Jakobi, 1972. Morphology would suggest that this species is most closely related to two other short range endemics from Yeelirrie: *K. linel* **sp. nov.** and *K. uranusi* **sp. nov.** (see below). Unfortunately, despite repeated attempts, we were not able to get any COI sequences of *K. esbe* to test this relationship by molecular methods. Besides shorter caudal rami, the latter two species differ from *K. esbe* in the ornamentation of the genital double-somite in female (only one row of large spinules laterally; arrowed in Fig. 11B), and to a smaller extent in the shape of the third leg apophysis in male. Relying only on morphological evidence, we would speculate that these three species represent a monophyletic group among Australian *Kinnecaris* members (and also on a global scale), but molecular results disprove a close relationship of *K. linel* and *K. uranusi* (see discussion further below).

Kinnecaris linel sp. nov.

(Figs. 11–14)

Type locality. Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line L, Snake Well, 27.3074˚S 120.1505977˚E.

Type material. Holotype male dissected on one slide (WAM C47188); allotype female dissected on one slide (WAM C47189); one paratype male and one paratype female on one SEM stub *in toto* coated with carbon (WAM C47190); one paratype male dissected on one slide (WAM C47191); one paratype female dissected on one slide (WAM C47192); one paratype female destroyed for DNA sequence (amplification successful; see Fig. 23); 10 paratypes (six males + two females + two copepodids) in alcohol (WAM C47193); all collected at type locality, leg. T. Karanovic & S. Callan, 18 March 2010, seLN8310.

Other material examined. One female destroyed for DNA sequence (amplification unsuccessful); 10 males + 19 females + 12 copepodids in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line L, bore L-UNK1, 27.329832˚S 120.15059˚E, leg. T. Karanovic & G. Perina, 16 March 2010, seLN8533.

Eleven males + 16 females + 12 copepodids in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line L, bore L-UNK1, 27.329832˚S 120.15059˚E, leg. T. Karanovic & S. Callan, 18 March 2010, seLN7139.

One female destroyed for DNA sequence (amplification successful; see Fig. 23); one female in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line L, bore L-UNK1, 27.329832˚S 120.15059˚E, leg. P. Bell & G. Perina, 14 November 2009, seLN7315.

Description. Male (based on holotype and several paratypes). Total body length from 365 to 424 µm (424 µm in holotype). Surface of integument of all somites with dense and shallow cuticular pits, and all somites after cephalothorax with numerous short rows of minute spinules; third and fourth urosomites with some additional large spinules ventrally or laterally. Colour, nauplius eye, rostrum, body segmentation, and pore and sensilla pattern of all somites as in *Kinnecaris esbe* (see above), as well as many other details listed below. Habitus (Fig. 11A) cylindrical and very slender, without any demarcation between prosome and urosome dorsally, but with urosome wider in lateral view; prosome/urosome ratio about 0.6; greatest width from dorsal view hard to establish. Body length/width ratio about 9.6; cephalothorax only slightly wider than genital somite in dorsal view. Integument strongly sclerotized as in *K. esbe*, and more strongly than in *K.lakewayi* and *K. barrambie*, and also with deep and irregular depressions on all somites but especially on cephalothoracic shield, and pleuras and tergites of three free prosomites. Cephalothorax with clearly visible (Fig. 11A) double dorsal cuticular window posteriorly; fourth and fifth urosomites with pair of lateral circular windows each, both clearly visible and one on fifth urosomite slightly larger than that on fourth urosomite (Fig. 11A).

Cephalothorax (Fig. 11A) about 1.7 times as long as wide in dorsal view; representing about 18% of total body length. Surface of cephalic shield ornamented as in *K. esbe*, as well as tergites and pleuras of free pedigerous somites; except for additional dorsal pore on fourth and fifth pedigerous somites.

Genital somite (Fig. 11A) ornamented with numerous short dorsolateral rows of spinules, in addition to three pairs of sensilla on posterior margin, and one pair of very small ventro-lateral cuticular pores in anterior part; no large spinules on this somite; spermatophore visible inside some paratypes and similar size and shape to that in *K. esbe*.

Third urosomite (Fig. 11A) ornamented with two dorso-lateral rows of large spinules in anterior half, six posterior sensilla, and many rows of minute spinules.

Fourth urosomite (Fig. 11A) ornamented with two ventro-lateral short rows of large spinules ventrally of large and somewhat swollen lateral cuticular window; additionally ornamented with six posterior sensilla and numerous minute spinules.

Fifth (preanal) urosomite (Fig. 11A) with even larger and more swollen windows than those on fourth urosomite but without any large spinules, sensilla or pores; only ornamentation shallow cuticular pits and numerous minute spinules, forming nearly continuous row along hyaline fringe.

Anal somite (Fig. 11A) ornamented with pair of large dorsal sensilla at base of anal operculum, pair of large cuticular pores laterally in anterior half, two pairs of minute cuticular pores laterally closer to posterior margin, and pair of slightly larger cuticular pores ventrally, at base of caudal rami, in addition to cuticular pits and rows of minute spinules. Anal operculum better developed than in *K. esbe*, unornamented on outer surface, ornamented with row of slender spinules on inner surface, with highly convex and smooth distal margin, not reaching posterior end of anal somite, representing 68% of somite width. Anal sinus widely opened, with two diagonal rows of slender spinules on ventral side and transverse row of spinules on dorsal side.

Caudal rami (Fig. 11A) about 5.5 times as long as greatest width and 1.2 times as long as anal somite, very cylindrical in all views, with only slight inflation around insertion of dorsal seta, nearly parallel, with space between them about 1.7 times one ramus width. Armature and ornamentation as in *K. esbe*, but because rami slightly less elongated position of dorsal and lateral setae and their relative lengths differs. Dorsal seta inserted closer to inner margin at about 3/5 of ramus length, 0.8 times as long as caudal ramus, triarticulate basally and smooth. Lateral setae also thin and smooth, inserted close to each other at 5/6 of ramus length; proximal seta which inserted closer to dorsal surface strongest and longest, about 0.2 times as long as ramus, twice as long as proximal seta which inserted closer to ventral side, and about 1.2 times as long distal lateral seta. Inner apical seta smooth and slender, inserted closer to ventral surface, about 0.32 times as long as ramus. Middle apical seta strongest, inserted distally, without breaking plane, smooth, slightly curled, about 2.1 times as long as outer apical seta and 0.2 times as long as whole body. Outer apical seta also strong and without breaking plane, but unipinnate distally and inserted closer to ventral side than middle apical seta, about 0.85 times as long as ramus.

Antennula (Fig. 13C), antenna, mouth appendages, and first two pairs of swimming legs as in *K. esbe*.

Third swimming leg (Fig. 13A) also very similar to that in *K. esbe* but apophysis proportionately larger and with much more incised apical notch; longitudinal row of large spinules on outer margin also missing as in *K. esbe*; exopodal spine about 1.2 times as long as apophysis.

Fourth swimming leg (Fig. 13B) with five small spinules on basis at base of endopod (but not very close to it), and endopod with seven (on right leg) or nine (on left leg) large spinules arranged into scoop-like structure. Apical seta on third exopodal segment 1.3 times as long as entire exopod and 3.4 times as long as outer spine.

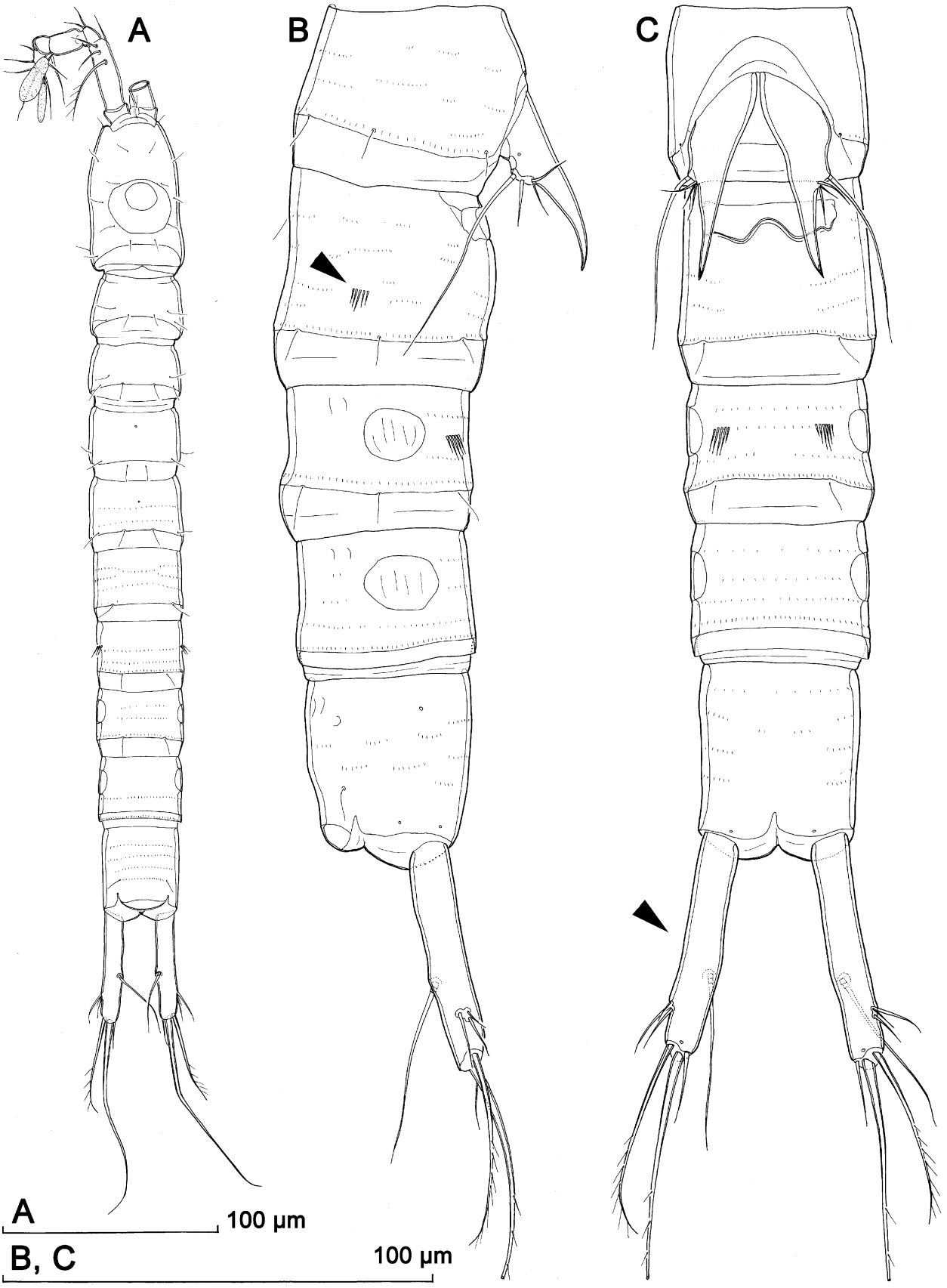

FIGURE 11. *Kinnecaris linel* **sp. nov.**, A, holotype male; B & C, allotype female: A, habitus, dorsal view; B, urosome, lateral view; C, urosome, ventral view. Arrows pointing reduced number of rows of large spinules on genital double-somite (B) and less elongated caudal rami (C) when compared to previous species.

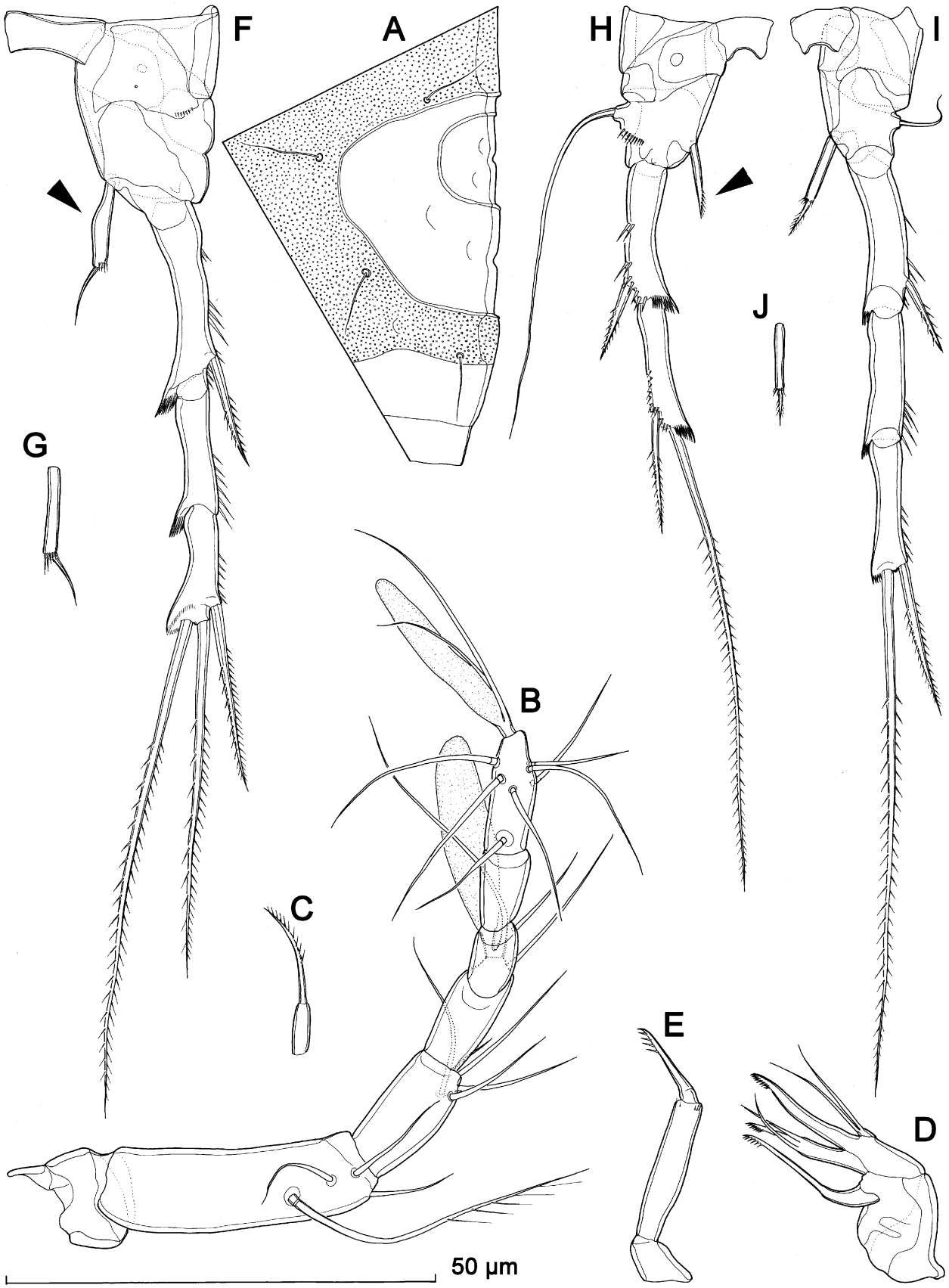

FIGURE 12. *Kinnecaris linel* **sp. nov.**, allotype female: A, double cuticular window on cephalothorax, lateral view; B, antennula, dorsal view; C, exopod of antenna, lateral view; D, maxilla, posterior view; E, maxilliped, anterior view; F, right second swimming leg, posterior view; G, endopod of left second swimming leg, posterior view; H, third swimming leg, anterior view; I, right fourth swimming leg, posterior view; J, endopod of left fourth swimming leg, posterior view. Scale 50 µm for all figures. Arrows pointing abnormal shape of second leg endopod (F) and more robust endopod of third swimming leg (H) when compared to previous species.

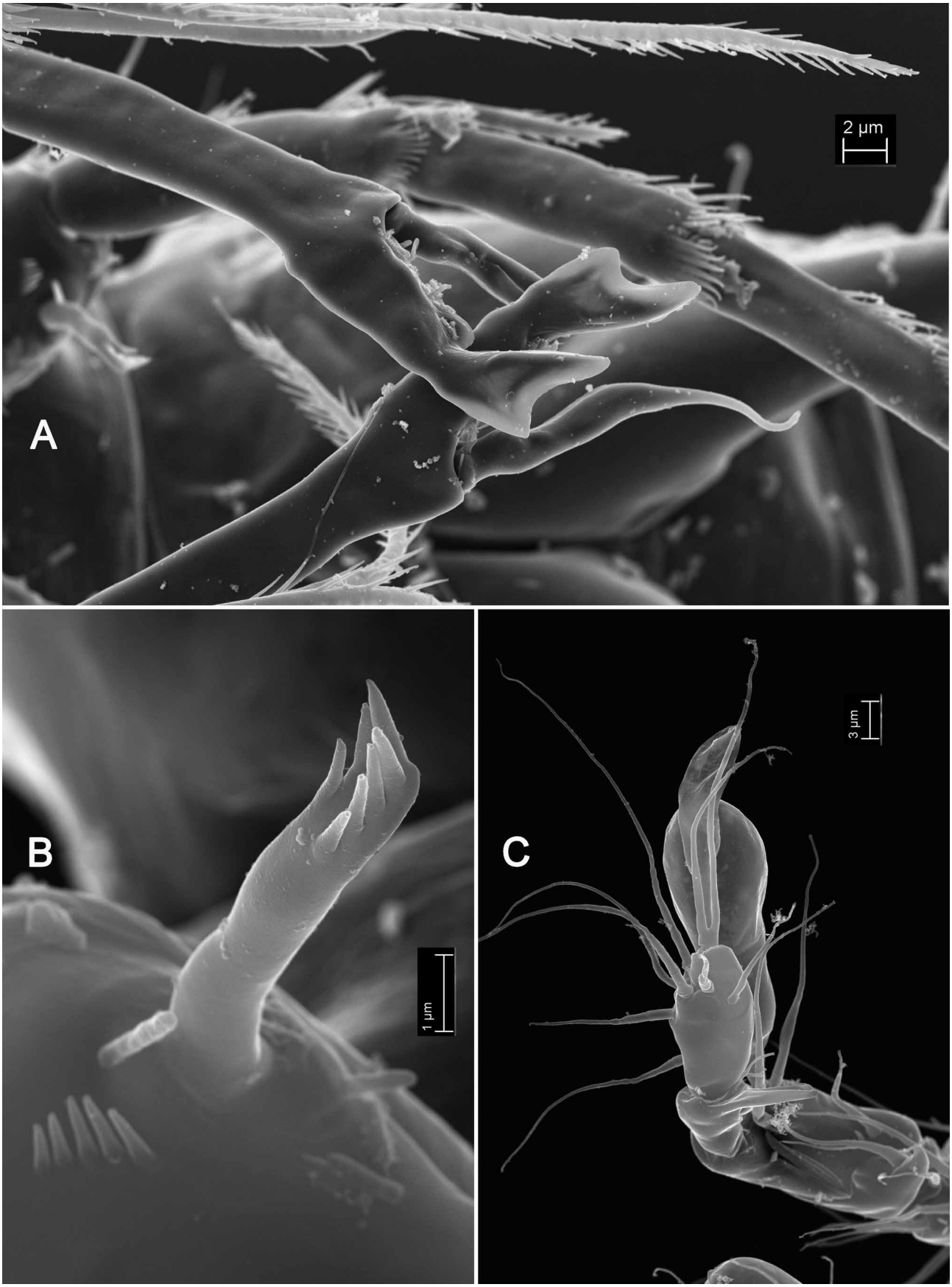

FIGURE 13. *Kinnecaris linel* **sp. nov.**, SEM photographs, paratype male: A, distal part of third swimming legs, anterior view; B, endopod of fourth swimming leg, antero-median view; C, distal part of antennula, ventral view.

