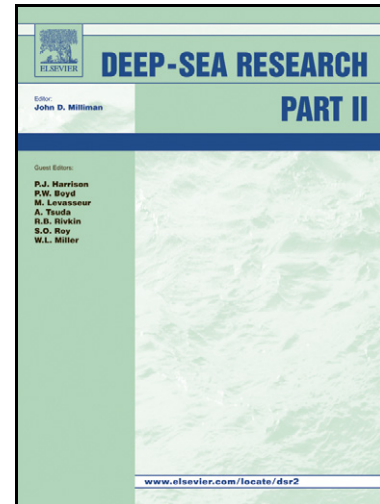


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A new species of *Eualus* Thallwitz, 1891 and new record of *Lebbeus antarcticus* (Hale, 1941) (Crustacea: Decapoda: Caridea: Hippolytidae) from the Scotia Sea

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Abstract

Eleven specimens representing two hippolytid genera, *Eualus* Thallwitz, 1891 and *Lebbeus* White, 1847, were sampled recently from the Scotia Sea (1517–2598 m). Seven specimens are described and illustrated as *Eualus amandae* sp. nov., and its morphology is compared with those of previously described species. Four female specimens, morphologically consistent with *Lebbeus antarcticus* (Hale, 1941), are described and illustrated to supplement previous descriptions of this rarely collected bathyal species. Partial COI mtDNA and 18S rDNA sequences were generated for both species. Only limited DNA sequences are available for the Hippolytidae. COI phylogenetic trees are presented to illustrate that the new species is genetically distinct from all other species in GenBank. This record enhances existing knowledge of Antarctic invertebrate biodiversity and species richness of decapod crustaceans in the Southern Ocean.

Keywords

Biodiversity, Deep-Sea, Hydrothermal vents, Southern Ocean, Phylogenetics, Polar

1. Introduction

Knowledge of the distribution of decapod crustaceans from the Southern Ocean has increased considerably in recent years (e.g. Raso et al., 2008; Rogers et al., 2012; Thatje and Arntz, 2004; Thatje and Lörz, 2005). Caridean shrimps cover the largest known bathymetric range of the Southern Ocean decapod fauna, distributed from the intertidal zone to the deep sea (Gorny, 1999). They are one of few groups of decapod crustaceans found south of the Antarctic Convergence (Arntz et al., 1999; Kirkwood, 1984; Thatje and Arntz, 2004; Yaldwyn, 1965), where they are represented by at least five families, nine genera and ten species (Boschi and Gavio, 2005). The caridean family Hippolytidae Spence Bate, 1888 is the most diverse decapod family south of the Antarctic Convergence (Boschi and Gavio, 2005; Gorny, 1999), represented to date by three species: *Chorismus antarcticus* (Pfeffer, 1887); *Eualus kinzeri* Tiefenbacher, 1990; *Lebbeus antarcticus* (Hale, 1941).

During a recent research cruise to the East Scotia Ridge and Kemp Caldera, Scotia Sea, a novel species of the hippolytid genus *Eualus* Thallwitz, 1892 was discovered and several specimens of *Lebbeus antarcticus* (Hale, 1941) were also sampled. The aims of this paper were to: (1) describe the new species and compare its morphology with those of previously described species; (2) describe and illustrate the new specimens of *L. antarcticus* to supplement previous descriptions (based on single or incomplete specimens) of this rarely collected bathyal species (Hale, 1941; Komai et al., 1996; Ward, 1985; Zarenkov, 1970); (3) use the COI mtDNA region to determine if the species are genetically distinct from other hippolytid species in the GenBank database. This record enhances existing knowledge of Antarctic invertebrate biodiversity and species richness of decapod crustaceans in the Southern Ocean.

2. Materials & Methods

2.1 Sample collection

The specimens were collected during the *RRS James Cook* cruise 042 (JC42) in January-February 2010 to the Scotia Sea (Fig. 1). All specimens were collected using sampling equipment attached to, or deployed by, the Remotely Operated Vehicle (ROV) *Isis*. Sampling data are summarised in Table 1.

2.2 Morphology

Prior to fixation, a pereopod was removed from each specimen for subsequent molecular analysis. Specimens were fixed in 10 % neutralised formalin and then transferred to 75% Industrial Methylated Spirits. Individuals were measured to the nearest 0.1 mm using Vernier callipers. Postorbital carapace length (CL) was measured from the posterior margin of the orbit to the posterior margin of the carapace and is used herein as an indication of specimen size. Individuals were sexed under a dissecting microscope. Illustrations were prepared with the aid of a camera lucida mounted onto a Leica MZ8 stereomicroscope, scanned and inked digitally using a WACOM™ digitiser and Adobe® Illustrator® software. Specimens were deposited in the invertebrate collection at the Natural History Museum, London

(NHMUK). Morphological terminology generally follows Komai and Hayashi (2002) and Komai et al. (2012).

2.3 Molecular

A pereopod from each specimen was immediately placed in 100% ethanol for molecular analysis. Genomic DNA was isolated from the pereopods. DNA was extracted with the DNeasy Tissue Extraction Kit (Qiagen, Crawley, West Sussex, United Kingdom) as directed by the manufacturer. Reactions were performed in 10 μ l volumes, containing 0.5 μ l of each primer (forward and reverse) at a concentration of 10 nmol, 5 μ l of Qiagen 10x PCR buffer, 1.5 μ l of MgCl₂ (25 mM), 1 μ l dNTPs (2nmol, Biotline), 0.25 μ l of Taq (5U/ μ l) and 1 μ l of DNA template (~ 30 ng). Partial 18S rDNA (~580 bps) was amplified using SSUA NSF4 (Hendriks et al., 1989; NSF4 5'-CTGGTTGATYCTGCCAGT-3') and SSUA NSR581 (Wilmotte et al., 1993 SSUA NSR581 5'ATTACCGCGGCTGCTGGC-3') under the following conditions: Initial denaturation at 96°C for 0.5 minute, followed by 40 cycles of 94°C for 0.5 min, 55°C for 0.5 min, 72°C for 1 min, and a final extension of 5 min at 72°C. Partial COI mtDNA (~700 bps) was amplified using LCO 1490 and HCO 2198 (Folmer et al., 1994; LCO 1490 5'-GGTCAACAAATCATAAAGATATTGG-3' HCO 2198 5'-TAAACTTCAGGGTGACCAAAAAATCA-3') under the following conditions: Initial denaturation at 94°C for 5 minutes, followed by 5 cycles of 94°C for 1 min, 45°C for 1.5 min, 72°C for 1.5 min, then 30 cycles of 94°C for 1 min, 50°C for 1 min, 72°C for 1 min, and a final extension of 5 min at 72°C.

DNA sequencing was performed at LGC Berlin Germany. All sequences were edited and proofread in CodonCode Aligner Version 3.5.6 (CodonCode Corporation 2006). Sequence quality was evaluated using “Phred” quality scores, excluding sequences with values <300 (Ewing et al., 1998a, b). Electropherograms were also manually examined for sequencing errors and, where possible, variable positions were confirmed by reference to the corresponding reverse sequences. The partial 18S sequences were blast search (blastn) to find the closest matching sequences. The partial COI mtDNA were checked for open-reading frames and blast searched (tblastx) to assess gene homology. The edited partial COI mtDNA (650-685 bps) were aligned with all hippolytid species available in GenBank (Table 2). If numerous COI sequences were available for a species, a maximum of six sequences were randomly selected for the alignment. *Alvinocaris longirostris* Williams and Chace, 1982 was selected as outgroup taxa for the COI dataset based on the affinity of alvinocaridids with the Hippolytidae, following Nye et al. (2012).

The COI dataset was aligned with reference to its protein translation and then manually adjusted by eye using Se-A1 v2.0a11 (Rambaut, 2002). The analysed alignment of 52 taxa was truncated to 657 basepairs which were analysed per individual codon position for chi-square of likelihood scores, constant, variable and parsimony informative sites. ModelTest v 3.7 (Posada and Crandall, 1998) was used to infer the best-fitting evolutionary model for the COI locus with a second-order Akaike Information Criterion correction (AICc) employed. Bayesian analyses were conducted using MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003). The Bayesian analysis was conducted by computing 10 million Markov chain Monte Carlo generations in two parallel runs, each with three cold chains and one hot chain. The initial 10% of each analysis was discarded as burn-in. Convergence was assessed

using TRACER v1.5 (Rambaut and Drummond, 2009) and all split frequencies were observed to be <0.01 before analyses were terminated.

3. Taxonomy

Order DECAPODA Latreille, 1802
 Infraorder CARIDEA Dana, 1852
 Superfamily ALPHEOIDEA Rafinesque, 1815
 Family HIPPOLYTIDAE Spence Bate, 1888

3.1 Genus *Eualus* Thallwitz, 1892

Eualus amandae sp. nov.

(Figures 2-6)

3.1.2 Material examined

Holotype: female (CL 10.1 mm), [NHMUK 2012.1523]. JC42 (*RRS James Cook* and *ROV Isis*), *Isis* dive #152, site JC-42-5-15, Kemp Caldera, Scotia Sea, 59°41'S, 28°21'W, 1517 m, 11 February 2010, suction sampler.

Paratypes: three females (CL 5.0-9.5 mm, [NHMUK 2012.1525, 2012.1526, 2012.1528], two males (CL 5.7-6.0), [NHMUK 2012.1524, 2012.1527]. Same data as holotype. One male (CL 6.5 mm), [NHMUK 2012.1522]. JC42 (*RRS James Cook* and *ROV Isis*), *Isis* dive #145, site JC-42-4-15, E9, Scotia Sea. 60°02'S, 29°58'W, 2401 m, 04 February 2010, suction sampler.

3.1.3 Description

Body (Fig. 2) moderately slender, integument glabrous.

Rostrum (Fig. 2, 3A-B, 4A) straight, slightly descending, directed forward; not reaching, reaching, or exceeding distal margin of first segment of antennular peduncle, but not reaching distal margin of second segment; 0.4-0.6 times carapace length. Dorsal margin armed with 5-9 teeth, including 4-6 on rostrum proper and 1-3 postrostral teeth along midline of the carapace; posteriormost tooth arising at 0.1-0.2 CL. Ventral margin with blade becoming somewhat deeper distally, with 0-4 teeth in distal 0.3; ventral blade less developed in males (Fig. 4A).

Carapace (Fig. 2, 3A-B, 4A) with low median portrostral carina extending 0.3 of carapace; dorsal profile in lateral view slightly convex. Orbital margin concave; suborbital lobe bluntly triangular, not reaching antennal tooth. Antennal tooth moderately strong, acute. Pterygostomial tooth small. Anterolateral margin between antennal tooth and pterygostomial tooth slightly sinuous.

Abdomen (Fig. 2) dorsally rounded, posterodorsal margin of third somite produced. Pleura of anterior four somites broadly rounded, unarmed marginally; fifth pleuron bearing one moderately strong posteroventral tooth and one moderately strong posterolateral tooth (Fig. 3C). Sixth somite approximately 1.8 times longer than fifth,

2.5 times longer than deep, with small posteroventral tooth; posterolateral process terminating in small tooth.

