Untersuchungen zur Biodiversität antarktischer benthischer Amphipoda (Malacostraca, Crustacea)

Studies on the biodiversity of Antarctic benthic Amphipoda (Malacostraca, Crustacea)

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Die vorliegende Arbeit ist die inhaltlich unveränderte Fassung einer Dissertation, die im Februar 2003 dem Fachbereich Zoologie der Universität Hamburg vorgelegt wurde.

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3. **Veröffentlichungen**

Zusammenfassung

Die Untersuchungen zur Biodiversität antarktischer benthischer Amphipoda beruhen zum großen Teil auf Material, das während der Expedition ANT XVII-3 (EASIZ III) mit dem FS *Polarstern* gefangen wurde. Tiere stammen hauptsächlich vom Schelf des östlichen Weddell-Meeres und von der antarktischen Halbinsel. Die Probennahme fand im antarktischen Herbst statt. Die kumulative Arbeit läßt sich in drei Bereiche gliedern, die sich überschneiden und ergänzen:

- Taxonomie und Systematik
- Abundanz und Diversität
- Phylogenie.

Taxonomie und Systematik wird in der folgenden Arbeit durch vier Veröffentlichungen adressiert. Es werden vier neue Arten aus vier verschiedenen Familien beschrieben und soweit möglich die Ökologie der Taxa untersucht. Bei einer neuen *Epimeria* Art (Epimeriidae) handelt es sich um eine weitere Art in einer in der Antarktis häufig vorkommenden Gattung. Hingegen wurde eine *Dikwa* beschrieben, die den zweiten Vertreter ihrer Familie und den ersten im Südlichen Ozean darstellt. Zudem scheint sie in symbiontischer Beziehung zu einer Hartkoralle zu stehen. Der sogenannte antarktische *Eusirus* Komplex (Eusiridae) wurde durch die Beschreibung einer neuen Art auf drei Vertreter unterteilt. Die Arten sind sich sehr ähnlich. Die Untersuchung zahlreicher Museumsbestände war nötig, um morphologische Unterscheidungsmerkmale darzustellen. Ein bisher unbekannter Lysianasside wurde zu mehreren Hundert Individuen aus dem Gewebe verschiedener Demospongiae präpariert.

Abundanz und Diversität von Amphipoden,die in Schwämmen leben wurde quantitativ und qualitativ untersucht. Aufgrund der Probennahme mit geschlepptem Gerät wurden nur die Flohkrebse ausgewertet, die sich in den Kanälchen des Schwammgewebes aufgehalten haben. Es befanden sich teilweise über 40 Individuen pro Liter. Dabeiwurden ausschließlich Männchen und Weibchen von sechs Arten aus fünf Familien gefunden, aber keine Juvenilen. Im Gegensatz zu den schwammbewohnenden Amphipoda zeigten suprabenthischen Peracarida während des antarktischen Herbstes relativ niedrige Abundanz und hohe Diversität. Die suprabenthische Probennahme fand 1.00-1.33 Meter über dem Boden mit einem modifizierten Epibenthsschlitten statt. Die Ergebnisse konnten mit suprabenthischen Proben der EASIZ II Expedition verglichen werden, die während des antarktischen Sommers stattfand.

Phylogenetische Fragestellungen der Amphipodenfamilien Epimeriidae und Iphimediidae wurden mit molekularen und morphologischen Methoden adressiert. Die resultierende Baumtopologien der verschiedenen Methoden sind sich relativ ähnlich, z.B. muss die Monophylie der Gattungen *Iphimediella* und *Gnathiphimedia* (Iphimediidae) bezweifelt werden. Während Sequenzvergleiche der Cytochrom Oxidase eine Artaufspaltung epimeriider Amphipoda lange nach der Abkühlung der Antarktis preisgaben, wurden bei den morphologischen Untersuchungen starke Variationen innerhalb derselben Arten festgestellt. Die relativ junge Trennung der Epimeria Arten kombiniert mit hoher intraspezifischer Varianz läßt auf eine momentan stattfindende rasche Speziation dieser Amphipoden in der Antarktis schließen.

Manche Autoren unterscheiden ökologischen von evolutionärem Erfolg antarktischer benthischer Invertebraten. Amphipoda erzielen in der Antarktis beides: sowohl evolutionären als auch ökologischen Erfolg.

Summary

This study on the biodiversity of Antarctic benthic Amphipoda is mainly based on material collected with RV *Polarstern* during the expedition ANT XVII-3 (EASIZ III). Most of the animals examined were obtained from the eastern Weddell Sea shelf and off the Antarctic Peninsula. The samples were taken in the Antarctic autumn, a time late in the season when only few samples were taken before. For the first time data of presence, abundance and reproduction are compared with similar data of Amphipoda taken during the Antarctic summer.

This thesis is separated in three parts, which overlap and complete each other:

- Taxonomy and Systematic
- Abundance and Diversity
- Phylogeny

Four manuscripts address taxonomic and systematic aspects, describing four new species from four different families. Their ecology is outlined as far as possible. *Epimeria reoproi* is a further species of the genus *Epimeria* that is common in Antarctic waters. *Dikwa andresi* is the second described species of the family Dikwidae and its first representative in the Southern Ocean. This species seems to live symbiotic with a hard coral. The Antarctic *Eusirus*-complex is enlarged by *Eusirus giganteus*. The three species of the *Eusirus*-complex look very much alike. Comprehensive museum material, consisting of several hundred specimens, had to be studied to extract, define and present morphological differences. Several hundred individuals of an unknown species of Lysianassidae were dissected from the tissue of different species of Demospongiae and described.

Abundance and diversity of amphipods living endozooically in sponges were studied qualitatively and quantitatively. Because of the qualitative kind of samples taken with dragged gear only amphipods were studied which lived within the sponge tissue. In some cases more than 40 individuals per litre were found. Females and males belonging to six species of five families were studied, but no juveniles were found. Compared with the highly abundant spongicolous amphipods the suprabenthic peracarids showed low abundance and high diversity during the Antarctic autumn. Suprabenthic samples were taken 1-1.33 meter above the ground by means of an epibenthic sledge modified after Rothlishberg & Pearcy (1977). The results of the analysis on the suprabenthic community were compared with similar data taken during EASIZ II, an Antarctic summer expedition.

The amphipod families Epimeriidae and Iphimediidae were phylogenetically approached with molecular and morphological methods. The resulting dendrograms are very similar. The genera *Iphimediella* and *Gnathiphimedia* (Iphimediidae) are most likely paraphyletic. The molecular study revealed a splitting of the species long after the cooling of Antarctica. The morphological investigation showed high intraspecific variation. The comparatively young separation of the species combined with high intraspecific morphological variations led to the picture of recent, relatively fast speciation of Antarctic Amphipoda.

Some authors distinguish ecological versus evolutionary success of Antarctic benthic invertebrates. Amphipoda in Antarctic waters gain both: ecological and evolutionary success.