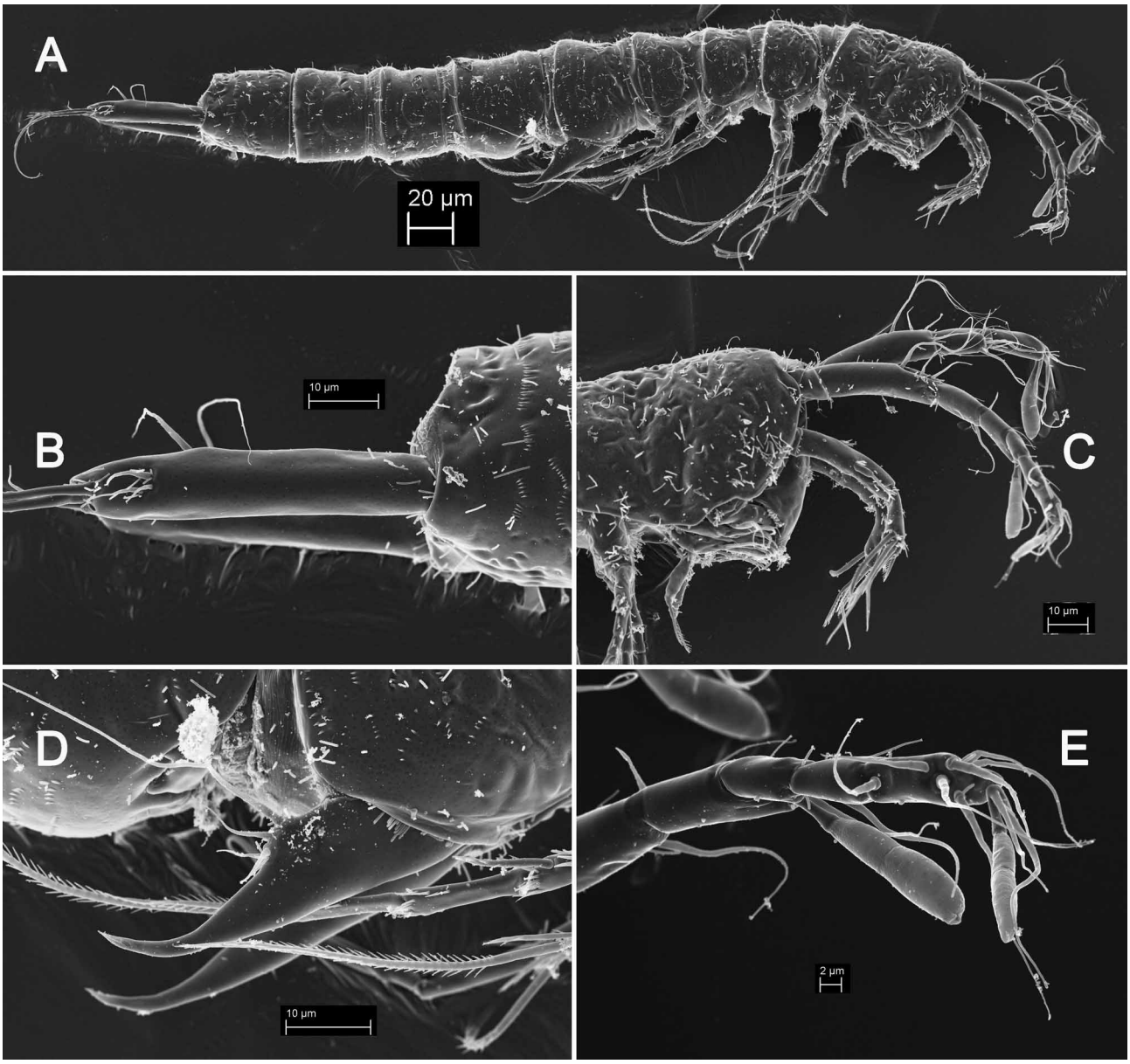

FIGURE 14. *Kinnecaris linel* **sp. nov.**, SEM photographs, paratype female: A, habitus, lateral view; B, anal somite and caudal rami, lateral view; C, cephalothorax, lateral view; D, fifth legs and anterior part of genital double-somite, lateral view; E, antennula, lateral view.

Fifth and sixth legs without any difference from those in *K. esbe*.

Female (based on allotype and several paratypes). Body length from 369 to 418 µm (408 µm in allotype). Habitus (Fig. 14A), ornamentation of cephalothorax (Fig. 12A) and free prosomites (Fig. 14A), colour, and nauplius eye similar to those in male, except genital and first abdominal somite fused into double-somite and middle part slightly less slender. Prosome/urosome ratio 0.68; greatest width from dorsal view hard to establish; body length/width ratio 8.1; cephalothorax only slightly wider than genital double-somite.

Genital double-somite (Fig. 11B, C) slightly longer than wide, without any trace of subdivision except for pair of ancestral dorso-lateral sensilla at middle; additionally ornamented with six posterior sensilla (two dorsal, two ventral and two lateral), several dorso-lateral rows of minute spinules, and one lateral short row of five large spinules in posterior half (arrowed in Fig. 11B), homologous to those on third urosomite in male. Genital complex (Figs. 11C, 14D) as in *K. esbe*.

Third urosomite (Figs. 11B, C, 14A) similar to that in male, with two groups of four large spinules ventro-laterally; lateral cuticular windows well developed and highly visible.

Fourth (preanal), and fifth (anal) urosomites also very similar to those in male (Figs. 11A, B, C, 14A, B), without any large spinules except those inside anal sinus.

Caudal rami (Figs. 11A, B, C, 14B) similar to those in male, but slightly inflated at middle in ventral view (arrowed in Fig. 11C) and more divergent; shorter than in previous species.

Antennula (Fig. 12B) very similar to that in *K. esbe*, only with somewhat more robust apical aesthetasc on seventh segment.

Antenna (Figs. 12C, 14C, E) very similar to that in *K. esbe*, exopodal seta twice as long as segment.

Maxilla (Fig. 12D) with three setae on distal endite of syncoxa, two smooth and with pore on tip, third with brush of spinules distally and strong; otherwise as in *K. lakewayi*.

Maxilliped (Fig. 12E) with several minute spinules at base of endopod, otherwise as in *K. lakewayi.*

Other mouth appendages (Fig. 14C), first swimming leg (Fig. 14A, C), second swimming leg (Fig. 12F, G), and exopod of fourth swimming leg (Fig. 12I) very similar to those in male and without any difference from those in *K. esbe*.

Endopod of second swimming leg (Fig. 12F, G), cylindrical, six times as long as wide, its apical seta 0.67 times as long as segment; one aberrant endopod in allotype inflated (arrowed in Fig. 12F).

Third swimming leg (Fig. 12H) similar to that in *K.esbe*, but with more spinules along distal inner margin of endopod (arrowed in Fig. 12H), which also longer.

Endopod of fourth swimming leg (Fig. 10I, J), small and slender, about seven times as long as wide, less than half as long as first exopodal segment, armed with single bipinnate seta apically; ornamented with several slender spinules along distal margin, at base of apical seta. Exopod similar to that in male.

Fifth leg (Figs. 11B, 14D) as in male, and without any difference from that in *K. esbe*; cuticular window also not observable under light microscope.

Sixth leg (Figs. 11C, 14D) vestigial, both fused into simple bilobate cuticular plate, covering gonopore, unornamented and unarmed; outer distal corners not produced into sharp processes, but well rounded and shorter than inner lobes.

Etymology. The species name comes from its type locality (line L; see Fig. 24), but should be treated as comprising an arbitrary combination of letters that can be treated as a Latin word and may be conceived as a noun in apposition to the generic name.

Variability. Body length in males ranges from 365 to 424 µm (398 µm average; n = 30), while in females it ranges from 369 to 418 µm (395 µm average; n = 42). Endopod of the female second swimming leg is always cylindrical, except in one leg in the allotype female, which is inflated at middle (arrowed in Fig. 12F). Endopod of the female fourth leg is always small and very slender (Fig. 12I, J), and endopods of the male fourth leg always have seven spinules on the right leg (Fig. 13B) and nine on the left, which is an unusual asymmetry, but it seems to be a constant character also in *K. esbe*. The shape of the apophysis of the male third leg (Fig. 13A) is not variable, and is a very good morphological character, as are the groups of large spinules on the female urosome (Fig. 11B, C).

Remarks. Morphology of this species is such that it is very hard indeed to find enough distinguishing characters between it and *K. uranusi* **sp. nov.** (see below), yet our molecular data do not support their sister-species relationship (see further below; Fig. 23). Some of the most important differences include the length and shape of the caudal rami (slightly longer and more cylindrical in *K. linel* **sp. nov.;** arrowed in Fig. 11C), fine ornamentation of urosomites (more rows of minute spinules in *K. linel*, especially dorsally on anal somite; Fig. 11A), as well as the shape of the third leg apophysis in male (with deep apical notch in *K. linel*; Fig. 13A). As remarked above, both species are also very similar to *K. esbe* **sp. nov.**, but differ in the ornamentation of the genital double-somite in female, length of the caudal rami, and some other minor details in proportion of certain armature elements and ornamentation of appendages. Molecular data suggest a sister relationship of *K. linel* and *K. lined* **sp. nov.**, although support for this clade is not very strong (Fig. 23). The two species, however, differ not only in the proportion of the caudal rami and ornamentation of urosomites, but also in the armature of the fourth leg basis and exopod in male, as well as in the third leg apophysis (see below).

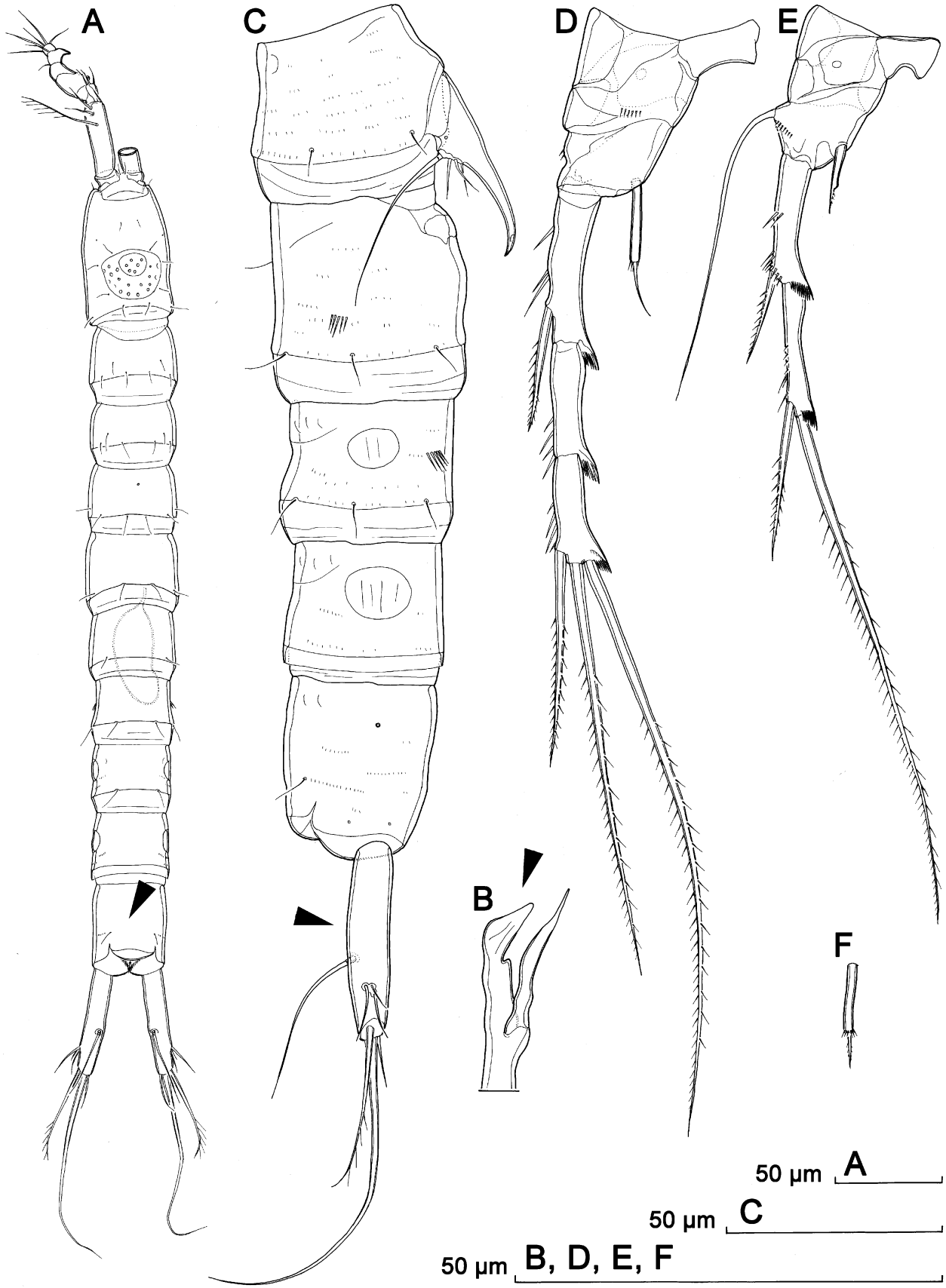

FIGURE 15. *Kinnecaris uranusi* **sp. nov.**, A & B, holotype male; C-F, allotype female: A, habitus, dorsal view; B, distal part of third swimming leg, anterior view; C, urosome, lateral view; D, second swimming leg, posterior view; E, third swimming leg, anterior view; F, endopod of fourth swimming leg, posterior view. Arrows pointing absence of minute spinules on anal somite (A), absence of notch on third leg apophysis (B), and shorter caudal rami (C) when compared to previous species.

***Kinnecaris uranusi* sp. nov.**
(Figs. 15–18)

Type locality. Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line 1, bore YYAC0016A, 27.1657429˚S 119.8722617˚E.

Type material. Holotype male dissected on one slide (WAM C47194); allotype female dissected on one slide (WAM C47195); one paratype male on SEM stub *in toto* coated with carbon (WAM C47196); one paratype male dissected on one slide (WAM C47197); one paratype female dissected on one slide (WAM C47198); five paratype males in alcohol (WAM C 47199); all collected at type locality, leg. T. Karanovic & S. Callan, 20 March 2010, seLN8415.

Other material examined. One female destroyed for DNA sequence (amplification successful; see Fig. 23); 1 female + 1 copepodid in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line H, bore TPB33-1, 27.133739˚S 119.827871˚E, leg. T. Karanovic & S. Callan, 18 March 2010, seLN8563.

One female destroyed for DNA sequence (amplification successful; see Fig. 23);one female on SEM stub *in toto* coated with carbon (WAM C47200); two males + one female + two copepodids in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line F, bore YU2, 27.137169˚S 119.853157˚E, leg. T. Karanovic & G. Perina, 17 March 2010, seLN8536.

One female destroyed for DNA sequence (amplification unsuccessful); four males + five females + 10 copepodids in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line K, bore YYHC085B, 27.247824˚S 120.054676˚E, leg. T. Karanovic & S. Callan, 18 March 2010, seLN7131.

Four males + two females on one SEM stub *in toto* coated with carbon (WAM C47201); four males + five females in alcohol (WAM C47202); 13 males + six females + 10 copepodids in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line K, bore YYHC085B, 27.247824˚S 120.054676˚E, leg. T. Karanovic & S. Callan, 20 March 2010, seLN8419.

One female destroyed for DNA sequence (amplification successful; see Fig. 23); seven males + 17 females in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line 1, bore YYD22, 27.167304˚S 119.870456˚E, leg. S. Callan & N. Krawczyk, 15 March 2010, seLN8496.

One male destroyed for DNA sequence (amplification unsuccessful); three males + one female in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line 1, bore YYD26, 27.1686738˚S 119.8701177˚E, leg. S. Callan & N. Krawczyk, 15 March 2010, seLN8479.