Telson (Fig. 4 B-C) damaged badly in all but two specimens [NHMUK 2012.1524, 2012.1527]. Length approximately 5 times anterior width, 1.1-1.2 times longer than sixth abdominal somite in dorsal midline; lateral margins parallel in anterior third, tapering posteriorly, bearing 3 dorsolateral spines on each side; posterior margin rounded, with 2 pairs of lateral spines (mesial pair longer) and 7-8 median spines.

Uropods (Fig. 4B) with broad rami exceeding distal margin of telson; exopod with distinct transverse suture, bearing small fixed spine and one moveable spine at distolateral angle; endopod shorter and narrower than exopod; posterolateral projection of protopod triangular with acute tip.

Eyes (Fig. 2, 3A-B, 4A) subpyriform with stalk narrowing proximally; cornea distinctly wider than stalk, its maximum width 0.1 times CL, darkly pigmented; ocellus apparently absent.

Antennular peduncles (Fig. 2, 3A-B, 4A) not quite extending to base of dorsolateral tooth of antennal scale. First segment longer than distal two segments combined, reaching 0.6-0.7 of antennal scale, with ventrolateral tooth, ventromesial margin armed with one prominent subdistal tooth; stylocerite not reaching, reaching, or exceeding slightly beyond distal margin of first segment of antennular peduncle, terminating in acute point, mesial margin sinuous. Second segment less than half length of first, with strong distolateral tooth. Third segment approximately half length of second, with small dorsodistal tooth. Lateral flagellum with thickened aesthetasc-bearing portion approximately 0.5 times CL.

Antenna (Fig. 2, 3D) with basicerite bearing small, acute ventrolateral tooth; carpocerite reaching to distal 0.6 of antennal scale. Antennal scale approximately 0.6 times CL, 3.0 times longer than wide; lateral margin straight; distolateral tooth falling short of rounded distal lamella of blade.

Mouthparts (Fig. 5) similar to those of other species of the genus, no specific characters. Mandible (Fig. 5A) composed of stout molar, flattened incisor and biarticulate palp; molar process subcylindrical with obliquely truncate grinding surface and area of dense setae distally; incisor process bearing four distal serrations; palp curved, shorter than incisor, distal article bearing several long setae (Fig. 5B).

Maxillule (first maxilla) (Fig. 5C) with well-developed endites; coxal endite bearing numerous long setae; basal endite with several rows of spines and stiff setae along the mesial margin; palp curved weakly, bilobed, bearing three distal setae.

Maxilla (second maxilla) (Fig. 5D) with bilobed upper endite, fringed with many setae, flanked by a well-developed palp with two distal setae; lower endite reduced, with several long setae; scaphognathite well developed, with rounded posterior lobe, fringed with numerous setae.

First maxilliped (Fig. 5E) with well-developed endites fringed with setae; palp biarticulate; exopod with caridean lobe; epipod large, bilobed.

Second maxilliped (Fig. 5F) with broad ultimate segment fringed with stiff setae; ischial segment with excavated mesial margin; exopod and epipod well-developed, epipod with podobranch present.

Third maxilliped (Fig. 5) moderately elongate and slender, exceeding antennal scale by approximately 0.6 of ultimate segment. Antepenultimate segment somewhat flattened proximally, approximately 0.9 times as long as two distal segments combined; distolateral and dorsodistal margins armed with a small tooth; small spine at ventrodistal angle (Fig. 5H); lateral surface with row of spiniform setae on blunt ridge parallel to dorsal margin. Ultimate segment approximately 2.8 times longer than penultimate segment, with dense tufts of setae; tapering distally, with short row of corneous spines distomesially and distolaterally (Fig. 5I).

Branchial formula summarised in Table 3.

First pereopod (Fig. 6A) moderately stout, extending to distal margin of antennal scale. Chela (Fig. 6B) approximately twice as long as carpus; dactylus approximately 0.6 times as long as palm, weakly curved distally, terminating in two darkly pigmented corneous claws; fixed finger terminating in one.

Second pereopod (Fig. 6C) distinctly more slender than first, extending beyond distal margin of antennal scale by approximately length of chela and 0.6 length of carpus. Chela small with subcylindrical palm; dactylus terminating in two darkly pigmented corneous claws; fixed finger terminating in one. Carpus composed of seven articles.

Third to fifth pereopods (Fig. 6D-H) similar in structure, long and slender. Third pereopod (Fig. 6D) dactylus approximately 0.1 length propodus, terminating in acute unguis and armed with seven darkly pigmented accessory spinules on flexor margin, (Fig. 6E); carpus approximately 0.5 as long as propodus; propodus with two rows of ventral accessory spinules; merus armed with one lateral spine.

Fourth pereopod (Fig. 6F) dactylus with 8 darkly pigmented accessory spinules on flexor margin; propodus with 2 rows of ventral flexor spinules; merus armed with one lateral spine.

Fifth pereopod (Fig. 6G) dactylus with eight darkly pigmented accessory spinules on flexor margin (Fig. 6H); propodus with two rows of ventral flexor spinules; merus armed with one lateral spine.

Female pleopods similar to those of other species of the genus, without distinctive feature. In males, first pleopod with endopod (Fig. 4D) elongate subtriangular, bearing setae on lateral margin; appendix interna terminal, elongate, approximately less than half length of endopod. Second pleopod with appendix masculina (Fig. 4E) of similar length to appendix interna, bearing several long setae.

3.1.4 Colouration in life

Unknown.

3.1.5 Distribution

Known only from non-hydrothermal areas in the Kemp Caldera and on the E9 segment of the East Scotia Ridge, Scotia Sea, 1517-2401 m (see Table 1).

3.1.6 Etymology

The new species is named after Dr Amanda J. Tyler.

3.1.7 Remarks

Eualus amandae sp. nov. belongs to the group of *Eualus* species characterised by the possession of epipods on the anterior three pairs of pereopods. It is morphologically most similar to: *E. avinus* (Rathburn, 1899); *E. berkeleyorum* Butler, 1971; *E. dozei* A. Milne-Edwards, 1891; *E. horii* Komai and Hayashi, 2002; *E. lineatus* Wicksten and Butler, 1983; *E. macilentus* (Krøyer, 1841); *E. spathulirostris* (Yokoya, 1933); *E. subtilis* Carvacho and Olson, 1984. Shared characters include the rostrum extending beyond distal extremity of the eye but not reaching distal margin of antennular peduncle, and the presence of a pterygostomial tooth.

The new species differs from all of these species (and other congeneric species) by the presence of two teeth on the posterolateral margin of the fifth pleura. Additional characters differentiating *Eualus amandae* sp. nov. from each species are discussed below.

Eualus amandae sp. nov. is similar to *E. berkeleyorum* in the unarmed margin of the fourth abdominal pleuron. It is distinguished easily from this species by the straight, slightly descending rostrum (versus strongly arched), armed with 5-9 (versus 12-14) dorsal teeth, the anterolateral margin of the carapace (slightly sinuous versus sinuous), and presence of a single spine (versus 4-5) on the meri of the third and fourth pereopods.

Eualus amandae sp. nov. is distinguished from *E. avinus*, *E. horii*, *E. lineatus*, *E. macilentus*, *E. spathulirostris* and *E. subtilis* by the lack of armature on the fourth pleuron (versus armed with a tooth) and presence of a single (versus multiple) meral spines on the third pereopod. The new species is separated further from *E. avinus*, *E. macilentus* and *E. spathulirostris* by the dorsal margin (straight versus convex) and armature of the rostrum in the former two species (5-9 dorsal teeth, versus 12-14 and 11-14 respectively).

Eualus amandae sp. nov. differs further from *E. horii* in the presence (versus absence) of a postrostral carina, and the proportionally longer sixth abdominal somite (1.8 times longer than fifth, versus 1.6-1.7 times) and telson (length five times anterior width, versus 2.8 times). Moreover, *Eualus horii* and *E. lineatus* possess a dorsal tooth on the stylocerite (this character is easiest to use for differentiation), absent in *E. amandae* sp. nov. The new species is distinguished further from *E. subtilis* by the presence of a suborbital lobe, and from *E. subtilis* and *E. lineatus* by differences in the armature of the antennular peduncles.

Eualus amandae sp. nov. is separated from *E. dozei* by the unarmed fourth abdominal pleuron, armature of the rostrum (5-9 dorsal teeth, 1-3 postrostral, versus three dorsal, none postrostral), and presence (versus absence) of a suborbital lobe.

To date, 36 species of *Eualus* (one of which has two subspecies) have been described, distributed primarily in cold and temperate waters of the world oceans at shallow to bathyal depths (De Grave and Fransen, 2011). *Eualus amandae* sp. nov. is the second member of the genus to be recorded from the Southern Ocean. *Eualus kinzeri* Tiefenbacher, 1990 was described from the Weddell Sea, from 673-782 m water depth (Arntz and Gorny, 1991; Tiefenbacher, 1990). Since then, it has been recorded north of the Antarctic Convergence, from the Magellan region in the waters around the southern islands off the eastern mouth of the Beagle Channel (Arntz et al., 1999).

The new species is distinguished readily from *Eualus kinzeri* by the presence of two teeth on the posterolateral margin of the fifth pleura. Further differences between these two Antarctic species include: proportionally shorter rostrum (not reaching distal margin of second segment of antennular peduncle, versus reaching beyond antennular peduncle) and armature of the ventral margin (0-4 versus 6-9 teeth), and the small (versus well developed) pterygostomial tooth.

3.2 Genus *Lebbeus* White, 1847

Lebbeus antarcticus (Hale, 1941)

(Figures 7-10)

Spirontocaris antarcticus Hale, 1941: 267, figures 5, 6.

Lebbeus antarctica: Zarenkov, 1968: 161; Hayashi, 1992: 109 (table).

Lebbeus antarcticus: Kirkwood, 1984: 27, figure 39; Ward, 1985: 58, figures 1-3; Komai et al., 1996: 195, figure 8; Komai et al., 2012: 25 (table).

3.2.1 Material examined

Female (CL 15.4 mm), [NHMUK 2012.1529]. JC42 (*RRS James Cook* and *ROV Isis*), *Isis* dive #133, site JC-42-3-15, E2, Scotia Sea, 56°05'S, 30°19'W, 2598 m, 23 January 2010, baited trap. Two females (CL 13.4, 15.2 mm), [NHMUK 2012.1531, 2012.1530]. JC42 (*RRS James Cook* and *ROV Isis*), *Isis* dive #135, site JC-42-3-18, E2, Scotia Sea, 56°05'S, 30°19'W, 2139 m, 25 January 2010, baited trap. Female (CL 12.0 mm), [NHMUK 2012.1532]. JC42 (*RSS James Cook* and *ROV Isis*), *Isis* dive #140, site JC-42-4-7, E9, Scotia Sea, 60°02'S, 29°58'W, 2402 m, 30 January 2010, biobox.

3.2.2 Description

Body (Fig. 7) moderately robust, integument glabrous.

Rostrum (Fig. 7, 8A-B) straight, directed forward, reaching to distal one-third of first segment of antennular peduncle but not to distal margin of first segment of antennular peduncle, 0.3-0.4 times carapace length. Dorsal margin armed with 5-6 teeth, including 3 on rostrum proper and 2-3 postrostral teeth along midline of the carapace, posteriormost tooth arising at 0.2-0.3 CL. Ventral margin armed with 1-2 teeth in distal 0.2, ventral lamina poorly developed.