1. Einleitung

1.1. Der Begriff „Biodiversität“

Es gibt zahlreiche Definitionen des Begriffes Biodiversität. Die bekannteste Definition wurde 1992 auf der UNCED (United Nations Conference on Environment and Development) in Rio de Janeiro in der „Konvention der Biologischen Diversität“ festgelegt, die von 156 Nationen unterschrieben wurde:

" 'Biological diversity' means the variability among living organisms from all sources including, inter alias, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems. "

Diese Definition ist sehr umfassend, alle biologischen Disziplinen, von einer Gensequenz bis zum Ökosystem, können sich darin wiederfinden. Wie Clarke und Johnston (im Druck) anmerken, kann sich diese Definition zwar gut in der Politik oder im Management bewähren, aber wahrscheinlich nicht in der wissenschaftlichen Entwicklung.
Das *Commitee on Biological Diversity in Marine Systems* (Butman et al. 1995) betont in diesem Kontext definierte geographische Regionen:

„Biodiversity is defined as the collection of genomes, species, and ecosystems occurring in a geographically defined region. “

Moderneren Definitionen nach ist Biodiversität vor dem Hintergrund definierter geographischer Regionen und Zeiteinheiten zu betrachten (z.B. Hubbell 2001):

„..synonymous with species richness and relative species abundance in space and time. Species richness is simply the total number of species in a defined space at a given time, and relative species abundance refers to their commonness or rarity"

Die detaillierte Entstehung und den Bedeutungswandel des Begriffes Biodiversität präsentiert Hobohm (2000). In der vorliegenden Arbeit wird Biodiversität im Sinne von Hubbell (2001) verstanden. Hinter dieser auf den ersten Blick sehr einfach erscheinenden Formulierung verbergen sich in der Praxis die Schwierigkeiten der Taxonomie, Arten gegeneinander abzugrenzen und methodische Herausforderungen, das räumliche und zeitliche Vorkommen dieser Arten in wissenschaftlich kompatible Einheiten zu zwängen.

Die vorliegende Arbeit behandelt Aspekte zur Biodiversität antarktischer Amphipoda aus den Bereichen der Taxonomie und Systematik, der Artenmannigfaltigkeit und Häufigkeit, sowie der molekular und morphologisch untersuchten Verwandtschaftsbeziehungen und Stammesgeschichte ausgewählter Taxa.

1.2. Die Amphipoda

Die Peracarida (Ranzenkrebse) werden in neun Ordnungen unterteilt (Martin & Davis 2001): 1) Spelaeogriphacea Calman 1904, 2) Thermosbaenacea Monod 1927, 3) Lophogastrida Sars 1870; 4) Mysida Haworth 1825, 5) Mictacea Bowman, Garner, Hessler, Iliffe & Sanders 1985, 6) Amphipoda Latreille 1816, 7) Isopoda Latreille 1817, 8) Tanaidacea Dana 1849 und 9) Cumacea Krøyer 1846. Westheide und Rieger (1996) unterscheiden sieben Ordnungen der Peracarida. Sie stellen die Thermosbaenacea (Pancarida), deren dorsale Carapaxhöhle sich zu einem Brutbeutel aufbläht, den Peracarida gegenüber, deren wichtigste Autapomorphie das Marsupium auf der Ventralseite des Thorax der geschlechtsreifen Weibchen darstellt. Im Gegensatz zu Martin und Davis (2001) fassen Westheide und Rieger (1996) die Mysida und die Lophogastrida in der Ordnung Mysidacea zusammen. Die Amphipoda (Flohkrebse) stellen das artenreichste Taxon.

Da es nur sehr wenige Funde fossiler Flohkrebse gibt, kann ihr Alter anhand morphologischer Merkmale nur grob geschätzt werden. Einige Fossilfunde sind aus dem oberen Eozän (vor ca. 55-34 Millionen Jahren) und Oligozän (vor ca. 34-24 Millionen Jahren) bekannt (Karaman 1984). Vielmehr bilden Verbreitungsmuster einzelner Gruppen die Grundlage zu Überlegungen zum phylogentischen Alter. Die rezente unterirdische Amphipodenfauna von Texas beinhaltet einige Crangonyctiden, Hadziiden und einen Bogidielliden. Die heutige Verbreitung der Crangonyctiden in der Nordhemisphäre, impliziert einen Ursprung in Laurasien vor dem Jura (Holsinger & Longley 1980). Die Bogidielliden und die Hadziiden entsprechen hingegen zirkumtropischen Gondwana und Thethys Typen. Die Grundwasserfauna von Texas beinhaltet 22 Arten, mehr als doppelt so viele wie die bekannten komplexen Höhlenfaunen. Dies impliziert ein sehr altes und stabiles Habitat. Schram (1986) postuliert das Alter dieses Refugiums auf mindestens 70 Millionen Jahre. Die Verbreitung von Astacuren (Decapoda), die durch Fossilfunde gut belegt ist, entspricht z.B. der einiger crangonyctider Süßwasseramphipoden. Crangonyctoidae gelten als sehr primitives Amphipodentaxon. Das Alter der Astacuren-Fossilien wird im Mesozoikum (vor 65-248 Millionen Jahren) vermutet (Bousfield & Shih 1994). Bousfield und Conlan (1990) vermuten den Ursprung der Amphipoda im späten Paläozoikum, vor ca. 300 Millionen Jahren. Aus dieser Zeit stammen Fossilien anderer Peracarida wie Isopoda, Cumacea und Tanaidacea.

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Innerhalb der Gruppen der Peracarida sind die Verwandtschaftsverhältnisse weitgehend ungeklärt. Während z.B. Dahl (1991) und Watling (1983) die Amphipoda als eine Schwestergruppe der Isopoda betrachten, postuliert Bousfield (1988) die Mysidacea als Schwestergruppe der Amphipoda. Andere Autoren, z.B. Ax (1999), begründen aufgrund eines den Amphipoda fehlenden Manca Stadiums eine Schwesterngruppenstellung zu allen anderen Taxa der Peracarida.

Ungeachtet der ungeklärten phylogenetischen Stellung innerhalb der Peracarida gilt die Monophylie der Amphipoda als unangefochten. Der Name Amphipoda bedeutet

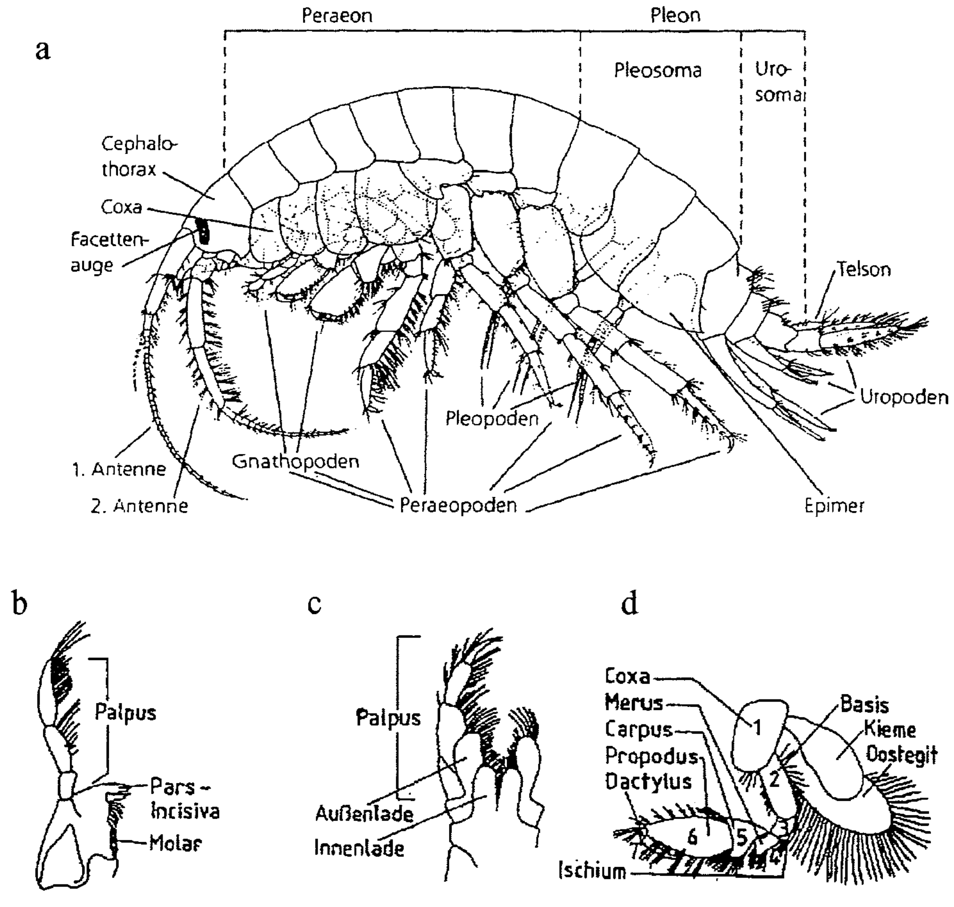

Abbildung 1. Bauplan eines typischen Gammaridea: a) Lateralansicht, b) Mandibel, c) Maxilliped, d) vierter Peraeopod; a) nach Bousfield (1973), leicht verändert aus Westheide & Rieger (1996); b-d) aus Sieg & Wägele (1990).