10 males + six females + 2 copepodids in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line 1, bore YYD26, 27.1686738˚S 119.8701177˚E, leg. T. Karanovic & S. Callan, 20 March 2010, seLN8296.

One male destroyed for DNA sequence (amplification unsuccessful); four males in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line 2, bore YYAC1006B, 27.1616404˚S 119.8866403˚E, leg. T. Karanovic & S. Callan, 21 March 2010, seLN8553.

One female in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line 2, bore YYAC1007A, 27.165236˚S 119.883142˚E, leg. S. Callan & N. Krawczyk, 16 March 2010, seLN8524.

Three females in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line 2, bore YYAC1007A, 27.165236˚S 119.883142˚E, leg. T. Karanovic & S. Callan, 21 March 2010, seLN8546.

One male in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line 2, bore YYAC1007A, 27.165236˚S 119.883142˚E, leg. P. Bell & G. Perina, 27 August 2009, seLN7312.

Two males + one female in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line 1, bore YYD22, 27.167304˚S 119.870456˚E, leg. P. Bell & G. Perina, 1 September 2009, seLN6610.

One male in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line H, bore TPB33-1, 27.133739˚S 119.827871˚E, leg. P. Bell & S. Callan, 01 September 2009, seLN7303.

One female destroyed for DNA sequence (amplification unsuccessful); Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line C, bore YYHC0037C, 27.2067173˚S 119.9845332˚E, leg. T. Karanovic & S. Callan, 19 March 2010, seLN8597.

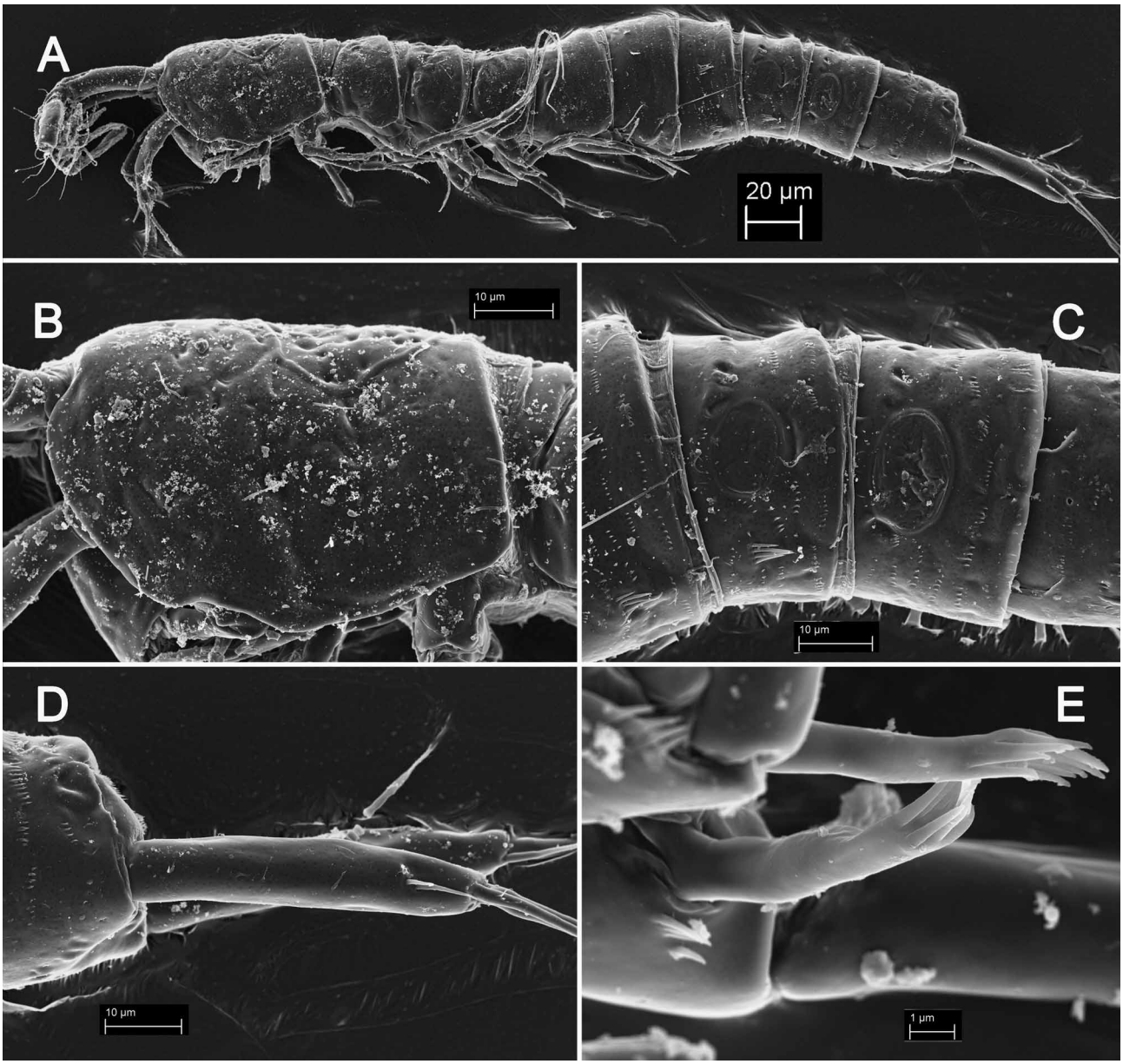

FIGURE 16. *Kinnecaris uranusi* **sp. nov.**, SEM photographs, paratype male: A, habitus, lateral view; B, cephalothoracic shield, lateral view; C, fourth and fifth urosomites, lateral view; D, anal somite and caudal rami, lateral view; E, endopods of fourth swimming legs, lateral view.

Description. Male (based on holotype, several paratypes, and many additional specimens examined). Total body length from 368 to 436 µm (434 µm in holotype). Morphology extremely similar to *Kinnecaris linel* (see above), and only minute differences observable. Surface of integument of all somites with dense cover of shallow cuticular pits, and all somites after cephalothorax with several short rows of minute spinules (Figs. 16A, 17A); third and fourth urosomites with additional larger spinules ventrally or laterally (Fig. 16C). Colour, naupliar eye, rostrum, body segmentation, and pore and sensilla pattern of all somites as in *K. linel*. Habitus (Figs. 15A, 16A, 17A) cylindrical and very slender, without any dorsal demarcation between prosome and urosome, but with urosome much wider in lateral view, especially in those specimens with completely formed spermatophore; prosome/urosome ratio about 0.65; greatest width from dorsal view hard to establish. Body length/width ratio about 9.6; cephalothorax as wide as genital somite in dorsal view. Integument equally strongly sclerotized as in *K. linel* or *K. esbe*, and also with deep and irregular depressions on all somites but especially on cephalothoracic shield and pleuras and tergites of three free prosomites. Cephalothorax with clearly visible double dorsal cuticular window poste-

riorly (Figs. 15A, 16B); fourth and fifth urosomites each with pair of lateral circular windows (Figs. 15A, 16C), that on fifth urosomite somewhat larger.

Cephalothorax (Figs. 15A, 16B, 17B) almost 1.8 times as long as wide in dorsal view; representing about 17.5% of total body length. Surface of cephalic shield (Figs. 15A, 16B) ornamented as in *K. linel*, as well as tergites and pleuras of free pedigerous somites (Figs. 16A, 17A), except for dorsal pore on fifth pedigerous somites being absent visible, and generally fewer rows of minute spinules on each somite.

Genital somite (Figs. 15A, 18A, B) ornamented with several dorso-lateral short rows of spinules, in addition to three pairs of sensilla on posterior margin, and one pair of very small ventro-lateral cuticular pores in anterior part; no large spinules on this somite; spermatophore visible inside holotype and several paratypes and similar in size to that in *K. esbe* and *K. lakewayi*.

Third urosomite (Fig. 16C) ornamented with four rows of five large spinules each in anterior half (two dorso-laterally and two ventro-laterally), in addition to six posterior sensilla, and many rows of minute spinules.

Fourth urosomite (Fig. 16C) ornamented with two ventro-lateral short rows of four large spinules, ventrally from large and somewhat swollen lateral cuticular window; additionally ornamented with six posterior sensilla and several rows of minute spinules.

Fifth (preanal) urosomite (Fig. 16C) with even larger and more swollen windows but without any large spinules, sensilla or pores; only ornamentation represented by shallow cuticular pits and numerous minute spinules, although not as many as in *K. linel* or *K. esbe*, and those along hyaline fringe very small and scarce.

Anal somite (Fig. 15A, 16A, 17A) ornamented with pair of large dorsal sensilla at base of anal operculum, pair of lateral large cuticular pores in anterior half, two pairs of minute cuticular lateral pores close to posterior margin, and pair of slightly larger ventral cuticular pores at base of caudal rami, in additional to cuticular pits and rows of minute spinules; minute spinules getting extremely scarce or completely absent on dorsal side of anal somite (arrowed in Fig. 15A). Anal operculum very similar to that of *K. linel*, unornamented on outer surface, ornamented with row of slender spinules on inner surface, with highly convex and smooth distal margin, not reaching posterior end of anal somite, representing 63% of somite width. Anal sinus widely opened, with two diagonal rows of slender spinules on ventral side and transverse row of spinules on dorsal side (Fig. 17C).

Caudal rami (Figs. 15A, 16D, 17C) about 4.8 times as long as greatest width and 1.15 times as long as anal somite, generally cylindrical in all views, buth with noticable inflation around insertion of dorsal seta, slightly divergent, with space between them about 1.5 times one ramus width. Armature and ornamentation as in *K. linel*, but, because rami slightly less elongated, position of dorsal and lateral setae slightly different, as well as their relative lengths. Dorsal seta inserted closer to inner margin at about 3/5 of ramus length, 0.85 times as long as caudal ramus, triarticulate basally and smooth. Lateral setae also thin and smooth, inserted close to each other at 3/4 of ramus length; proximal seta which inserted closer to dorsal surface strongest and longest, about 0.3 times as long as ramus, twice as long as proximal seta which inserted closer to ventral side, and about 1.4 times as long distal lateral seta. Inner apical seta smooth and slender, inserted close to ventral surface, about 0.38 times as long as ramus. Middle apical seta strongest, inserted distally, without breaking plane, smooth, slightly curled, twice as long as outer apical seta and 0.2 times as long as whole body. Outer apical seta also strong and without breaking plane, but unipinnate distally and inserted closer to ventral side, about 0.9 times as long as ramus.

Antennula (Fig. 16A), antenna (Fig. 16A), mouth appendages (Figs. 17B, 18C), and first two pairs of swimming legs (Figs. 17A, B, 18C) as in *K. linel*.

Third swimming leg (Figs. 15B, 17D) also very similar to that in *K. linel* but apophysis proportionally longer, more tridimensional, and without apical notch (arrowed in Fig. 15B); longitudinal row of large spinules on outer margin also missing as in *K. linel* and *K. esbe*; exopodal spine about 1.2 times as long as apophysis.

Fourth swimming leg (Figs. 16E, 17E) basis with five small spinules at base of endopod (but not very close to it), and endopod with seven (on right leg) or nine (on left leg) large spinules arranged into scoop-like structure. Apical seta on third exopodal segment 1.2 times as long as entire exopod and 3.2 times as long as outer spine.

Fifth and sixth legs (Fig. 18A, B) without almost any difference from those in *K. linel* or *K. esbe*; except fifth leg perhaps slightly more slender in distal part and reaching further posteriorly.

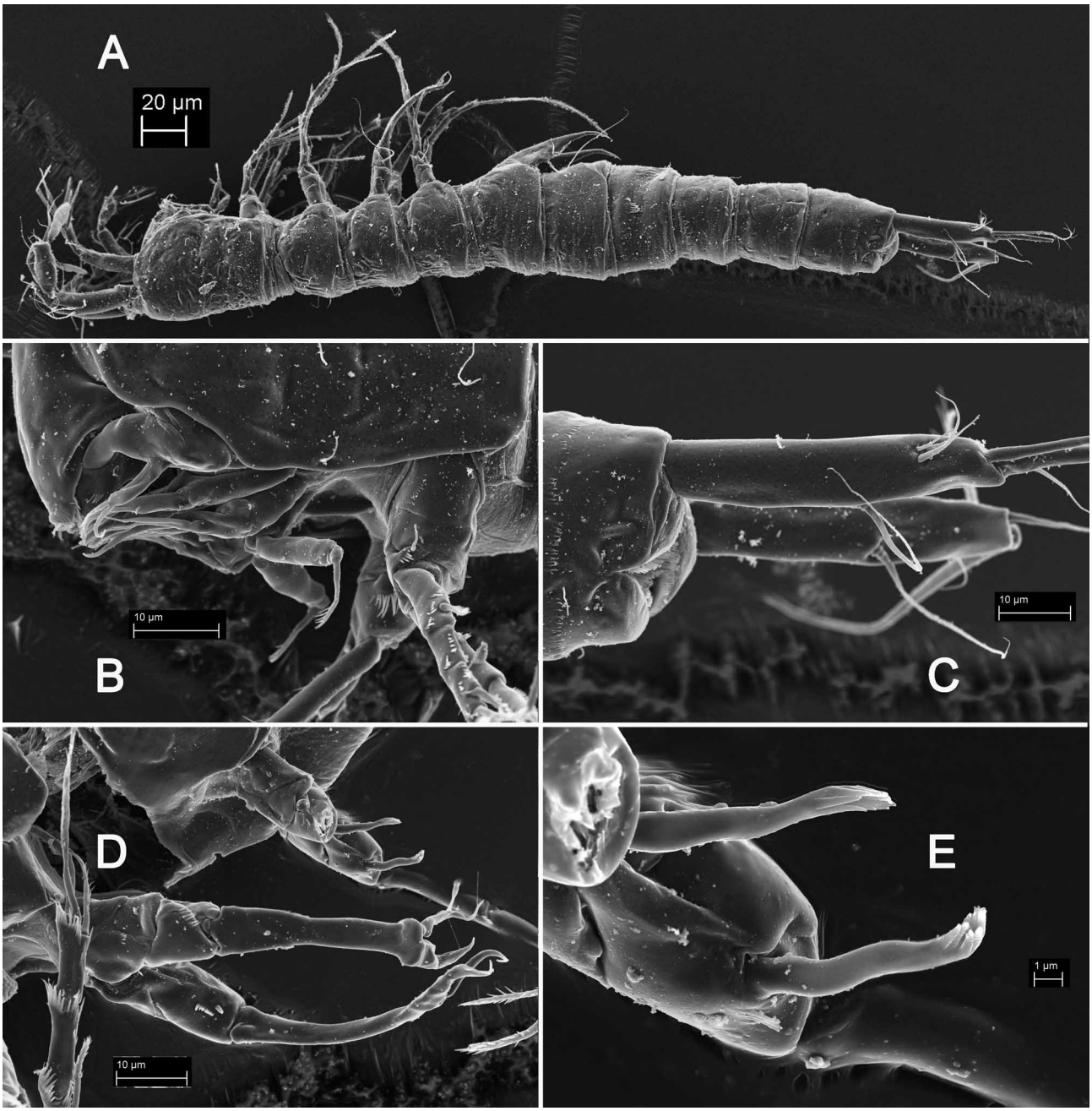

FIGURE 17. *Kinnecaris uranusi* **sp. nov.**, SEM photographs, A & C, male I from bore YYHC085B1 (line K); B, D & E, male II from the same bore; A, habitus, lateral view; B, mouth appendages, lateral view; C, anal somite and caudal rami, lateral view; D, third swimming legs, lateral view; E, endopods of fourth swimming legs, lateral view (note: exopod of left leg broken off).

Female (based on allotype, several paratypes, and many additional specimens). Body length from 354 to 426 µm (405 µm in allotype). Habitus (Fig. 18E), ornamentation of cephalothorax and free prosomites, colour and naupliar eye similar to those of male, except genital and first abdominal somite fused into double-somite and middle part slightly less slender in dorsal view, but more slender in lateral view. Prosome/urosome ratio 0.7; greatest width from dorsal view hard to establish; body length/width ratio 7.9; cephalothorax only slightly wider than genital double-somite.

