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Do circum-Antarctic species exist in peracarid Amphipoda? A case study in the genus *Epimeria* Costa, 1851 (Crustacea, Peracarida, Epimeriidae)

Anne-Nina Lörz[1,†], Elizabeth W. Maas[1,‡], Katrin Linse[2,§],
Charles Oliver Coleman[3,|]

1 *National Institute of Water and Atmospheric Research, Private Bag 14-901, Kilbirnie, Wellington, New Zealand* **2** *British Antarctic Survey, Natural Environmental Research Council, High Cross, Madingley Road , Cambridge, CB3 0ET, United Kingdom* **3** *Museum für Naturkunde Berlin, Invalidenstraße 43, D-10115 Berlin, F.R.G.*

† *urn:lsid:zoobank.org:author:9442484E-43A4-4383-A1A6-AE493087BCA1*
‡ *urn:lsid:zoobank.org:author:3B44FEC0-DF77-4074-BADD-EF549F6A0F74*
§ *urn:lsid:zoobank.org:author:E6628609-3C45-4A45-9337-D05303AABD23*
| *urn:lsid:zoobank.org:author:1EC18609-2D14-462B-8E59-B1CE40166FAF*

Corresponding author: *Anne-Nina Lörz* (a.loerz@niwa.co.nz)

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Abstract

The amphipod genus *Epimeria* is species rich in the Southern Ocean and at present eight of its 19 species are reported with circum-Antarctic distributions. For the first time, specimens of epimeriid species from the Antarctic Peninsula, the Weddell Sea and the Ross Sea were analysed using partial COI genes sequences and morphological characters. In total 37 specimens of 14 species of *Epimeria* and two species of *Epimeriella* were analysed and the resulting molecular topology checked by critically reviewing taxonomic characters. The genus *Epimeriella*, genetically grouping within *Epimeria* is synonymised with the genus *Epimeria*. Sequences distances between populations of the nominal species *Epimeria robusta* from the Weddell and Ross Sea led to detailed morphological investigations, resulting in the description of *Epimeria robustoides* **sp. n.** from the Weddell Sea. *Epimeria robusta* Barnard, 1930 from the Ross Sea is redescribed. Sequences of a damaged *Epimeria* specimen of a species new to science from the lower continental shelf of the eastern Weddell Sea were included. Based on the current study, the hypothesis of circum-Antarctic species' distributions in brooding amphipods proved to be unlikely.

Keywords

Circum-Antarctic distribution, COI, Antarctica, New Zealand, Amphipoda, *Epimeriella*, *Epimeria* sp. n.

Introduction

In the Southern Ocean's benthic ecosystem, crustaceans are by far the most specious taxon. Among the crustaceans, amphipods are the most numerous group with more than 815 recorded species (De Broyer et al. 2007). The globally distributed amphipod family Epimeriidae Boeck, 1871 (formerly Paramphithoidae) belongs to the dominant members of Antarctic shelf benthos (Coleman 2007). Twenty-five species of Epimeriidae are known from Antarctic waters, that is 19 *Epimeria* Costa, 1851, four *Epimeriella* Walker, 1906, one *Metepimeria* Schellenberg, 1931a and one *Uschakoviella* Gurjanova, 1955b.

Based on their distribution records from the Weddell and Ross Sea shelves, eight species of Epimeriidae (*Epimeria grandirostris, E. inermis, E. macrodonta, E. puncticulata, E. "robusta", E. macronyx, E. walkeri* and *E. scabrosa*) are believed to have circum-Antarctic distributions. *Epimeria robusta* Barnard, 1930 was originally described from the Ross Sea but because of insufficient descriptions and images Coleman (1994) redescribed *E. robusta* based on specimens from the Weddell Sea. Five of the epimeriid species (*Epimeria extensa*, *E. heldi*, *E. reoproi*, *E. vaderi* and *E. truncata*) are known from locations only on the Antarctic Peninsula. Two species, *Epimeria rimicarinata* Watling and Holman, 1980 and the recently described *E. schiaparelli* Lörz, Maas, Linse and Fenwick, 2007 are found exclusively in the Ross Sea.

Epimeriella macronyx is known from the eastern Antarctic Peninsula, Davis Sea, Ross Sea, South Orkney Islands, South Shetland Islands and the Weddell Sea. *Epimeriella scabrosa* was found at Oats Coast and the Weddell Sea. *Epimeriella truncata* is known only from the type locality, at the western Antarctic Peninsula. *Epimeriella walkeri* has a distribution at the Davis Sea, Palmer Archipelago, Ross Sea, South Shetland Islands and Weddell Sea. The monotypic genus *Metepimeria* has never been found again after its original description and the finding of *Uschakoviella* by Watling and Holman (1981) could not be confirmed. All other known species of *Uschakoviella* are restricted to the Arctic Ocean.

The Antarctic Epimeriidae mostly occur on the continental shelves and upper slopes. So far only one epimeriid specimen has been caught on the deep slope (2157 m) off Kapp Norvegia in the Weddell Sea during the ANDEEP III expedition. This damaged species of *Epimeria* sp. proved to be new to science (authors personal observation).

Outside of the Southern Ocean only a few species of Epimeriidae have been described from the Southern Hemisphere. With the exception of *Epimeriella victoria* (Hurley, 1957) these belong to the genus *Epimeria* and show bathymetric affinities to the deep continental slopes and deep sea. Three have been found in depths greater than 1500 m off the Brazilian coast: *E. bathyalis* Wakabara and Serejo, 1999 (1200–1575 m), *E. rotunda* Wakabara and Serejo, 1999 (1190–1205 m) and *E. ultraspinosa* Wakabara and Serejo, 1999 (830 m). The deepest species of Epimeriidae found is *Epimeria bispinosa* Ledoyer, 1986 off Madagascar in 3450 m water depth. *Epimeria* *longispinosa* Barnard, 1916 occurs off eastern Florida and False Bay, South Africa at depths of 345–750 m. The New Zealand Epimeriidae so far only comprises of four species [*Epimeria glaucosa* Barnard, 1961, 3710 m; *E. bruuni* Barnard, 1961, 2470 m; *E. horsti* Lörz, 2008, 1030m; and *E. victoria* (Hurley, 1957), 140 m] and to date none have been found in Australian waters (Lörz et al. 2008).

The first combined molecular and morphological phylogeny of Antarctic Epimeriidae and Iphimediidae was based on a total of 16 taxa. It was presented by Lörz and Held (2004) and proved the monophyly of the families Epimeriidae and Iphimediidae. This preliminary study based on only 16 specimens from the Weddell Sea included six species of *Epimeria* (Epimeriidae) and eight species of *Iphimediella*, *Echiniphimedia* and *Gnathiphimedia* (Iphimediidae).

Lörz and Brandt (2004) published the first extensive morphology-based phylogeny of Antarctic *Epimeria* based on all 17 Antarctic species described at that time, including species of the genera *Epimeriella* and *Metepimeria*. The resulting topology of this study confirmed the monophyly of the Epimeriidae and Iphimediidae but was not convincingly able to determine relationships between and within the genus *Epimeria*. *Epimeriella* and *Metepimeria* species appeared amongst the species of *Epimeria*, suggesting polyphyly for the latter genus.

Recent expeditions to the Ross Sea, seamounts off New Zealand and the Weddell Sea collected new epimeriid material, which was preserved in a state suitable for genetic studies. This new material enables us is to shed light on open questions regarding the evolution of Southern Hemisphere Epimeriidae:

1. Do circum-Antarctic distributions occur amongst species of epimeriid Amphipoda?
2. How are New Zealand and Antarctic *Epimeria* species related? Do the Southern Ocean epimeriids form an Antarctic clade?
3. Are the genera *Epimeria* and *Epimeriella* monophyletic?

Our recent study contributes to the ongoing investigation and census of the Southern Ocean benthic biota, its diversity and biogeographic history.

Material and methods

Taxon sampling. During recent expeditions of RV *Tangaroa* to the Ross Sea (BioRoss, TAN0402; IPY, TAN0802) and seamounts off New Zealand (TAN0413, TAN0602), as well as RV *Polarstern* to the Weddell Sea (ANT XXI/2, BENDEX und ANDEEP III) new amphipod material was collected. Amphipods were sorted from collections immediately (often alive), fixed in 98% ethanol and later transferred to 70% ethanol. Of these collections 30 specimens of Epimeriidae and 1 specimen of Iphimediidae were identified to species level and included in the molecular analysis (Table 1).

The final phylogenetic dataset includes the 31 new sequences of 14 epimeriid and one iphimediid species and 17 published sequences of six species of Epimeriidae, nine of Iphimediidae and *Eusirus* cf. *perdentatus* (Eusiridae).

Morphological description. Specimens were examined and dissected using a Leica MZ9.5 stereomicroscope and drawn using a camera lucida attachment. Small appendages (mouthparts, uropods, telson) were temporarily mounted in lactic acid, examined and drawn using a Nikon compound microscope fitted with a camera lucida. The body lengths of specimens examined were measured by tracing individual's mid-trunk lengths (tip of the rostrum to end of telson) using a camera lucida.

All illustrations were drawn by using the digital inking illustration method described by Coleman (2003). Within the description, abbreviations are used for slender setae (SS) and robust setae (RS). Type material was deposited in the Natural History Museum Berlin, Germany, and the NIWA Marine Invertebrate Collection Wellington, New Zealand. We cross checked with the type material from *E. robusta*, held at the Natural History Museum London (BMNH 1930.8.1.303–309). Coloured photographs of *Epimeria robusta* and *E. robustoides* sp. n. were taken on board immediately after the specimen were caught.

DNA extraction and analysis. Genomic DNA was isolated from amphipod pereopods using the DNEasy tissue extraction kit (Qiagen Ltd) and quantified using the PicoGreen quantification kit (Molecular Probes, Invitrogen Ltd). The partial mitochondrial cytochrome oxidase subunit I (COI) gene was amplified using the universal primers described by Folmer et al. 1994 using PuReTaq Ready-To-Go™ PCR Beads (GE Healthcare), 0.2 µM of each primer and between 20–200 ng of genomic DNA. PCR reactions were carried out in a GeneAmp 2720 thermocycler (Applied Biosystems, Foster City, California, USA) using the following conditions: an initial hold at 95°C for 5 minutes and then 30 cycles of 95°C for 30 seconds; 45°C for 30 seconds; 72°C for 1.5 minutes; and a final extension at 72°C for 7 minutes. PCR products were purified using QIAquick Spin Columns (Qiagen Ltd) and quantified using the PicoGreen Kit (Molecular Probes, Invitrogen Ltd). Sequencing of the COI gene was carried out at Macrogen Ltd, Korea, using the amplification primers.

The proof-read sequences of the 31 specimens were aligned using ARB software (Ludwig et al. 2004) against COI sequences available in EMBL of seven *Epimeria* species, three *Echiniphimedia* species, three *Iphimediella* species, two *Gnathiphimedia* species and *Eusirus* cf. *perdentatus* Chevreux, 1912 (Table 1). The Iphimediidae and *Eusirus* cf. *perdentatus* were chosen as the outgroup taxa, since Lörz and Held (2004) showed them to be the sister taxa of the Epimeriidae.

Evolutionary distances were calculated from sequence pair dissimilarities using only unambiguously sequenced positions. The partial COI gene sequences determined in this study are deposited in the EMBL database and the accession number for each specimen is shown in Table 1. The amphipod specimens are registered and curated at the National Institute for Water and Atmospheric Research (NIWA) (Table 1).

Phylogenetic analysis. Sequences were analyzed using maximum parsimony (MP) and maximum likelihood (ML) criteria in PAUP*4.0b10 (Swofford 2002). MP analyses were implemented in PAUP* as heuristic search, tree bisection-reconnection (TBR), random addition sequence. All characters were unordered and

Table 1. EMBL accession numbers, NIWA registration numbers and station data of specimens analysed.