Wechselfüßer und bezieht sich auf die innerhalb der höheren Krebse einzigartige Anordnung der Paraeopoden. Die vorderen vier Paare sind nach vorn, die hinteren drei Paare nach hinten abgewinkelt. Oftmals sind die beiden ersten Paare subchelat und werden als Gnathopoden bezeichnet. Die typische Form von Habitus und Mundwerkzeugen eines gammariden Amphipoden mit den Bezeichnungen, die in der vorliegenden Arbeit verwendet werden, zeigt Abbildung 1.

Von ca. 6000 weltweit bekannten Amphipodaarten gehören etwa 85 % zu den Gammaridea. Traditionell werden die Amphipoda in vier Großgruppen aufgeteilt (Martin & Davis 2001):
1) Gammaridea Latreille 1802, 2) Caprellidea Leach 1814, 3) Hyperiidea Milne Edwards 1814 und 4) Ingolfiellidea Hansen 1903. Myers & Lowry (im Druck) präsentieren eine neue Unterordnung der Amphipoda: Corophiidea. Diese enthält die Infraordnungen Corophiida und Caprellida. Während Ingolfiellidea mit sehr kleinen wurmförmigen Körpern typische Sandlückenfauna darstellen, kommen Hyperiidea ausschließlich im marinen Pelagial vor. Caprellidea halten sich meist mit den Peraeopoden 5-7 am Substrat fest und filtrieren mit ihren Antennen Nahrungspartikel aus dem Wasser. Die auf Walen parasitierenden sogenannten Walläuse der Familie Cyamidae gehören ebenfalls zu den Caprellidea, bzw. Caprellida der Unterordnung Corophiidea (Myers & Lowry im Druck).

Die vorliegende Arbeit behandelt nahezu ausschließlich Taxa der Gammaridea. Eine Ausnahme stellt der Caprellidae *Aeginoides gaussi* Schellenberg 1926 dar, der an zwei Stationen zwischen 1.00 m und 1.33 m über dem Boden gefangen wurde (s. achte Veröffentlichung).

1.3. Gammaridea der Antarktis

Peracaride Krebse sind die artenreichste Tiergruppe des antarktischen Benthos. Die Amphipoda sind das häufigste Taxon innerhalb der Peracarida (De Broyer & Jazdzewski 1996). Diese Daten basieren vorrangig auf Schelfuntersuchungen. Ob sie auch in der Tiefsee zutreffen, muss noch erforscht werden.

Aus dem Südozean sind über 700 benthische Arten von Amphipoda bekannt, von diesen gehören 97 % zu den Gammaridea (De Broyer & Jazdzewski 1996). Dies entspricht knapp 12 % der weltweit vorkommenden Arten. In der Antarktis sind ca. 86 % der benthischen Arten von Flohkrebsen endemisch, während die benthischen Familien nur 5 % Endemismen zeigen (De Broyer & Jazdzewski 1996). Die Anzahl neu beschriebener Arten ist in den letzten zwei Jahrzehnten rapide angestiegen, da sich die logistischen Möglichkeiten für Probennahmen im Südozean durch den Einsatz verschiedener Forschungsschiffe wie PFS *Polarstern*, RRS *James Clarke Ross*, RV *Nathaniel Palmer* und FFS *Victor Hensen* sehr verbessert haben.

Es gibt kaum ein Habitat auf dem antarktischen Schelf, welches nicht von Amphipoda besiedelt wird. Der hohe evolutionäre Erfolg der Amphipoda liegt unter anderem in ihrer großen Anpassungsfähigkeit, verschiedene Nahrungsressourcen zu nutzen. Dauby et al. (2001a) teilen die Amphipoda des Weddell-Meeres aufgrund von Mageninhaltsuntersuchungen und Aquarienbeobachtungen in acht Ernährungstypen ein: 1) Filtrierer, 2) Detritus-Fresser, 3) opportunistisch- räuberische Detritus-Fresser, 4) opportunistische Räuber, 5) räuberische mikrophage Weidegänger, 6) räuberische Makrophagen, die z.T. auch Nekrophagie zeigen, 7) opportunistische und 8) wahre Aasfresser. Diese Ernährungsformen beinhalten alle bekannten Fraßtypen mit Ausnahme der makroherbivoren Weidegänger. Makroherbivore Gammariden fehlen in tieferen antarktischen Gewässern aufgrund der Abwesenheit von Makroalgen unterhalb 100 Metern (Wiencke 1995).

Bei Nahrungsspezialisten kann die Nahrungskonkurrenz ausgeschlossen oder als vernachlässigbar eingestuft werden. Zum Beispiel gibt es für die Bryozoen fressende Art *Gnathiphimedia mandibularis* K.H. Barnard 1930 als Nahrungskonkurrenten im hochantarktischen Benthos neben einigen Gastropoden nur den Echinoiden *Sterechinus neumayeri* (Meissner 1900) (Klages 1993). Schwämme werden u.a. aufgrund ihrer Nadeln von den meisten Tieren als Nahrung vermieden, jedoch gibt es Amphipodaarten, die sich auf Schwämme spezialisiert haben (Coleman 1989b). Der in der vorliegenden Arbeit beschriebene Lysianassidae, *Pseudokoroga spongiophila* Lörz & De Broyer im Druck, scheint das Gewebe seiner Wirte, verschiedene Hornkieselschwämme, als opportunistische Nahrung zu nutzen. Erstmalig im Südozean wird ein Amphipode beschrieben, der mit einer Hartkoralle eine Lebensgemeinschaft bildet, *Dikwa andresi* Lörz & Coleman im Druck.
Die trophische Bedeutung benthischer Gammariden für andere Gruppen in der antarktischen Schelfgemeinschaft ist vor allem für die Fische Nothothenioidae und Artedidraconidae bekannt (Kock 1992, Olaso et al. 2000). Brandt (2000) postuliert, dass es sich bei den stacheligen Fortsätzen auf den Körpern der Peracarida möglicherweise um Anpassungen zum verbesserten Fraßschutz handeln könnte. Ein polymorphes Muster der Cuticulapigmente könnte zur Camouflage der antarktischen Ranzenkrebse beitragen (Wägele 1986). Die Amphipoden haben ebenfalls eine große Bedeutung als Nahrung für Pinguine, Robben und

verschiedene Invertebraten im Südozean. Sie werden z.B. von Octopoden, Garnelen und Isopoden konsumiert. Die Wassertiefen des antarktischen Schelfs vermindern den Feinddruck durch Seevögel, die in Flachwassergemeinschaften der Subantarktis große Mengen an Amphipoda erbeuten können (Bregazzi 1972, Rauschert 1991). Insgesamt stellen Amphipoda ein wichtiges Glied im Nahrungsnetz der Antarktis dar.