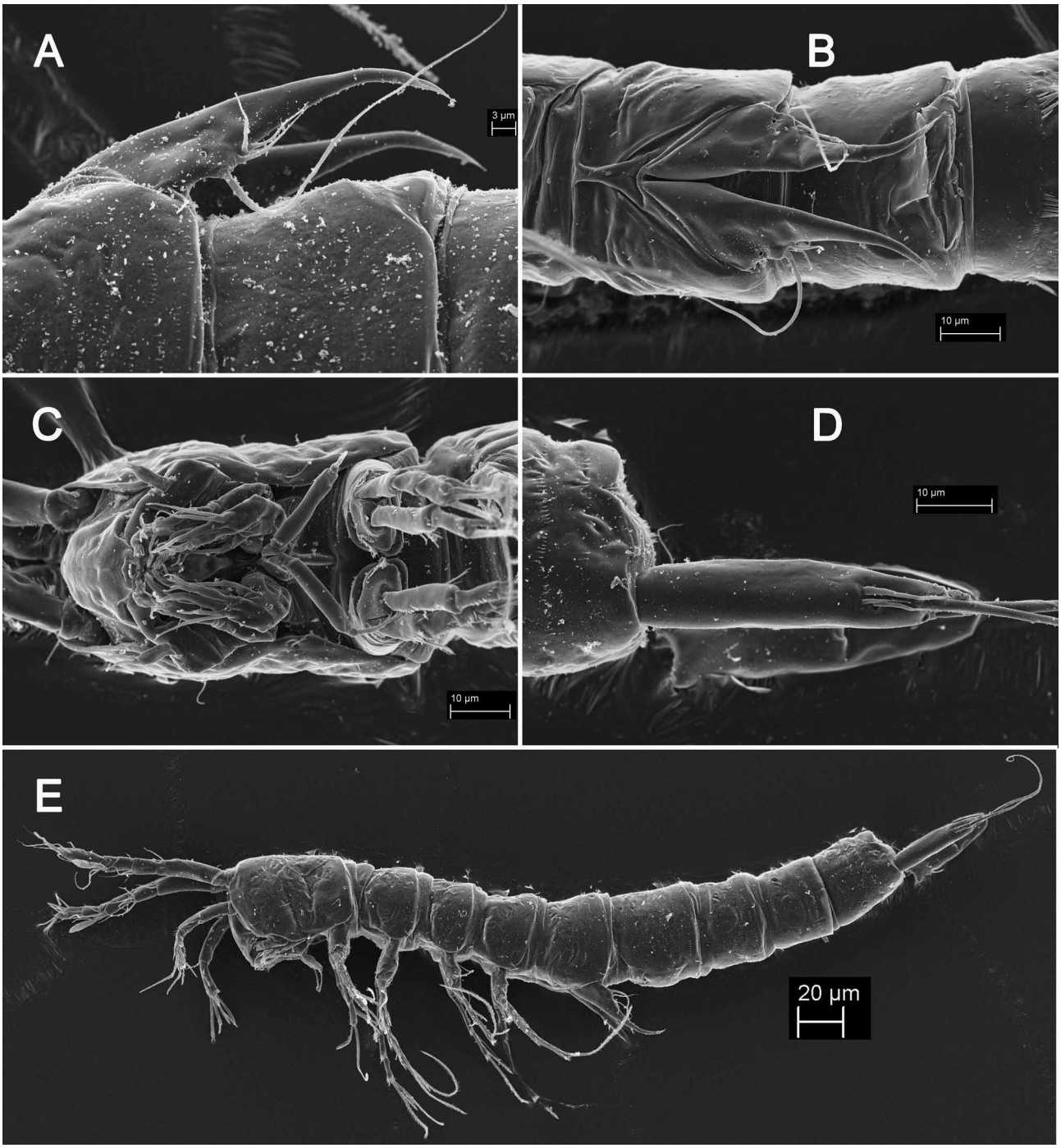

FIGURE 18. *Kinnecaris uranusi* **sp. nov.**, SEM photographs, A, male I from bore YYHC085B1 (line K); B & C, male III from the same bore; D & E, female from the same bore: A, fifth and sixth legs, lateral view; B, first two urosmal somites, ventral view; C, cephalothorax, ventral view; D, anal somite and caudal rami, lateral view; E, habitus, lateral view.

Genital double-somite (Figs. 15C, 18E) slightly longer than wide, without any trace of subdivision except for pair of ancestral dorso-lateral sensilla at middle; additionally ornamented with six posterior sensilla (two dorsal, two ventral, and two lateral), several dorso-lateral rows of minute spinules, and one short row of five lateral large spinules in posterior half, as in *K. linel*. Genital complex (Figs. 15C, 18E) also similar to that in *K. linel*, but outer distal corners of operculum slightly more produced posteriorly (although not pointy).

Third urosomite (Figs. 15C, 18E) similar to that in male, with two groups of four large ventro-lateral spinules; lateral cuticular windows well developed and highly visible.

Fourth (preanal), and fifth (anal) urosomites also very similar to those in male (Figs. 15C, 18E), without any large spinules, except those in anal sinus.

Caudal rami (Figs. 15A, 18D) similar to those in male, slightly shorter than those in *K. linel* and significantly shorter than those in *K. esbe*, also more inflated at middle (arrowed in Fig. 15C).

Antennula (Fig. 18E) also similar to that in *K. linel*, but with much more slender aesthetascs.
Antenna, mouth appendages, first swimming leg, second swimming leg (Fig. 15D), and exopod of fourth swimming leg (Fig. 15E) very similar to those in male and without any difference from those in *K. linel*.

Endopod of second swimming leg (Fig. 15D), cylindrical, six times as long as wide, its apical seta 0.68 times as long as segment.

Third swimming leg (Fig. 15E) similar to that in *K.linel*, but with less spinules along inner margin of endopod and with characteristic hump at ancestral border between segment and apical armature element.

Endopod of fourth swimming leg (Fig. 15G), small and very slender, about seven times as long as wide, half as long as first exopodal segment, armed with single bipinnate seta apically; ornamented with few slender spinules along distal margin, at base of apical seta. Exopod similar to that of male.

Fifth leg (Fig. 15C) as in male, and without any difference from that in *K. linel*; cuticular window not observable.

Sixth legs (Fig. 18E) vestigial, fused into simple bilobate cuticular plate, covering gonopore, unornamented and unarmed; outer distal corners well rounded (not produced into sharp processes), and slightly shorter than inner lobes.

Etymology. The name refers to Uranus, the ancient Greek deity of the sky, which gave name to a planet in our solar system, which in turn gave name to the chemical element Uranium, one of the important mineral deposits in the distribution range of this species, which was experimentally mined at Yeelirrie in the 1970s. The specific name is a noun in the genitive singular.

Variability. Body length in males ranges from 368 to 436 µm (395 µm average; n = 50), while in females it ranges from 354 to 426 µm (392 µm average; n = 50). Despite a relatively wide distribution of this species in Yeelirrie, no significant variable features were discovered, except the body length. Careful examination and many SEM photographs taken of specimens from the northern part of its range (Figs. 15, 16) and those from line K (Figs. 17, 18) also failed to reveal any geographical variation. Endopod of the male fourth leg always has seven spinules on the right leg and nine on the left (Figs. 16E, 17E), which is an unusual asymmetry, but it seems to be a character also in *K. esbe* **sp. nov.** and *K. linel* **sp. nov.**. The shape of the apohysis of the third leg in male (Fig. 15B) is not variable, and is a very good morphological character, as are the groups of large spinules on the female urosome (Fig. 15C); although latter do not differ from those in *K. linel*.

Remarks. Major similarities and differences between *K. uranusi* **sp. nov.** and *K. linel* **sp. nov.** are given in the remarks section for the latter species (see above), and the two seem to share the greatest number of morphological characters. Molecular data (Fig. 23), on the other hand, suggest that these two species are not so closely related, but rather indicate that *K. uranusi* is more closely related to an undescribed species from line P (*Kinnecaris* sp.) and to *K. linesae* **sp. nov.** The latter species, however, differs from *K. uranusi* in so many morphological characters that we have to accept the results of our molecular analysis with some reservation. Among other morphological differences suffice to mention here: the caudal rami shape (Figs. 16D, 21G), ornamentation of urosomites (Figs. 18E, 22A), ornamentation of the fourth leg basis and exopod in male (Figs. 16E, 17E, 21F), and shape of the third leg apophysis in male (Figs. 17D, 21E).

Kinnecaris lined sp. nov.

(Fig. 19)

Type locality. Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line D, bore D-Trog, 27.2828034˚S 120.1113122˚E.

Type material. Holotype male dissected on one slide (WAM C47203); allotype female dissected on one slide (WAM C47204); two paratype females destroyed for DNA sequences (both amplifications successful; see Fig. 23); two paratype males dissected on one slide each (WAM C47205 and C47206); two paratype females dissected on one slide each (WAM C47207 and C47208); 30 paratypes (three males + 27 females) in alcohol (WAM C 47209); all collected at type locality, leg. S. Callan & G. Perina, 23 September 2010, seLN100401.

Description. Male (based on holotype and several paratypes). Total body length from 355 to 395 µm (388 µm in holotype). Surface of integument of all somites with numerous shallow cuticular pits (Fig. 19B). Colour, naupliar eye, rostrum, body segmentation, and pore and sensilla pattern of all somites as in *Kinnecaris lakewayi* (see above), except for large dorsal pore on second pedigerous somite dorsally. Habitus (Fig. 19A) cylindrical and very slender, without any demarcation between prosome and urosome dorsally, but with urosome somewhat wider in lateral view; prosome/urosome ratio about 0.8; greatest width from dorsal view hard to establish. Body length/width ratio about 8.8; cephalothorax 1.07 times as wide as genital somite. Integument relatively weakly sclerotized, smooth, without rows of minute spinules; larger spinules only present on fourth urosomite ventrally. Cephalothorax with clearly visible double dorsal cuticular window posteriorly (Fig. 19A); fourth and fifth urosomites with pair of oval lateral cuticular windows each.

Cephalothorax (Fig. 19A) about 1.6 times as long as wide in dorsal view; representing about 19% of total body length. Surface of cephalic shield ornamented as in *K. lakewayi*, as well as tergites and pleuras of free pedigerous somites, except for presence of shallow cuticular pits.

Genital somite (Fig. 19A) ornamented with three pairs of sensilla on posterior margin and one pair of very small cuticular pores in anterior part ventro-laterally; spermatophore not visible inside.

Third urosomite (Fig. 19A) without any spinules, ornamented only with six posterior sensilla.

Fourth urosomite (Fig. 19A) ornamented with two ventral rows of four large spinules at middle, ventrally from well developed oval cuticular window, and six posterior sensilla.

Fifth (preanal) urosomite (Fig. 19A) with windows similar to those on fourth urosomite but without any large spinules, sensilla or pores; only ornamentation shallow cuticular pits.

Anal somite (Fig. 19A) with pair of large dorsal sensilla at base of anal operculum, pair of large lateral cuticular pores (one pore on each side) in anterior half, two lateral pairs of minute cuticular pores close to posterior margin, and ventral pair of slightly larger cuticular pores at base of caudal rami, in addition to cuticular pits; no spinules of any size. Anal operculum well developed, unornamented on outer surface, ornamented with row of slender spinules on inner surface, with convex and smooth distal margin, not reaching posterior end of anal somite, representing 67% of somite width. Anal sinus widely opened, with two diagonal rows of slender spinules on ventral side and transverse row of spinules on dorsal side (below anal operculum).

Caudal rami (Fig. 19A, B) slightly divergent, with space between them about 1.5 times one ramus' width, about 3.6 times as long as greatest width (dorsal view) and 0.7 times as long as anal somite, generally cylindrical in dorsal and ventral view (although distal part somewhat tapering), but slightly inflated at midlength in lateral view, with proximal part of inner margin slightly convex in dorsal (or ventral) view; base not much narrower than rest of ramus. Armature and ornamentation as in *K. lakewayi*, but lateral setae inserted slightly more posteriorly (i.e. at about 3/4 of ramus length).

Antennula, antenna, mouth appendages, and first two pairs of swimming legs very similar to those of *K. lakewayi*.

Third swimming leg (Fig. 19C, D, E) also generally similar to *K. lakewayi* but apophysis much larger, not bilobate, with sharper tip (i.e. more like that in *K. esbe*, although more robust and without apical notch); ornamentation same as in *K. lakewayi*, including longitudinal row of large spinules on outer margin of first exopodal segment distally; exopodal spine about 1.2 times as long as apophysis.

Fourth swimming leg (Fig. 19F) with eight very long spinules on basis at base of endopod; endopod spiniform with spinules along distal third of outer margin, not arranged in scoop-like structure, but in simple row (proximalmost largest). First exopodal segment with several very long spinules on posterior surface at about midlength. Apical seta on third exopodal segment 1.2 times as long as entire exopod and about three times as long as outer spine.

Fifth leg without any difference from that in *K. lakewayi*, except maybe slightly more slender in distal third; no visible outline of cuticular window.

Sixth legs as in *K. lakewayi*.

Female (based on allotype and several paratypes). Body length from 362 to 403 µm (392 µm in allotype). Habitus, ornamentation of prosomites (Fig. 19G, inset), colour, and naupliar eye similar to those in male, except genital and first abdominal somite fused into double-somite and middle part slightly less slender. Prosome/urosome ratio 0.8; greatest width from dorsal view hard to establish; body length/width ratio also 8.5; cephalothorax 1.1 times as wide as genital double-somite.

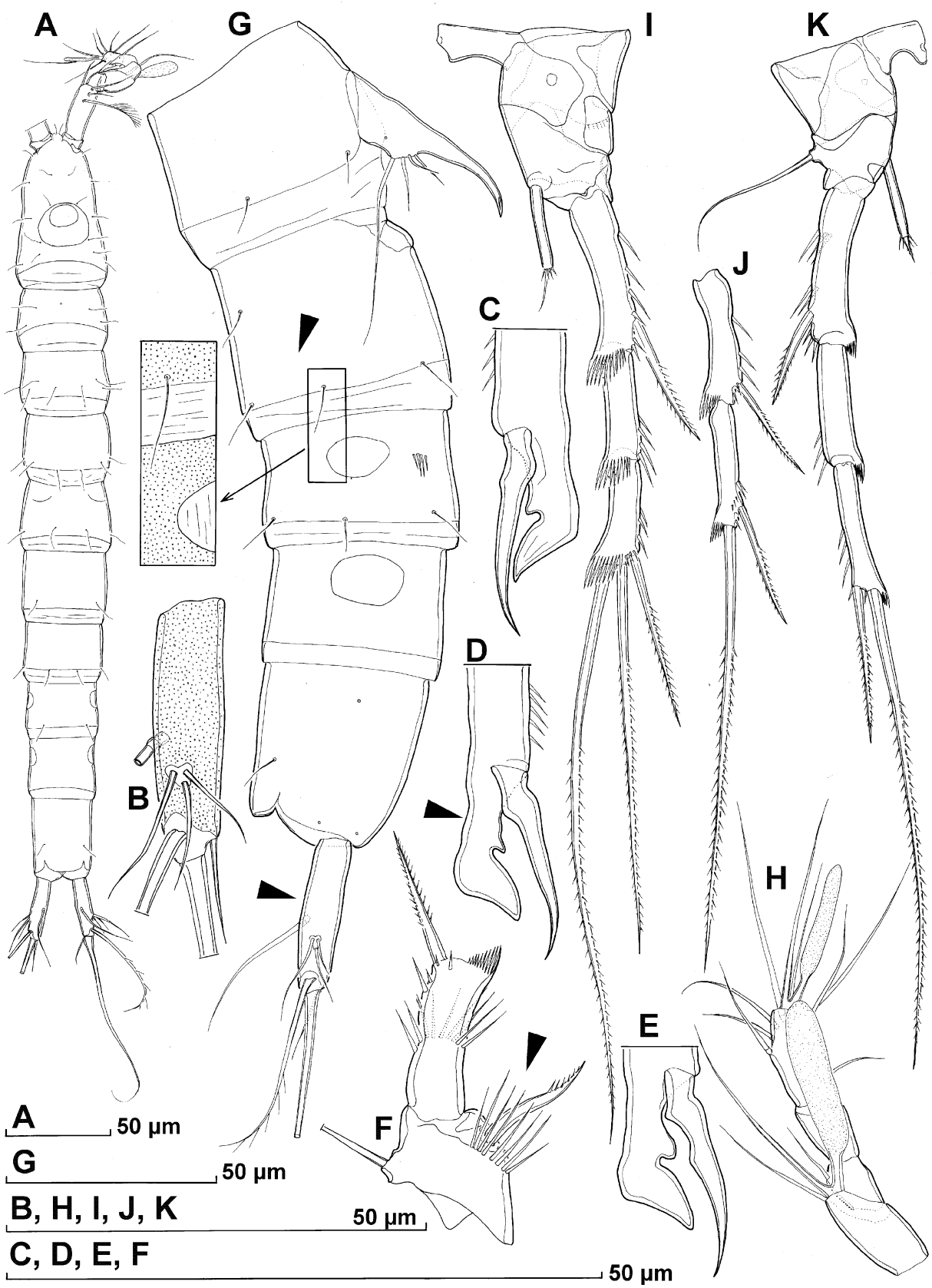

FIGURE 19. *Kinnecaris lined* **sp. nov.**, A-C & F, holotype male; D, paratype male I; E, paratype male II; G-K, allotype female: A, habitus, dorsal view; B, right caudal ramus, lateral view; C-E, distal part of third swimming leg, anterior view; F, basis, endopod, and first exopodal segment of fourth swimming leg, anterior view; G, urosome, lateral view; H, distal part of antennula, ventral view; I, second swimming leg, anterior view; J, exopod of third swimming leg, anterior view; K, fourth swimming leg, posterior view. Inset showing cuticular pits and fine ornamentation of urosome. Arrows pointing shorter caudal rami than in previous species and absence of large spinules on genital double-somite (G), characteristic shape (absence of apical notch) of third leg apophysis (D), and very long basal spinules at base of fourth leg endopod (F).

Genital double-somite (Fig. 19G) about 1.1 times longer than wide in dorsal view, without any trace of subdivision except for pair of ancestral dorso-lateral sensilla in anterior half; additionally ornamented with six posterior sensilla; no dorso-lateral rows of large spinules (condition arrowed in Fig. 19G). Genital complex (Fig. 19G) as in *K. lakewayi*, but sixth legs without spiniform processes.

Third urosomite (Fig. 19G) similar to that in male, with two ventro-lateral rows of four large spinules and clearly visible lateral cuticular windows.

Fourth (preanal), and fifth (anal) urosomites (Fig. 19G) also very similar to those in male, without any large or small spinules, except those in anal sinus.

Caudal rami (Fig. 19G) also very similar to those in male, slightly inflated at middle from lateral view (arrowed in Fig. 19G).

Antennula (Fig. 19H) very similar to that in *K. lakewayi*, with slightly more robust apical aesthetasc.
Antenna, mouth appendages, first swimming leg, second swimming leg (Fig. 19I), and exopod of fourth swimming leg (Fig. 19K) very similar to those of male and almost without any difference from those in *K. lakewayi*.
Endopod of second swimming leg (Fig. 19I) 7.2 times as long as wide, its apical seta very slender and only half as long as segment.

Third swimming leg (Fig. 19J) similar to *K. lakewayi*, with only slightly proportionately longer apical seta on second segment and more strongly expressed cuticular plates on praecoxa and coxa.

Endopod of fourth swimming leg (Fig. 19K) about seven times as long as wide, half as long as first exopodal segment, armed with short bipinnate element apically, ornamented with six spinules along distal margin, at base of apical seta. Exopod similar to that in male, but without large spinules on posterior surface of first exopodal segment.