	Accession Number	NIWA Registration number	Expedition / Station	Latitude	Longitude W or E and in min and dec not all dec	Start Depth (m)	Finish Depth (m)	Region
Epimeriidae								
Epimeria schiaparelli	FM955284	18186	TAN0402/25	71°47′55″ S	170°55′58″ E	127	140	Ross Sea
E. inermis	FM955280	20164	TAN0402/ 94	71°31′48″ S	170°06′40″ E	220	191	Ross Sea
E. inermis	FM955281	20169	TAN0402/ 184c	71°30′20″ S	171°36′25″ E	480	491	Ross Sea
E. inermis	FM955282	20171	TAN0402/233	67°25′40″ S	163°54′56″ E	230	227	Balleny Islands
E. inermis	FM955292	20168	TAN0402/134	71°38′30″ S	170°09′90″ E	65	64	Ross Sea
E. inermis	FM955285	20162	TAN0402/33	71°45′17″ S	171°25′10″ E	282	278	Ross Sea
E. robusta	FM955279	20263	TAN0402/25	71°47′55″ S	170°55′58″ E	127	140	Ross Sea
E. robusta	FM955283	20273	TAN0402/150	71°58′46″ S	171°58′5″ E	480	461	Ross Sea
E. robusta	FM955286	20257	TAN0402/22	71°48′40″ S	170°56′29″ E	151	180	Ross Sea
E. robusta	FM955287	20266	TAN0402/105	71°15′27″ S	170°38′50″ E	470	458	Ross Sea
E. robustoides	FM955288	34934	ANT XXI/2 PS65-293	72°51′54″ S	019°39′19″ W	541	518	Weddell Sea
E. robusta	FM955289	20261	TAN0402/39	71°45′18″ S	171°08′33″ E	251	253	Ross Sea
E. robusta	FM955291	20258	TAN0402/25	71°47′55″ S	170°55′58″ E	127	140	Ross Sea
E. robusta	FM955290	20274	TAN0402/154	72°00′50″S	172°13′20″ E	536	586	Ross Sea
E. annabellae	FM955293	34935	ANT XXI/2 PS 65-337	70°56′41″ S	010°32′70″ W	306		Weddell Sea
Epimeria new species 1	FM955295	34937	ANDEEPIII PS67-078-11	71°09′39″ S	013°59′33″ W	2157	2147	Weddell Sea
E. horsti	FM955296	34938	TAN0604-111 #1119	42°47′51″ S	179°59′16″ E	970	1040	New Zealand
E. horsti	FM955297	34939	TAN0604-106 #990	42°43′36″ S	180°06′20″ E	1030	1156	New Zealand
E. bruuni	FM955298	4088	TAN0413-200 #2708 (3A)	39°22′34″ S	179°50′35″ E	2526	2550	New Zealand
E. rimicarinata	FM955300	19639	TAN0402/105	71°15′27″ S	170°38′50″ E	470	458	Ross Sea
E. rimicarinata	FM955302	19645	TAN0402/108	71°16′19″ S	170°35′59″ E	400	405	Ross Sea
E. rimicarinata	FM955304	19644	TAN0402/108	71°16′19″ S	170°35′59″ E	400	405	Ross Sea
E. rimicarinata	FM955303	19634	TAN0402/22	71°48′40″ S	170°56′29″ E	151	180	Ross Sea
E. georgiana	FM955299	34940	ANT XXI/2 PS 65-232	71°18′37″ S	013°56′70″ W	910	899	Weddell Sea

	Accession Number	NIWA Registration number	Expedition / Station	Latitude	Longitude W or E and in min and dec not all dec	Start Depth (m)	Finish Depth (m)	Region
E. georgiana	FM955305	34941	ANT XXI/2 PS65- 232	71°18′37″ S	013°56′70″ W	910	899	Weddell Sea
E. puncticulata	FM955301	34943	ANT XXI/2 PS65-121	70°50′50″ S	010°35′32″ W	268	274	Weddell Sea
E. grandirostris	FM955307	34945	ANT XXI/2 PS65-144	70°57′10″ S	010°48′26″ W	401	406	Weddell Sea
E. walkeri	FM955308	20255	TAN0402/63	72°19′18″ S	170°28′43″ E	303	293	Ross Sea
E. walkeri	FM955306	34946	ANT XXI/2 PS65-90	70°56′8″ S	010°31′42″ W	274	288	Weddell Sea
E. macronyx	FM955309	20254	TAN0402/76	72°8′16″ S	172°41′25″ E	496	501	Ross Sea
E. georgiana	AF451341	x	see Lörz and Held 2004	62°49′30″ S	060°49′18″ W	202		Antarctic Peninsula
E. reoproi	AF451342	x	see Lörz and Held 2004	63°00′60″ S	060°31′00″ W	48		Antarctic Peninsula
E.macrodonta	AF451343	x	see Lörz and Held 2004	71°11′54″ S	012°20′42″ W	316		Weddell Sea
E.robustoides	AF451344	x	see Lörz and Held 2004	71°11′54″ S	012°20′42″ W	323		Weddell Sea
E. rubrieques	AF451345	x	see Lörz and Held 2004	71°16′40″ S	013°45′47″ W	648		Weddell Sea
E. similis	AF451346	x	see Lörz and Held 2004	71°16′40″ S	013°45′47″ W	648		Weddell Sea
E. georgiana	AY061802	x	see Väinölä et al. 2001	Weddell				Antarctic Peninsula
Iphimediidae								
Echiniphimedia scotti	FM955294	34936	TAN0602-442	66°45′22″ S	163°03′37″ E	1930	1940	Ross Sea
Iphimediella rigida	AF451347	x	see Lörz and Held 2004	71°11′54″ S	012°20′42″ W	323		Weddell Sea
I. cyclogena	AF451348	x	see Lörz and Held 2004	71°11′54″ S	012°20′42″ W	323		Weddell Sea
I. georgei	AF451349	x	see Lörz and Held 2004	71°11′54″ S	012°20′42″ W	316		Weddell Sea
E. hodgsoni	AF451350	x	see Lörz and Held 2004	71°11′54″ S	012°20′42″ W	323		Weddell Sea
E. waegelei	AF451351	x	see Lörz and Held 2004	70°50′24″ S	010°35′12″ W	266		Weddell Sea
E.echinata	AF451352	x	see Lörz and Held 2004	70°50′24″ S	010°35′12″ W	266		Weddell Sea
Gnathiphimedia mandibularis	AF451353	x	see Lörz and Held 2004	70°50′12″ S	010°34′53″ W	269		Weddell Sea
G. sexdentata	AF451354	x	see Lörz and Held 2004	71°12′11″ S	012°19′10″ W	318		Weddell Sea
Eusiridae								
Eusirus cf. *perdentatus*	AF451355	x	see Lörz and Held 2004	63°01′12″ S	59°09′12″ W	673		Antarctic Peninsula

analyses were conducted under equal weights. Topological robustness was assessed using 1000 bootstrap replicates (Felsenstein 1985) and parsimony jackknifing (Farris et al. 1996). Jackknife frequencies were calculated in PAUP* using 1000 pseudoreplicates under a heuristic search with 30% character deletion. The ML analysis used the HKY85 model. The ML analysis was conducted using the heuristic search option in PAUP* and starting branch lengths were obtained using Rogers-Swofford approximation method. Bootstrap values for the ML tree were obtained from 100 replicates.

Morphological descriptions. The taxonomic differentiation within and between genera of the Epimeriidae is often based on a few morphological characters (Coleman and Barndard 1991, Lörz and Brandt 2004). A key to the Antarctic species of Epimeriidae was published by Coleman (2007). The morphological characterisation in Epimeriidae is hindered by the high plasticity of characters depending on sex and age of the specimens (Lörz and Brandt 2004), therefore taxon specific characteristics can the misinterpreted as intraspecific variability. Genetic information, here COI mtDNA, is used as additional characters to clarify and validate the taxonomic classification (Figure 1).

Here we give a new diagnosis of the genus *Epimeria* after placing *Epimeriella* in synonymy, describe one species new to science, *Epimeria robustoides* sp. n. and redescribe *Epimeria robusta*.

Systematics

Order AMPHIPODA Latreille, 1816
Suborder GAMMARIDEA Latreille, 1802
Family EPIMERIIDAE Boeck, 1871

Genus *Epimeria* Costa, 1851 in Hope, 1851

?*Vertumnus* White, 1847: 89 [*nomen nudum*].

Epimeria Costa, 1851: 24 [*nomen nudum*].– Costa in Hope 1851: 46. – Karaman and Barnard 1979: 108.– Watling and Holman 1980: 642.– Coleman 2007: 31.

Pseudepimeria Chevreux, 1912: 9 (type species *Pseudepimeria grandirostris* Chevreux, 1912; original designation).

Subepimeria Bellan-Santini, 1972b: 225 (type species *Subepimeria geodesiae* Bellan-Santini, 1972; original designation).

Epimeriella.– Walker 1906: 17.– Karaman and Barnard 1979: 107.– Coleman 2007: 56 (type species *Epimeriella macronyx* Walker, 1906; by monotypy). syn. n.

Type species. *Epimeria tricristata* Costa, 1851 in Hope, 1851; by monotypy.

Remarks. The most recent family diagnoses for the Epimeriidae is that of Coleman (2007), Coleman and Barnard (1991), and Barnard and Karaman (1991).

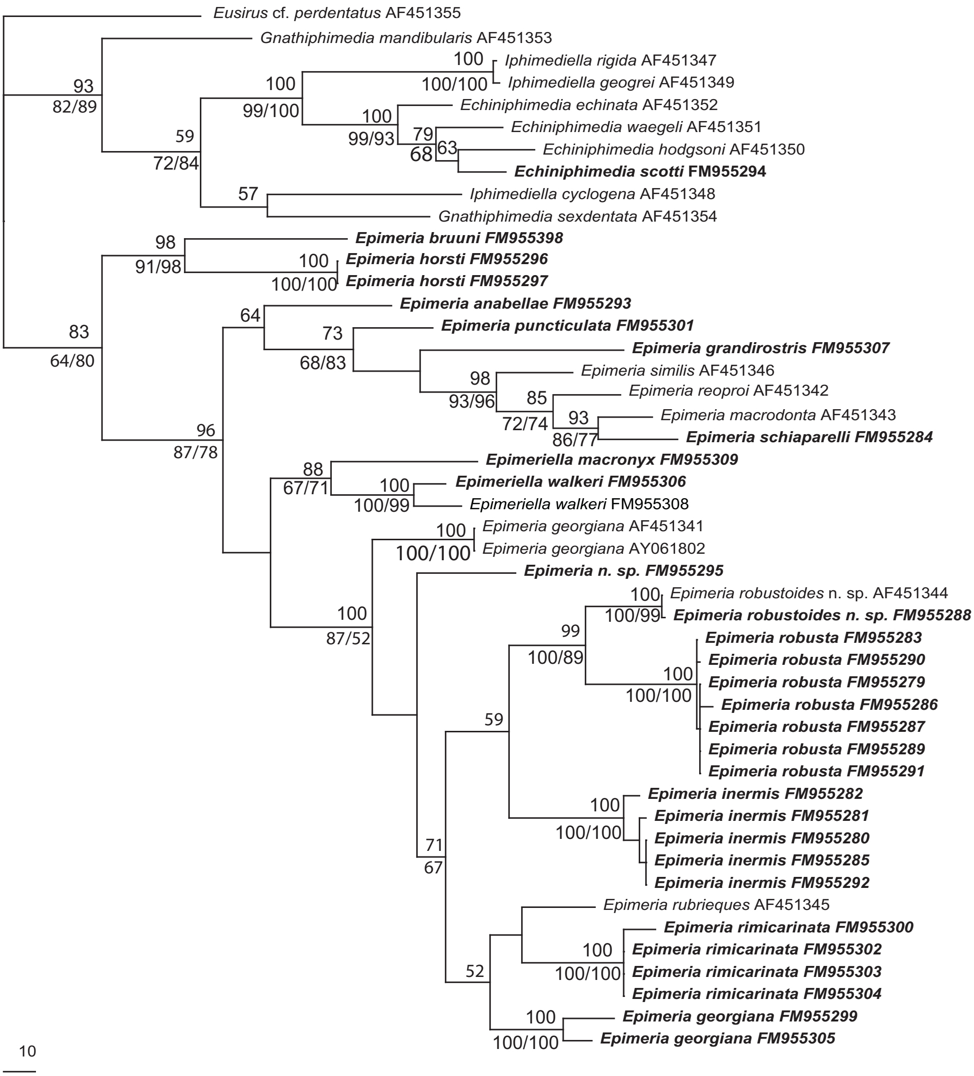

Figure 1. Maximum parsimony topology (length 1599, CI 0.33, RI 0,6815). Branch support values are given: jackknife above, parsimony / likelihood bootstrap below branches. Sequences obtained in this study are marked in bold. The scale bar gives the number of nucleotide substitutions per branch length.

Based on the genetic data presented in the following and a detailed morphological evaluation of the weak morphological separation criteria between *Epimeriella* and *Epimeria* we herewith synonymize *Epimeriella* with *Epimeria*. Since we transfer the species *Epimeriella macronyx* Walker, 1906; *Epimeriella scabrosa* Barnard, 1930; *Epimeriella truncata* Andres, 1985; *Epimeriella victoria* (Hurley, 1957a) and *Epimeriella walkeri* Barnard, 1930 to the genus *Epimeria*, we herewith give a new genus diagnosis.

The diagnosis has been broadened from that given by Barnard and Karaman (1991) since it now included characters formerly predominantly occurring in the genus *Epimeriella* such as a smooth body and the laminar, none triturative pars molaris.

Diagnosis. Body covered with teeth or processes or body poorly armed, almost smooth. Antenna 1 peduncular article 2 shorter than 1. Accessory flagellum present or absent. Mouthparts projecting quadrately. Upper lip incised or almost entire; epistome not very broad. Mandibular incisor ordinary, toothed, setal row present; molar blunt, strong, triturative or simple, conical or laminar. Lower lip inner lobes absent, outer lobes relatively broad. Hypopharyngeal gap sometimes widened. Maxilla 1 palp 2-articulate, article 2 ordinary. Maxilla 2 inner plate without facial row of setae. Maxilliped inner plate narrower but as long as outer plate, latter elongate; palp article 2 narrow and unproduced; palp article 4 well developed, unguiform or serrate. Coxae 1–4 progressively longer; coxae 4–5 forming ventral arc; coxa 4 long, polycuspidate. Gnathopods alike, articles 5–6 elongate, subchelate (typical), sometimes simple . Telson incised or cleft.