Als ein weiterer Grund für die erfolgreiche Besiedlung des antarktischen Schelfs durch die Amphipoda wird die Brutpflege diskutiert. Neben Peracarida betreiben auch einige Echinoiden, Asteroiden, Crinoiden, Polychaeten sowie manche Bivalven und Gastropoden Brutpflege (z.B. Hain & Arnaud 1992, Knox 1977, Linse & Page im Druck, Poulin & Féral 1996). Diese Form der Reproduktion scheint ein besonderer Vorteil in Polarregionen zu sein, da starke Saisonalität mit reduziertem Nahrungsangebot und Lichtmangel eine besondere Herausforderung an das Überleben der Larven stellt. Poulin et al. (2002) stellen dem evolutionären Erfolg zahlreicher Brutpflege betreibender Taxa den ökologischen Erfolg der benthischen Invertebraten mit planktotropher Entwicklung gegenüber. Der Hauptvorteil der Entwicklung mit pelagischen Larven in der Antarktis liegt in der Besiedlung unstabiler Gebiete. Eisberge können durch den antarktischen Schelf bis zu einer Tiefe von mehreren hundert Metern pflügen (Gutt 2001, Peck et al. 1999). Etablierte Faunengemeinschaften werden so zerstört und neue Habitate geschaffen.

Es gibt die Möglichkeit, dass auch innerhalb der Peracarida die Juvenilen ein anderes Habitat im Südozean besiedeln als die Adulten. Während Juvenile der Gnathiiden (Isopoda) Blut an Fischen saugen, leben die Adulten in Schwämmen, in denen auch die Fortpflanzung stattfindet (Wägele 1988). In der vorliegenden Arbeit wurden Demospongiae und ihre kommensalistischen Amphipoda während des antarktischen Herbstes untersucht. Dabei wurden ausschließlich adulte Flohkrebse gefunden (Lörz 2001).

Poulin et al. (2002) unterscheiden ökologischen von evolutionärem Erfolg antarktischer benthischer Invertebraten. Amphipoden erzielen in der Antarktis beides: sowohl evolutionären als auch ökologischen Erfolg.

1.4. Ziele dieser Arbeit

Diese Arbeit „Untersuchungen der Biodiversität antarktischer Amphipoda“ behandelt benthische und suprabenthische Flohkrebse des Weddell-Meeres, der Antarktischen Halbinsel und des Scotia Bogens. Die Biodiversitätsstudien verfolgen sowohl einen taxonomischen als auch einen ökologischen Ansatz. Phylogenetische Fragestellungen zu ausgewählten Taxa der Amphipoda werden mit morphologischen und molekularen Methoden bearbeitet. Die Ziele lassen sich wie folgt zusammenfassen:

1. **Taxonomie und Systematik**
   Beschreibung neuer Arten der Amphipoda, Differenzialdiagnose und Verbreitung ausgewählter Taxa.

2. **Abundanz und Diversität**
   Wie hoch sind diese Werte während des antarktischen Herbstes von
   a) Amphipoda, die in Symbiose mit Schwämmmen leben?
   b) Peracarida, die suprabenthisch auf dem Shelf leben? (Probennahme 1.00-1.33 m)

3. **Phylogenie**
   Stammesgeschichtliche Untersuchungen der Familien Epimeriidae und Iphimediidae mittels mitochondrialer Gensequenzen der Cytochromoxidase I sowie klassischer morphologischer Methoden.
   Sind die Ergebnisse dieser Methoden vergleichbar?
   Kann die Phylogenie helfen, Fragen der Herkunft und des Alters ausgewählter Gruppen zu erörtern?

2. Probennahme

2.1. Untersuchungsgebiet

Ein Großteil der untersuchten Amphipoda wurde während der *Polarstern* Expedition ANT XVII-3 gefangen. Diese Fahrt, EASIZ III (Ecology of Antarctic Sea Ice Zone), begann am 18. März 2000 in Kapstadt, Südafrika, und endete am 11. Mai 2000 in Punta Arenas, Südchile. Die häufigen Untersuchungsgebiete deutscher Antarktis-Expeditionen sind in Abbildung 2 dargestellt. Die meisten Proben für die vorliegende Arbeit stammen aus dem Weddell-Meer bei Kapp Norvegia und den Gebieten an der Antarktischen Halbinsel. Stationen, an denen Proben mit dem Epibenthosschlitten (EBS) genommen wurden, befinden sich bei Kapp Norvegia und bei den Süd Shetland Inseln, Abbildung 3.

Die antarktischen Schelfregionen unterscheiden sich hinsichtlich ihrer großen Wassertiefe, ihrer Tiefenzunahme in Richtung des Kontinents und ihrer rauen Topographie von allen anderen kontinentalen Schelfen (Melles 1990).

2.2. Fanggeräte

Für die vorliegende Arbeit wurden ausschließlich Proben von geschleppten Geräten verwendet: Grundschleppnetz (GSN), Agassiz-Trawl (AGT), Rauschert Dredge (RD) und Epibenthosschlitten (EBS). Mit großen Schleppnetzen, GSN und AGT, wird der Boden nur qualitativ beprobt, jedoch werden relativ große Areale befischt. Somit erhöht sich die Wahrscheinlichkeit, dass ein großer Prozentsatz der dort vorkommenden Organismen erfasst wird, wenn sie in Hinblick auf Größe und Lebensraum den Fangcharakteristika des verwendeten Gerätes entsprechen. Das AGT hat eine Maschenweite von mindestens 10 mm, das GSN von mindestens 135 mm. Eine ausführlichere Funktion der Geräte beschreibt Klages (1991). Da die Mehrzahl der Amphipoda kleiner als 10 mm sind, eignen sich Fanggeräte mit kleinmaschigen Netzen besser für Probennahmen, die Biodiversitätsstudien dienen. Die Analysen zur Biodiversität kommensalistisch in Schwämmen lebender Amphipoda beruhen allerdings auf Schwammproben von den großen geschleppten Geräten.

Die Netze der RD und des EBS weisen Maschenweiten von 500 µm auf. Genauere Beschreibungen zu Aufbau und Funktion der Rauschert Dredge befinden sich bei Lörz et al. (1999), zum EBS bei Brandt & Barthel (1995).

Die weitere Bearbeitung des Materials wird in den jeweiligen Abschnitten „Material & Methods“ der Veröffentlichungen beschrieben.