Fifth leg (Fig. 19G) similar to that in male, but slightly more elongated, with narrower distal part.

Sixth leg (Fig. 19G) vestigial, both fused into simple bilobate cuticular plate, covering gonopore, unornamented and unarmed; outer distal corners well rounded, not produced into sharp processes, slightly shorter than inner lobes.

Etymology. The species name comes from its type locality (line D; see fig. 23), but should be treated as comprising an arbitrary combination of letters that can be treated as a Latin word and may be conceived as a noun in apposition to the generic name.

Variability. Body length of males ranges from 355 to 395 µm (384 µm average; n = 6), while in females it ranges from 362 to 403 µm (388 µm average; n = 30). No other significant forms of variability or asymmetry were observed. The shape of the apohysis of the male third leg (Fig. 19C, D, E) is a very good morphological character, showing very little variability in shape or size, and then mostly due to slightly different angle of observation.

Remarks. This species does not show some remarkable autapomorphic morphological features, but is distinct from all other Australian congeners in at least one or two characters, and COI data also suggest its separate specific status. Phylogenetic analyses of the COI data suggest a sister relationship of *K. lined* **sp. nov.** and *K. linel* **sp. nov.**, although support for this clade is not very strong (Fig. 23). The two species, however, differ not only in the proportion of the caudal rami and ornamentation of urosomites, but also in the armature of the fourth leg basis and exopod in male, as well as in the third leg apophysis (arrowed in Fig. 19D, F, G). A very strong ornamentation of the fourth leg basis in male (Fig. 19F) distinguishes at once *K. lined* from *K. lakewayi* **sp. nov.**, *K. barrambie* **sp. nov.**, *K. esbe* **sp. nov.**, *K. linel*, and *K. uranusi* **sp. nov.** Similarly strong ornamentation was observed only in *K. eberhardi* (Karanovic, 2005) and *K. linesae* **sp. nov.** (see below). The former species, however, has the apical part of the fourth leg endopod completely smooth (Karanovic, 2005), while the latter has much shorter caudal rami, smooth cuticle (no pits), no large spinules on the third urosomite in female, as well as a different shape of the third leg apophysis in male. *Kinnecaris solitaria* (Karanovic, 2004) is probably the most similar species to *K. lined* in morphology; this species was described from Depots Spring station, some 70 km south of Yeelirrie and in a different palaeochannel. Unfortunately, *K. solitaria* is still known only after females, so no male characters can be compared. The females differ slightly in the caudal rami shape, which are more cylindrical in dorsal (or ventral) view in *K. solitaria*, and the number of lateral setae on them (only two in *K. solitaria*). The reduced number of lateral caudal setae is an autapomorphic feature of *K. solitaria* among Australian congeners, although it was reported for several species from Africa (Karanovic, 2004). No doubt, this reduction originated convergently and does not indicate a closer phylogenetic relationship. It is also possible that the smallest lateral seta has been overlooked in some earlier descriptions, so we cannot put too much emphasis on this character. *Kinnecris lined* differs from *K. solitaria* also

by the densely pitted cuticle (inset in Fig. 19G), more slender anal somite (Fig. 19A), and stronger and ornamented endopod of the fourth leg (Fig. 19K).

Kinnecaris linesae sp. nov.

(Figs. 20–22)

Type locality. Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line A, Wirraway Bore, 27.097464˚S 119.760755˚E.

Type material. Holotype male dissected on one slide (WAM C47210); allotype female dissected on one slide (WAM C47211); one paratype male and one paratype female on one SEM stub *in toto* (WAM C47212); one paratype female destroyed for DNA sequences (amplification unsuccessful); two paratype females dissected on one slide each (WAM C47213 and C47214); four paratype females in alcohol (WAM C 47215); all collected at type locality, leg. T. Karanovic & G. Perina, 15 March 2010, seLN8504. Additional paratypes: three males + three females + two copepodid in alcohol, collected at type locality, leg. T. Karanovic & S. Callan, 18 March 2010, seLN8558. Additional paratype female in alcohol, collected at type locality, leg. P. Bell & S. Callan, 15 November 2009.

Other material examined. One female destroyed for DNA sequence (amplification successful; see Fig. 23); 2 males in alcohol (WAM C47216); Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line E, bore YYHHC0118A, 27.0354526˚S 119.7159141˚E, leg. S. Callan & G. Perina, 22 September 2010, seLN100379.

One female destroyed for DNA sequence (amplification successful; see Fig. 23);one male and one female in alcohol; Australia, Western Australia, Yilgarn region, Yeelirrie pastoral station, bore line E, bore YYHHC0103B, 27.035571˚S 119.717257˚E, leg. S. Callan & G. Perina, 22 September 2010, seLN100387.

Description. Male (based on holotype and four paratypes). Total body length from 312 to 354 µm (330 µm in holotype). Surface of integument of all somites extremely smooth, without minute spinules or cuticular pits (Fig. 21). Colour, naupliar eye, rostrum, body segmentation, and pore and sensilla pattern of all somites as in *Kinnecaris lakewayi* (see above). Habitus (Fig. 21A) cylindrical and slender, without any demarcation between prosome and urosome in dorsal or lateral view; prosome/urosome ratio about 0.74; greatest width from dorsal view hard to establish. Body length/width ratio about 8.4; cephalothorax about as wide as genital somite. Integument relatively weakly sclerotized, smooth, without rows of minute spinules; large spinules present only on third urosomite ventrally (Fig. 21A). Cephalothorax with clearly visible double dorsal cuticular window posteriorly; fourth and fifth urosomites each with pair of oval lateral cuticular windows (Fig. 21A).

Cephalothorax about 1.5 times as long as wide in dorsal view; representing about 19% of total body length. Surface of cephalic shield ornamented as in *K. lakewayi*, as well as tergites and pleuras of free pedigerous somites. Genital somite (Fig. 21A) ornamented with three pairs of sensilla on posterior margin and one pair of ventro-lateral very small cuticular pores in anterior part; spermatophore visible inside in holotype and two paratypes, similar size to that in *K. lakewayi*.

Third urosomite (Fig. 21A) ornamented with two rows of four large spinules ventrally and with six posterior sensilla.

Fourth urosomite (Fig. 21A) ornamented with two ventral rows of large spinules at middle, in front of relatively small, but clearly visible, lateral cuticular windows; additionally ornamented with six posterior sensilla.

Fifth (preanal) urosomite (Fig. 21) with larger lateral cuticular windows but without any ornamentation.

Anal somite (Figs. 20A, 21A, G) 1.3 times as long as preanal somite (more than in any other species described here), ornamented with pair of large dorsal sensilla at base of anal operculum, lateral pair of large cuticular pores (one pore on each side) in anterior half, two lateral pairs of minute cuticular pores close to posterior margin, and ventral pair of slightly larger cuticular pores, at base of caudal rami; no spinules of any size on outer surface. Anal operculum well developed, unornamented on outer surface, with row of slender spinules on inner surface, with smooth and nearly straight distal margin, reaching posterior end of anal somite, representing 67% of somite width. Anal sinus widely opened, with two diagonal rows of slender spinules on ventral side and transverse row of spinules on dorsal side (below anal operculum).

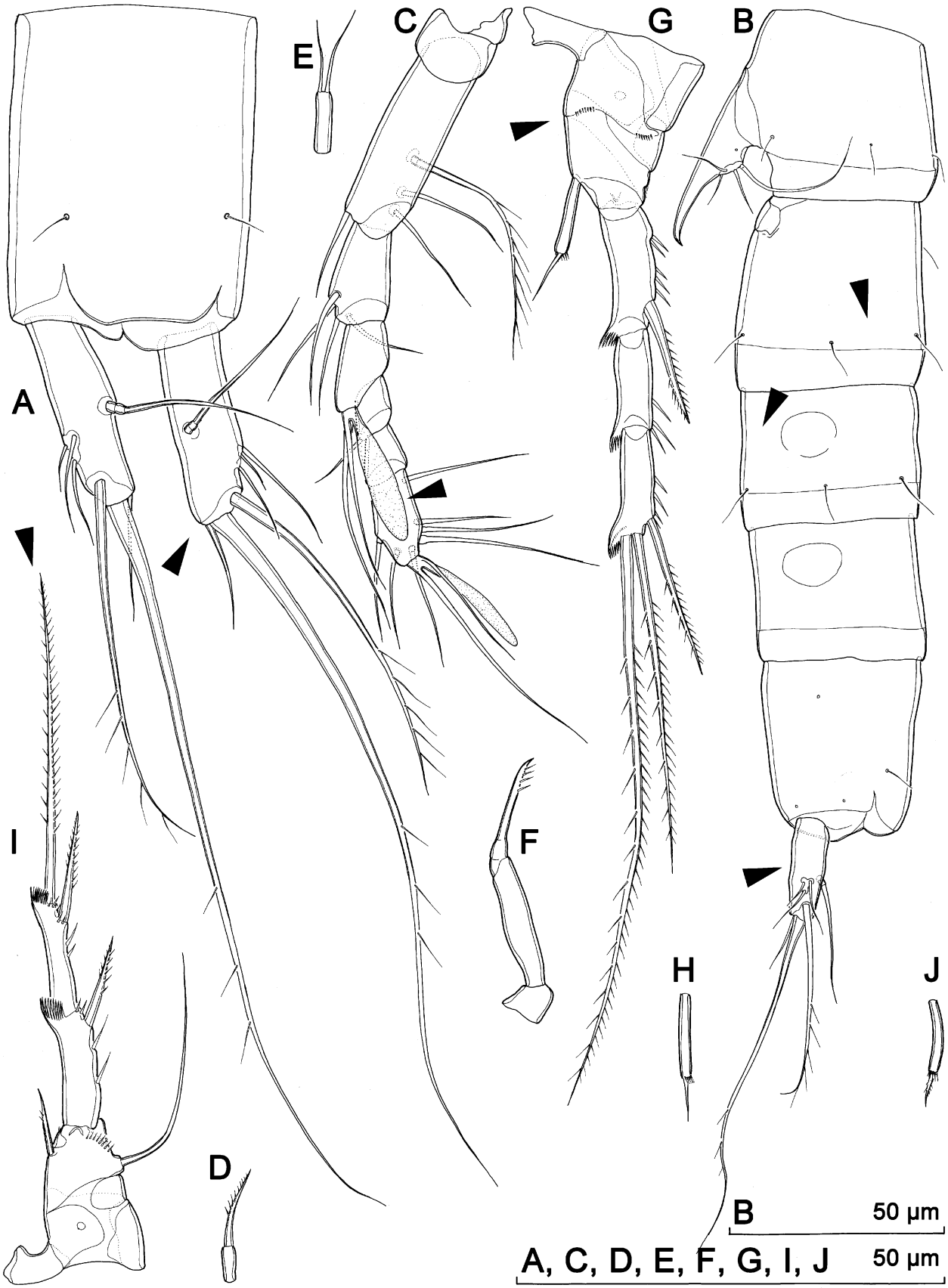

FIGURE 20. *Kinnecaris linesae* **sp. nov.**, A, holotype male; B-J, allotype female: A, anal somite and caudal rami, dorsal view; B, urosome, lateral view; C, antennula, ventral view; D, exopod of antenna, lateral view; E, mandibular palp, posterior view; F, maxilliped, anterior view; G, right second swimming leg, posterior view; H, endopod of left second swimming leg, anterior view; I, third swimming leg, anterior view; J, endopod of fourth swimming leg, posterior view. Arrows pointing numerous features different from previous species: shorter caudal rami (A & B), absence of any spinules on urosome (B), short easthetasc on antennula (C), additional row of spinules on second leg coxa (G), and shorter apical seta on third leg (I).

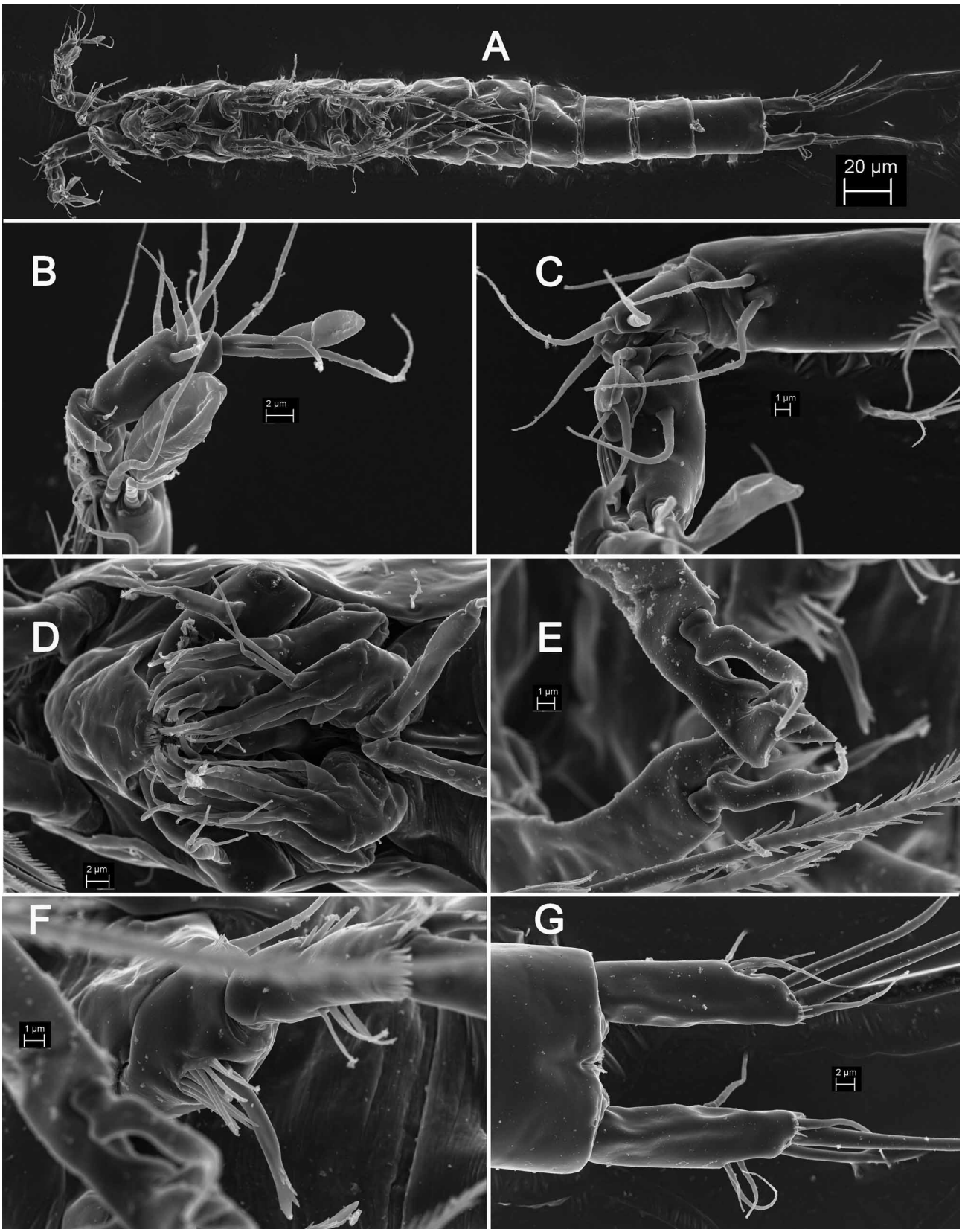

FIGURE 21. *Kinnecaris linesae* **sp. nov.**, SEM photographs, paratype male: A, habitus, ventral view; B, distal part of left antennula, ventral view; C, proximal part of right antennula, ventral view; D, mouth appendages, ventral view; E, distal parts of third swimming legs, anterior view; F, basis and endopod of fourth swimming leg, anterior view; G, anal somite and caudal rami, ventral view.

Caudal rami (Figs. 20A, 21G) parallel, with space between them about 1.3 times one ramus width, about 3.1 times as long as greatest width (dorsal view) and 0.7 times as long as anal somite, generally cylindrical in anterior half, but somewhat tapering in distal half and with diagonal distal margin (inner corner being much more produced than outer corner in dorsal or ventral view; arrowed in Fig. 20A), slightly inflated at midlength in lateral view; base about as wide as rest of ramus. Armature and ornamentation as in *K. lakewayi*, but lateral setae inserted more posteriorly (at about 3/4 of ramus' length) and principal apical seta with straight tips.

Antennula (Fig. 21B, C), antenna (Fig. 21A), mouth appendages (Fig. 21D), and first two pairs of swimming legs (Fig. 21A) very similar to those in *K. lakewayi*.

Third swimming leg (Fig. 21E) also generally similar to *K. lakewayi* but apophysis much larger, not bilobate, with very broad distal part (more than in any other species described here), with slightly concave distal margin and apical tip at about same level as inner distal corner; ornamentation same as in *K. lakewayi*, including longitudinal row of large spinules on outer margin of first exopodal segment distally; exopodal spine about 1.2 times as long as apophysis, but unlike in other species bent inwards at 90° angle, its distal tip touching distal margin of apophysis.

Fourth swimming leg (Fig. 21F) with nine very long spinules on basis at base of endopod, both similar to *K. lined*; endopod spiniform with five small spinules along distal quarter of outer margin, not arranged in scoop-like structure. First exopodal segment with several very long spinules on posterior surface at about midlength. Apical seta on third exopodal segment about as long as entire exopod and about three times as long as outer spine.

Fifth leg (Fig. 21A) without any difference from that in *K. lakewayi*, except for absence of cuticular pits.

Sixth legs (Fig. 21A) as in *K. lakewayi*.

Female (based on allotype and several paratypes). Body length from 322 to 364 µm (343 µm in allotype). Habitus, ornamentation of prosomites (Fig. 22A), colour, and naupliar eye similar to those in male, except genital and first abdominal somite fused into double-somite and middle part slightly less slender, as well as absence of large spinules on urosome. Prosome/urosome ratio 0.8; greatest width from dorsal view hard to establish; body length/width ratio about 8.2; cephalothorax 1.1 times as wide as genital double-somite.