After synonymising *Epimeriella* with *Epimeria,* the genus *Epimera* now includes 46 species:

Epimeria annabellae Coleman, 1994;
Epimeria bathyalis Wakabara and Serejo, 1999;
Epimeria bispinosa Ledoyer, 1986;
Epimeria bruuni Barnard, 1961;
Epimeria cora Barnard, 1971;
Epimeria concordia Griffiths, 1977;
Epimeria cornigera (J.C. Fabricius, 1779);
Epimeria extensa Andres, 1985;
Epimeria georgiana Schellenberg, 1931;
Epimeria glaucosa Barnard, 1961;
Epimeria grandirostris (Chevreux, 1912);
Epimeria heldi Coleman CO (1998a);
Epimeria horsti Lörz, 2008;
Epimeria inermis Walker, 1903;
Epimeria intermedia Schellenberg, 1931;
Epimeria longispinosa Barnard, 1916;
Epimeria loricata G.O. Sars, 1879;
Epimeria macrodonta Walker, 1906;
Epimeria macronyx (Walker, 1906), comb. n.;
Epimeria monodon Stephensen, 1947;
Epimeria obtusa Watling, 1981;
Epimeria oxicarinata Coleman, 1990;
Epimeria pacifica Gurjanova, 1955;
Epimeria parasitica (M. Sars, 1858);

Epimeria pelagica Birstein and M. Vinogradov, 1958;
Epimeria pulchra Coleman, 1990;
Epimeria puncticulata Barnard, 1930;
Epimeria reoproi Lörz and Coleman, 2001;
Epimeria rimicarinata Watling and Holman, 1980;
Epimeria robusta Barnard, 1930;
Epimeria robustoides Lörz & Coleman, 2009, sp. n.;
Epimeria rotunda Wakabara & Serejo, 1999;
Epimeria rubrieques De Broyer & Klages, 1991;
Epimeria scabrosa (Barnard, 1930), comb. n.;
Epimeria schiaparelli Lörz, Maas, Linse and Fenwick 2007;
Epimeria semiarmata Barnard, 1916;
Epimeria similis Chevreux, 1912;
Epimeria subcarinata Nagata, 1963;
Epimeria tuberculata G.O. Sars, 1895;
Epimeria truncata (Andres, 1985), comb. n.;
Epimeria ultraspinosa Wakabara and Serejo, 1999;
Epimeria vaderi Coleman CO (1998b);
Epimeria victoria (Hurley, 1957), comb. n.;
Epimeria walkeri (Barnard, 1930), comb. n.;
Epimeria yaquinae McCain, 1971.

***Epimeria robustoides* Lörz & Coleman, sp. n.**

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Figs 2–5

Epimeria robusta.– Bamard, 1958: 108; 1961: 103.– McCain 1971: 161.– De Broyer and Klages 1991: 164.– Coleman 1994: 560.

Material examined. Holotype. Ovig. female 40 mm. 72°35.67´5S, 18°8.17´W, depth 604–656 m, collected during the *Polarstern* cruise ANT III 1985 by Agassiz-trawl, 27.I.1985, station 273.

Etymology. The species is named *robustoides* because of its morphological similarity to *Epimeria robusta*.

Diagnosis. Body (Fig. 2A, B) robust. Posterior margin of pereonites 5–6 with small medial protrusion, pereonite 7 with shallow keel, pereonite 7 and posterior margins of metasome segments 1–2 with an elevation (in lateral view). Metasome segments 1–3 with mid-dorsal keel, metasome segment 3 and urosomite 1 with pointed tooth. Urosomite 3 with shallow mid-dorsal keel. Coxa of pereopods 1–3 tapering distally, apically rounded (Figs 4A, B, E). Propodus of gnathopods 1–2 expanded distally, with well-developed palm. Coxa of pereopod 4 very large, with wide posteroventral angle projecting somewhat ventrally. Pereopod 5 (Fig. 5D) ba-

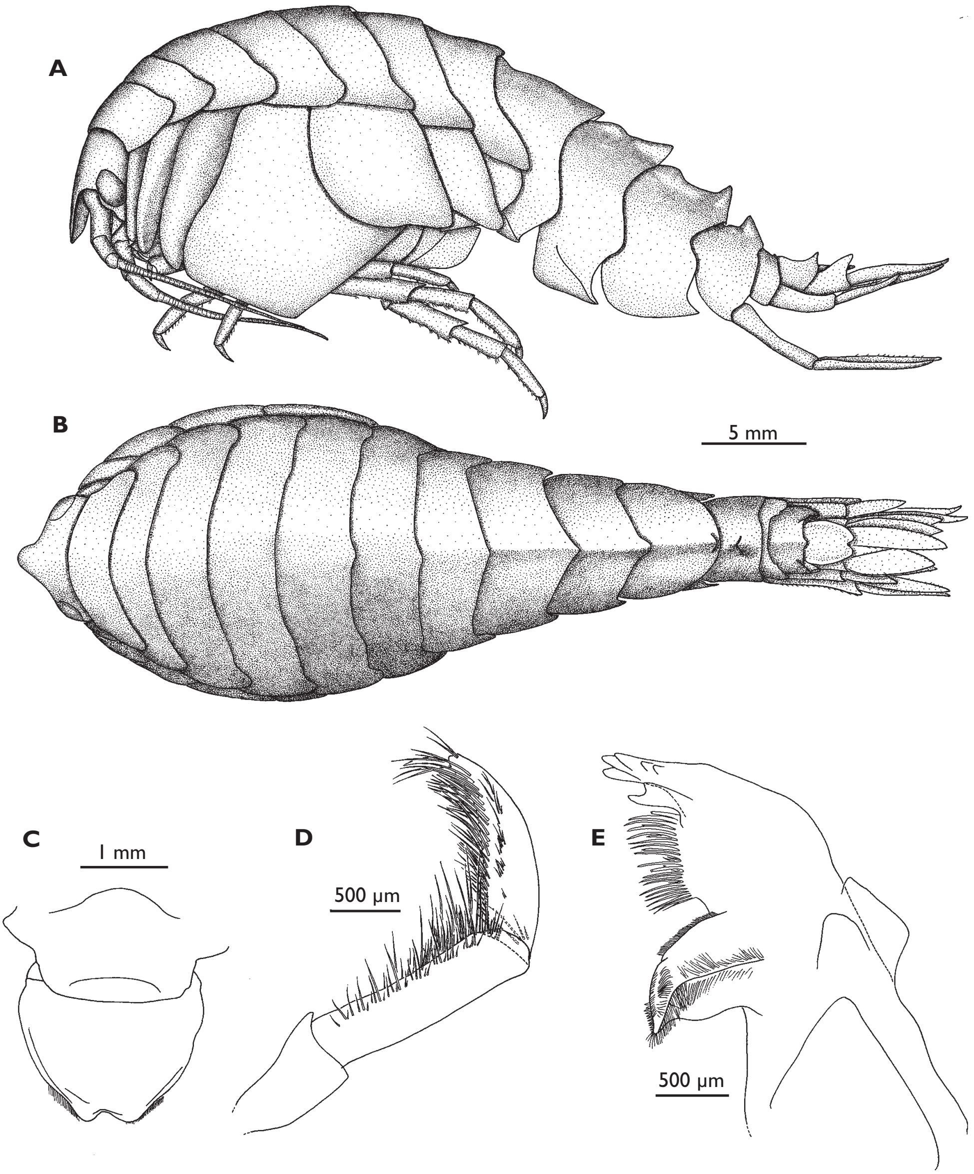

Figure 2. *Epimeria robustoides* sp. n., female, 40 mm. **A** Lateral habitus **B** dorsal habitus **C** labrum **D** mandibular palp **E** mandibular body.

sis with posteromarginal tooth, basis of pereopod 6 with similar tooth but larger, pereopod 7 basis (Fig. 5C) widened proximally, but without tooth, only posterodistal angle pointed.

Distribution. Weddell Sea, 604–656 m.

Description. Anterior cephalic margin sinuous, lateral cephalic lobe slightly produced; rostrum same length as head, reaching proximal part of antenna 1 peduncle

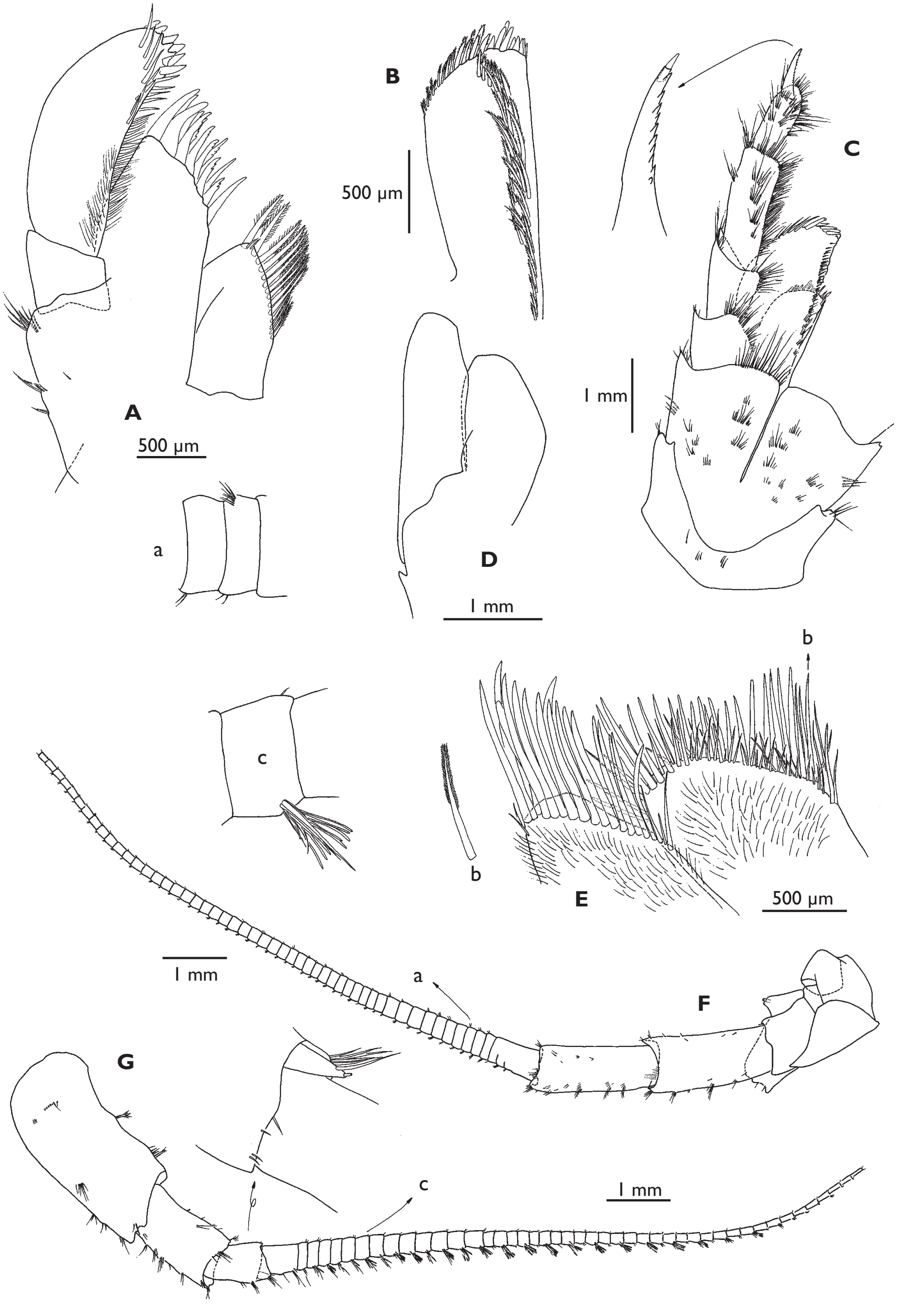

Figure 3. *Epimeria robustoides* sp. n., female, 40 mm. **A** Maxilla I **B** frontal face of inner maxillipedal endite **C** maxilliped. left palp and endites omitted **D** shape of maxilla 2 **E** details of maxilla 2 **F** antenna 2 **G** antenna 1.