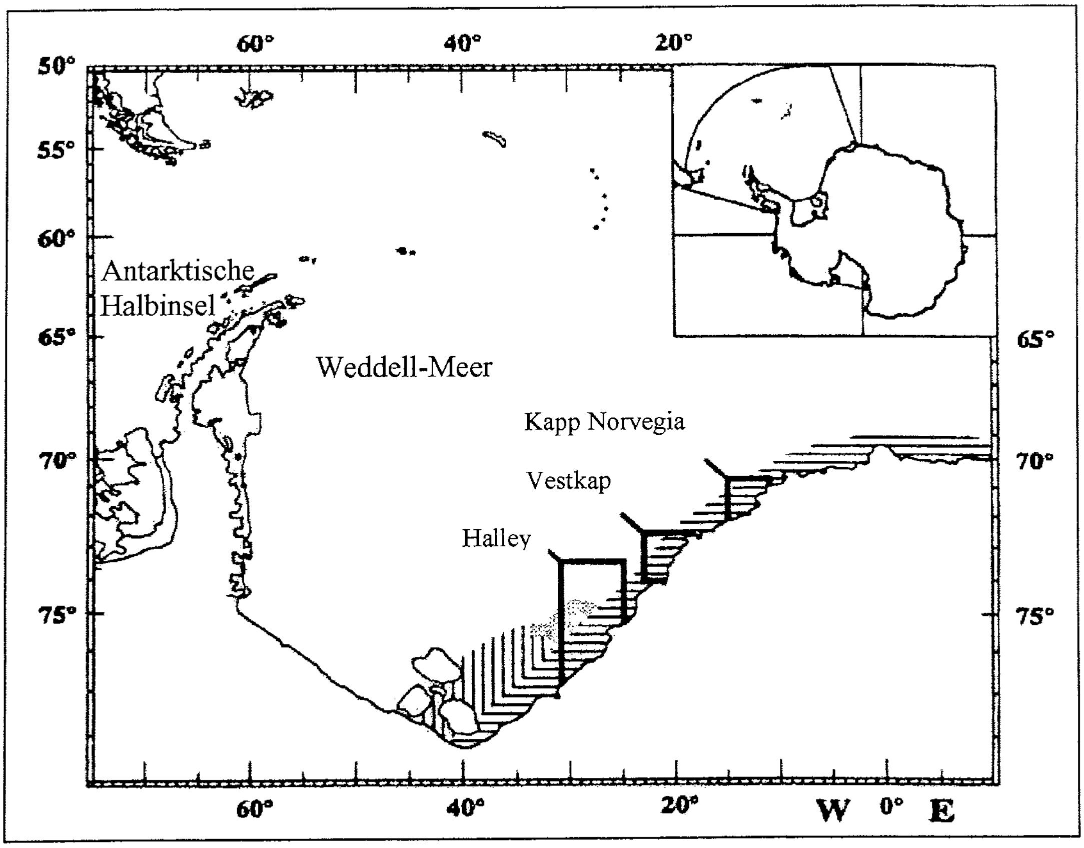

Abbildung 2. Deutsche Hauptuntersuchungsgebiete im Weddell-Meer und an der Antarktischen Halbinsel. Die Gebiete der Probennahme, auf denen viele Ergebnisse dieser Arbeit beruhen, befinden sich bei Kapp Norvegia und der Antarktischen Halbinsel (verändert nach Voß 1988).

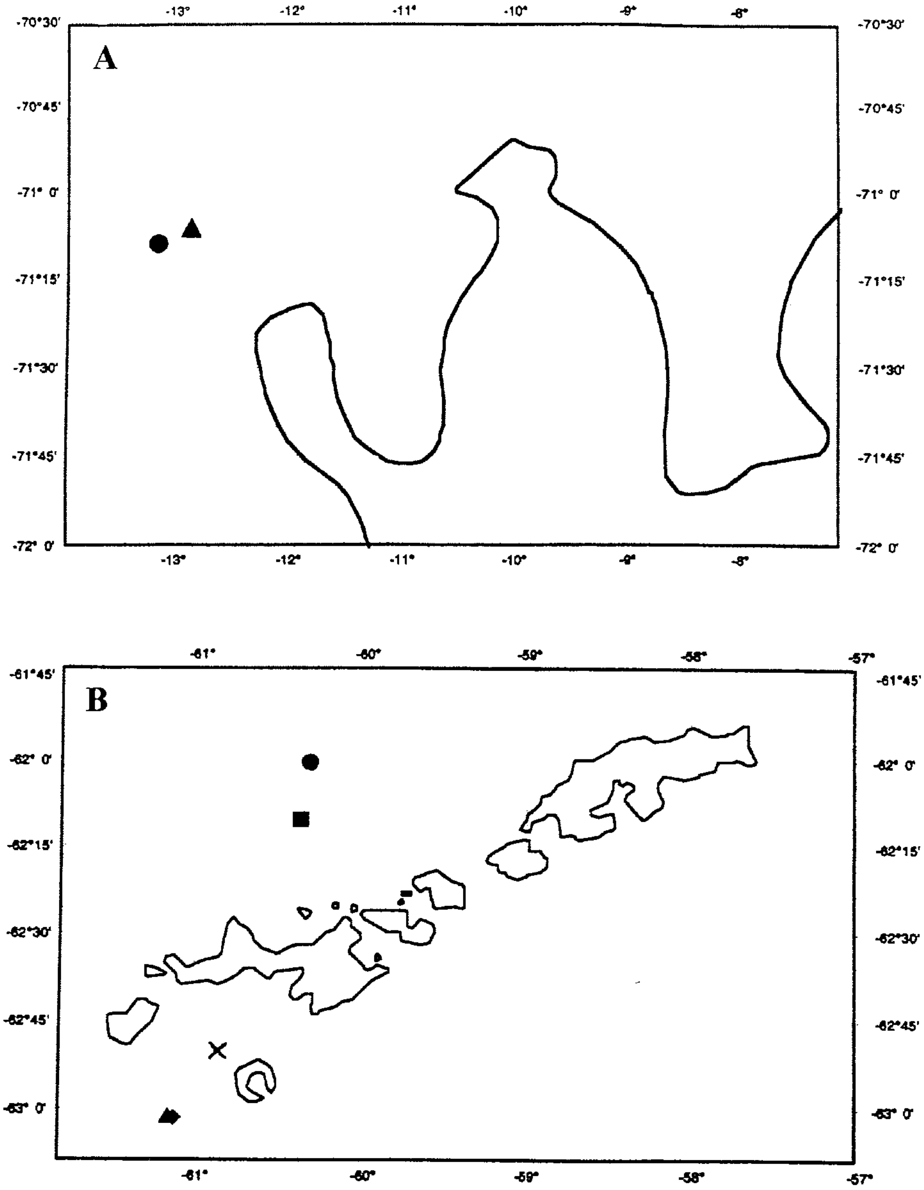

Abbildung 3. Stationen, die während ANT XVII-3 mit dem Epibenthosschlitten (EBS) beprobt wurden.
A vor Kapp Norvegia: ▲: Stat. 97-1, 743 m; ●: Stat. 138-1, 840 m
B Süd Shetland Inseln: ▲: Stat. 174-1, 365 m;◆ : Stat. 175-1, 305 m; **X**: Stat. 177-2, 206 m; ■: Stat. 180-2, 200 m; ●: Stat. 184-2, 399 m.

Veröffentlichung I

Low diversity of spongicolous Amphipoda (Crustacea) observed in the Antarctic autumn

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Abstract

Sponges represent a major component of the Antarctic zoobenthos. They are known to act as hosts for several invertebrates. In the present investigation a total of 1193 specimens of Amphipoda living in the sponge tissue of three species of Demospongiae were observed. The sponges were collected in the Weddell Sea and at the Antarctic Peninsula in April, during the Antarctic autumn 2000. The population density, species richness, composition, and reproductive biology of the spongicolous Amphipoda was studied. More than 40 individuals were collected per 1000 cm^3 sponge tissue. Females of all species had eggs or embryos in their marsupia. Interestingly, their young will be released - even though most of the studied species are filter feeders - in the Antarctic autumn and winter. Spongicolous inquiline Amphipoda may therefore not be influenced by the seasons as much as their free living relatives.

Keywords: Amphipoda, Antarctica, Demospongiae, reproduction, seasonality, symbiosis

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Introduction

Sponges are the major component of many Antarctic benthic communities (Barthel & Gutt 1992; Mc Clintock 1987; Cattaneo-Vietti et al. 1999). Several Antarctic species of Demospongiae are used by other organisms as hosts. Amphipoda (Crustacea) are known to be an important component of the fauna associated with sponges. Several studies have focused on ecological or taxonomic aspects of amphipods associated with sponges (e.g. Biernbaum 1981; Costello & Myers 1987; Serejo 1998), but little is known about amphipods associated with sponges from the Weddell Sea (Kunzmann 1996). Until now nothing was known about the species composition of associated amphipods and their reproduction during the Antarctic autumn.