Genital double-somite (Figs. 20B, 22A, C) about 1.1 times as long as wide in dorsal view, without any trace of subdivision except for pair of ancestral dorso-lateral sensilla in anterior half; additionally ornamented with six posterior sensilla; no rows of large spinules dorso-laterally (condition arrowed in Fig. 20B). Genital complex (Fig. 22C) as in *K. lakewayi*, with outer distal corners of genital operculum (fused sixth legs) produced into short and sharp spiniform processes.

Third urosomite (Figs. 20B, 22A) similar to that of male, without any ventro-lateral large spinules (condition arrowed in Fig. 20B), and with clearly visible small lateral cuticular windows.

Fourth (preanal), and fifth (anal) urosomites (Fig. 20B) also very similar to those of male, without any large or small spinules, except those in anal sinus.

Caudal rami (Fig. 20B, 22B) very similar to those of male, although slightly inflated at middle from lateral view (arrowed in Fig. 20B).

Antennula (Figs. 20C, 22A) very similar to that in *K. lakewayi*, with only slightly shorter proximal aesthetasc (arrowed in Fig. 20C).

Antenna (Fig. 20D), mouth appendages (Figs. 20E, F, 22D), first swimming leg (Fig. 22A, D), second swimming leg (Fig. 20G, H), and exopod of fourth swimming leg (Fig. 22A) very similar to those of male and almost without any difference from those of *K. lakewayi*.

Endopod of second swimming leg (Fig. 20G, H) about seven times as long as wide, its apical seta very slender and only half as long as segment.

Third swimming leg (Fig. 20I) similar to *K. lakewayi*, but with proportionately shorter apical seta on second segment (arrowed in Fig. 20I) and more strongly expressed cuticular plates on praecoxa and coxa.

Endopod of fourth swimming leg (Fig. 20J) about seven times as long as wide, half as long as first exopodal segment, armed with short bipinnate element apically, ornamented with six spinules along distal margin, at base of apical seta. Exopod similar to that of male, but without large spinules on posterior surface of first exopodal segment.

Fifth leg (Figs. 20B, 22C) similar to that of male, but slightly more elongated, with narrower distal part; cuticular window visible (although not well defined) with scanning electron microscope, but not visible with light microscope.

Sixth legs (Fig. 22C) vestigial, fused into simple bilobate cuticular plate, covering gonopore, unornamented and unarmed; outer distal corners produced into short and sharp spiniform processes, but significantly shorter than inner lobes.

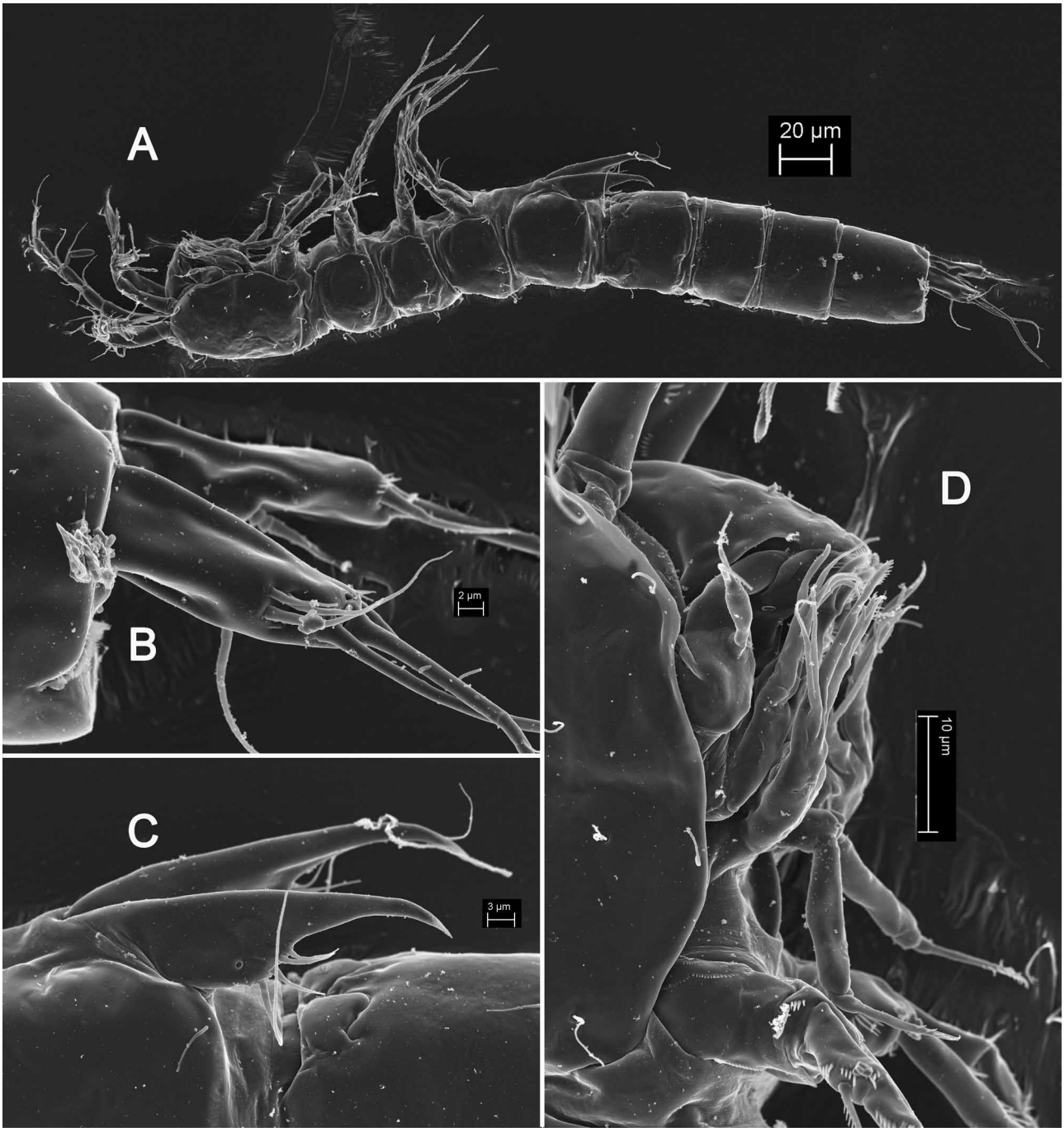

FIGURE 22. *Kinnecaris linesae* **sp. nov.**, SEM photographs, paratype female: A, habitus, lateral view; B, anal somite and caudal rami, lateral view; C, fifth legs and anterior part of genital double-somite lateral view; D, mouth appendages, lateral view.

Etymology. The species name comes from the two bore lines where it was collected (lines A and E; see fig. 23), but should be treated as comprising an arbitrary combination of letters that can be treated as a Latin word and may be conceived as a noun in apposition to the generic name.

Variability. Body length of males ranges from 312 to 354 µm (337 µm average; n = 5), while in females it ranges from 322 to 364 µm (344 µm average; n = 13). No other significant forms of variability or asymmetry were observed. The shape of the apohysis of the male third leg (Fig. 21E) is extremely conservative, as is the somite ornamentation (or the lack of it).

Remarks. This species differs from all other eight Australian congeners by the absence of all spinules on all somites in female, including those on the third urosomite ventrally (arrowed in Fig. 20B); the only spinules left are those on the male third urosomite ventro-laterally (Fig. 21A). It also has the shortest caudal rami of all Australian species, with diagonal distal margin in ventral view (Fig. 21G), as well as an extremely broad distal part of the third leg apophysis in male (Fig. 21E). Cuticle is extremely smooth in this species, without any cuticular pits. The only other Australian *Kinnecaris* Jakobi, 1972 that lacks cuticular pits is *K. solitaria* (Karanovic, 2004), which is unfortunately still only known after females, so the male characters cannot be compared. The latter species, however, can easily be distinguished from *K. linesae* **sp. nov.** by the reduced number of lateral caudal setae, longer caudal rami, presence of minute spinules on the anal somite, and presence of large spinules on the third urosomite. Molecular data (Fig. 23) suggest that *K. linesae* is more closely related to *K. uranusi* **sp. nov.** (and one undescribed species from line P: *K.* sp.) than to *K. linel* **sp. nov.** or to *K. lined* **sp. nov.** Morphological data do not support this relationship, and differences between *K. linesae* and *K. uranusi* are numerous, while the latter species is morphologically very similar to *K. linel* (see above).

Molecular results

DNA was extracted and the COI fragment successfully PCR-amplified from 12 parastenocaridid specimens (Table 2) using a nested combination of primers given in Table 1. Unfortunately, despite repeated attempts, we were not able to successfully amplify COI fragment of *Kinnecaris esbe* **sp. nov.**, and for *K. barrambie* **sp. nov.** we did not have enough material for both morphological and molecular analysis. Research on *K. lakewayi* **sp. nov.** was supported from a different project, without any budget for molecular work; moreover, material was originally not preserved with molecular work in mind (70% ethanol), so no specimens of this species were used for molecular studies either. One juvenile specimen from the Yeelirrie bore line P (100411b *Kinnecaris* sp.) was the only representative of its genus from this line, so we decided to sequence it. It probably represents a separate species (Fig. 23), but without any material left for morphological observations it could not be described and named. Given the subtle nature of morphological differences between different species described in this paper, it is also quite clear that we would not be able to recognize or describe this species based on a single juvenile specimen. Because sampling in this remote region has been completed for now, and we had no other means of collecting more specimens of this potentially new species, we decided to present our results in their somewhat incomplete form. Both morphological and molecular data are available so far only for four *Kinnecaris* Jakobi, 1972 species (Table 2).

The edited COI sequences were imported into the program MEGA v. 4 (Kumar et al., 2008) and aligned using CLUSTAL W. All the sequences were translated into protein using MEGA and were shown to have no evidence of stop codons indicative of non-functional copies of COI. BLAST analyses of GenBank revealed that the obtained sequences are copepod in origin and not contaminants, although none of the GenBank COI sequences were included in our phylogenetic analyses.

Average pairwise distances between morpho-taxa were found to be very high, with the lowest divergence (8.2%) between *Kinnecaris linesae* **sp. nov.** and *Kinnecaris* sp. (Table 3). Second (8.4 %) and third (9.6%) lowest divergences were found between *Kinnecaris* sp. and *K. uranusi* **sp. nov.** and between *K. linesae* and *K. uranusi* respectively, while those between all other taxa were in excess of 12%. The latter high divergence values are generally indicative of distinct species by comparison with other crustaceans (Lefébure et al., 2006). Average pairwise distances among the three Australian parastenocaridid genera were all about 20% or higher, indicating only a remote relationship, and are comparable to those among some well accepted canthocamptid genera (Karanovic & Cooper in press).

The highest divergences within morpho-taxa were those between three specimens of *K. uranusi* (0.3%), which came from three different bore lines (F, H & 1; see Fig. 24). Two specimens of *K. linel* **sp. nov.** came from two different bores on line L, with the divergence between them being about 0.2%. These are all indicative of intraspecific variability (Lefébure et al., 2006). Two specimens of *K. linease* came from two different bores on line E, with zero divergence between their sequences. Zero divergence was also observed between two specimens of *K. lined* **sp. nov.**, although these came from a single bore (and thus are more likely to be kin).

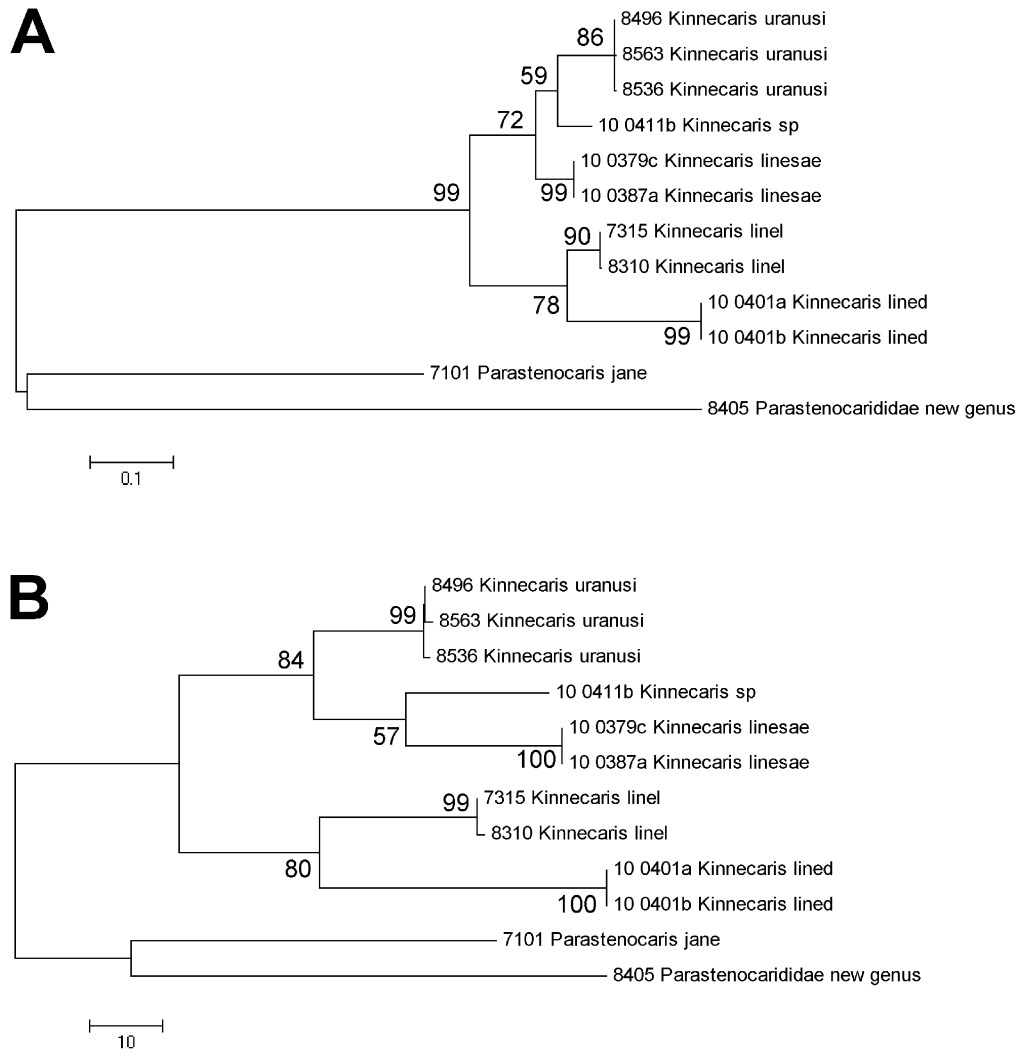

FIGURE 23. Two cladograms based on COI sequence data from copepod specimens of the Yeelirrie calcrete and the Pilbara region: A, maximum likelihood (ML) tree constructed using MEGA v 5.0.3 and an HKY+G model of evolution (selected using a Bayesian Information Criterion as being the optimal model), with the numbers on the branches representing bootstrap values from 500 pseudoreplicates; B, single maximum parsimony (MP) tree, with a length of 324 steps, and bootstrap values shown on some branches. The cladograms are drawn to scale and specimen numbers correspond to those in table II.

TABLE 3. Average pairwise NJ distances (P-distance model) among COI sequences between seven morpho-species of Australian Parastenocarididae (lower diagonal) and within morpho-species (diagonal).

Species	1	2	3	4	5	6	7
1. *Kinnecaris linel*	0.002						
2. *Kinnecaris uranusi*	0.131	0.003					
3. *Kinnecaris lined*	0.121	0.168	0.000				
4. *Kinnecaris* sp.	0.157	0.084	0.152	-			
5. *Kinnecaris linease*	0.123	0.096	0.158	0.082	0.000		
6. *Parastenocaris jane*	0.201	0.198	0.218	0.218	0.224	-	
7. New Genus	0.221	0.226	0.226	0.242	0.220	0.220	-

All analyses (Fig. 23) indicated the presence of at least seven genetically divergent lineages, each supported with high bootstrap values. Tree generated with Neighbour Joining (NJ) was very similar to that generated with Maximum Likelihood (ML), so only the latter is presented here. Overall tree topology did not differ significantly

for NJ, ML or MP analyses, which shows robustness of our data for this analysis. Maximum Parsimony (MP) method produced a single tree of 324 steps (Fig. 23B), which differs from the ML tree only slightly in the position of *Kinnecaris* sp. (showing it to be a sister clade of *K. linesae* rather than of *K. uranusi*). This clade, however, has a very low bootstrap value in both analyses, and because *Kinnecaris* sp. was not studied morphologically in this study, these differences are of little importance. Three genera formed three separate clades with a bootstrap support of 99% or 100% in all analyses. Unfortunately, two major clades of *Kinnecaris* were not that well supported: the *uranusi/sp./linesae* clade has a support of only 72% in our ML analysis, while it is slightly better supported (84%) in our MP analysis (Fig. 23A, B). The *linel/lined* clade was slightly better supported in our MP analysis (80%) than in our ML analysis (78%), but this cannot be considered a strong support, and is also contradicted by our morphological data (see below). The lineage with the weakest support (59% in ML and 57% in PM analyses) is the one determining the sister relationship of *Kinnecaris* sp., but because of the lack of morphological data for this haplotype we will not comment on it any more.