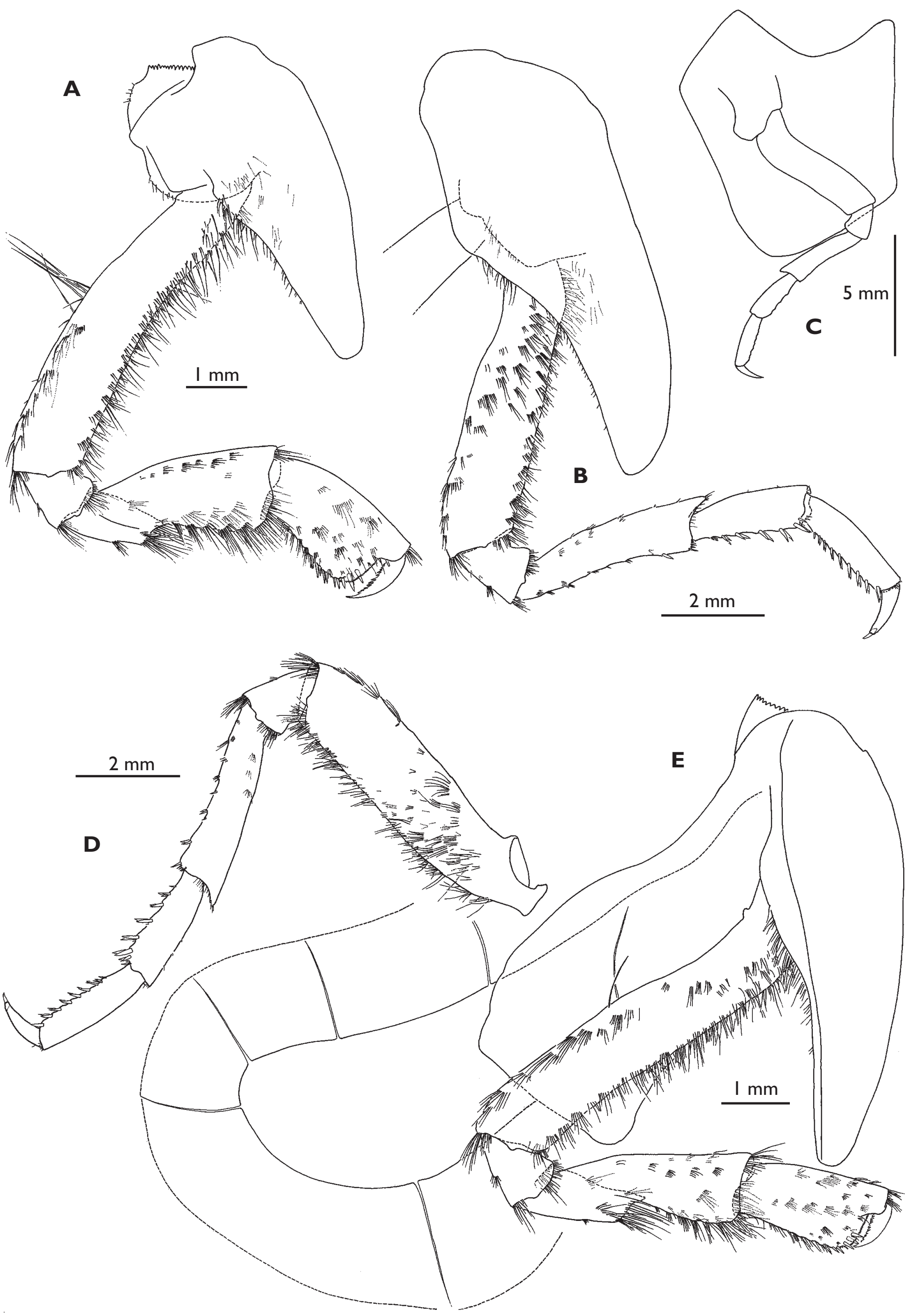

Figure 4. *Epimeria robustoides* sp. n*,* female, 40 mm. **A** Pereopod 1 **B** pereopod 3 **C** pereopod 4, medial face, setae omitted **D** pereopod 4, coxa dissected **E** pereopod 2, dotted line indicates length of oostegite setae, of which only some examples are given.

G

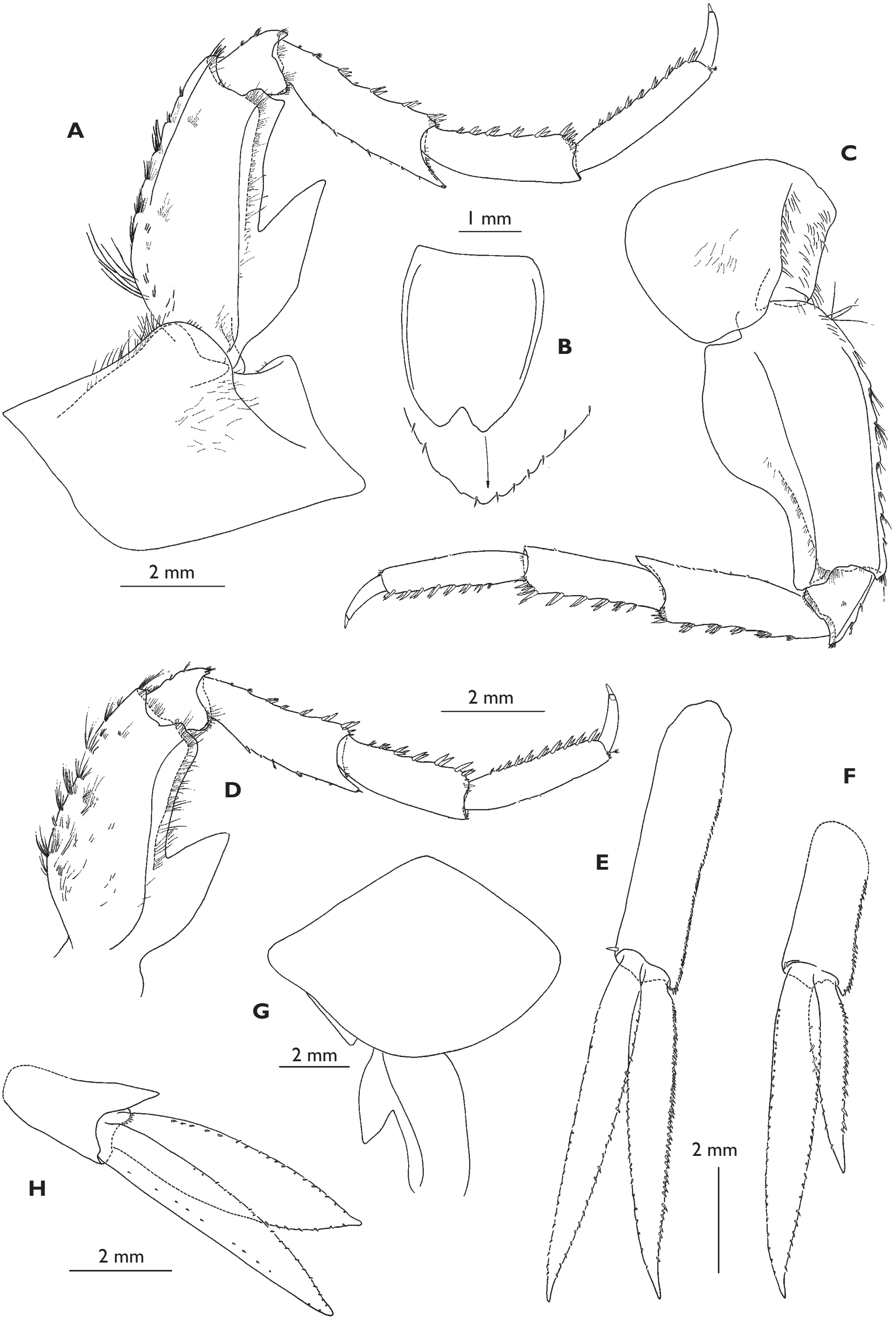

Figure 5. *Epimeria robustoides* sp. n. **A** Pereopod 6 **B** telson **C** pereopod 7 **D** pereopod 5. coxa dissected **E** uropod 1 **F** uropod 2 **G** coxa and part of basis of pereopod 5 **H** uropod 3.

article 1; eyes present, oval, 0.4 × head height. Pereonite 1 subequal in length to head (excluding rostrum), pereonite 2 approx. 0.75 x length of pereonite 1, pereonites 1 to 6 lacking mid-dorsal or dorsolateral processes; pereonite 7 posterior margin with dorsolateral carina weakly developed; pleonites 1–3 with carinae, pereonite 3 and urosomite 1 with acute mid-dorsal process. Urosomite 2 shortest, lacking mid-dorsal process, urosomite 3 with pointed posterior process.

Epimeron. 1 antero- and posteroventral angle rounded; epimeron 2 and 3 posteroventral angle produced.

Antenna. 1 peduncle article 1 with 2 small processes; article 2 with no process, shorter than article 1; article 3 shortest; accessory flagellum scale-like; primary flagellum of 45 articles. Antenna 2 articles 1–5 lacking distal processes, flagellum with 53 articles.

Mandible. Incisor and lacinia mobilis strongly dentate; molar produced and triturative; palp article 3 densely setose medially, with long stout SS distally. Maxilla 1 medial plate subtriangular, obliquely convex inner margin with 11 stout, plumose SS; lateral plate distal margin oblique, with medially lobate RS; palp strongly exceeding outer plate; palp article 1 short, article 2 slightly curved medially with stout SS distomedially, stout RS distally. Maxilla 2 with long, distally crenulate setae distally on lateral and medial plates. Maxilliped lateral plate broadly rounded distally, medial plate with nodular RS and a row of long plumose SS on medial, anterior face; palp medial margin strongly setose; merus distally slightly expanded; dactyl with serrate medial margin.

Pereopods. Gnathopod 1: coxa 1 long and slender, basis linear, slender, posterior margin with numerous fine SS; merus slightly longer than ischium, anterior margin very short, distal margin oblique, posterodistal angle acute, setose; carpus linear, distal half of posterior margin with long SS; propodus slightly expanded distally, anterior margin naked except for distal fringe of short SS, palm finely crenulate, slightly oblique, with cluster of RS defining rounded distal margin, posterior margin with numerous long SS; dactylus slender, slightly curved, posterior margin strongly serrate. Gnathopod 2: coxa 2 wider than coxa 1, basis linear, ischium anterior margin very short, distal margin obliquely articulating with carpus, carpus linear, anterior margin naked except for transverse row of SS distally, posterior margin with numerous stout SS distally; propodus linear, palm almost transverse, rounded, finely crenulated, lined with numerous submarginal RS; dactylus large, not exceeding palm, posterior margin serrate. Pereopod 3: coxa similar to coxa 2, basis linear, anterior and posterior margin finely setulose; merus slightly expanded distally; carpus shorter than merus, anterior margin naked, posterior margin with 6 pairs of RS; propodus naked anteriorly, posterior margin with 9 pairs of RS; dactylus stout, curved. Pereopod 4: coxa much larger than 3, wide posteroventral angle projecting somewhat ventrally; basis to dactylus as for pereopod 3. Pereopod 5: coxa rectangular; basis bearing posteromarginal tooth; merus drawn out posterodistally; carpus slightly widened distally, posterior margin with 7 pairs of RS; propodus linear, posterior margin with 10 pairs of RS; dactylus curved, stout, approx. 0.3 × propodus length. Pereopod 6: coxa anterior half hidden by coxa 5, anterior margin weakly concave, posterior margin slightly drawn out; basis posteromarginal tooth larger than in pereopod 5; merus drawn out posterodistally, ischium to dactylus as in pereopod 5. Pereopod 7: coxa subrectangular; basis widened distally, but without tooth, only posterodistal angle pointed; ischium to dactylus as in pereopods 5 and 6.

Urosome and telson. Uropod 1: peduncle subequal in length to inner ramus, medial margin with 1 RS distally, distal margin with close row of short RS; inner ramus lateral margin with spaced row of short RS, medial margin with sparse RS; outer ramus marginally shorter than inner. Uropod 2: peduncle with row of short setae; inner ramus nearly twice the length outer ramus, both margins sparse lined with RS; outer ramus, both margins with few short RS. Uropod 3: peduncle short, approx. 0.3 × length of inner ramus, medial and inner margins of both rami with sparse row of short RS. Telson slightly longer than wide, u-shaped emargination 0.2 × lengths, lobes triangular, broadly rounded apically.

Coloration. Freshly captured specimen (s) of *Epimeria robustoides* show distinct red eyes (Fig. 10 A) and some bear orange patches on their bodies.

Epimeria robusta Barnard, 1930

Figs 6–9

Epimeria robusta Barnard, 1930: 375, 449, figs 40a, 41.

Figured individual: NIWA 20257, TAN0402/22, 71.8010°S, 170.9413°E, 151–180m, 09 02 2004 female, 37 mm.

Additional material examined. The following *Epimeria robusta* specimen were collected during "The International Polar Year" expedition TAN0802: NIWA 36856, NIWA 36618, st 100, 76°12.13′S, 176°14.86′E, 447 m; NIWA 37110, NIWA 37148, st 117, 72 35.41 S, 175 20.53 E, 475 m; NIWA 37209, st 115, 72 35.10 S, 175 18.49 E, 447 m; NIWA 37613, st 157, 72 01.41 S, 173 10.81 E, 814 m. Following *Epimeria robusta* specimen were collected during the BioRoss expedition TAN0402: NIWA 20258, NIWA 20259, NIWA 20263, st 25, 71 47.92 S, 170 55.96 E, 140 m; NIWA 202760, NIWA 20261, st 39, 71 45.30 S, 171 08.55 E, 251 m; NIWA 20262, st 48, 72 19.00 S, 170 21.73 E, 132 m; NIWA 20264, NIWA 20265, NIWA 20267, st 105, 71 15.45 S, 170 38.08 E 470 m; NIWA 202668, st 124, 71 18.58 S, 170 28.63 E, 212 m; NIWA 20269, st 126, 71 18.55 S, 170 27.01 E, 161 m; NIWA 20270, st 130, 71 19.80 S, 170 27.55 E, 120 m; NIWA 20271, st 140, 72 00.81 S, 170 46.47 E, 231 m; NIWA 20272, st 149, 71 58.87 S, 171 57.99 E, 456 m; NIWA 20273, st 150, 71 58.77 S, 171 58.09 E, 480 m; NIWA 20274, st 153, 72 00.51 S, 172 13.36 E, 540 m; NIWA 20275, NIWA 20276, st 154, 72 00.07 S, 172 13.33 E, 586 m; NIWA 20277, st 157, 71 59.11 S, 172 10.71 E, 737 m; NIWA 20278, st 190, 71 34.75 S, 170 52.36 E, 230 m.