Carapace (Fig. 7) with low but distinct median portrostral carina extending at least one-third of carapace; dorsal profile in lateral view convex. Supraorbital tooth moderately strong, arising posterior to rostral base, slightly ascending, not reaching

tip of suborbital lobe and antennal tooth; deep U-shaped notch inferior to base of supraorbital tooth. Orbital margin weakly concave; suborbital lobe bluntly triangular. Antennal tooth well-developed, acute, reaching tip of suborbital lobe. Pterygostomial tooth small, not reaching antennal tooth. Anterolateral margin between antennal tooth and pterygostomial tooth strongly sinuous with deep excavation below antennal tooth.

Abdomen (Fig. 7) dorsally rounded. Second somite with transverse groove on tergum, forming low ridge posteriorly; posterodorsal margin of third somite produced. Pleura of anterior three somites broadly rounded, unarmed marginally; fourth pleuron (Fig. 8C), with or without small posteroventral tooth (tooth present in two specimens); fifth pleuron bearing moderately strong posteroventral tooth (Fig. 8C). Sixth somite approximately 1.5-1.7 times longer than fifth, 1.9-2.0 times longer than deep, with small posteroventral tooth; posterolateral process terminating in small, acute tooth.

Telson (Fig. 7, 8D-E), length 3.6-3.9 times anterior width, 1.2-1.5 times longer than sixth abdominal somite in dorsal midline; lateral margins parallel in anterior third, tapering posteriorly, bearing 3-5 dorsolateral spines on each side; posterior margin obtusely triangular, with two pairs of lateral spines (mesial pair longer) and 4-7 median spiniform setulose setae.

Uropods (Fig. 8D) with broad rami exceeding distal margin of telson; exopod with distinct transverse suture, bearing small fixed spine and 1-2 moveable spines at distolateral angle; endopod shorter and narrower than exopod; posterolateral projection of protopod triangular with acute tip.

Eyes (Fig. 7, 8A-B) subpyriform with stalk narrowing proximally; cornea distinctly wider than stalk, its maximum width 0.1 times CL; ocellus absent.

Antennular peduncles (Fig. 7, 8A-B) extending to base of dorsolateral tooth of antennal scale. First segment longer than distal two segments combined, reaching midlength of antennal scale, dorsodistal margin armed with 2-4 slender teeth (variable within specimens), ventromesial margin armed with 1 prominent subdistal tooth; stylocerite reaching at least two-thirds along first peduncular segment to just falling short of distolateral angle of first peduncular segment, terminating in acute point, mesial margin sinuous. Second segment approximately 0.4 length of first segment, with strong distolateral tooth. Third segment less than half as long as second, with small dorsodistal tooth. Lateral flagellum with thickened aesthetasc-bearing portion approximately 0.4 times CL.

Antenna (Fig. 7, 8F) with basicerite bearing small, acute ventrolateral tooth; carpocerite reaching midlength to 0.6 of antennal scale. Antennal scale approximately 0.6 times CL, three times longer than wide; lateral margin straight; distolateral tooth falling short of rounded distal lamella of blade.

Mouthparts (Fig. 9) similar to those of other species of the genus, no specific characters. Mandible (Fig. 9A-B) composed of flattened incisor, stout molar and biarticulate palp; incisor process bearing four distal serrations and several fine setae on mesial margin; molar process subcylindrical with obliquely truncate grinding surface and area of dense setae distally; palp curved, shorter than incisor, basal article broad with few short setae, distal article bearing numerous long setae.

Maxillule (first maxilla) (Fig. 9C) with well-developed endites; coxal endite bearing numerous long setae; basal endite with row of spines and several rows of stiff setae along the mesial margin; palp curved weakly, slightly bilobed, bearing two distal setae.

Maxilla (second maxilla) (Fig. 9D) with bilobed upper endite, fringed with many setae, flanked by a well-developed palp with two distal setae; lower endite reduced, bearing several long setae; scaphognathite well developed, with rounded posterior lobe, fringed with numerous setae on all margins.

First maxilliped (Fig. 9E) with well-developed endites fringed with setae; palp biarticulate; exopod with caridean lobe; epipod large, bilobed.

Second maxilliped (Fig. 9F) with broad ultimate segment fringed with stiff setae; ischial segment with excavated mesial margin; exopod and epipod well-developed, epipod with podobranch present.

Third maxilliped (Fig. 9G) exceeding antennal scale by half length of ultimate segment. Antepenultimate segment approximately 0.7 times as long as two distal segments combined; armed with a small tooth and two long spiniform setae on distolateral and dorsodistal margins, with a small spine at ventrodistal angle (Fig. 9H); lateral surface bearing row of spiniform setae on blunt ridge parallel to dorsal margin. Ultimate segment approximately 2.5 times longer than penultimate segment, with dense tufts of setae; tapering distally, with short row of corneous spines distomesially and distolaterally (Fig. 9I).

Branchial formula summarised in Table 4.

First pereopod (Fig. 10A) moderately stout, extending to distal margin of antennal scale. Chela (Fig. 10B) approximately 1.5 as long as carpus; dactylus approximately 0.5 times as long as palm, strongly curved distally, terminating in two corneous claws; fixed finger terminating in one.

Second pereopod (Fig. 10C) distinctly more slender than first, extending beyond distal margin of antennal scale by approximately 0.2 length of carpus. Chela small; dactylus terminating in two corneous claws; fixed finger terminating in one corneous claw. Carpus composed of 6-9 articles (left/right: 8/8, 7/7, 9/7, 7/5).

Third to fifth pereopods (Fig. 10D-G) similar in structure, long and slender, decreasing in length and stoutness posteriorly. Third pereopod (Fig. 10D) overreaching antennal scale by approximately 0.9 length of propodus; dactylus approximately 0.1 length propodus, terminating in acute unguis and armed with seven accessory spinules on flexor margin, distalmost spinule distinctly larger than others, making dactylus tip appear biunguiculate (Fig. 10E); carpus approximately 0.6 as long as propodus; propodus with two rows of ventral accessory spinules; merus armed with 5-8 lateral spines.

Fourth pereopod (Fig. 10F) overreaching antennal scale by approximately 0.6 length of propodus; dactylus with seven accessory spinules on flexor margin; propodus with two rows of ventral flexor spinules; merus armed with 3-6 lateral spines.

Fifth pereopod (Fig. 10G) overreaching antennal scale by approximately 0.2 length of propodus; dactylus with seven accessory spinules on flexor margin; propodus with two rows of ventral flexor spinules; merus armed with one lateral spine.

Female pleopods similar to those of other species of the genus, without distinctive feature.

3.2.3 Colouration in life

Carapace red-orange, becoming paler dorsally, translucent. Abdomen pale with scattered red chromatophores. Rostrum and cephalic appendages pale red-orange. Cornea darkly pigmented. Third maxilliped red-orange; corneous spinules on ultimate article darkly pigmented. Pereopods red-orange; chelae of anterior two pairs terminating in darkly pigmented claws; dactyli of posterior three pairs pale, with darkly pigmented corneous spines and ungui. Gills white.

3.2.4 Distribution

Known previously from Antarctic waters, 450-920 m: Terre Adélie, 66°21'S 138°28'E, 63°53'S 114°01'E, 67°45'S 147°10'E (Hale, 1941; Zarenkov, 1968, 1970); Lützw-Holm Bay, 69°10'S, 37°30'E (Nunanami et al., 1984); from Weddell seal stomachs, Jones Ice Shelf East, 67°30'S, 67°00'W, and Bagnold Point, 67°02'S, 67°29'W (Ward, 1985); southeastern Weddell Sea, Halley Bay and Vestkapp (Arntz and Gorny, 1991); Lararev Sea (Gorny et al., 1992); Prtyz Bay, 69°12'S, 75°30'E (Komai et al., 1996). Also recorded north of the Antarctic Convergence: off Patagonia and Tierra del Fuego "from stations well below 1000 m" (Arntz et al., 1999); off Chile 22°48'S, 70°42'W, 1775 m (Guzmán and Quiroga, 2005; this record is questionable).

The present specimens are from the periphery of diffuse-flow vent fields on the E2 and E9 segments of the East Scotia Ridge, East Scotia Sea, 2139-2598 m (Table 1).

3.2.5 Remarks

Several specimens of *Lebbeus antarcticus* have been described previously. Some minor differences are apparent when the present specimens are compared with previous descriptions. In the original description of the male holotype, Hale (1941) stated that the rostrum is half as long as the rest of the carapace; it is 0.3-0.4 times the carapace length in the present specimens. The number of rostral and post-rostral teeth documented in this study (see above) differ from those in the single specimens studied by Hale (1941) and Komai et al. (1996), but fall within the range for the species (Ward, 1985).

The specimens studied to date have exhibited variation in the armature of the fourth abdominal pleura, with either the presence (Ward, 1985) or absence (Hale, 1941; Komai et al., 1996) of a posteroventral tooth. Based on the evidence available at the time, Komai et al. (1996) suggested that this feature may be sexually dimorphic. The

present specimens, however, exhibit variation in this feature and are all female. The sixth abdominal somite in the specimen of Komai et al. (1996) is 1.8 times longer than the fifth somite; it is approximately 1.5-1.7 times longer in the present specimens.

The proximal segment of the antennular peduncle has been shown to bear two (Hale, 1941; Komai et al., 1996) or three (Ward, 1985) teeth on the dorsodistal margin, compared with 2-4 in the present specimens. The specimen described by Komai et al. (1996), and those described herein, differ from those in Hale (1941) and Ward (1985) in the longer third maxilliped (exceeding antennal scale by half length of ultimate segment versus reaching slightly beyond antennal scale). The armature of the antepenultimate segment of this appendage consists of a small distolateral tooth in the specimen of Komai et al. (1996), whereas the present specimens are armed with a small tooth and two long spiniform setae on the distolateral and dorsodistal margins, and a small ventrodistal spine.

The division of the carpus of the second pereopod into seven articles is a diagnostic feature of *Lebbeus* (Hayashi, 1992; Holthuis, 1993). Three of the present specimens are peculiar in exhibiting variation in the number of articles of the carpus of the second pereopod (left/right: 8/8, 9/7, 7/5). All four specimens, however, conform to the other diagnostic characters of the genus, as defined by Hayashi (1992). Moreover, the description given herein is consistent with previous descriptions of *L. antarcticus* in all other respects. Given the sampling location, and morphological similarities with the specimens described previously, the most conservative approach is to assign these specimens to *L. antarcticus*, while acknowledging that the number of carpal articles on the second pereopod is variable within this genus. Variation in the number of carpal articles of the second pereopod in species of *Lebbeus* has been described previously by Chang et al. (2010). Review of the literature describing *Lebbeus* species indicates that the number of carpal articles is fairly consistent; however the character is not absolutely reliable for generic diagnosis.