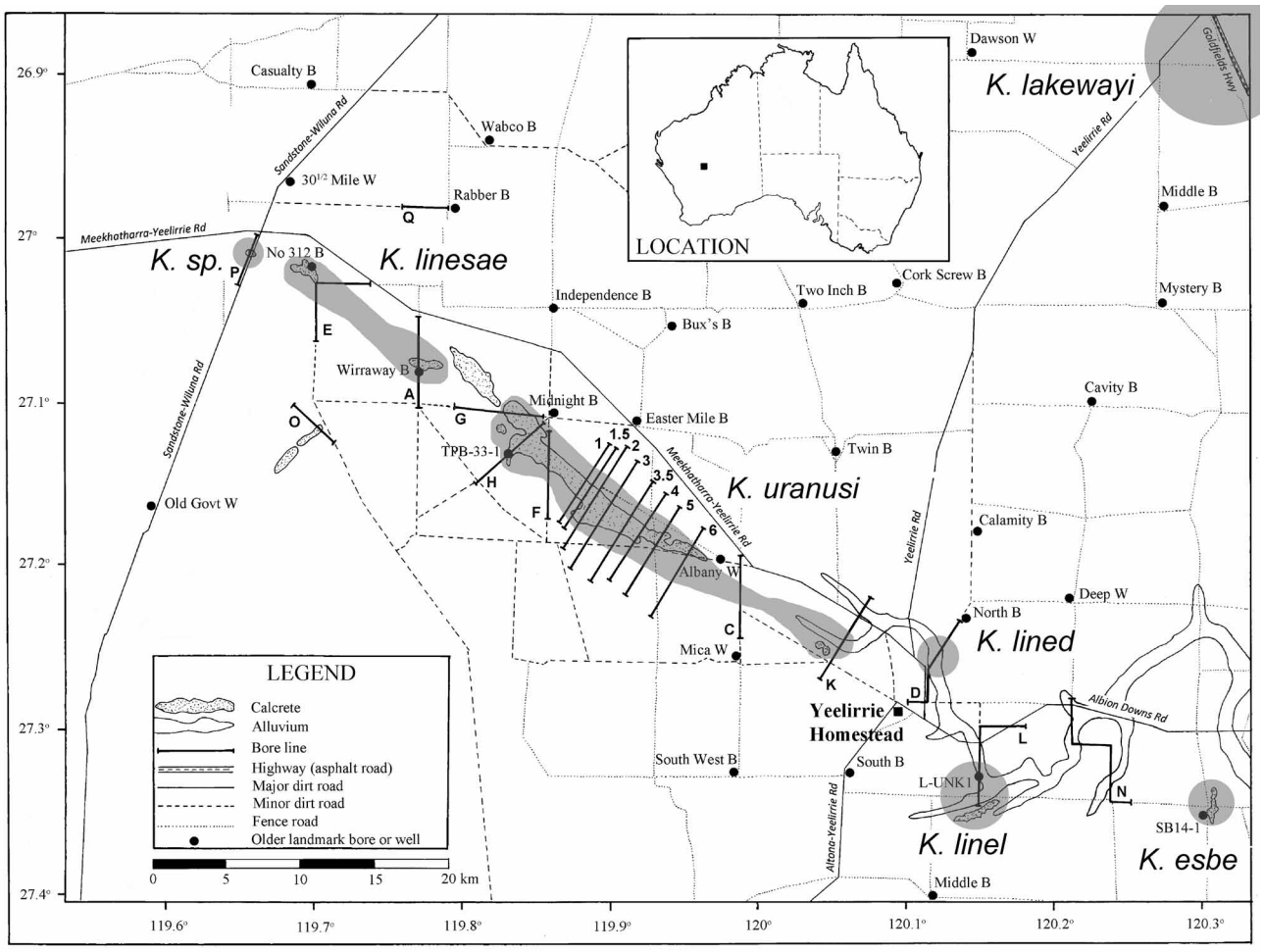

FIGURE 24. Distributional ranges of six short range endemics from the genus *Kinnecaris* Jakobi, 1972 in the Yeelirrie palaeochannel (distribution of *K. lakewayi* **sp. nov.** in a parallel palaeochannel only partly shown in the right top corner). Map of the area investigated shows only some of the sampling localities (bores and wells) in Yeelirrie; all others lie on the following 21 bore lines (from north-west to south-east): P, Q, O, E, A, G, H, F, 1, 1.5, 2, 3, 3.5, 4, 5, 6, C, K, D, L, and N. The water flow in the palaeochannel is also in this direction. Upper inset shows the location of the area in Australia.

Discussion

Diversity in the Yeelirrie calcretes. The new parastenocaridid genus and five of the seven *Kinnecaris* species described here come from Yeelirrie, a newly investigated locality for groundwater fauna (Fig. 24) in the Yilgarn region (not surveyed in Karanovic 2004), which revealed an unprecedented diversity of copepod crustaceans. Up to seven species per single bore in a single sampling event were quite normal (Fig. 26), but this number was as high as

ten when counting all sampling occasions from a single locality. The Yeelirrie area, which contains one of the largest calcretes in the uppermost reaches of the Carey palaeochannel (Timms 1992), is only about 75 km long and less than 10 km wide, but the surface area of suitable habitats (calcretes) is probably less than 100 km^2 (see Fig. 24). Using morphological methods we were able to distinguish 22 different species and subspecies here, from six copepod families. Sequence analyses of the mitochondrial COI gene supported the presence of all these species and additionally revealed the presence of three potential cryptic species (Karanovic & Cooper in press, submitted, in preparation). This finding equates to about 70% of previously recorded diversity in the whole Yilgarn region, and this region was relatively well surveyed (Karanovic 2004). The harpacticoid genus *Schizopera* G.O. Sars, 1905 is especially diverse here, containing nine different species in this calcrete (almost twice the number of species previously known from this whole region), and up to four species in a single sampling bore (Fig. 26). This diversity of species is usually associated with a remarkable size differentiation, comparable only to that previously observed in some dytiscid beetles (Leys & Watts 2008). On the other hand, both morphological and molecular data confirm that other major stygofauna groups (ostracods, amphipods, isopods, and dytiscids) in this calcrete are much less diverse, containing the usual number of one to three species, which would suggest different ages and colonization histories for different groups (Karanovic & Cooper submitted).

Unlike members of *Schizopera*, species of the genus *Kinnecaris* are all allopatric in distribution and differ very little morphologically, including their size. Interestingly, distributional ranges of the new parastenocaridid genus and the genus *Kinnecaris* overlap only partly (on lines E, P, & A), and there is a marked size difference between them (Karanovic & Cooper in press), suggesting a potential niche partitioning with minimal competition for resources. The former lives in the upper reaches of the palaeochannel, in relatively freshwater, while the latter seems to have been adapted to waters of increased salinity, although we do not know the precise habitat of any taxon in a given bore, and it may be that *Kinnecaris* inhabits only a first few centimetres of the water column, where the water layer is relatively fresh (most of these habitats in Western Australia behave like anchialine systems, especially after a significant rain event, with a shallow top layer of freshwater laying on top of much deeper layer of saline and sometimes hypersaline water; Humphreys 2006; Humphreys et al. 2009).

Distributions and affinities of the new species. *Kinnecaris lakewayi* **sp. nov.** was collected in bores around Lake Way (Figs. 24, 25), just south-east of the small township of Wiluna. Subterranean waters in this area are also a tributary of the Carey Palaeochannel, which runs parallel to the Yeelirrie tributary and the two join at Lake Darlot, about 100 km south-east (Timms 1992; Johnson et al. 1999). This palaeochannel lies east of a major drainage divide which separates palaeochannels flowing west to the Indian Ocean from channels that drain east into the interior of Australia (Beard 1998). As mentioned above, we did not have a chance to do any molecular work on this species, but the geographical distance of nearly 200 km between it and the closest species from the Yeelirrie area (when measured downstream and then upstream the palaeochannel, see Timms 1992) would suggest only a remote relationship with other species described here. This is supported by our morphological studies, and *K. lakewayi* differs from all other Australian congeners by some additional armature on the urosomites, as well as by its unusual caudal rami shape (see above). Surprisingly, this species is morphologically most similar to *K. barrambie* **sp. nov.**, although some of the similarities are probably plesiomorphic character states and thus indicative of shared ancient ancestry rather than close phylogenetic relationships. Interestingly, *K. barrambie* was collected from a calcrete aquifer within the Cogla Downs system on the Yarrabubba pastoral lease, approximately 30 km north of Barrambie (Fig. 25). Cogla Downs is in the uppermost reaches of the extensive Nowthanna/Lake Annean palaeodrainage system that drains to the Indian Ocean. Thus, the distance between the two species is enormous, and dispersal unlikely, unless it is possible for these animals to distribute laterally and across ridges in the uppermost reaches of neighbouring palaeochannels, and then colonise their waters downstream. We will discuss this dispersal scenario further below. Unfortunately, only three specimens of *K. barrambie* were ever collected, which did not leave any material for our molecular analysis. Morphology of this species is a strange mixture of plesiomorphic and apomorphic character states, with the ornamentation of the genital double-somite and shape of the caudal rami being autapomorphic features. The only other *Kinnecaris* with two rows of large spinules on the genital double-somite laterally is *K. esbe* **sp. nov.** (see above), but this species has much longer caudal rami, much denser minute ornamentation on most somites, as well as a very different shape of the third leg apophysis in male. Also, the rows of large spinules on the genital double-somite are much closer to each other and clearly parallel in *K. esbe*, which makes us question their homology (or at least one of them) in these two species. Most probably, *K. barrambie* is not very closely related to any currently known Australian congener. Two other Australian species of *Kinnecaris* were described earlier by

Karanovic (2004, 2005), and we also did not have any suitable material of them for the molecular analysis. *Kinnecaris eberhardi* (Karanovic, 2005) was described from the south-western corner of Western Australia, some 800 km south from any other Australian species. Not surprisingly, it shows a number of unique features among its congeners, including posteriorly inflated caudal rami, and a smooth endopod of the male fourth leg. Absence of any large spinules on the female urosomites and very large basal spinules on the male fourth leg are features it shares with *K. linease* **sp. nov.**, a species from the uppermost reaches of the Yeelirrie palaeochannel, but the urosomal spinules may have been lost independently and basal spinules are most probably a plesiomophic character state. The two species differ in many characters, most notably in the shape of the male third leg apophysis and caudal rami (see above; Karanovic 2005). *Kinnecaris solitaria* (Karanovic, 2004) was described less than 70 km south of Yeelirrie, from Depots Spring pastoral station (Fig. 25). This area, however, belongs to the Raeside Palaeochannel, which runs parallel to the Carey Palaeochannel, and also belongs to the internal drainage. Unfortunately, this species is still known only after females, so many important male morphological characters cannot be compared (Karanovic, 2004). Females are probably most similar to those of *K. lined* **sp. nov.** (see above), but they differ in the caudal rami shape and the number of lateral setae on them (latter being an autapomorphic feature of *K. solitaria* among Australian congeners). The reduced number of lateral caudal setae was also reported for several African species (Chappuis 1936, 1952, 1955; Fryer 1956; Wells 1964), but this reduction probably originated convergently and does not indicate a closer phylogenetic relationship. At this stage we cannot put too much emphasis on this character, as it is also possible that the smallest lateral seta has been overlooked in some earlier descriptions. *Kinnecris lined* differs from *K. solitaria* also by a densely pitted cuticle, more slender anal somite, and stronger and ornamented endopod of the fourth leg. Unfortunately, we were not able to test if these two species are closely related by molecular methods, and this remains one of the highest priorities for our future research, as it may help answer some questions of dispersal of stygofauna along and across palaeochannels and their dividing ranges.

A dendritic system of palaeodrainage channels is a prominent feature of the Yilgarn Craton of Western Australia, which are usually betrayed on the surface by chains of linear playa lakes (Clarke 1994). However, parastenocarids seem to be very rare here, possibly due to increased salinity in many aquifers (Beard 1976, Holmgren et al. 2006). That is probably the main reason why all discovered species so far are distributed in the uppermost reaches of their respective palaeochannels. One is almost tempted to predict that future discoveries in the Yilgarn will be along the drainage dividing line, in aquifers that are least affected by increased salinity.

Short range endemism. Five of the seven new species described in this paper are short range endemics, with allopatric distributions along the Yeelirrie palaeochannel (Figs. 24, 25). Another possible new species remained undescribed (*Kinnecaris* sp.), its only juvenile specimen being destroyed for COI sequence (Fig. 23). This species seems to be restricted to the smallest patch of calcrete in the area, in the north-western part of Yeelirrie, on bore line P (Fig. 24). This calcrete, along with that on line O (which lies on a small subterranean tributary of the main palaeochannel), has very fresh waters; our measurements in the field confirmed that salinity generally increases downstream (from north-west to south-east), although it may differ significantly on one transverse bore line, depending on the exact location in the calcrete (Karanovic & Cooper submitted). Molecular data (Fig. 23B) indicate that *K.* sp. is probably most closely related to *K. linesae* **sp. nov.**, which is quite logical and may indicate a recent speciation event, as the latter species was found on the closest bore lines further downstream of the boreline where *K.* sp. was collected (lines E & A; see Fig. 24). As no morphology is known for *K.* sp., we will not discuss it any further here. Further downstream from lines E and A is the largest calcrete body in the area (Fig. 24), which is home to *K. uranusi* **sp. nov.**, along with many other copepod species (Fig. 26). We were able to get COI sequences from three specimens collected on three different bore lines (H, F & 1), and the divergence between them was only 0.3% (Table 3). This would indicate a relatively high gene flow inside this calcrete, and is congruent with our discoveries in the genus *Schizopera* here (Karanovic & Cooper submitted), as well as in some other major groups of stygofauna (T. Finston pers. comm.). Although calcrete disappears on the surface between Albany Well and line K, it is quite possible that there is an underground narrow vain that connects the two, because besides *K. uranusi* a number of other stygobites (including some copepods) have been found in both areas, and COI data suggest a relatively high gene flow (Karanovic & Cooper submitted; in preparation; T. Finston pers. comm.). Unfortunately we did not manage to amplify COI from *K. uranusi* from line K, but detailed morphological observations with SEM (Figs. 16, 17, 18) showed no differences whatsoever. Our molecular analyses suggest *K. uranusi* to be a sister clade to the *linease/sp* clade (Fig. 23), but morphological data contradict this hypothesis. This would have to be resolved using different genes and more specimens, but at the moment we argure in favour of morphological data. *Kinnecaris ura-*

nusi is very different morphologically from *K. linesae*, but it is so similar to *K. linel* **sp. nov.**, that the two can be distinguished only by the most minute differences in the ornamentation of urosomites and proportions of the caudal rami (see above). They, together with *K. esbe* **sp. nov.,** undoubtedly represent a closely related group of species, defined by a number of synapomorphies: strongly elongated caudal rami, dense ornamentation of somites with minute spinules, similar ornamentation of urosomites with large spinules, reduced ornamentation on the male fourth leg basis at the base of the endopod, endopods of the male fourth legs with spinules arranged into scoop-like structures apically, with always seven spinules on the right leg endopod and nine on the left one. There is very little chance that all these characters may have originated independently driven by selection, or that they are plesiomorphic.

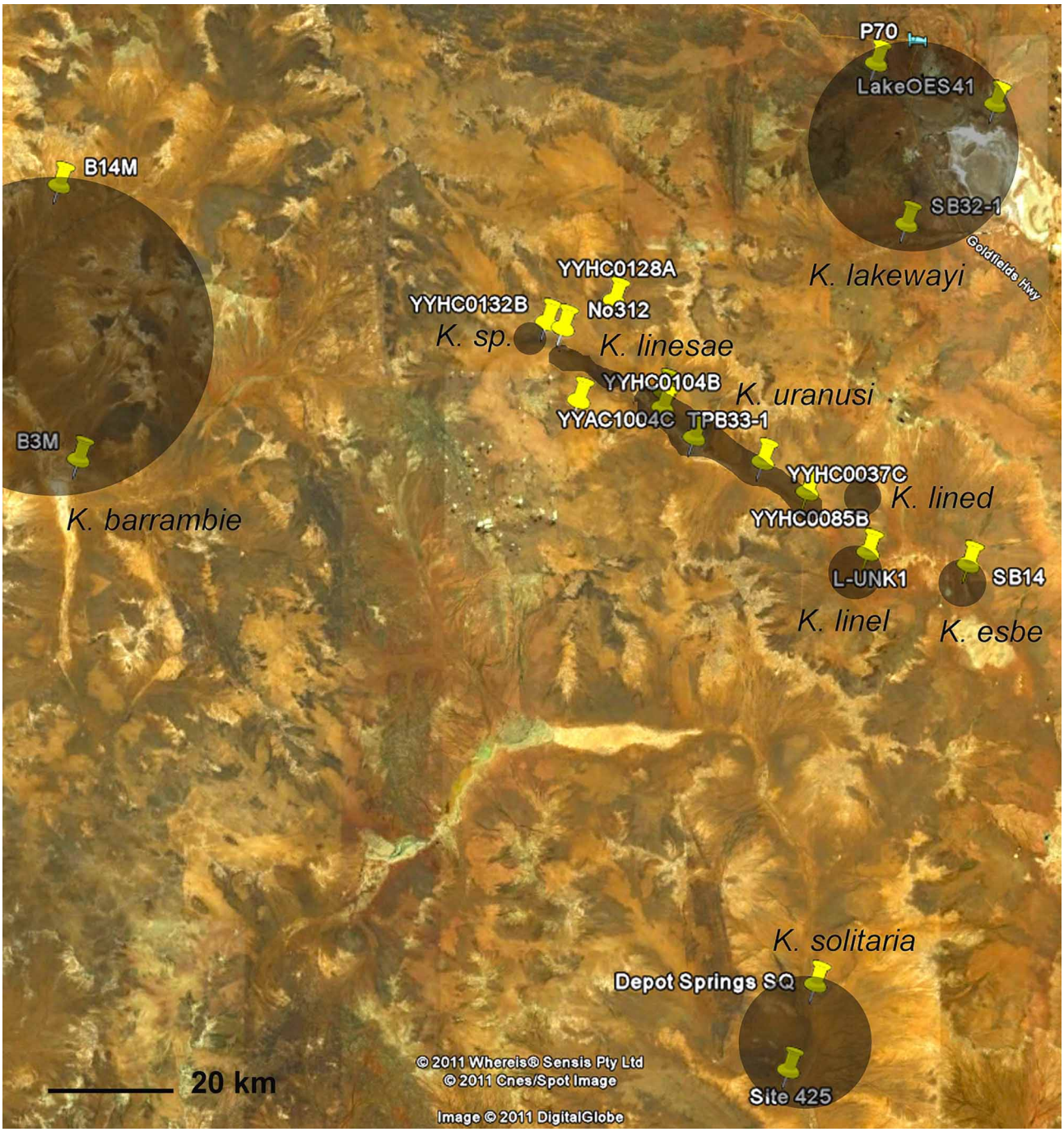

FIGURE 25. Distributional ranges (shaded areas) of all nine short range endemics from the genus *Kinnecaris* Jakobi, 1972 in the Yilgarn region: *K. lakewayi* **sp. nov.**, *K. barrambie* **sp. nov.**, *K. sp.*, *K. linesae* **sp. nov.**, *K. uranusi* **sp. nov.**, *K. lined* **sp. nov.**, *K. linel* **sp. nov.**, *K. esbe* **sp. nov.**, and *K. solitaria* (Karanovic, 2004). Pins show locations of some of the more prominent bores in the area, with bore names in white font. Map modified from Google Earth. Note that the only other Australian congener, *K. eberhardi* (Karanovic, 2005), is not a short range endemic, and lives almost 800 km south-west from the area shown on this map.