The main objectives of this paper are to analyse the abundance and composition of the amphipod fauna in sponges and outline their reproductive biology in the Antarctic autumn.

Material & Methods

During the crüise ANT XVII-3 of RV "Polarstern" several sponges and sponge pieces were collected in April 2000 by means of a bottom trawl. Demospongiae with commensally living amphipods were sampled close to the German station Neumayer (station 119-1, 266 m, 70°50.40'S, 10°35.20'W & station 124-1, 269 m, 70°50.20'S, 10°34.89'W) and at the Antarctic Peninsula (station 166-1, 673 m, 63°01.20', 59°09.20'W).

The volume of the sponges was measured by the multiplication of length, height and width. The tissue was afterwards dissected with a pair of tweezers and rinsed with seawater to collect the amphipod infauna. The small sponge pieces were examined under a stereoscope for further remaining animals. The samples were sieved through a mesh size of 300 µm. Most animals were fixed in buffered formalin (4 %) and later transferred into ethanol (70 %).

For comparison of abundance on different sponge species the numbers of inhabiting individuals were calculated for 1000 cm^3 (=1 l). Only amphipods living within the sponge tissue, not outside on the surface, were considered. A length-frequency distribution was drawn up for the most common amphipod species. The body length of the Amphipoda was measured from the tip of the rostrum to the base of the telson. Additionally the length of the oostegite at pereiopod four was measured. Win STAT Version 3.1 was used for statistical analyses.

Of all spongicolous amphipod species the eggs / embryos were counted and measured. They were considered as brood size if the oostegites forming the brood pouch were not damaged.

The specimens are deposited in the Zoological Museum of Hamburg (ZMH K39818 - 39829) and at the Zoological Museum of Tromsø (TM 11024 - 11028).

Results

Population density : Different numbers of amphipods living within the sponge tissue were observed for the three species of Demospongiae (see table 1). Up to 25 pieces of sponge tissue were observed for each sponge species at each station. The richest amphipod density was found in *Jophon spatulatus* (Kirkpatrick,1907) at a depth of 269 m: more than 40 individuals per 1000 cm^3 tissue.

Species richness and composition : The 1193 spongicolous amphipods consisted of six species, belonging to five different families: *Colomastix fissilingua* (Schellenberg, 1926) (Colomastigidae), *Andaniotes linearis* (K.H. Barnard, 1932) (Stegocephalidae), *Stegosoladidus ingens* (Chevreux, 1906) (Stegocephalidae), *Pseudokoroga* n. sp. (Lysianassidae), *Leucothoe spinicarpa* (Abildgaard ,1789) (Leucothoidae) and *Polycheria antarctica* (Stebbing, 1875) (Dexaminidae).
The three sponge species were inhabited by different species percentages (Fig. 1). At Kapp Norvegia, Colomastigidae and Lysianassidae were the clearly dominant taxa living in the sponges *Jophon spatulatus* (Kirkpatrick, 1907) and *Clathria pauper* (Broenstedt, 1926). At the Antarctic Peninsula, Stegocephalidae constituted 98 % of the amphipod fauna inhabiting *Microxina simplex* (Topsent, 1916).

Reproductive biology : The length-frequency distribution was studied for the most common species *Colomastix fissilingua* (Fig. 2). This member of the family Colomastigidae shows a strong sexual dimorphism, the males have extremely enlarged second gnathopods. The males which in total were larger than the females show two size classes. No clearly separated size class can be seen among the females, their body length is distributed between 2,2 mm and 6,8 mm.
All except two females of *Colomastix fissilingua* had well-developed oostegites. The length of the oostegites measured at the fourth pereiopod showed a highly significant correlation to the body length, $p< 0,001$ (Fig. 3). Setae are grown when the oostegite reaches a size of 0,49 mm. No juveniles of *Colomastix fissilingua* were found in the sponge tissue. All individuals showed characters which Holman and Watling (1983) classified as distinguishing for adults,

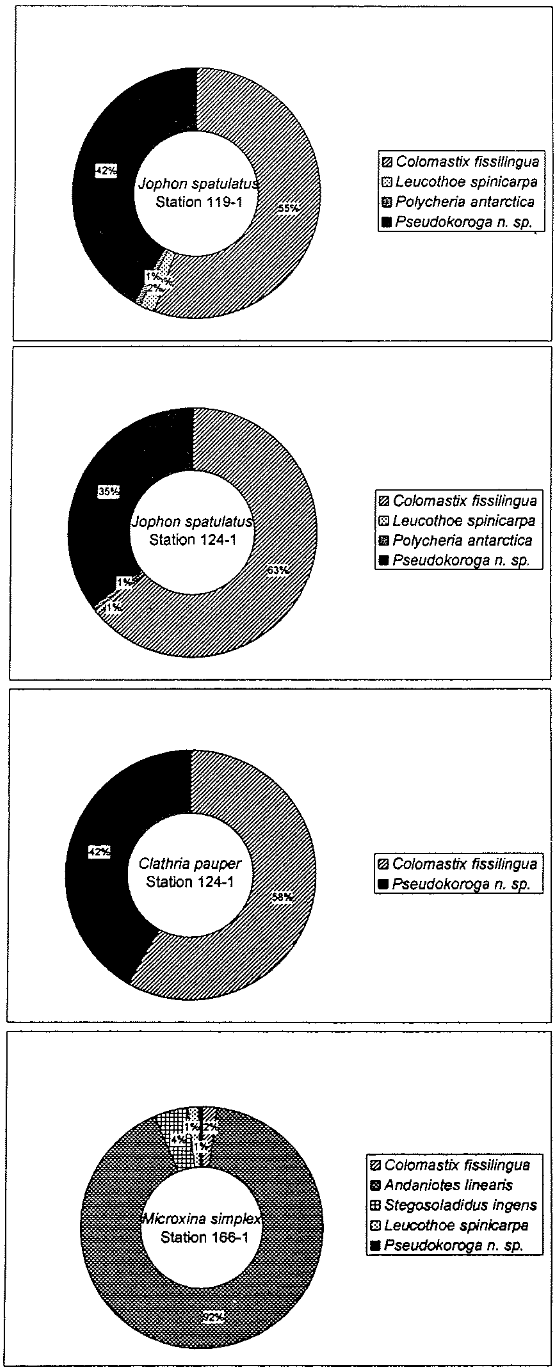

Fig. 1. The inquiline amphipods of different Demospongiae.

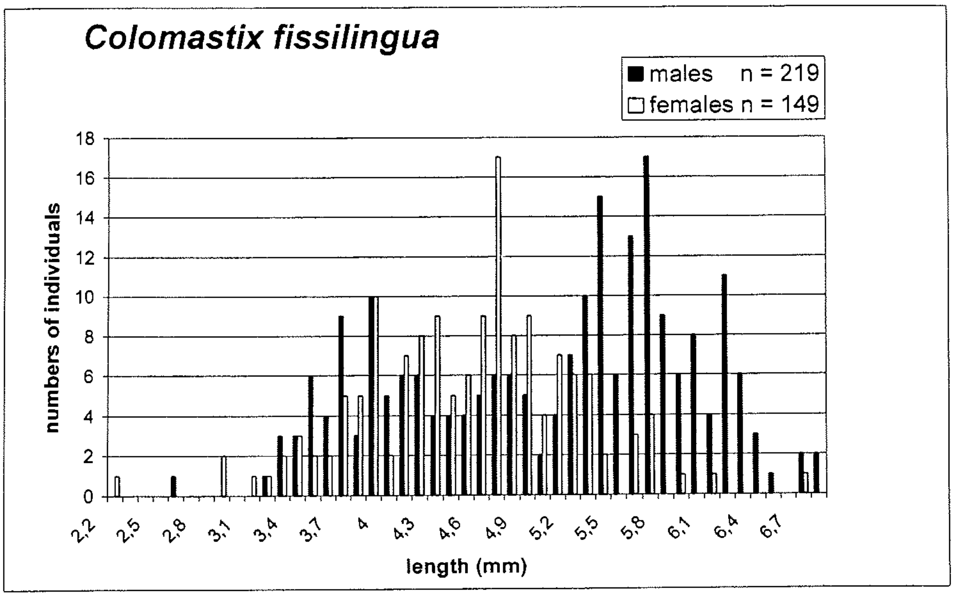

Fig. 2. Length-frequency distribution of *Colomastix fissilingua*.