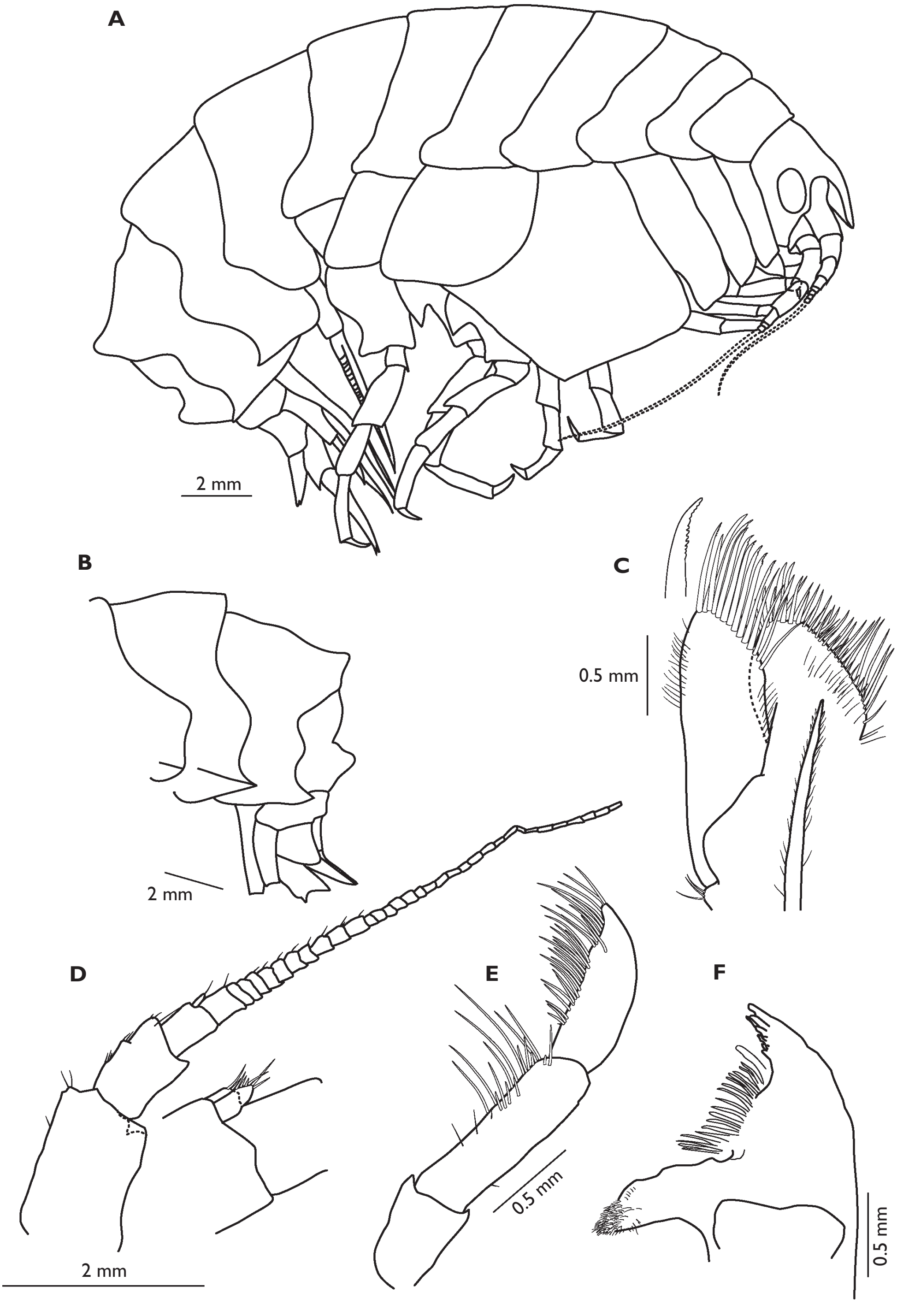

Figure 6. *Epimeria robusta,* NIWA 20257, female, 37 mm. **A** Lateral habitus **B** metasome and urosome **C** maxilla 2 **D** antenna 1 **E** mandibular palp **F** mandibular body.

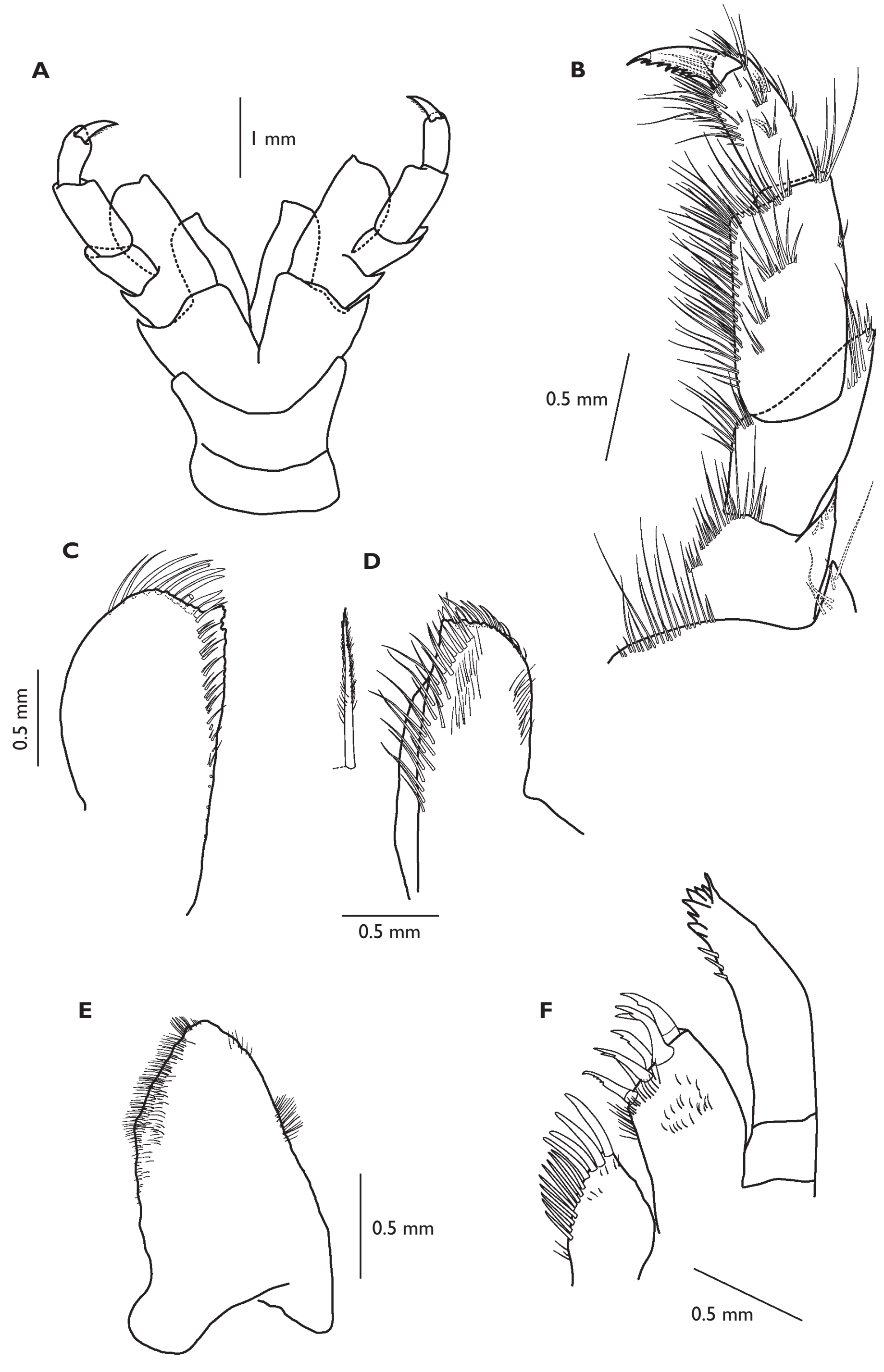

Figure 7. *Epimeria robusta,* NIWA 20257, female, 37 mm. **A** Maxilliped **B** maxillipedal palp **C** frontal face of inner maxillipedal endite **D** frontal face of outer maxillipedal endite **E** labrum **F** maxilla 1.

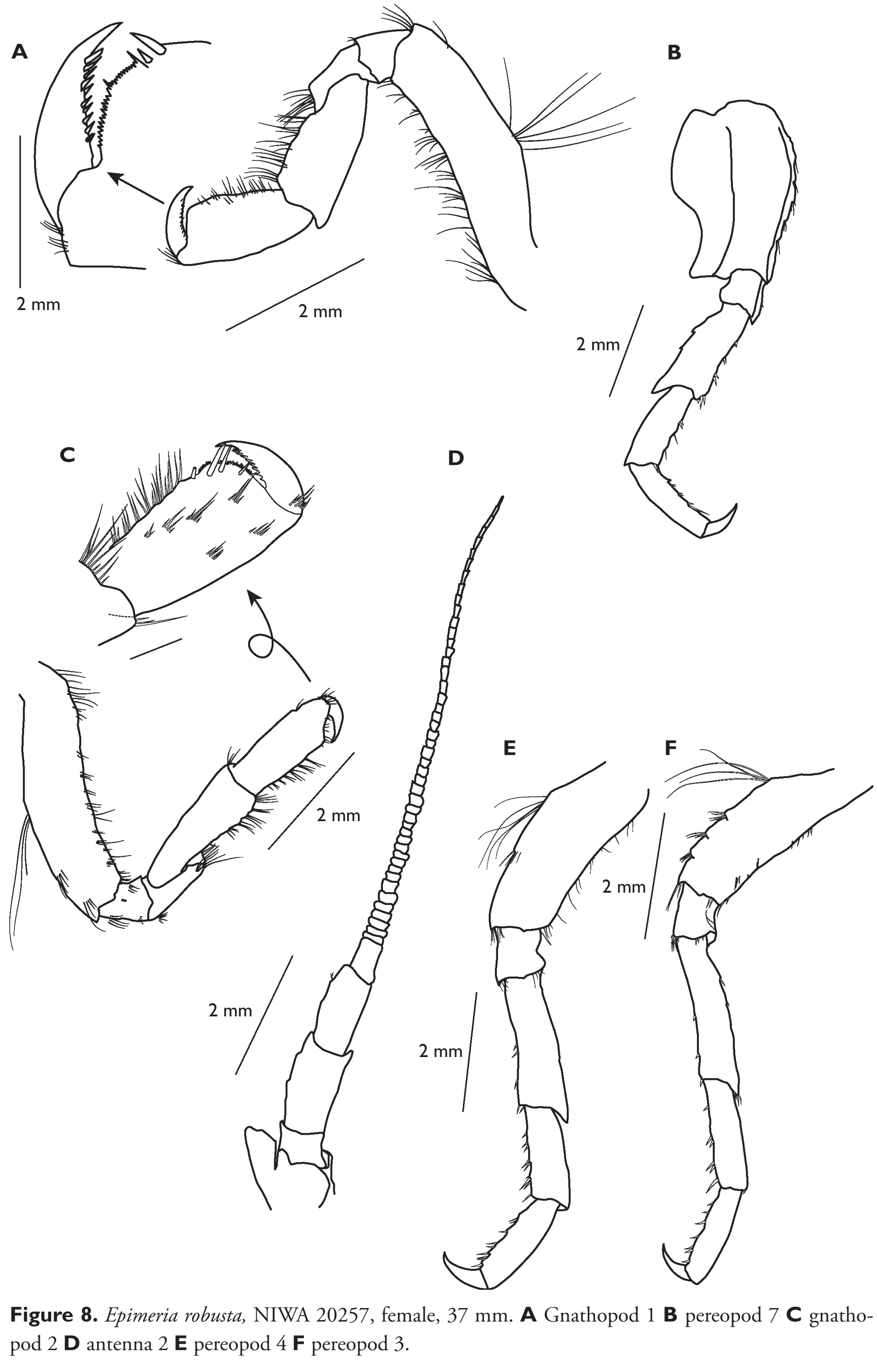

Figure 8. *Epimeria robusta,* NIWA 20257, female, 37 mm. **A** Gnathopod 1 **B** pereopod 7 **C** gnathopod 2 **D** antenna 2 **E** pereopod 4 **F** pereopod 3.