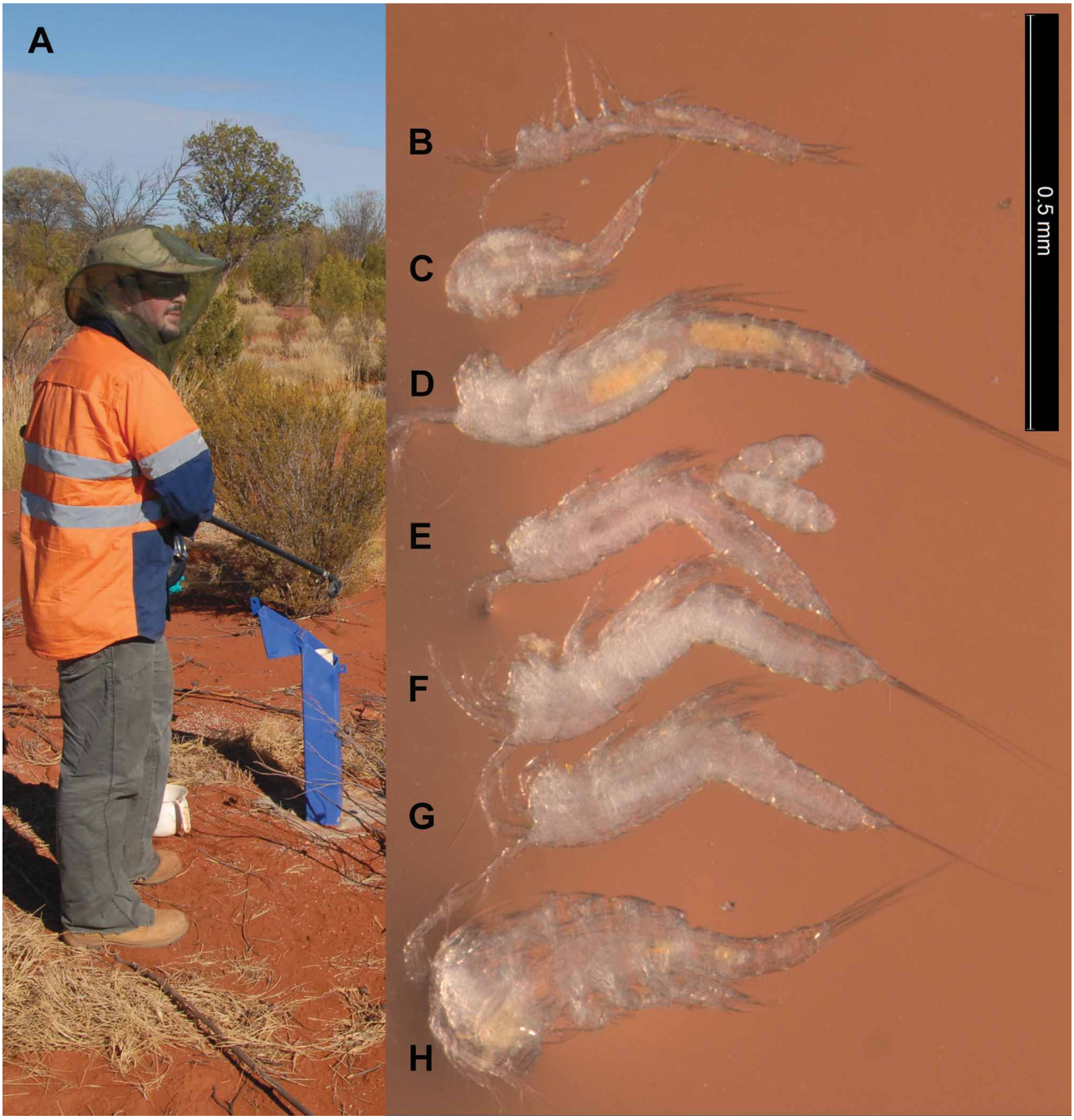

FIGURE 26. Seven sympatric copepod species from bore YYD26 (bore line 1): A, Mr Shae Callan sampling from the bore; B, *Kinnecaris uranusi* **sp. nov.**, adult female; C, *Pseudectinosoma* sp., adult female; D, *Nitocra* sp., adult female; E, *Schizopera* sp. 1, ovigerous female; F, *Schizopera* sp. 2, adult female; G, *Schizopera* sp. 3, adult female; H, *Halicyclops eberhardi* De Laurentiis, Pesce & Humphreys, 2001.

Morphological evidence would suggest a downstream colonisation history in the genus *Kinnecaris*, where the most plesiomorphic form (*K. linesae*) lives in the uppermost reaches of the palaeochannel, and the trend in the caudal rami elongation and denser somite ornamentation is obvious downstream the palaeochannel (*K. uranusi*, *K. linel*, and then *K. esbe*; see Fig. 24), with the only exception being *K. lined* which is probably an independent colonisation event. This colonisation history seems likely as parastenocarids are copepods of freshwater origin, and one can imagine dispersal of this group down the palaeochannel during periods of increased rainfall, with evolution into separate species in isolated calcrete pockets during periods of increased aridity. Our molecular data suggest a relatively close relationship between *K. lined* and *K. linel* (Fig. 23), which also have neighbouring areas of distribu-

tion in the lower part of the Yeelirrie palaeochannel (Fig. 24), but that is again contradicted by our morphological observations (see above). The two species differ in many characters, including the ornamentation of urosome, caudal rami shape, ornamentation of the endopods and bases of the male fourth leg, and even somewhat in the shape of the male third leg apophysis. The latter species is, as already mentioned, morphologically extremely similar to *K. esbe* and *K. uranusi*, with many characters in their transitional form between these two species, and also with an area of distribution that lies between those of *K. esbe* and *K. uranusi* (see Fig. 24). Although many of these questions will probably remain unanswered for quite some time, our current detailed morphological and molecular studies provide strong evidence that we are not dealing with one widely distributed and very variable species in the Yilgarn region but rather with a complex of short range endemics (Harvey 2002).

Intraspecific morphological uniformity. No Australian species of *Kinnecaris* shows dimorphism or polymorphism in the caudal rami shape, although caudal rami differ significantly between species. Dimorphism and even polymorphism in the caudal rami shape have been frequently reported for parastenocarids (see Schminke 1991), and also for several species of *Kinnecaris* (Fryer 1956; Wells, 1964; Ranga Reddy & Schminke 2009). Our experience with these and other harpacticoids is such that we would suggest reexamination of those cases also with molecular methods, as some of those "forms" may actually be closely related (but distinct) sympatric species. We recorded several such cases in the genus *Schizopera* recently also in the Yeelirrie palaeochannel (Karanovic & Cooper submitted). Interestingly, most of them were large species living sympatrically (ranges of the two most closely related overlap only partly), and the most obvious differences were found in the caudal rami, structures responsible for sexual recognition. In most harpacticoid copepods a male grabs a female by the caudal rami with their antennulae, at the start of the copulation process (Lang 1948; Dahms 1988; Huys & Boxshall 1991). This can be especially significant in subterranean environments, where several closely related species live together, with a limited possibility for species recognition using light or chemical signals.

This study was the first ever attempt at a molecular analysis of parastenocaridid copepods, and our amplification success rates were very low with universal primers of Folmer et al. (1994). That is why we used additional 'nested' primers (Table 1), designed from preliminary copepod COI sequence data, in combination with universal primers to improve the PCR-amplification efficiency. Even then our success rates were about 50% on average. This may be due to the very small size of specimens and correspondingly low amount of DNA isolate, but it is probably also because we are yet to find an optimal procedure and combination of primers for this group.

Seasonal dynamics in subterranean habitats. Here we shall mention one other important chance discovery during our work in the Yeelirrie area: that of very strong seasonal dynamics in this styofaunal community, which is a novel concept for subterranean ecosystems (Karanovic & Cooper in press, submitted & unpublished). It is almost common knowledge that stygobitic animals exhibit a reduction or loss of eyes and pigments, have enhanced non-optic sense organs, and species that are inhabiting interstitial spaces are most often vermiform (Culver et al. 1995). It is also a widely accepted view that many convergent physiological adaptations occur, especially lower metabolic rates and loss of circadian periodicity and seasonal dynamics (Gibert et al. 1994, Langecker 2000). Stygobiotic animals also lack resting stages, have fewer young and are longer lived than their surface relatives (Coineau 2001). Case studies of subterranean animals in Europe have revealed, for example, that embryonic development in the single egg of a bathynellid can take up to nine months (Coineau 2001). Studies on population dynamics and seasonal variability of stygobitic copepods in France and Slovenia (Lescher-Moutoué 1973, Pipan & Brancelj 2003, 2004) confirmed the generally accepted view that these ecosystems are indeed very stable, slow to recover, and intrinsically vulnerable to anthropogenic effects (Culver & Pipan 2009). This notion was applied to Australian subterranean environments uncritically (Humphreys 2001, 2008), although with some puzzling observations concerning the long persistence of stygofauna in subterranean habitats through geological eras and massive climatic changes. That is why we were so surprised to see pronounced differences in our stygofauna survey results in Yeelirrie in different months, despite very stable physical environmental conditions. Although most of the results are still awaiting publication, and in this paper we are only discussing one harpacticoid genus, it may be interesting to mention some observations. One species of the genus *Schizopera* was collected from the same bore (SB14-1) on three separate occasions, once in March 2009 and twice in March 2010, but was absent in January 2010, although we tried very hard to collect samples for DNA analysis (Karanovic & Cooper submitted). In fact, in January 2010 all harpacticoids were absent from this bore, and they include another new species of *Schizopera*, *Kinnecaris esbe* **sp. nov.,** and as yet undescribed new species each from the genera *Nitocra* Boeck, 1865, and *Pseudectinosoma* Kunz, 1935. In January 2010, the only copepod in the bore SB14-1 was *Halicyclops eberhardi* De Laurentiis, Pesce &

Humphreys, 2001. This bore was no exception, as many other localities produced very few or no harpacticoid specimens, despite an enormous sampling effort and negligible changes in the water level and salinity when compared to our field trip in November 2009. There were no significant rain events in Yeelirrie between January and March 2010, and the water level was even slightly lower and salinity generally slightly higher across the area (unfortunately, precise data are still considered confidential by the private consulting company and their client). It is easy to imagine our surprise when we discovered an amazing diversity and density of copepods in the March 2010 sampling round. This would imply a very strong seasonal dynamics in this subterranean community, but more targeted research is needed to confirm and explain these initial observations. Interestingly, and this may be just a coincidence, at the end of this sampling round there was a massive rain event in the area, which made some roads unusable and prevented us from taking last few planned samples. It was almost like subterranean copepods (and other stygofauna) had an ability to predict the incoming rain and hatched to make the most of the incoming food input! This phenomenon is certainly worth further investigation, as significant rain events in these arid regions are highly irregular and hard to predict (Beard 1976, Holmgren et al. 2006), but, needless to say, at this stage this is just a speculation.

Affinities of Australian to non-Australian *Kinnecaris*. Notoriously inaccurate and/or incomplete descriptions of many species, as well as those based on only one sex, make the comparison of many morphological details in the family Parastenocarididae very hard or impossible (Galassi & De Laurentiis 2004; Schminke 2010), which is also one of the main obstacles for any phylogenetic analysis of this family (Karanovic 2006; Corgosinho et al. 2010). The genus *Kinnecaris* is not an exception, except for recently described taxa from Australia, Papua New Guinea, and India (Karanovic 2004, 2005; Schminke 2008; Ranga Reddy & Schminke 2009). We will outline here, where possible, only some of the most important morphological differences between non-Australian and Australian taxa, because both morphological and molecular data suggest that Australian species are relatively closely related and probably represent a monophyletic group. The Indian *K. godavari* Ranga Reddy & Schminke, 2009 has a completely straight genital operculum in the female, as well as a continuous row of large spinules on the genital double-somite ventrally (see Ranga Reddy & Schminke 2009). The Papua New Guinean *K. giselae* Schminke, 2008 has a more complex endopod of the male fourth leg and three large spinules at its base (Schminke 2008). The Madagascan *K. variolata* (Chappuis, 1952) differs from all Australian species by its male fourth leg, with the endopod ornamented with very large spinules all along its outer margin and no spinules on the basis (Chappuis 1952). Another Madagascan species, *K. forficulata* (Chappuis, 1952), has a distally inflated endopod of the male fourth leg, as well as a concave anal operculum (Chappuis 1952). The Madagascan *K. madagascarensis* (Chappuis, 1952) has a much smaller male fifth leg, and inwardly curved endopod of the male fourth leg, which is also trilobate apically (Chappuis, 1952); note that this is the only species with significant sexual dimorphism in the fifth legs, and questionably a member of *Kinnecaris*, although we do not have enough information even to confirm that males and females belong to the same species. The Madagascan *K. arenicola* (Chappuis, 1954) has a large endopod of the male fourth leg, which is ornamented with extremely large spinules all along its outer surface, as well as an extremely small exopodal spine on the male third leg (Chappuis, 1954). The Sierra Leonean *K. lyncaea* (Cottarelli & Bruno, 1994) has a concave anal operculum and much shorter inner distal process on the male fifth leg (Cottarelli & Bruno 1994). Lake Tanganyika's *K. cornuta* (Chappuis, 1955) also has a concave anal operculum and fifth legs with shorter inner distal processes in both sexes (Chappuis, 1955). A concave anal operculum is also present in the Zimbabwean *K. sinoiaica* (Wells, 1964), while another Zimbabwean species, *K. fluviatilis* (Wells, 1964), differs from the Australian congeners by its almost posteriorly placed dorsal and lateral armature of the caudal rami (Wells 1964). Lake Nyasa's *K. arenosa* (Fryer, 1956) has an apically inflated and almost perfectly round male third leg apophysis, as well as a very short exopodal spine on the male third leg, and a very different endopod of the male fourth leg (Fryer 1956). The Ethiopian *K. aethiopica* (Cottarelli & Bruno, 1995), *K. quollenis* (Cottarelli & Bruno, 1995), and *K. impervia* (Cottarelli & Bruno, 1995) all have different endopods of the male fourth leg from the Australian congeners (Cottarelli & Bruno 1995). A very different endopod of the male fourth leg is also present in two Kenyan species, *K. caffer* (Chappuis, 1936) and *K. muscicola* (Chappuis, 1936), and the latter also has a concave anal operculum (Chappuis 1936; Lang 1948). Unfortunately, incomplete descriptions of many of these species and unknown males for two species (*K. fluviatilis* and *K. solitaria*) prevent us from performing a cladistic analysis of the genus *Kinnecaris* based on morphological characters. As stated by Schminke (2008), even the generic placement of some of them is only provisional, and awaits complete redescriptions. Although making a key to all species of *Kinnecaris* would be possible at this stage, because of the many incomplete descriptions such a key would have

to be largely based on trivial characters. However, as the number of know parastenocarids in Australia increases, we think a simple key to the Australian species of the genus *Kinnecaris* may be beneficial for further studies and specimen identification.

Key to Australian species of *Kinnecaris*

1. Preanal somite without large spinules ventrally 2
– This somite with four groups of large spinules . . . . . *K. lakewayi* **sp. nov.**
2. Third urosomite in female (fourth in male) with at most two groups of large spinules ventrally 3
– This somite with four groups of large spinules . . . . . *K. barrambie* **sp. nov.**
3. Third urosomite in female (fourth in male) with no large spinules 8
– This somite with two groups of large spinules ventrally 4
4. Genital double-somite without large spinules laterally 7
– This somite with at least one group of large spinules laterally 5
5. Genital double-somite with one group of large spinules laterally 6
– This somite with two parallel groups of large spinules laterally . . . . . *K. esbe* **sp. nov.**
6. Male third leg apophysis with deep apical notch; caudal rami very slender in lateral view; anal somite with many rows of minute spinules dorsally . . . . . *K. linel* **sp. nov.**
– Male third leg apophysis without apical notch; caudal rami slightly inflated at middle in lateral view; anal somite with few minute spinules dorsally . . . . . *K. uranusi* **sp. nov.**
7. Caudal rami with two lateral setae . . . . . *K. solitaria* (Karanovic, 2004)
– Caudal rami with three lateral setae . . . . . *K. lined* **sp. nov.**
8. Caudal rami inflated distally; somites with cuticular pits . . . . . *K. eberhardi* (Karanovic, 2005)
– Caudal rami not inflated distally; somites with smooth cuticle . . . . . *K. linesae* **sp. nov.**

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