4. Molecular results

Partial sequences of the COI mtDNA (650-685 bp) and 18S rDNA (519-531 bp) regions were amplified from five specimens of *Eualus amandae* sp. nov. and four specimens of *Lebbeus antarcticus* (Table 2). Partial sequences of COI and 18S were identical amongst specimens of *E. amandae* sp. nov. and distinct from all those in GenBank. The nearest match for *E. amandae* sp. nov. COI was *E. gaimardii* *gaimardii* voucher EG01CN0506 with 82% maximum identity (mi) over 93% of query coverage (qc), and for 18S to *E. gaimardii* isolate KC3056 with 99% mi over 96% qc. Partial sequences of COI and 18S were identical amongst *L. antarcticus* specimens and distinct from those of *E. amandae* sp. nov. and all species in GenBank. The closest match for *L. antarcticus* for COI was *L. carinatus* isolate IcP02-1 with 95% mi over 87% qc and for 18S it was *Thoralus cranchii* voucher ULLZ6969 with 99% mi over 100% qc, followed by *E. gaimardii* isolate KC3056 with 99% mi over 94% qc.

The COI dataset had 374 constant, 51 variable and 232 parsimony informative sites. The third codon position was particularly variable: it had seven constant, one variable and 211 parsimony informative sites. The COI dataset strongly rejected base compositional heterogeneity at the 3rd codon positions ($\chi^2 = 329$, $p > 0.01$), and nearly every site at the 3rd codon position was parsimony informative (211/219 sites), suggesting substantial saturation as well as potentially erroneous phylogenetic signal due to the highly heterogeneous base composition. Consequently the Bayesian COI phylogeny was estimated in two different ways: (1) evolutionary rate parameters estimated separately ('partitioned') for codon positions (1+2) and 3 (each partition GTR+I+G), in order that the phylogenetic signal from the highly variable 3rd codon positions is weighted equally with the less variable 1st and 2nd codons (Shapiro et al., 2006), and (2) translating 3rd codon position DNA into purines (A and G = R) and pyrimidines (C and T = Y; 'RY' coding). MrBayes was run subsequently for the RY coded third position dataset and the unchanged dataset. The resulting topologies are shown in Fig. 11.

The two treatments of the COI dataset yielded different clade groupings with weak support on branches other than species groups, including *Eualus amandae* sp. nov. and *Lebbeus antarcticus* (Fig. 11). In both treatments, significant support (1/0.99 Bayesian posterior probabilities) is found for the sister grouping of *L. antarcticus*, *L. laurentae* and *L. virentova* (Fig. 11). The *Eualus* affinity is not resolved by these analyses, as expected for a limited dataset of this kind, although the phylogenetic position is similar with both dataset treatments, suggesting this is independent of base composition heterogeneity.

5. Discussion

Morphological analysis of *Eualus amandae* sp. nov. reveals it to be a new species in the genus *Eualus*, distinguished from all other *Eualus* species by the presence of two teeth on the posterolateral margin of the fifth pleura (section 3.1.7). Consistency in partial sequences of the COI mtDNA gene between specimens and significant support for the species clade in the Bayesian analyses confirms that they belong to a single species. The presence of fixed and unique mutations in the sequences indicates that they are genetically distinct from all other species in GenBank.

Morphological study of four specimens of *Lebbeus antarcticus* suggests that one of the defining features for this species (number of carpal articles of the second pereopod) is variable within and between individuals (section 3.2.5). Consistency in partial sequences of COI mtDNA between individuals and support for the species clade in the Bayesian analyses confirms that they belong to a single species. Unique and fixed mutations within the sequences indicate that they are genetically distinct from all other species in GenBank. Additional sequences of *L. antarcticus* from other Antarctic locations, however, were not available for comparison.

5.1 Conclusions

This study reveals the presence of a new species, *Eualus amandae* sp. nov., and new records of *Lebbeus antarcticus* from the Scotia Sea. These findings enhance existing knowledge of the biodiversity and distribution of caridean shrimps in the Southern Ocean.

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Figure legends

Fig. 1. Map showing sampling locations E2, E9, and Kemp Caldera in the Scotia Sea. Dashed line represents the Antarctic Convergence.

Fig. 2. *Eualus amandae* sp. nov., holotype, female (Carapace length 10.1 mm), [NHMUK 2012.1523], from Kemp Caldera, Scotia Sea, 1517 m. Entire animal, lateral view. Scale bar = 5 mm.

Fig. 3. *Eualus amandae* sp. nov., holotype, female (Carapace length 10.1 mm), [NHMUK 2012.1523], from Kemp Caldera, Scotia Sea, 1517 m: A, anterior part of carapace and cephalic appendages, lateral view; B, same, dorsal view; C, posterolateral margins of right pleura of fourth and fifth abdominal somites, lateral view; D, left antennal peduncle and scale, ventral view. Scale bars = 2mm.

Fig. 4. *Eualus amandae* sp. nov., paratype, male (Carapace length 6.0 mm), [NHMUK 2012.1524], from Kemp Caldera, Scotia Sea, 1517 m: A, anterior part of carapace and cephalic appendages, lateral view; B, telson and left uropod, dorsal view; C, posterior part of telson, dorsal view; D, endopod of first left pleopod, ventral view; E, appendix masculina and appendix interna of left second pleopod, mesial view. Scalebars: A, B = 2 mm; C-E = 1mm.

Fig. 5. *Eualus amandae* sp. nov., A-F, holotype, female (Carapace length 10.1 mm), [NHMUK 2012.1523], from Kemp Caldera, Scotia Sea, 1517 m; G-I, paratype, male (Carapace length 6.5 mm), [0499 add registration no.], same data: A, left mandible, ventral view; B, same, palp and incisor process; C, left maxillule (first maxilla), ventral view; D, left maxilla (second maxilla), ventral view; E, left first maxilliped, ventral view; F, left second maxilliped, ventral view; G, right third maxilliped, lateral view; H, same, distal part of antepenultimate segment, lateral view; I, distal part of ultimate segment of right third maxilliped, dorsal view. Scale bars = A, C-G = 2 mm; B, H-I = 1 mm.

Fig. 6. *Eualus amandae* sp. nov., A-B, G-H, paratype, female (Carapace length 7.6 mm), [NHMUK 2012.1526], from Kemp Caldera, Scotia Sea, 1517 m; C, F, paratype, male (Carapace length 6.5 mm), [0499 add registration no.], same data; D, E, paratype, male (Carapace length 6.5 mm), [NHMUK 2012.1522], same data: A, right first pereopod, lateral view; B, same, carpus, mesial view; C, left second pereopod, lateral view; D, right third pereopod, lateral view; E, same, dactylus and distal part of propodus, lateral view; F, left fourth pereopod, lateral view; G, left fifth pereopod, lateral view; H, same, dactylus and distal part of propodus, mesial view. Scale bars: A, C-D, F-G = 2 mm; B, E, H = 1mm.

Fig. 7. *Lebbeus antarcticus* (Hale, 1941). Female (Carapace length 13.4 mm), [NHMUK 2012.1531], from the E2 segment of the East Scotia Ridge, Scotia Sea, 2139 m. Entire animal, lateral view. Scale bar = 5mm.

Fig. 8. *Lebbeus antarcticus* (Hale, 1941). Female (Carapace length 13.4 mm), [NHMUK 2012.1531], from the E2 segment of the East Scotia Ridge, Scotia Sea, 2139 m: A, anterior part of carapace and cephalic appendages, dorsal view; B, same, lateral view; C, posterolateral margins of right pleura of fourth and fifth abdominal

somites, lateral view; D, telson and left uropod, dorsal view; E, posterior part of telson, dorsal view; F, left antennal peduncle and scale, ventral view; G, coxae of right first to fourth pereopods, showing presence of epipod on third pereopod and corresponding setobranch on fourth pereopod, lateral view. Scale bars = 2mm.

Fig. 9. *Lebbeus antarcticus* (Hale, 1941). Female (Carapace length 13.4 mm), [NHMUK 2012.1531], from the E2 segment of the East Scotia Ridge, Scotia Sea, 2139 m. Left mouthparts: A, mandible, ventral view; B, same, palp and incisor process; C, maxillule (first maxilla), dorsal view; D, maxilla (second maxilla), ventral view; E, first maxilliped, ventral view; F, second maxilliped, ventral view; G, third maxilliped, lateral view; H, same, distal part of antepenultimate segment, lateral view; I, distal part of ultimate segment of third maxilliped, dorsal view. Scale bars: A-F, G-H = 1 mm; G = 2mm.

Fig. 10. *Lebbeus antarcticus* (Hale, 1941). Female (Carapace length 13.4 mm), [NHMUK 2012.1531], from the E2 segment of the East Scotia Ridge, Scotia Sea, 2139 m. Left pereopods: A, first pereopod, lateral view; B, same, chela and carpus, mesial view; C, second pereopod, lateral view; D, third pereopod, lateral view; E, same, dactylus and distal part of propodus, lateral view; F, fourth pereopod (incomplete), lateral view; G, fifth pereopod, lateral view. Scale bars: A-D, F-G = 2 mm E = 1mm.

Fig. 11. Bayesian analysis of cytochrome oxidase I of *Lebbeus* and *Eualus*. A, 3rd codon positions RY coded; B, Gene partitioned into codon positions (1+2) and 3 (each partition GTR+I+G). Bayesian posterior probabilities shown on branches.

Table 1. Sampling data

Species	NHMUK Reg. no.	Site	Area	Latitude (S)	Longitude (W)	Depth (m)	Date	Dive no.	Method
<i>Eualus amandae</i> sp. nov.	2012.1522	JC42-4-15	E9	60°02.580	29°58.837	2401	04/02/2010	145	Suction sampler
<i>Eualus amandae</i> sp. nov.	2012.1523	JC42-5-15	Kemp Caldera	59°41.973	28°21.01	1517	11/02/2010	152	Suction sampler
<i>Eualus amandae</i> sp. nov.	2012.1524	JC42-5-15	Kemp Caldera	59°41.973	28°21.01	1517	11/02/2010	152	Suction sampler
<i>Eualus amandae</i> sp. nov.	2012.1525	JC42-5-15	Kemp Caldera	59°41.973	28°21.01	1517	11/02/2010	152	Suction sampler
<i>Eualus amandae</i> sp. nov.	2012.1526	JC42-5-15	Kemp Caldera	59°41.973	28°21.01	1517	11/02/2010	152	Suction sampler
<i>Eualus amandae</i> sp. nov.	2012.1527	JC42-5-15	Kemp Caldera	59°41.973	28°21.01	1517	11/02/2010	152	Suction sampler
<i>Eualus amandae</i> sp. nov.	2012.1528	JC42-5-15	Kemp Caldera	59°41.973	28°21.01	1517	11/02/2010	152	Suction sampler
<i>Lebbeus antarcticus</i>	2012.1529	JC42-3-15	E2	56°05.307	30°19.094	2598	23/01/2010	133	Baited trap
<i>Lebbeus antarcticus</i>	2012.1530	JC42-3-18	E2	56°05.324	30°19.107	2139	25/01/2010	135	Baited trap
<i>Lebbeus antarcticus</i>	2012.1531	JC42-3-18	E2	56°05.324	30°19.107	2139	25/01/2010	135	Baited trap
<i>Lebbeus antarcticus</i>	2012.1532	JC42-4-7	E9	60°02.568	29°58.89	2402	30/01/2010	140	Biobox

Table 2. Taxonomy, voucher catalogue numbers and GenBank accession numbers for gene sequences used herein.