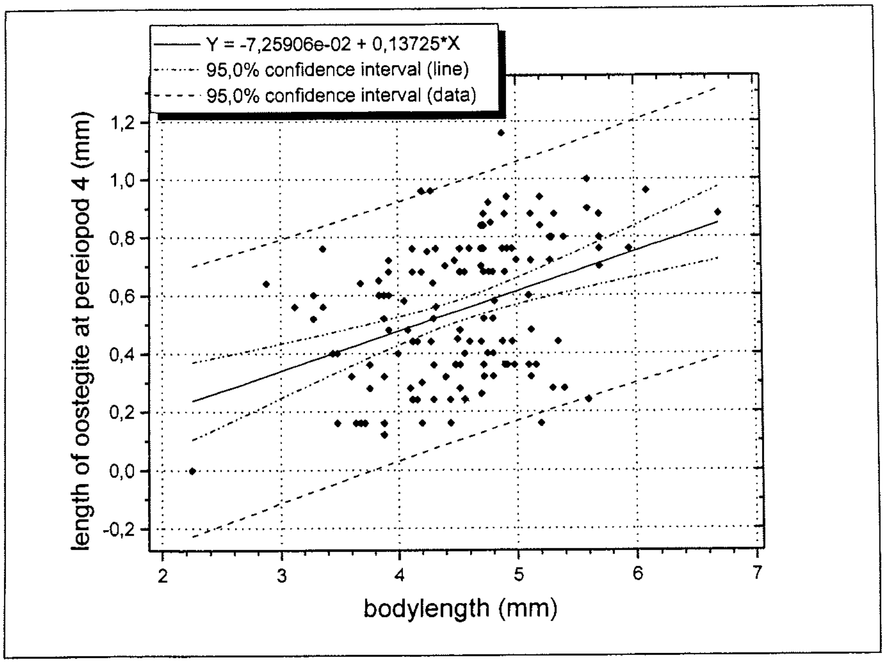

Fig. 3. Plot of oostegite length against body length of *Colomastix fissilingua*.

Tab. 1. Number of commensal amphipods per volume sponge .

Demospongiae	Station	Depth	Mean (Max.) number of Amphipoda per 1000 cm³ tissue
Jophon spatulatus	119-1	266 m	23 (39)
Jophon spatulatus	124-1	269 m	34 (43)
Clathria pauper	124-1	269 m	35 (35)
Microxina simplex	166-1	666 m	10 (13)

Tab. 2. Mean female length, embryo diameter and number of well developed embryos in the marsupia of two spongicolous Amphipoda.

Species	Mean female length (mm)	Mean embryo diameter (mm)	Mean brood size
Colomastix fissilingua	5	0,9	21
Andaniotes linearis	10	1,2	12

for example the length of the outer branch of the third uropod; in juveniles it does not reach 80 % of the length of the inner branch, in all studied species it does.

Some females of all four families Colomastigidae, Leucothoidae, Lysianassidae and Stegocephalidae carried eggs, embryos or young in their marsupia.

Discussion

Population density : Only very few quantitative studies of Amphipoda associated with sponges were completed in the past. Occasionally the number of amphipod species which inhabit a sponge were correlated to the weight of the sponge (Kamaltynov et al. 1993).

The spongicolous amphipod fauna which is associated with sponges is usually divided into two groups: species that are inquiline, and species that inhabit the outer surface of the sponge (Costello & Myers 1987). In the present study the latter are neglected because in samples taken with a bottom trawl it is impossible to distinguish benthic amphipods from those inhabiting the outer surface of the sponges. Kunzmann (1996) worked with two species of

Antarctic Demospongiae (*Mycale acerate* and *Tedania trirhaphis*) which were inhabited by even larger numbers of Amphipoda than *Jophon spatulatus*, but in that paper Amphipoda on the sponge surface were considered too, wherefore the estimated abundance might be unreliable.

Species richness and composition : While the abundance of spongicolous amphipods in Antarctic Demospongiae is very high, their diversity seems to be relatively low compared to species richness of spongicolous Amphipoda found in temperate climate. More than 15 species of amphipods were found in subtidal sponges in a shallow saltmarsh creek in South Carolina (Biernbaum 1981), but here again also individuals inhabiting the sponge surface were taken into consideration. Kamaltynov et al. (1993) list 13 species of Amphipoda associated with the sponge *Lubomirska baicalensis* in Lake Baikal, East Siberia, but only one species of these is considered infaunal. Kunzmann (1996) found a maximum of 7 amphipod species in one species of Antarctic Demospongiae: *Tedania oxeata*, but among these some individuals were only identified to family level and – as mentioned above- surface associated amphipods were also considered.

Reproductive biology : The fact that no juveniles of *Colomastix fissilingua* were found associated with any of the three sponge species and that nearly all females bear oostegites may lead to the assumption that this species inhabits sponges during its reproductive period only. At first glance a strong seasonality and a short individual life-span might explain the absence of juveniles, but many females had large oostegites with long setae, juveniles had been released from these marsupia shortly before and were not found in the sponge tissue. LeCroy (1995) proclaimed that there is no apparent reproductive season for the genus *Colomastix* as a whole, although not considering *Colomastix fissilingua*. There may be a constant level of reproduction throughout the year, at least in deeper waters. Here the seasonal fluctuations in water temperature are somewhat moderated, the increased protection and readily available food supply afforded by this habitat may facilitate the constant level of reproduction (LeCroy 1995). It has to be considered that LeCroy worked in the not very seasonal Gulf of Mexico. Focusing on Antarctica, ecological parameters such as ice covering in winter and phytoplankton spring bloom have to be thought of. Many Antarctic organisms are known to release their young during the Antarctic summer (e.g. White 1977). Oligotrophic conditions in the water column in Antarctic winter (Matsuda et al. 1987) could represent a metabolic constraint for filter-feeding organisms. Many sponges adopted their trophic strategy; they take up and preserve dense concentrations of diatoms to overcome severe food fluctuations typical for the Antarctic environment (Cattaneo-Vietti et al. 1999). While providing similar conditions throughout the year for their symbionts the sponge hosts buffer extreme seasonality of the Antarctic environment. Therefore spongicolous amphipods, especially inquilinous species, may not be influenced by the seasons as much as free living amphipods.

A correlation of body length and length of the right oostegite at pereiopod four was expected for *Colomastix fissilingua*, as it has been shown for other Antarctic amphipod species such as *Eusirus perdentatus* (Klages 1993). Surprisingly, some large females had very small oostegites without setae. Nevertheless the correlation of body length and length of the oostegite was highly significant. Sagar (1980) has observed that the oostegites of the Antarctic amphipod *Paramoera walkeri* (Stebbing, 1906) degenerate shortly after the release of young from the brood pouch. Maybe the oostegites of *Colomastix fissilingua* also degenerate and grow again after renewed fertilisation. However, it is also possible, and energetically logical, that females only grow their brood pouch once after being fertilised the first time.