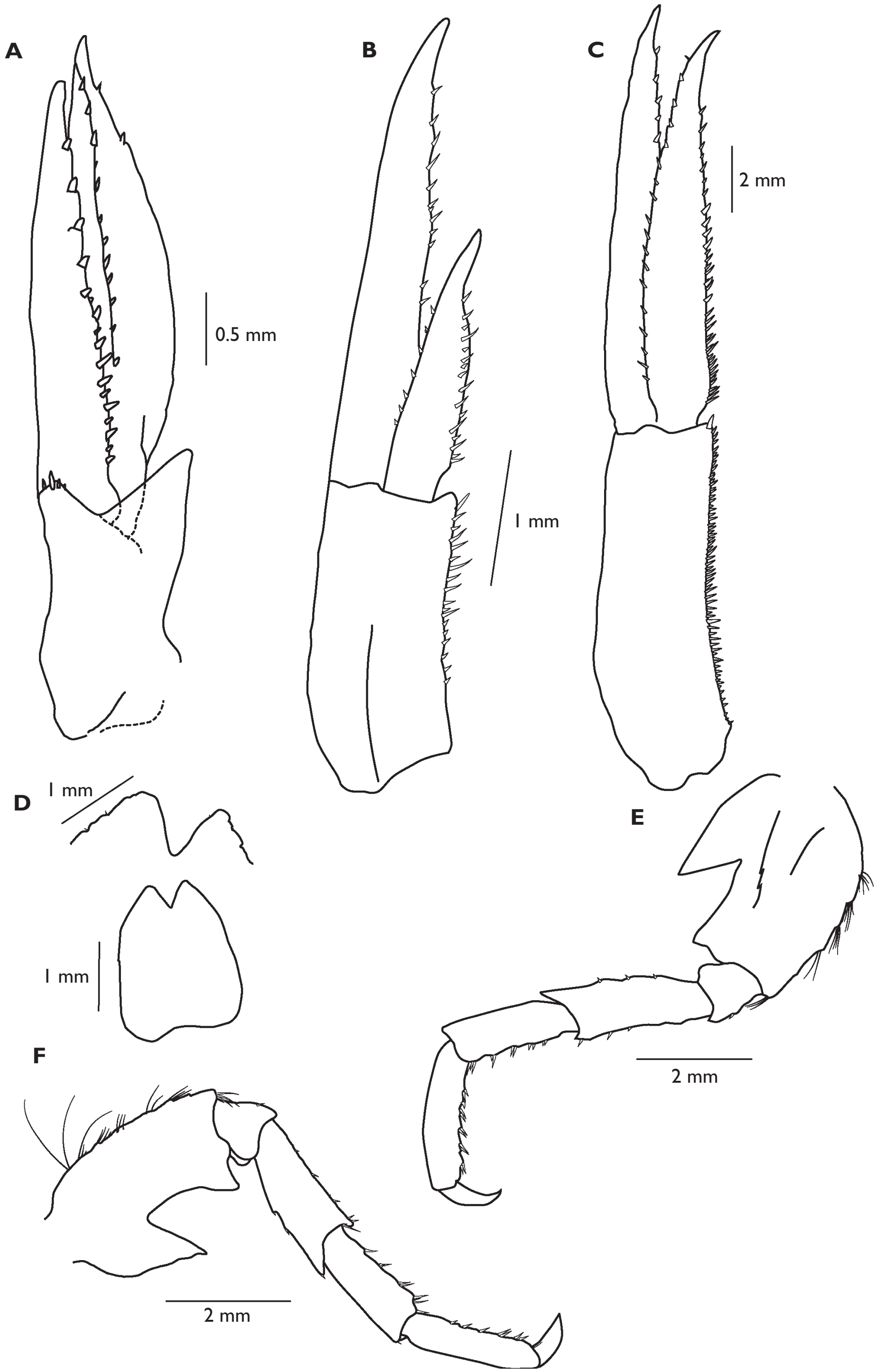

Figure 9. *Epimeria robusta,* NIWA 20257, female, 37 mm. **A** Uropod 1 **B** uropod 2 **C** uropod 3 **D** telson **E** pereopod 6 **F** pereopod 7.

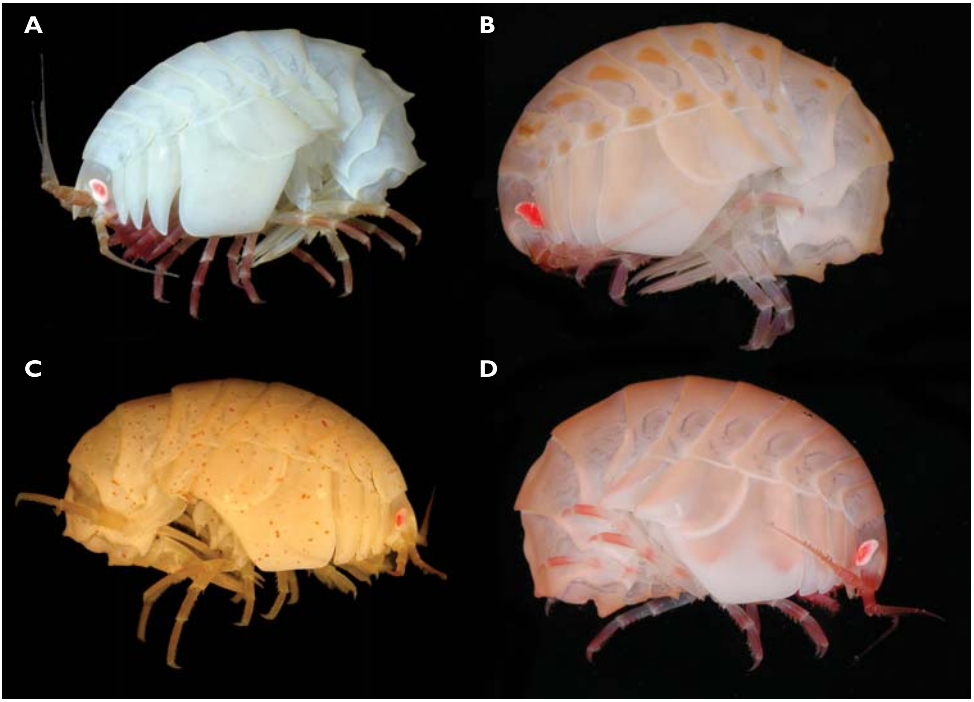

Figure 10. A *Epimeria robustoides* sp. n. Weddell Sea, photographed by Dr. Martin Rauschert on RV *Polarstern* **B-D** colour variations of *Epimeria robusta* from the Ross Sea pictured by Dr. Stefano Schiaparelli on RV *Tangaroa* **B** NIWA 37110, TAN0802/117 **C** NIWA 20270 TAN0402/130 **D** NIWA 37109, TAN0802/117.

Description. Anterior cephalic margin sinuous, lateral cephalic lobe slightly produced; rostrum same length as head, reaching proximal part of antenna 1 peduncle article 1; eyes present, oval, 0.4 × head height. Pereonite 1 subequal in length to head (excluding rostrum), pereonite 2 approx. 0.75 × length of 1, pereonites 1 to 6 lacking mid-dorsal or dorsolateral processes; pereonite 7 posterior margin with dorsolateral carina weakly developed; pleonite 1 shallow keel, post margin not drawn out straight, pleonite 2 with shallow keel, pleonite 3 with carinae. Urosomite 2 shortest, lacking mid-dorsal process, urosomite 3 with pointed posterior process.

Epimeron 1 antero- and posteroventral angle rounded; epimeron 2 and 3 posteroventral angle produced.

Antenna 1 peduncle article 1 with 2 small processes; article 2 with no process, shorter than article 1; article 3 shortest; accessory flagellum scale-like; primary flagellum of 45 articles. Antenna 2 articles 1–5 lacking distal processes, flagellum with 53 articles.

Mandible Incisor and lacinia mobilis strongly dentate; molar produced and triturative; palp article 3 densely setose medially, with long stout SS distally. Maxilla 1 medial plate subtriangular, obliquely convex inner margin with 11 stout, plumose SS; lateral plate distal margin oblique, with medially lobate RS; palp strongly exceeding outer plate; palp article 1 short, article 2 slightly curved medially with stout SS distomedially, stout RS distally. Maxilla 2 with long, distally crenulate setae distally on lateral and medial plates. Maxilliped lateral plate broadly rounded distally, medial plate with nodular RS and a row of long plumose SS on medial, anterior face; palp medial margin strongly setose; merus distally slightly expanded; dactyl with serrate medial margin.

*Pereopods***.** Gnathopod 1: coxa 1 long and slender, basis linear, slender, posterior margin with numerous fine SS; merus slightly longer than ischium, anterior margin very short, distal margin oblique, posterodistal angle acute, setose; carpus linear, distal half of posterior margin with long SS; propodus slightly expanded distally, anterior margin naked except for distal fringe of short SS, palm finely crenulate, slightly oblique, with cluster of RS defining rounded distal margin, posterior margin with numerous long SS; dactylus slender, slightly curved, posterior margin strongly serrate. Gnathopod 2: coxa 2 wider than coxa 1, basis linear, ischium anterior margin very short, distal margin obliquely articulating with carpus, carpus linear, anterior margin naked except for transverse row of SS distally, posterior margin with numerous stout SS distally; propodus linear, palm almost transverse, rounded, finely crenulated, lined with numerous submarginal RS; dactylus large, not exceeding palm, posterior margin serrate. Pereopod 3: coxa anteroventrally obliquely truncate, basis linear, anterior and posterior margin finely setulose; merus slightly expanded distally; carpus shorter than merus, anterior margin naked, posterior margin with 6 pairs of RS; propodus naked anteriorly, posterior margin with 9 pairs of RS; dactylus stout, curved. Pereopod 4: coxa much larger than 3, wide posteroventral angle projecting somewhat ventrally; basis to dactylus as for pereopod 3. Pereopod 5: coxa posteroventrally subacute, pointed; basis bearing posteromarginal tooth; merus drawn out posterodistally; carpus slightly widened distally, posterior margin with 7 pairs of RS; propodus linear, posterior margin with 10 pairs of RS; dactylus curved, stout, approx. 0.3 × propodus length. Pereopod 6: coxa posteroventrally subacute, pointed, anterior half hidden by coxa 5, anterior margin weakly concave, posterior margin slightly drawn out; basis posteromarginal tooth larger than in pereopod 5; merus drawn out posterodistally, ischium to dactylus as in pereopod 5. Pereopod 7: coxa subrectangular; basis widened distally, but without tooth, posterodistally and posteroventrally pointed; ischium to dactylus as in pereopods 5 and 6.

Urosome and telson. Uropod 1: peduncle subequal in length to inner ramus, medial margin with 1 RS distally, distal margin with close row of short RS; inner ramus lateral margin with spaced row of short RS, medial margin with sparse RS; outer ramus marginally shorter than inner. Uropod 2: peduncle with row of short setae; inner ramus nearly twice the length outer ramus, both margins sparse lined with RS; outer ramus, both margins with few short RS. Uropod 3: peduncle short, approx. 0.3 × length of inner ramus, medial and inner margins of both rami with sparse row of short RS. Telson slightly longer than wide, u-shaped emargination 0.2 × lengths, lobes triangular, broadly rounded apically.

Remarks

Coleman (1994) based a detailed redescription of *E. robusta* on material from the Weddell Sea, while the type material of *Epimeria robusta* is from the Ross Sea. He found minute morphological differences between material of the opposing Antarctic shelves but interpreted them as intraspecific variation (Coleman 1994). Results of the phylogenetic analysis (see below) showed an *Epimeria robusta* species-complex comprising of a species each in the Weddell Sea and the Ross Sea.

The new species, *Epimeria robustoides* sp. n. from the Weddell Sea (Figs 2–5; Fig. 10a) is morphologically very similar to *Epimeria robusta* Ross Sea (Figs 6–9, Fig. 10b-d). There is morphological variation amongst the *E. robusta* specimens from the Ross Sea: 1) in the relative length of pereonite 3 bearing a shallow mid dorsal keel and 2) coxae 2 and 3 are more acute in some specimen, not as obliquely truncate as in the pictured specimen. The morphological differences between *Epimeria robusta* and *E. robustoides* are summarized in the following:

	Epimeria robusta	***E. robustoides* sp. n.**
posteroventral corner of coxa 5 and 6	subacute/ pointed	more rounded
coxa 3 anteroventrally	obliquely truncate	tapering
epimeral plate 2 dorsally	shallow keel	pointed posterior process
pereopod 7 basis posteroventrally	pointed process	angular corner
urosomite 3	smooth	bearing process
pleonite 1	shallow keel posterior margin not drawn out straight	posterior part of dorsal keel elevated and drawn out straight

Coleman (1994, 2007) pointed out some morphological variation between the type specimen from the Ross Sea and a redescription of material from the Weddell Sea and Elephant Island. We studied more than 30 *E. robusta* specimens from the Ross Sea and all agree with the type description (contrasting the Weddell Sea specimen): having a keel pleonite only well developed on segment 3, the posterior margin of pleonite 1 is drawn into a tooth and short teeth occur only on pleonite 3 and urosomite 1.

The main difference to the Coleman (1994) description is that our animal has a rostrum reaching the end of the second article of antenna 1, whereas Coleman's redescription shows a rostrum just reaching the end of the first article of antenna 1. The morphological variation of *Epimeria* species, including the high variability of rostrum length of *E. robusta* related to size has been studied in detail by Lörz (2003).

Our current genetic analysis shows that *Epimeria georgiana* contains at least two species (see below). *Epimeria georgiana* is very similar to *E. rimicarinata* and *E.inermis*. *Epimeria georgiana* has the lateral face of coxa 4 sculptured, posterodistal and apical margins concave, the distal margin of coxa 4 is not curved around the ventral body side; and bases 5–7 notched posteromarginally, whereas in *E. inermis* coxa 4 is smooth, shield-like curved, with a somewhat convex ventral margin and a straight posterodistal margin, slightly curved under the ventral body side. Bases 5–7 are excavate, but not notched. *E. rimicarinata* has similarly shaped coxae as *E. georgiana*, however, the dorsal carinae are bilobed from lateral view, there are additional dorsolateral teeth on pereonites 5–7 and rounded humps on pleonites 1–3; basis 5 is not notched, basis 6 with a posteromarginal tooth, but this is directing posteriorly and not ventrally as in *E. georgiana*. We assume that specimen(s) that key out to *E. georgiana* belong to a species complex containing more than the two species shown by the present genetic separation. We are currently collating material of the different morphotypes of *E. georgiana* at the moment, but presently have too little material to discriminate sufficiently what minor morphological differences are non-variable features. Potentially, specimen from South Georgia, Bransfield Strait, Palmer Archipelago, South Shetland Islands and the eastern Weddell Sea shelf may be distinct species.