Taxa	Voucher nos.	GenBank accession nos. COI
Alvinocarididae Christoffersen, 1986		
<i>Alvinocaris longirostris</i> Kikuchi and Ohta, 1995	-	AB222050
Hippolytidae Spence Bate, 1888		
<i>Eualus amandae</i> sp. nov.	2012.1522	TBA
<i>Eualus amandae</i> sp. nov.	2012.1523	TBA
<i>Eualus amandae</i> sp. nov.	2012.1524	-
<i>Eualus amandae</i> sp. nov.	2012.1525	TBA
<i>Eualus amandae</i> sp. nov.	2012.1526	TBA
<i>Eualus amandae</i> sp. nov.	2012.1527	TBA
<i>Eualus amandae</i> sp. nov.	2012.1528	-
<i>Eualus avinus</i> (Rathburn, 1899)	SQB213A	DQ882065
<i>Eualus avinus</i>	SQB213B	DQ882064
<i>Eualus avinus</i>	SQB213C	DQ882063
<i>Eualus barbatus</i> (Rathburn, 1899)	SQC11A	DQ882066
<i>Eualus barbatus</i>	SQC11B	DQ882067
<i>Eualus barbatus</i>	SQC9A	DQ882069
<i>Eualus barbatus</i>	SQC9B	DQ882070
<i>Eualus barbatus</i>	SQC9C	DQ882068
<i>Eualus biunguis</i>	SQE11A	DQ882074
<i>Eualus biunguis</i> (Rathburn, 1902)	SQE11B	DQ882073
<i>Eualus biunguis</i>	SQE13A	DQ882072
<i>Eualus biunguis</i>	SQE13B	DQ882071
<i>Eualus cranchii</i> (Leach, 1817)	JSDUK185	JQ306050
<i>Eualus fabricii</i> (Krøyer, 1841)	BSM	FJ581627
<i>Eualus fabricii</i>	L90	FJ581628
<i>Eualus gaimardii gaimardii</i>	DPA12	DQ882075
<i>Eualus gaimardii gaimardii</i>	JSD	JQ305958
<i>Eualus gaimardii gaimardii</i>	EG01CN0506	FJ581629
<i>Eualus macilentus</i> (Krøyer, 1841)	BSM07T11-04	FJ581635
<i>Eualus macilentus</i>	BSM07T11-05	FJ581634
<i>Eualus macilentus</i>	EM01CN0606	FJ581633
<i>Eualus macilentus</i>	EM02CN0606	FJ581632
<i>Eualus macilentus</i>	TE-004T141	FJ581630
<i>Eualus macilentus</i>	TE-004T21	FJ581631
<i>Eualus suckleyi</i> (Stimpson, 1864)	SQJ242A	DQ882076
<i>Eualus suckleyi</i>	SQJ242B	DQ882077
<i>Eualus suckleyi</i>	SQJ39	DQ882078
<i>Hippolyte inermis</i> Leach, 1816	CCDB 2783	JF794740
<i>Hippolyte obliquimanus</i> Dana, 1852	CCDB 2033	JF794736
<i>Hippolyte williamsi</i> Schmitt, 1924	CCDB 2382	JF794738
<i>Lebbeus antarcticus</i> (Hale, 1941)	2012.1529	TBA
<i>Lebbeus antarcticus</i>	2012.1530	TBA
<i>Lebbeus antarcticus</i>	2012.1531	TBA
<i>Lebbeus antarcticus</i>	2012.1532	TBA
<i>Lebbeus groenlandicus</i> (Fabricius, 1775)	DPA06	DQ882084
<i>Lebbeus groenlandicus</i>	SPE26A	DQ882083

<i>Lebbeus groenlandicus</i>	SPE26B	DQ882082
<i>Lebbeus groenlandicus</i>	TE-004T141	FJ581737
<i>Lebbeus laurentae</i> Wicksten, 2010	-	AF125421
<i>Lebbeus polaris</i> (Sabine, 1824)	TE-004T181	FJ581738
<i>Lebbeus polaris</i>	LP01	FJ581739
<i>Lebbeus virentova</i> Nye et al., 2012	-	JQ837266
<i>Lysmata pederseni</i> Rhyne and Lin, 2006	-	EU135869
<i>Lysmata wurdemanni</i> (Gibbs, 1850)	-	EU135867
<i>Spirontocaris spinus</i> (Sowerby, 1805)	FC-DPA10	DQ882163
<i>Thor amboinensis</i> (De Man, 1888)	-	JQ180245

TBA: To be added.

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Table 3. *Eualus amandae* sp. nov. Branchial formula

Thoracic somites	1	2	3	4	5	6	7	8
	Maxillipeds				Pereopods			
	1	2	3	1	2	3	4	5
Pleurobranchs	-	-	-	1	1	1	1	1
Arthrobranch	-	-	-	-	-	-	-	-
Podobranch	-	1	-	-	-	-	-	-
Epipods	1	1	1	1	1	1	-	-
Setobranchs	-	-	-	+	+	+	+	-
Exopods	1	1	1	-	-	-	-	-

Table 4. *Lebbeus antarcticus* (Hale, 1941). Branchial formula

Thoracic somites	1	2	3	4	5	6	7	8
	Maxillipeds				Pereopods			
	1	2	3	1	2	3	4	5
Pleurobranchs	-	-	-	1	1	1	1	1
Arthrobranch	-	-	-	-	-	-	-	-
Podobranch	-	1	-	-	-	-	-	-
Epipods	1	1	1	1	1	1	-	-
Setobranchs	-	-	-	+	+	+	+	-
Exopods	1	1	-	-	-	-	-	-

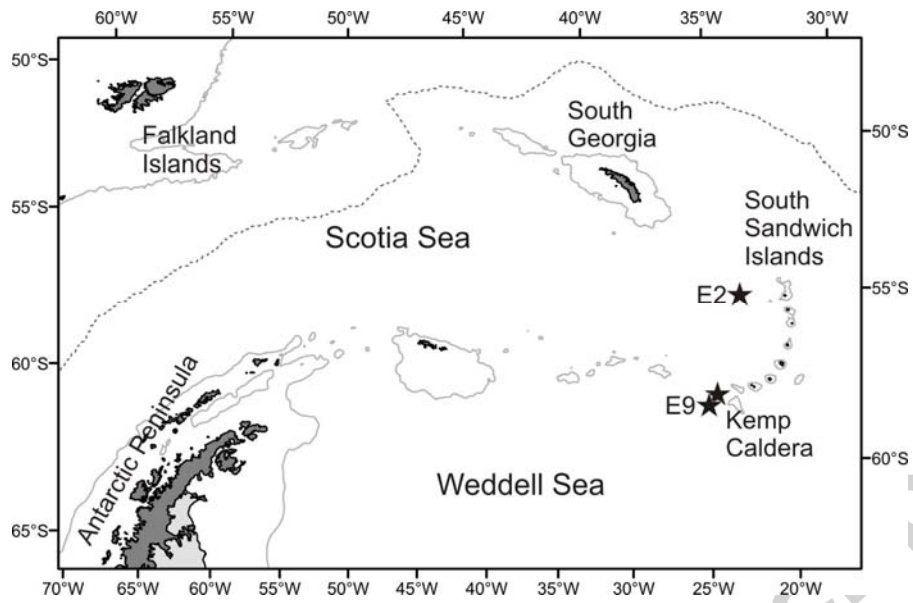


Fig. 1

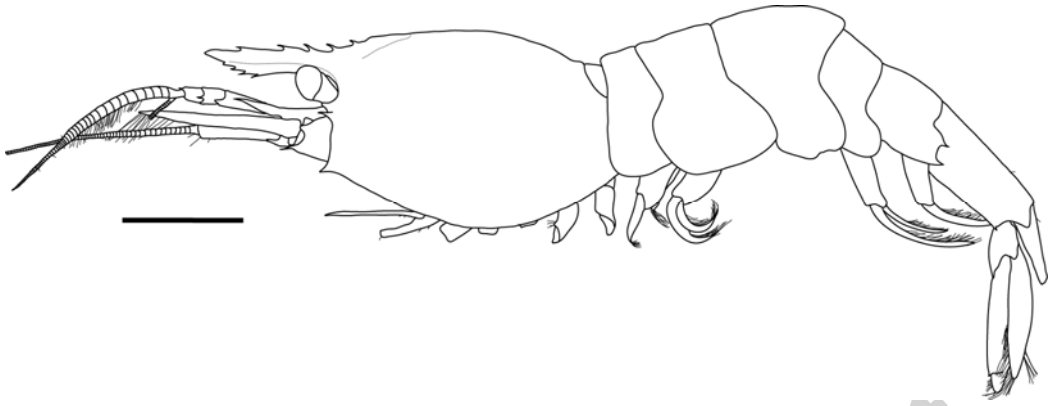


Fig. 2

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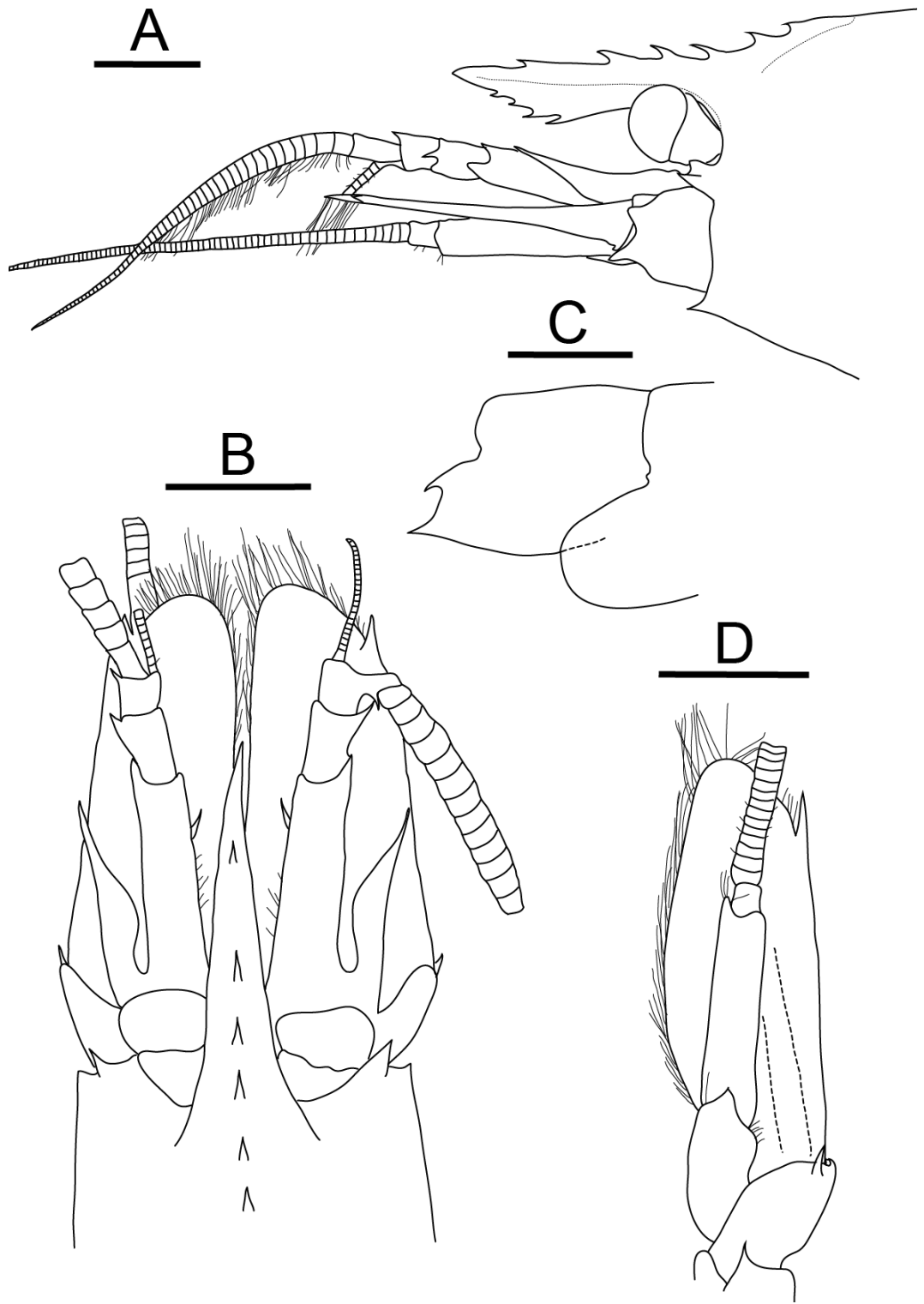


Fig. 3

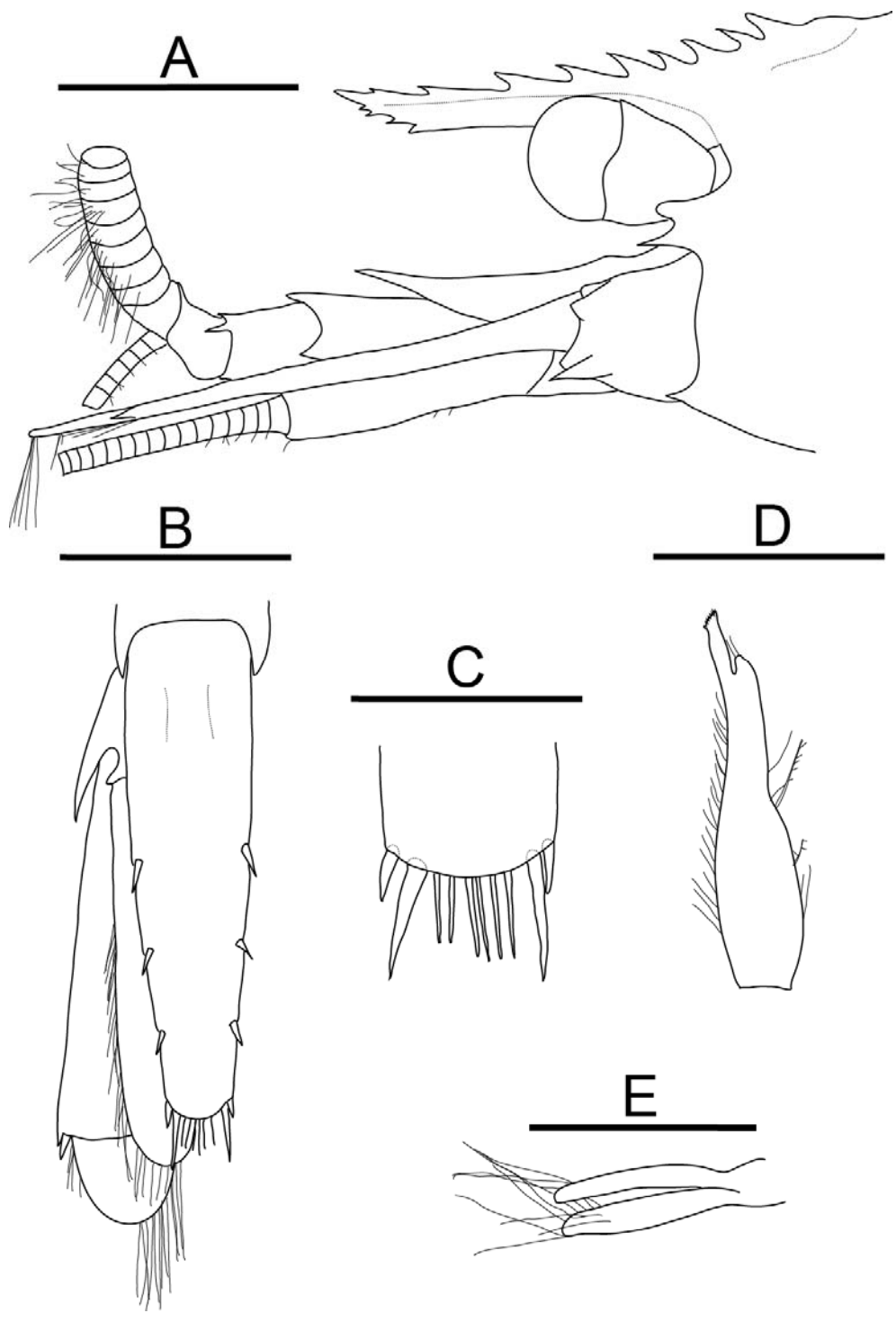


Fig. 4

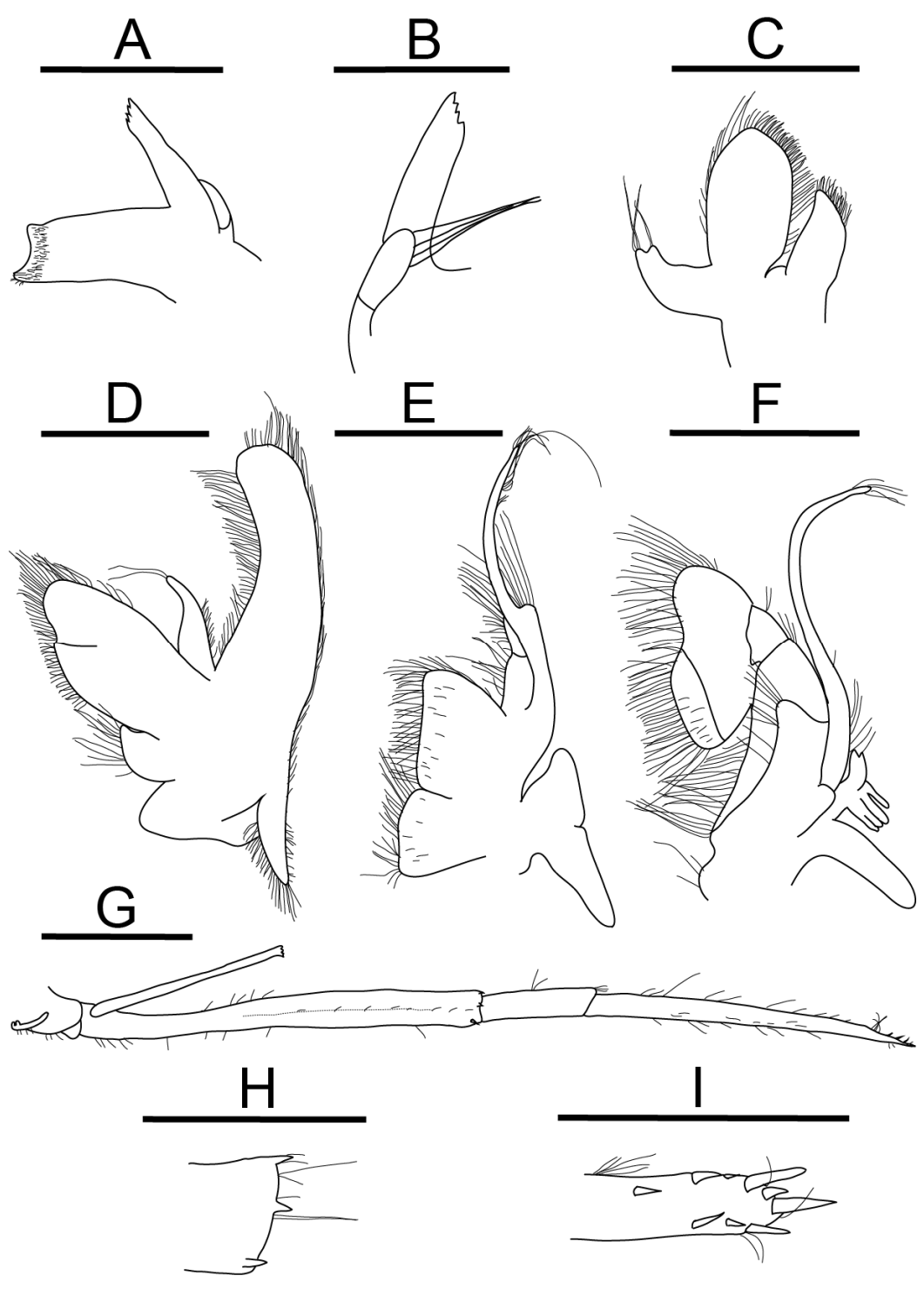


Fig. 5

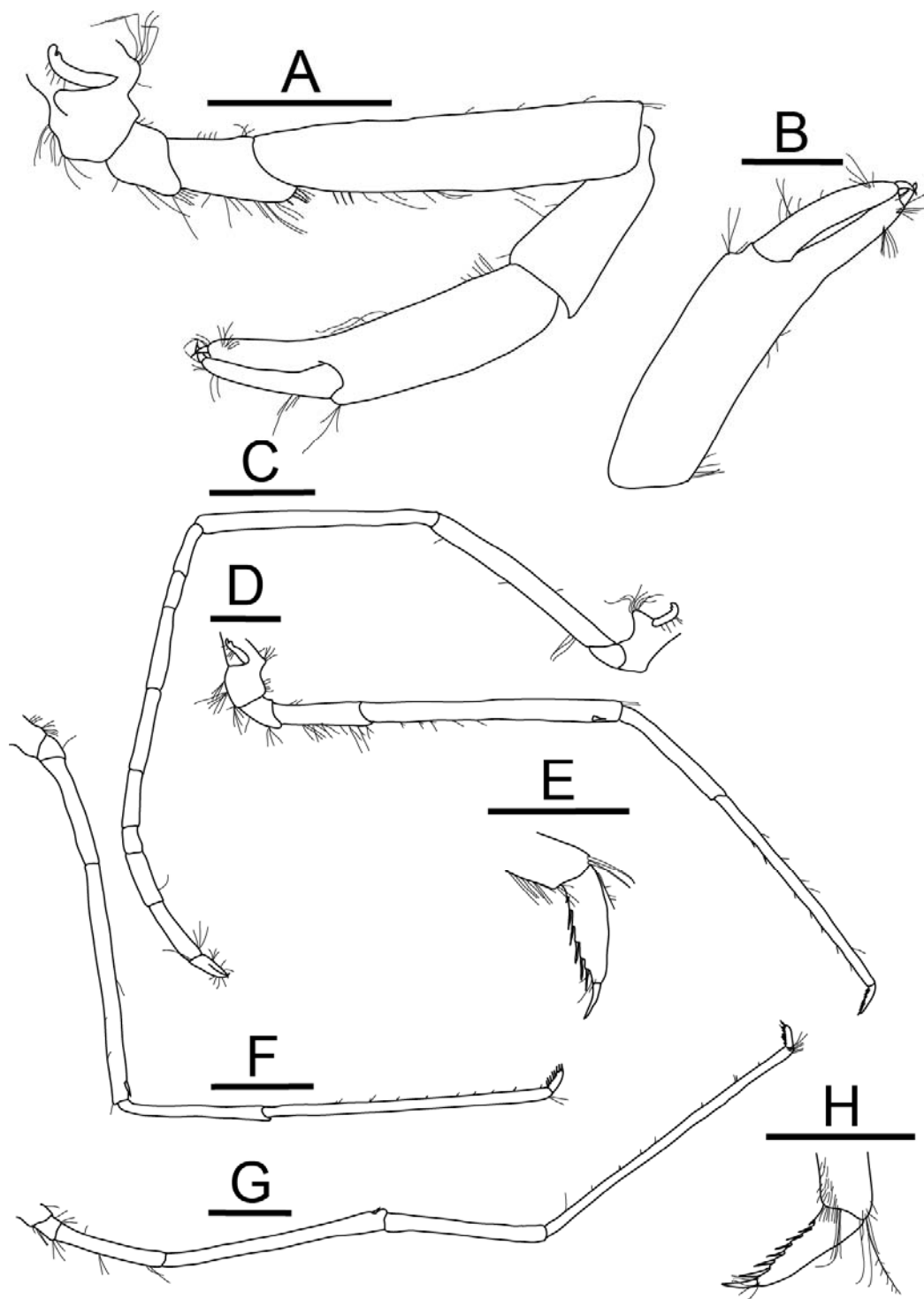


Fig. 6.