Phylogenetic analysis

Partial COI mtDNA sequences for 31 amphipod specimens were generated to examine the intraspecific and phylogenetic relationships in Southern Hemisphere Epimeriidae (EMBL Assession numbers FM955279-FM955309, Table 1). In addition 17 sequences of Antarctic Epimeriidae, Iphimediidae and *Eusirus* cf. *perdentatus* were downloaded from EMBL, the latter two taxa as outgroup sequences (Table 1).

COI analysis

In the final analysis dataset comprised 47 sequences of 28 species. The total length of the partial COI mtDNA sequence was 496 characters of which 274 were variable and 254 were parsimony informative. The mean nucleotide composition is A=0.27604, C=0.24216, G=0.16383, T=0.31794. The amino acid translation with invertebrate mitochondrial code revealed no stop codons. A heuristic search found three most parsimonious trees when transitions and transversions are weighted equally (length 1599, CI 0.3333, RI 0.6815). The consensus maximum parsimony tree is shown in Fig. 1. The HKY85 maximum likelihood tree (data not shown) was similar in its topology except for changes in the position of clades while the species composition within the clades was retained. The bootstrap values performed for the Maximum Likelihood analysis are given after the bootstrap values performed for the Maximum Parsimony analysis.

The tree inferred from maximum parsimony analysis was rooted with *Eusirus* cf. *perdentatus* (Fig. 1). The Iphimediidae (jk=93, bs=82/89) and Epimeriidae (jk=83, bs=64/80) formed well-supported monophyletic clades. Within the Iphimediidae two of the three anaylsed genera, *Gnathiphimedia* and *Iphimediella*, showed paraphyly, while only *Echiniphimedia* appeared to be monophyletic. Within the Epimeriidae the two species from the New Zealand seamounts (*E. bruuni* and *E. horsti*) formed a supported sister group (jk=98, bs=91/98) to the Southern Ocean species group (jk=96, bs=87/78). The latter group split into two clades of lower support, one containing seven species from the shelves of the Weddell and Ross Seas, the other comprising nine nominal species from the shelves and slopes of the Antarctic Peninsula, Weddell Sea and Ross Sea. The two species identified as *Epimeriella* before, *E. macronyx* and *E. walkeri*, form a well-supported group (jk=88, bs=67/71). The specimens examined from *Epimeria georgiana* showed paraphyly, forming two groups. One group consisted of the two specimens from the Antarctic Peninsula (AF452341 and AY061802), the other of two specimens from the Weddell Sea (FM955299, FM955305). *Epimeria robustoides* and *E. robusta* form a well-supported sister group to *E. inermis*. Within the well-supported species *Epimeria robusta* (jk=100, bs=100/100) four haplotypes were identified. Three haplotypes were found in *E. inermis* from the Ross Sea area, where the specimen from the Balleny Islands (FM955282) formed a sister lineage to the Victoria Land specimens.

Pairwise sequence divergences between and within the genera and species of the Epimeriidae and Iphimediidae were highly variable (Table 2, 3).

Intergeneric distances

The maximum uncorrected distances between epimeriid and iphimediid genera varied from 23.99 to 35.2% (Table 2). Within the genera of the Iphimediidae uncorrected COI distances varied from 21 to 31.1%. As the Epimeriidae were represented by only one genus, no intergeneric distances could be analysed.

Interspecific distances

Interspecific uncorrected COI sequence distances in the Iphimediidae varied from 7.9% (*Echiniphimedia scotti* to *E. hodgsoni*) to 29.5% (*Iphimediella cyclogena* to *I. georgei*)

Echiniphimedia scotti collected from the Ross Sea has a genetic distance of 7.9–8.5 to the *Echiniphimedia* species *E. waegeli, E. hodgsoni* and *E. echinata* from the Weddell Sea. The Weddell Sea species have interspecific distances of 9.9–10.5% amongst each other.

Within the Epimeriidae sequences distances varied from 8.5% (*E. schiaparelli* to *E. macrodonta*) to 26.15% (*E. horsti* to *E. annabellae*) (Table 2). The species from New Zealand's seamounts, *Epimeria horsti* and *E. bruuni* had more similar genetic sequences to each other than to any of the Antarctic *Epimeria* species, but the distance between them was high with nearly 20%. *Epimeria walkeri* and *E. macronyx* showed an interspecific distance of 15.7–17.1%. The new deep-water species, *Epimeria new* species 1, from 2157 m in the eastern Weddell Sea (Table 1) was

Table 2. Uncorrected genetic COI distances between epimeriid and iphimediid genera and species.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1	*Epimeria annabellae* FM955293																											
2	*E. bruuni* FM955298	25.8																										
3	*E. georgiana* AF451341	20.4	24.6																									
4	*E. georgiana* FM955299	21.4	25.0	15.3																								
5	*E. grandirostris* FM955307	23.8	27.8	22.2	23.8																							
6	*E. horsti* FM955297	26.0	20.0	24.2	24.0	28.0																						
7	*E. inermis* FM955281	21.8	27.6	19.4	19.2	22.0	25.0																					
8	*E. macrodonta* AF451343	19.2	25.6	19.8	22.2	21.8	25.4	21.8																				
9	*E. macronyx* FM955309	20.2	24.8	22.8	19.8	25.6	26.0	23.0	20.4																			
10	*Epimeria* n. sp. FM955295	20.8	25.4	14.7	14.5	22.2	23.8	17.1	21.0	20.2																		
11	*E. puncticulata* FM955301	18.2	25.6	20.8	20.6	21.6	25.4	20.6	14.3	19.4	19.6																	
12	*E. reoproi* AF451342	19.4	26.2	22.2	22.6	22.4	28.2	22.4	10.5	20.6	20.4	15.3																
13	*E. rimicarinata* FM955304	21.4	24.6	11.9	16.9	22.4	23.0	18.2	20.0	21.8	14.1	19.8	23.2															
14	*E. robusta* FM955279	20.8	26.8	18.8	18.6	26.0	25.8	18.6	19.6	21.8	20.2	22.4	21.6	16.5														
15	*E. robustoides* AF451344	20.6	25.4	14.1	16.5	23.6	24.0	17.1	19.6	20.8	16.7	18.6	21.6	16.1	21.1													

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
16	*E. rubrieques* AF451345	20.6	24.8	11.7	15.1	24.8	24.6	17.7	18.4	19.6	14.1	19.8	21.2	11.1	16.3	12.7												
17	*E. schiaparelli* FM955284	20.0	25.4	21.2	24.0	22.8	26.6	22.2	8.5	23.2	22.8	15.1	11.5	21.8	22.0	20.4	20.0											
18	*E. similis* AF451346	20.6	25.8	21.2	23.0	21.2	27.0	23.0	12.7	20.8	22.0	14.7	11.7	23.4	22.4	20.0	21.0	13.3										
19	*E. walkeri* FM955308	18.2	24.0	19.0	18.6	23.0	24.0	20.8	20.6	17.0	18.6	18.4	19.8	21.0	22.0	19.8	18.8	21.2	19.8									
20	*Echiniephimedia echinata* AF451352	30.9	30.9	30.1	32.9	30.5	30.3	33.9	30.5	30.9	31.7	29.7	30.9	29.9	32.9	31.9	31.5	31.7	30.3	29.1								
21	*E. hodgsoni* AF451350	30.5	30.5	32.3	33.7	30.5	30.3	33.5	31.5	31.5	32.5	31.5	31.1	31.9	33.1	30.9	33.5	30.5	30.9	28.7	10.1							
22	*E. scotti* FM955294	29.7	30.5	29.9	31.7	29.9	30.1	33.1	30.9	31.1	31.3	30.5	30.1	29.9	33.1	31.5	30.9	31.3	29.5	28.5	8.3	7.8						
23	*E. waegelei* AF451351	30.1	29.5	30.3	31.1	30.5	29.9	32.3	30.1	30.7	30.9	29.1	31.1	29.5	31.5	30.3	30.3	30.9	31.1	27.5	9.9	10.5	8.5					
24	*Gnathiphimedia sexdentata* AF451354	29.0	28.4	27.2	28.0	28.2	26.6	28.8	28.0	29.2	26.2	28.0	28.2	27.2	28.8	25.4	27.0	30.0	27.2	27.8	23.0	23.2	22.8	23.2				
25	*G. mandibularis* AF451353	24.0	27.6	24.0	26.8	28.2	28.6	28.8	25.8	25.8	28.0	25.6	25.2	25.8	29.2	25.8	25.0	25.4	24.4	24.6	26.1	26.7	24.7	25.1	23.6			
26	*Iphimediella cyclogena* AF451348	29.9	24.0	29.2	29.2	29.4	27.2	28.4	30.7	29.8	29.4	28.8	29.0	27.4	31.1	27.8	28.6	30.0	31.1	28.6	26.7	26.1	25.5	26.5	22.6	23.0		
27	*I. georgei* AF451349	31.5	31.3	30.3	32.9	33.5	31.3	35.2	30.7	35.2	31.7	31.5	30.3	29.7	33.9	33.1	31.7	33.1	31.7	31.1	21.0	22.4	21.2	21.6	28.3	27.9	29.5	
28	*I. rigida* AF451347	31.3	31.1	30.1	32.7	33.1	31.1	35.0	30.3	35.0	31.5	31.1	29.9	29.5	33.7	32.9	31.5	32.7	31.3	30.9	20.6	22.0	20.8	21.2	28.1	27.3	29.3	0.6

Table 3. Uncorrected genetic COI distances within selected *Epimeria* species

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	*E. georgiana* AF451341																									
2	*E. georgiana* AY061802	4.44																								
3	*E. georgiana* FM955299	15.3	14.7																							
4	*E. georgiana* FM955305	15.3	14.7	0																						
5	*E. horsti* FM955296																									
6	*E. horsti* FM955297					0																				
7	*E. inermis* FM955280																									
8	*E. inermis* FM955281							0.81																		
9	*E. inermis* FM955282							2.22	2.42																	
10	*E. inermis* FM955285							0	0.81	2.22																
11	*E. inermis* FM955292							0	0.81	2.22	0															
12	*E. rimicarinata* FM955300																									
13	*E. rimicarinata* FM955302												2.02													
14	*E. rimicarinata* FM955303												2.02	0												
15	*E. rimicarinata* FM955304												2.02	0	0											
16	*E. robusta* FM955279																									
17	*E. robusta* FM955283																0.2									
18	*E. robusta* FM955286																0.81	1.01								
19	*E. robusta* FM955287																0	0.2	0.81							
20	*E. robusta* FM955289																0	0.2	0.81	0						
21	*E. robusta* FM955290																0.4	0.2	1.21	0.4	0.4					
22	*E. robusta* FM955291																0	0.2	0.81	0	0	0.4				
23	*E. robustoides* AF451344																									
24	*E. robustoides* FM955288																							0.2		
25	*E. walkeri* FM955306																									
26	*E.walkeri* FM955308																									5.04

closest related to *Epimeria georgiana* and *E rubrieques* from the Weddell Sea, with interspecific distances of 14.72% and 14.11% respectively. Sequence distances between *Epimeria robusta* from the Ross Sea and *E. robustoides* from the Weddell Sea were 12.3 to 13.1%.

Intraspecific distances

Analysing the intraspecific differences the partial COI gene showed 0.0–1.2% sequence divergence within the seven *E. robusta* specimens from the Ross Sea and 0.2% sequence divergence within *E. robustoides* from the Weddell Sea. Sequence distances of 0.0–2.4% were found between the four *E. inermis* specimens, collected at four stations within the Ross Sea. The four *E. rimicarinata* specimens were collected from three different stations of the Ross Sea and had intraspecific distances of less than 2.1%. The two specimens of *Epimeria walkeri* collected in the Weddell and Ross Seas showed 5.04% sequence divergence while within *Epimeria georgiana* the two specimens collected at the Antarctic Peninsula varied by ~15% from the two speciemens collected in the eastern Weddell Sea.

Discussion

Taxonomic implications

In amphipod taxonomy it is common to have small morphological distances for separation between genera and even families (e.g. Coleman and Barnard 1991). The three families examined in this study, the Epimeriidae, Iphimediidae and Eusiridae, have only a few characters distinguishing them. Therefore members of the Iphimediidae and Eusiridae were chosen as outgroups in the molecular part of this study. Iphimediidae differ from Eusiridae in having at least one of coxae 1–4 being pointed (Barnard and Karaman 1991). The family Iphimediidae only differs from the Epimeriidae in having at least one pair of chelate gnathopods and in lacking the mandibular raker spines (Coleman and Barnard 1991).