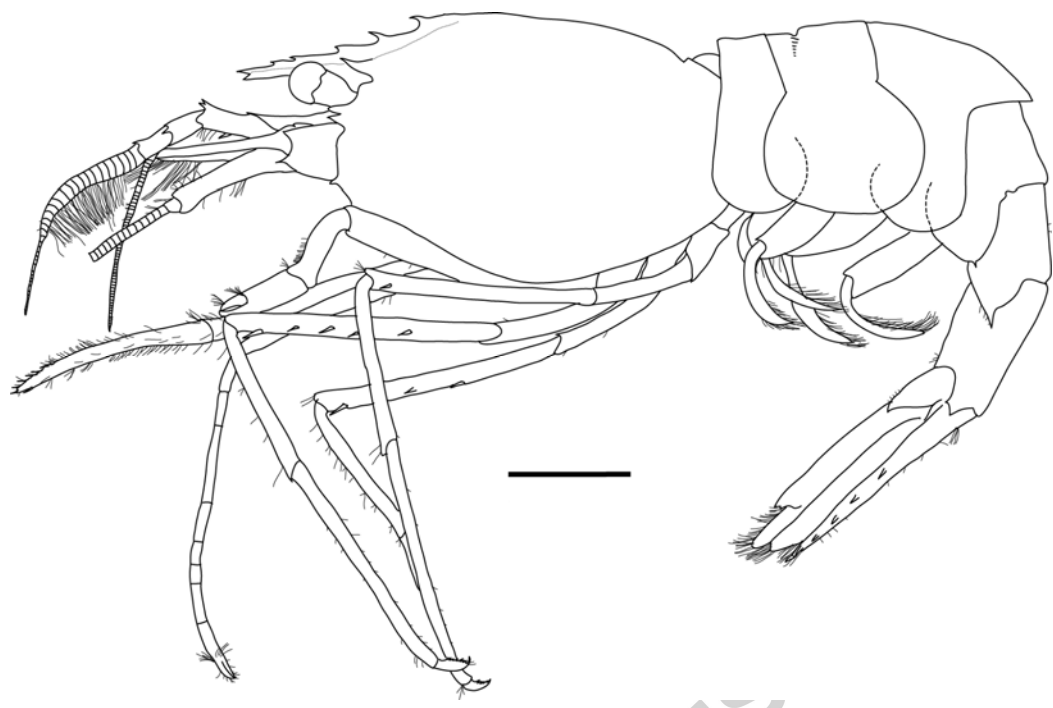


Fig. 7

Accepted manuscript

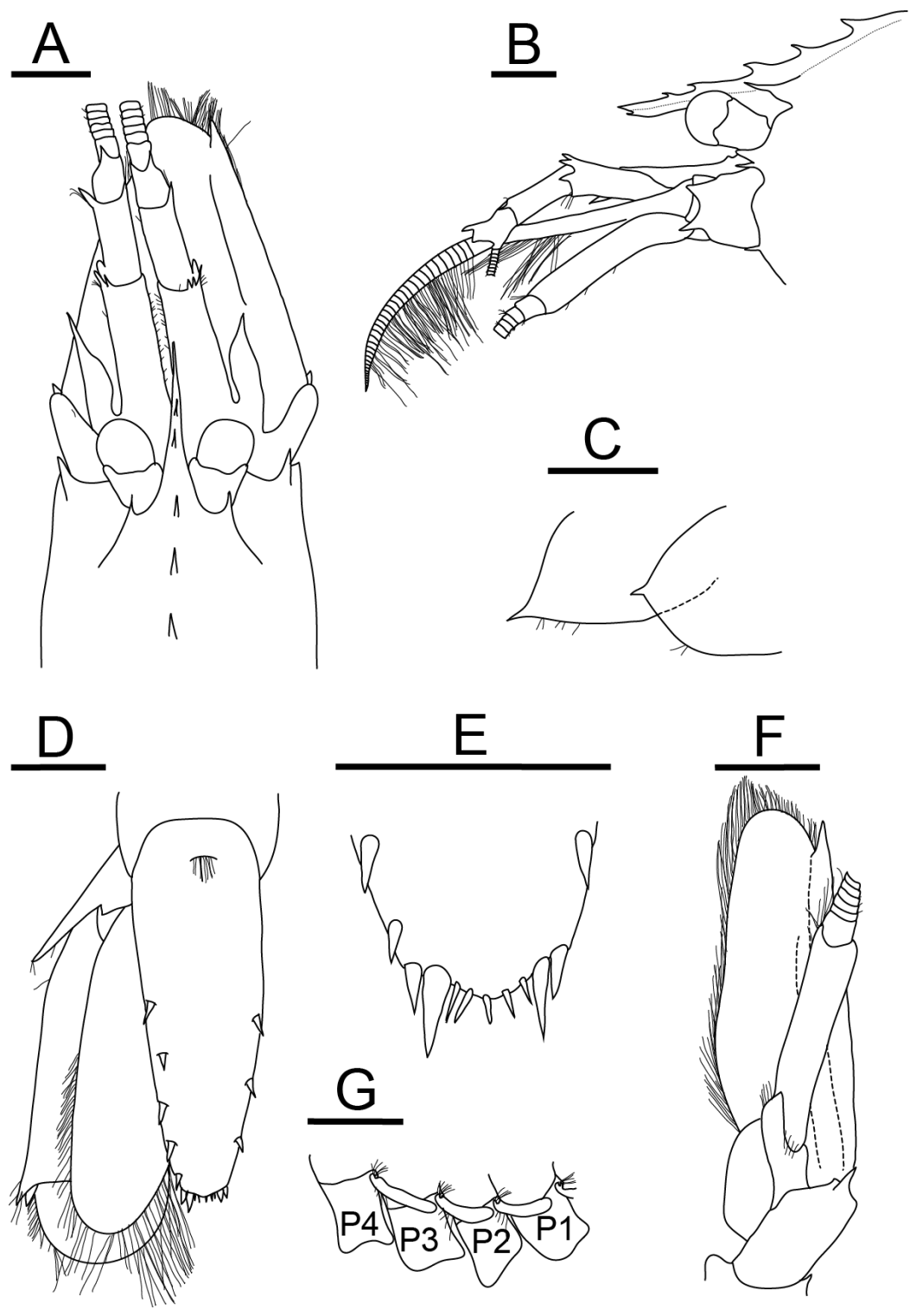


Fig. 8

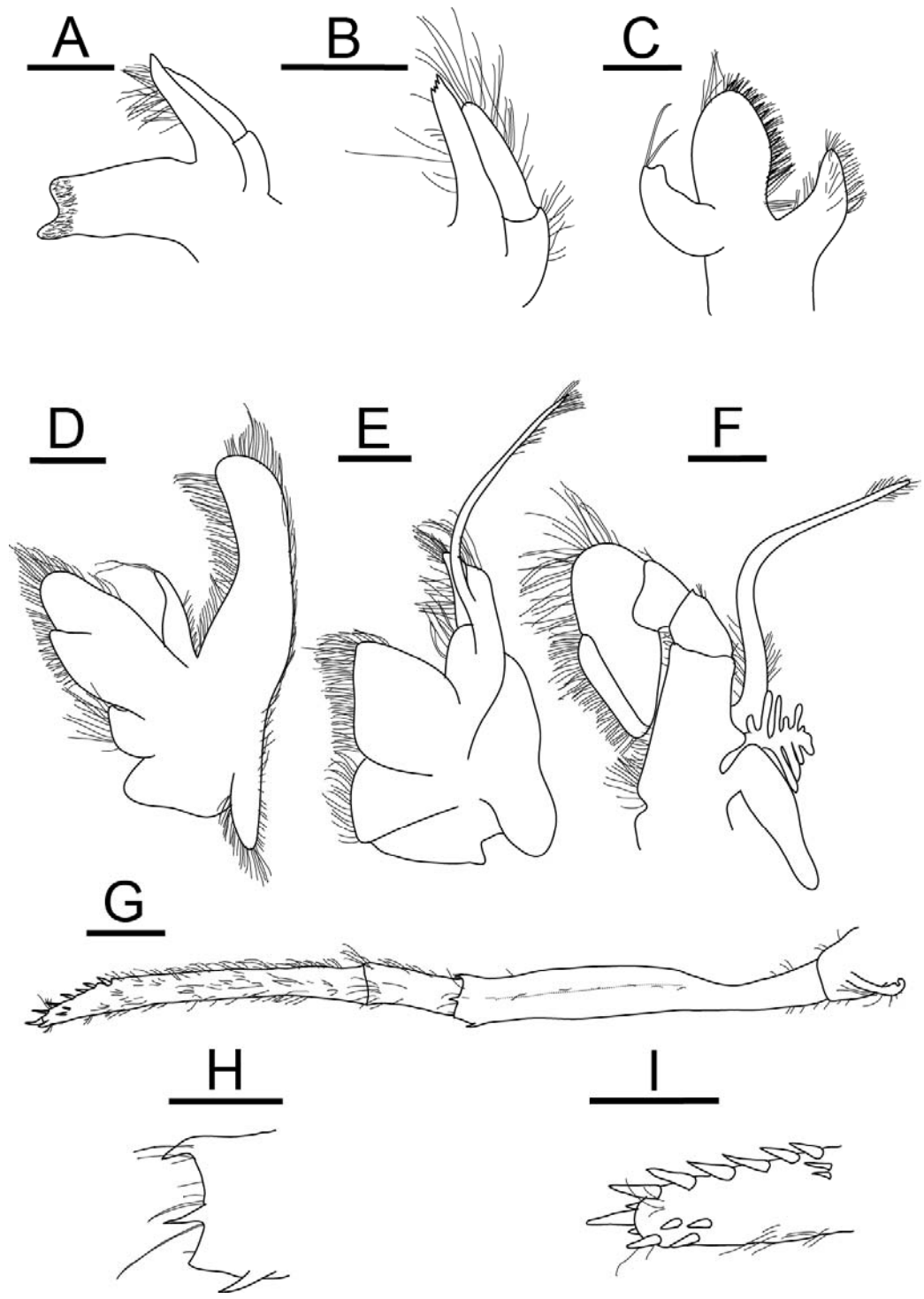


Fig. 9

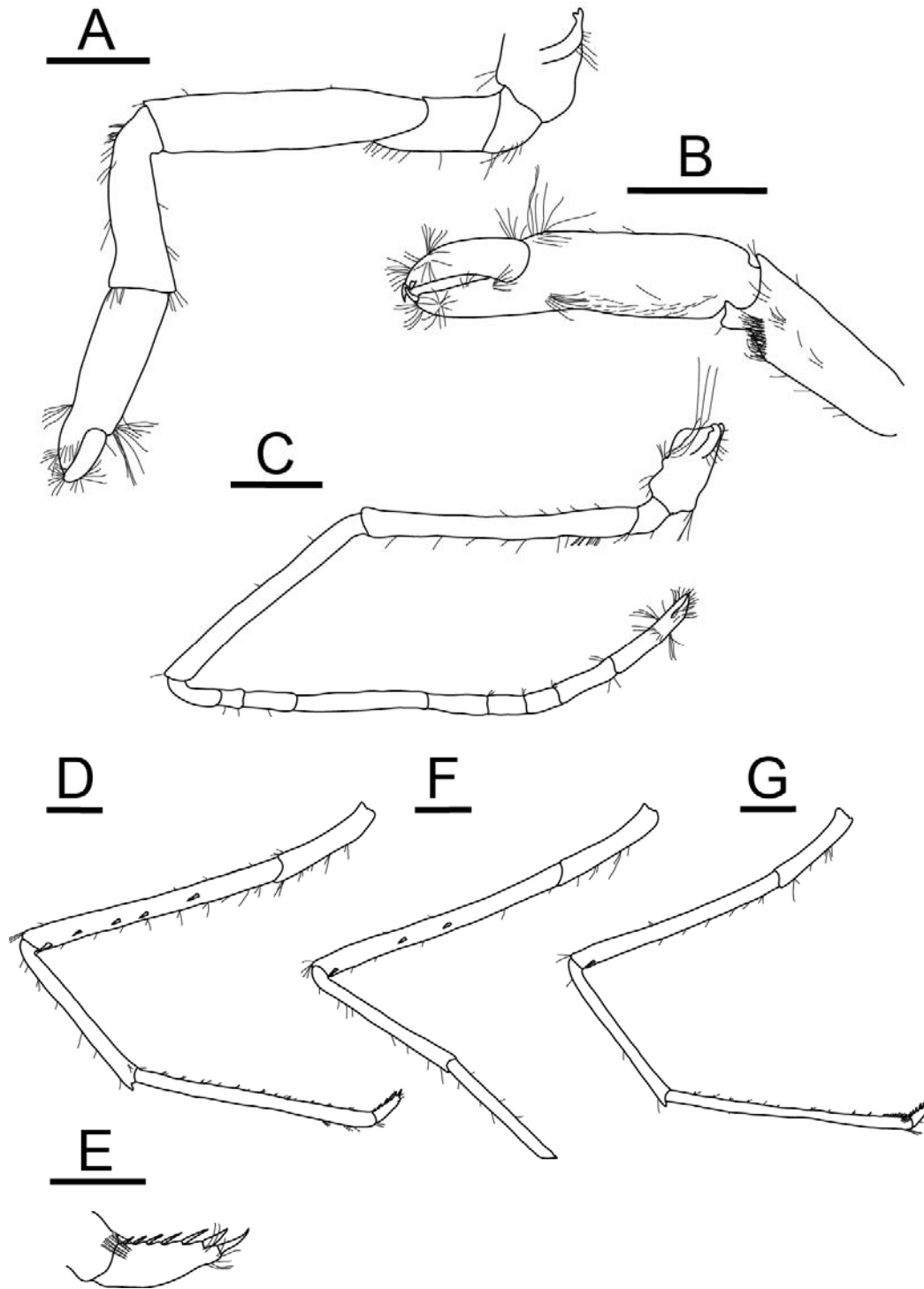


Fig. 10

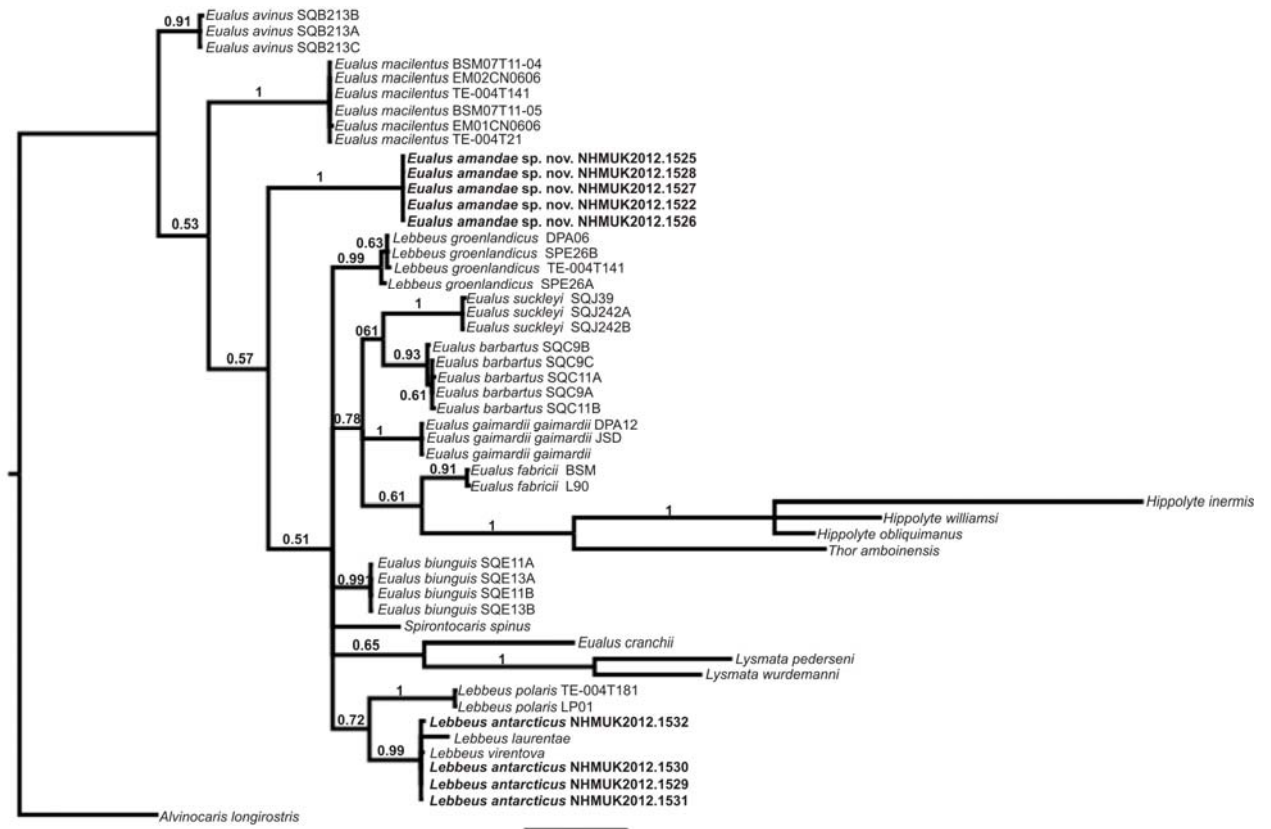


Fig. 11 A

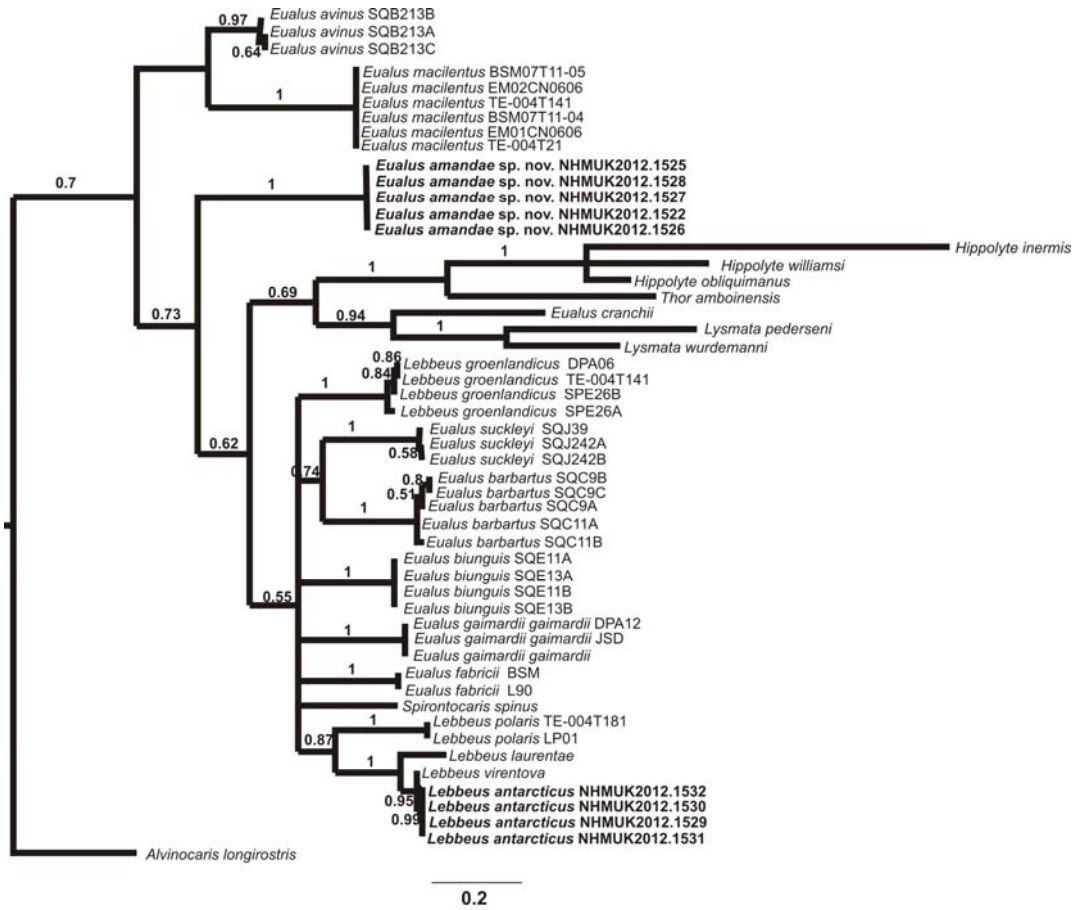


Fig. 11 B