Within the Epimeriidae, *Metepimeria* is separated from *Epimeria* by bearing a 3-articulate maxilliped palp, vs the 4 articulate maxilliped palp of *Epimeria*. The only morphological separation of *Epimeria* and *Epimeriella* was the latter having a drawn out pars molaris without triturative surface and the lower lip bearing a wide hypopharyngeal gap. However, it was questionable whether this is a strong enough character for a valid generic distinction. Lörz and Brandt (2004) measured the variability in width of the hypopharyngal gap within selected epimeriid species and found no significant differences between *Epimeria macrodonta* and *Epimeriella truncata*. Lörz and Brandt (2004) discussed that *Epimeriella* shows plesiomorphic characters of Antarctic *Epimeria* and indicated that the genus should therefore be synonymised with *Epimeria*. In their phylogeny based on 106 morphological characters, they analysed two *Epimeriella* species grouped within the Antarctic species of *Epimeria* and formed a clade with *Epimeria annabellae* (Lörz and Brandt 2004). The habitus of these three dorsally smooth species is similar (see e.g. Coleman 2007). The present molecular investigation shows the analysed species of *Epimeriella*, *E. macronyx* and *E. walkeri*, amongst the Antarctic *Epimeria* clade, supporting the former morphological studies by Lörz and Brandt (2004) of paraphyletic genera. Based on the here presented genetic data and a detailed morphological evaluation of the weak morphological separation criteria between *Epimeriella* and *Epimeria* we herewith synonymise *Epimeriella* with *Epimeria*. The topology of the molecular phylogeny showed the iphimediid genera *Iphimediella* and *Gnathiphimedia* to be paraphyletic taxa. The Iphimediidae, like the Epimeriidae, require more detailed morphological and molecular investigations to reveal their taxonomic characters.

Phylogeny of Southern Hemisphere *Epimeria*

The molecular phylogenetic analysis revealed the presence of a New Zealand seamount clade and an Antarctic clade of *Epimeria*. *Epimeria horsti*, collected from the New Zealand Ghoul and Gothic seamounts, is genetically closest to *E. bruuni* collected from the Young Hicks seamount, Hikurangi Plateau in New Zealand. Even though the New Zealand species have a genetic distance of over 20% from any *Epimeria* in the Southern Ocean, these two *Epimeria* species from rather close geographic localities also show a very large genetic distance, nearly 20% (Table 2). The New Zealand specimens show a strong monophyletic support (Fig. 1) whereas the support for the monophyly of Antarctic species is not so high in the likelihood analysis (78 bootstrap value), but the parsimony analysis shows higher values (bootstrap 87, jackknife 96). Without sequences of *Epimeria* outside of New Zealand and Antarctic waters it is not possible to determine the origin of the species based on this data. One likely scenario is that epimeriid amphipods "populated" New Zealand waters many million years ago or that several colonizations from the Ross Sea shelf to New Zealand shores have taken place. Another even more probable scenario is that epimeriids are Gondwanan and became isolated during sea-floor spreading in the Cretaceous. Our hypotheses are that all non-Antarctic epimeriids are monophyletic. Lörz and Brandt (2004) studied the phylogeny of *Epimeria* via morphological characters, with exception of *E. loricata* the species studied occurring beyond Antarctic waters form a well supported clade with the following synapomorphies: produced and pointed ventral angle of coxa 5; midventrally pointed coxa 4; lateral surface of coxa 5 bearing bump or tooth; merus of P5–P7 not produced. Based on their morphological characters, the two recently described and redescribed New Zealand species, *E. horsti* and *E. bruuni*, would be part of this non-Antarctic clade.

The specimens identified as *Epimeria georgiana* show a genetic distance of ~15%, a distance value that proved to separate species within the Epimeriidae. Therefore we take this high genetic difference as evidence for dealing with a *Epimeria-georgiana* species complex consisting of at least two different species. According to Coleman (2007) *E. georgiana* occurs at South Georgia, in the Bransfield Strait, along the Palmer Archipelago (latter two both Western Antarctic Peninsula), the South Shetland Islands, and eastern shelf of the Weddell Sea. Coleman noted (pers. com.) that the fourth coxa of *E. georgiana* specimen from the Antarctic Peninsula is quite different compared to the specimen from the Weddell Sea. The latter specimen resembled *E. inermis*, but show hooks at the basis of pereopods five and six. Väinölä et al. (2001) included cytochrome oxidase sequences from an *Epimeria georgiana* specimen in their "Phylogeography of "glacial relict" *Gammaracanthus* from boreal lakes and the Caspian and White seas", but did not note the exact sampling location. The *E. georgiana* specimens in this study are from the Weddell Sea and the Antarctic Peninsula. We will separate the two cryptic species keyed out to *Epimeria georgiana* following the identification key of Coleman (2007) in the near future.

Previous analysis of the partial COI gene showed 0.0–2.2% sequence divergence within eleven specimens of the *E. schiaparelli* from the Ross Sea (Lörz et al. 2007) forming a distinct group within *Epimeria*. This intraspecific divergence within *E. schiaparelli* is much less than this group's divergence from *E. macrodonta* (8.93–8.38%), the most closely related species. Divergences between other species were much larger (e.g. 12.02% divergence for *E. similis* and *E. macrodonta*) further supporting the conspecificity of all specimens identified as *E. schiaparelli*, despite conspicuous variation in morphological characters as pointed out by Lörz et al. (2007).

It is remarkable that the interspecific variation of the iphimediid genus *Echiniphimedia* is smaller between the Ross Sea species *E. scotti* and any of the three Weddell Sea species than any distance of the Weddell Sea species to each other (Tab. 2). A possibility is that the origin of the genus *Echiniphimedia* is in the Ross Sea and it has "populated" the Antarctic shelf several times. However, the Ross Sea shelf has been overrun by grounding ice sheets several times during the last glacial maxima. According to literature records, *Echiniphimedia scotti, E. hodgsoni* and *E. echinata* are accounted to have circum-Antarctic distributions with occurrences in the Ross Sea and at the Antarctic Peninsula (Coleman 2007). No records are known from a species of *Echiniphimedia* below 720 m, with the exception of *Echiniphimedia hodgsoni* (1120m). Unfortunately not enough material had been available of any of the three species from both geographic distant locations and none suitably fixed for genetic studies.

The interspecific genetic differences between species of the genus *Epimeria* are 12–26%, those of *Echiniphimedia* 7.8–29.1% (Table 2), the genetic distances between genera of Epimeriidae and Iphimediidae is 23–32% (Table 2). Molecular studies on the COI gene of non-Antarctic amphipods found 33.6–36.4% sequence differences between species in *Gammarus* (Meyran et al. 1997, Hou et al. 2007) Cristeascu and Herbert (2005) discovered ~28% sequence divergence in Ponto-Caspian amphipods of the genera *Dikerogammarus*, *Echinogammarus*, *Obesogammarus* and *Pontogammarus*. Witt et al. (2006) found COI nucleotide divergences among these *Hyalella* species ranging from 4.4% to 29.9%.

The interspecific divergence of Epimeriidae and Iphimediidae from the Southern Ocean compared with the studied Gammaridae is low (Meyran et al. 1997, Hou et al. 2007) but similar to the divergences discovered in *Hyalella* (Witt et al. 2006). A low interspecific divergence indicates a relatively recent speciation. One reason for a successful recent speciation could be their variety in feeding patterns (Coleman 1989, Dauby et al. 2001, DeBroyer et al. 2001). Examination of the mandibles (mouthparts) of some species underscores their specialised food preferences. *Gnathiphimedia mandibularis*, which feeds on bryozoan colonies, has hammer-like mandibles (non-cutting) to crush the bryozoans' calcareous (calcium carbonate) exterior. The mandibles of *Echiniphimedia hodgsoni*, however, have sharp cutting edges for biting through tough sponge tissue (Coleman 1989).

Dauby et al. (2001) have identified eight different feeding types among Antarctic amphipods, members of Epimeriidae and Iphimediidae are suspension feeders, deposit feeders, deposit feeders coupled with predation, opportunistic predators, micropredatory browsing, macropredation coupled with opportunistic necrophagy.

Another explanation for the recent speciation could be the variety in modes of mobility (Dauby et al. 2001). Epimeriidae and Iphimediidae show a great variation in their ability to move around, from sedentary (*Epimeria georgiana, Epimeria rubrieques*) to highly mobile (*Epimera walkeri*). Their degree of mobility is closely related to their food preferences, with the less mobile species more likely to be suspension-feeders and the more agile more inclined to be predators (Dauby et al. 2001).

The colour variation of these families might also add to their rate of speciation. These specimens are predominantly red. Some species, such as *Epimeria inermis*, occur in several colours. *Epimeria schiaparelli*, comes in two different patterns: striped and speckled, DNA analysis proved that both forms are the same species (Lörz et al. 2007).

Many specimens are covered with extravagantly long spines. We can only speculate on the role of these spines, since we know so little about the creatures' biology. A spiny exterior may offer protection from predators by breaking up the body outline and making the animal harder to see, or by rendering it unpleasant to eat. *Echiniphimedia hodgsoni* lives in sponges, and its many small white spines camouflage it within the sponge tissue.

The diversity of microhabitats and of potential foods combined with the different mobility patterns most likely encouraged the spread and speciation of Southern Ocean amphipods.

Does circum-Antarctic distribution occur amongst species of epimeriid Amphipoda?

Our present genetic and morphological studies revealed no circum-Antarctic epimeriid species in the examined specimens. Intraspecific genetic divergence in specimens from the same species from the same region was generally under 2.3%, except *Epimeria walkeri,* for example Ross Sea *E. robusta* (n=7, <1.2%); *E. inermis* (n=4, <2.4%), *E. rimicarinata* (n=4, <2.1%) or *E. schiaparelli* (in Lörz et al. 2007) (n=11, 0–2.19% sequence divergence). However, the specimen keyed out as *E. robusta* from the Weddell Sea showed a distance over 12% to the Ross Sea *E. robusta*, definitely suggesting a new species, thus described as *Epimeria robustoides* above.

The two species are morphological very similar; the table above shows the morphological features separating *Epimeria robusta* and *E. robustoides*. Previous collections of *Epimeria robusta* from the Weddell Sea most likely have to be treated as findings of *Epimeria robustoides*, unless further genetic studies reveal a sympatric distribution of *E. robustoides* and *E. robusta*.

Epimeria walkeri shows a genetic distance of 5.04% between the Ross Sea and the Weddell Sea. A COI sequence divergence value of >4% is often applied for separating marine invertebrate species in molecular barcoding (Witt et al. 2006). Since our data either show intraspecific variation of less than 2.5%, and an interspecific variation of at least 8.4%, we suggest that *Epimeria walkeri* is in the process of speciation.

The taxonomic relationships within the nominal *Epimeria-georgiana*-group were discussed above. The genetic sequence distances of ~15% between specimens from the Antarctic Peninsula and the eastern Weddell Sea are enough evidence for the existence of two species and to state that *E. georgiana* does not have a circum-Antarctic distribution but consists of a complex of cryptic species.

High values of intraspecific mitochondrial gene sequence divergence (COI and 16S mtDNA) indicating the existence of cryptic species are not only found in Antarctic species of Amphipoda from distant localities on the Southern Ocean. Similar results were found in studies on Isopoda (e.g. Held and Wägele 2005, Raupach and Wägele 2006, Raupach et al. 2007, Brökeland and Raupach 2008), Bivalvia (Linse et al. 2007), Octopoda (Allcock et al. 2004, Strugnell et al. 2008), Pycnogonida (Mahon et al. 2008), Crinoidea (Wilson et al. 2007) and benthic fish (Smith et al. 2008). Some reasons for the possible circum-Antarctic distribution of some breeding taxa is the dispersal via the Antarctic Circumpolar Current (ACC hypothesis) or extinction of a high proportion of taxa with pelagic development during vicariant events (extinction hypothesis) or the speciation enhanced in taxa with nonpelagic development in refuges during glacial maxima over the Antarctic Continental Shelf in the Pliocene/Pleistocene (ACS hypothesis) (Pearse et al. 2009). Nominal species collected at several distant localities, for example from the eastern Weddell Sea and Antarctic Peninsula or the Weddell Sea and Ross Sea, resulted in the discoveries of species complexes.

Conclusions. The morphological and molecular analysis on the validity of the epimeriid genus *Epimeriella* Walker, 1906 confirmed earlier the suggestion by Lörz and Brandt (2004) that this genus is a junior subjective synonym of *Epimeria* Costa, 1851. Five species are affected by this and are now named *Epimeria macronyx* comb. n., *E. scabrosa* comb. n, *E. truncata* comb. n., *E. victoria* comb. n. and *E. walkeri* comb. n. The analysed epimeriid specimens from New Zealand's seamounts and Antarctic localities formed two distinct clades separated by their geographic distributions. Within the Antarctic clade no further phylogeographic separation based on the species' distributions were observed. In order to evaluate the relationships between the Southern Hemisphere Epimeriidae, species from the Northern Hemisphere need to be included in the analysis. The use of the barcoding gene COI showed high sequence distances (12–13%) in the formerly circum-Antarctic distributed species *Epimeria robusta* and led to the description of *Epimeria robustoides* new species. The sequence distances within *Epimeria georgiana* of 15% between specimens from the Antarctic Peninsula and the eastern Weddell Sea gives evidence of another species complex in the Epimeriidae. Morphological variations in Antarctic amphipod populations from distant geographic localities have to be treated with care, potentially indicating the existence of cryptic species, all new to science. Based on our results, the hypothesis of circum-Antarctic species' distributions in brooding amphipods proved to be unlikely.

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