Females of *Andaniotes linearis* are about twice as long as *Colomastix fissilingua* while they are carrying far less embryos of a similar size. While the shapes of the embryos are very similar, the shapes of the females differ. *Andaniotes linearis* is curled up as is typical for Stegocephalidae, whereas *Colomastix fissilingua* is stretched like a tanaidacean. Generally, amphipod lineages that are parasitic or obligate associates of other animals display consistently smaller body sizes than their closest free-living relatives (Poulin & Hamilton 1995).

It is remarkable that very different stages of development were found in different marsupia of one species in the Antarctic autumn. Some females apparently had just released their young because big oostegites with long setae were still present. The development time is not known for either *Colomastix fissilingua* or *Andaniotes linearis*, but for two members of Lysianassidae, *Tryphosella kerkueleni* and *Cheirimedon femoratus*, the mean development time is about 3 months (Bregazzi 1973). Assuming similar development times, it is most probable that the studied species release their young in the Antarctic winter.

Acknowledgements

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Veröffentlichung II

Epimeria reoproi n. sp., a new amphipod (Epimeriidae) from the Antarctic

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Abstract

The amphipod *Epimeria reoproi* n. sp., collected from the Antarctic Ocean, is described in detail. It has a smooth anterior pereon and a carina that begins on pereonite 5. This is similar to *Epimeria vaderi* Coleman, 1998 and to a specimen that has been described by Andres (1985). The carinal processes increase in size on the pleon in posterior direction. The head bears a strongly flexed rostrum. Pereiopod coxa 4 is characteristically shaped, it is drawn out into a long, posteriorly flexed, acute apex. The posteroventral angles of the bases of pereiopods 5-6 are acutely produced.

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Introduction

During an expedition of the R/V "Polarstern", cruise ANT XVII-3 to the Weddell Sea and the Antarctic Peninsula, many amphipods were collected by various types of gears. Compared to previous expeditions, the Epimeriidae and Iphimediidae were not the dominant families of gammaridean Amphipoda. Nevertheless, in one of the dredge samples a interesting species of epimeriid amphipod was collected that turned out to be new to science, and that is described in detail herein.

Material & Methods

The animals were fixed in 70% ethanol, transferred into glycerol for study, and drawn with a camera lucida mounted on a Leica-Wild M8 dissecting microscope. The specimens were dissected and appendages and mouthparts transferred onto slides in glycerol, and drawn under a Leica DMLB and a Dialux Leitz Wetzlar compound microscope using a camera lucida, as well. The type material of the new species is deposited in the Zoological Institute and Zoological Museum of Hamburg.

SYSTEMATICS

Epimeria reoproi n. sp.

(fig. 1-5)

Material examined - Holotype, a specimen of 20 mm (without female or male sexual characters expressed). "Polarstern" ANT XVII-3, Sta. 171-3: 63°00.10'S 60°31.00'W, 29 April 2000, leg. M. Rauschert, depth 48 m, gear: dredge, mesh size 1 mm. ZMH K 38976. Two paratypes, 9 mm and 16 mm long, ZMH K 38977.

Etymology - The specific name is dedicated to a product of the Lilly company, i. e.: Reopro, an inhibitor of platelet aggregation. The epitheton is a norm in the genitive singular.

Description - Head with strongly flexed rostrum (fig. 1a), reaching distal margin of the first peduncular article of antenna 1; eyes large, round, rather prominent. Pereonite 1 less than half the length of the head; pereonite 2 shortest; pereonite 3 somewhat shorter than 1; pereonites 4-6 subequal in length, with subacute posteroventral angles; pereonite 7 slightly longer than 6; pleonite 1 and 3 shorter than 2 (fig. 1a). Pereonites 1-4 dorsally smooth, pereonites 5-7 with dorsal teeth increasing in size; pleonites 1-3 with strongly posteriorly curved dorsal teeth (fig. 1a). Posterolateral margin of pereonite 6 roundly produced, that of pereonite 7 with one tooth on both sides, and

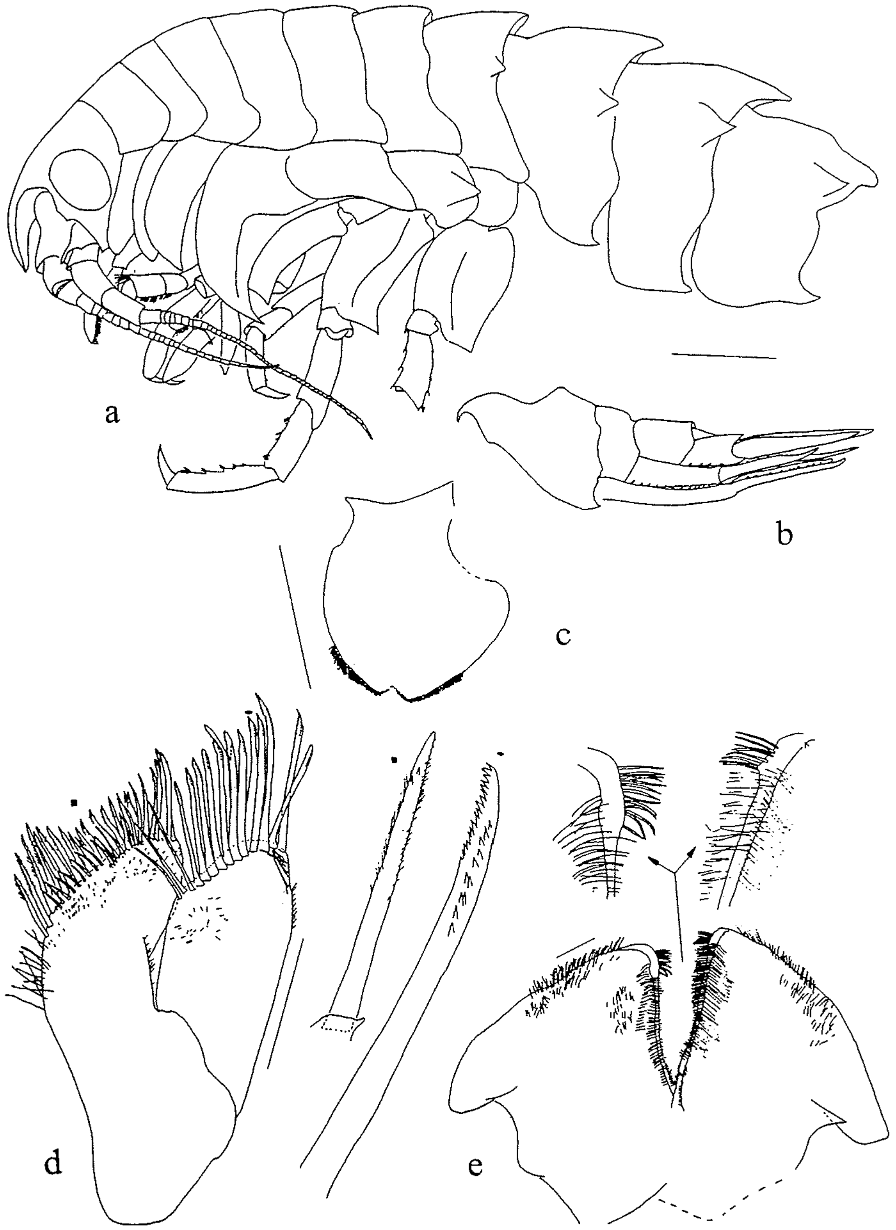

Fig. 1. *Epimeria reoproi* n. sp., holotype, 20 mm. a, lateral habitus without urosome; b, urosomite 1-3 with uropods, left lateral aspect.; c, labrum; d, maxilla 2, second row of shorter setae on outer plate omitted; e, lower lip. Scale bars: a-c, 2 mm; d, 500 µm, e, 200 µm.

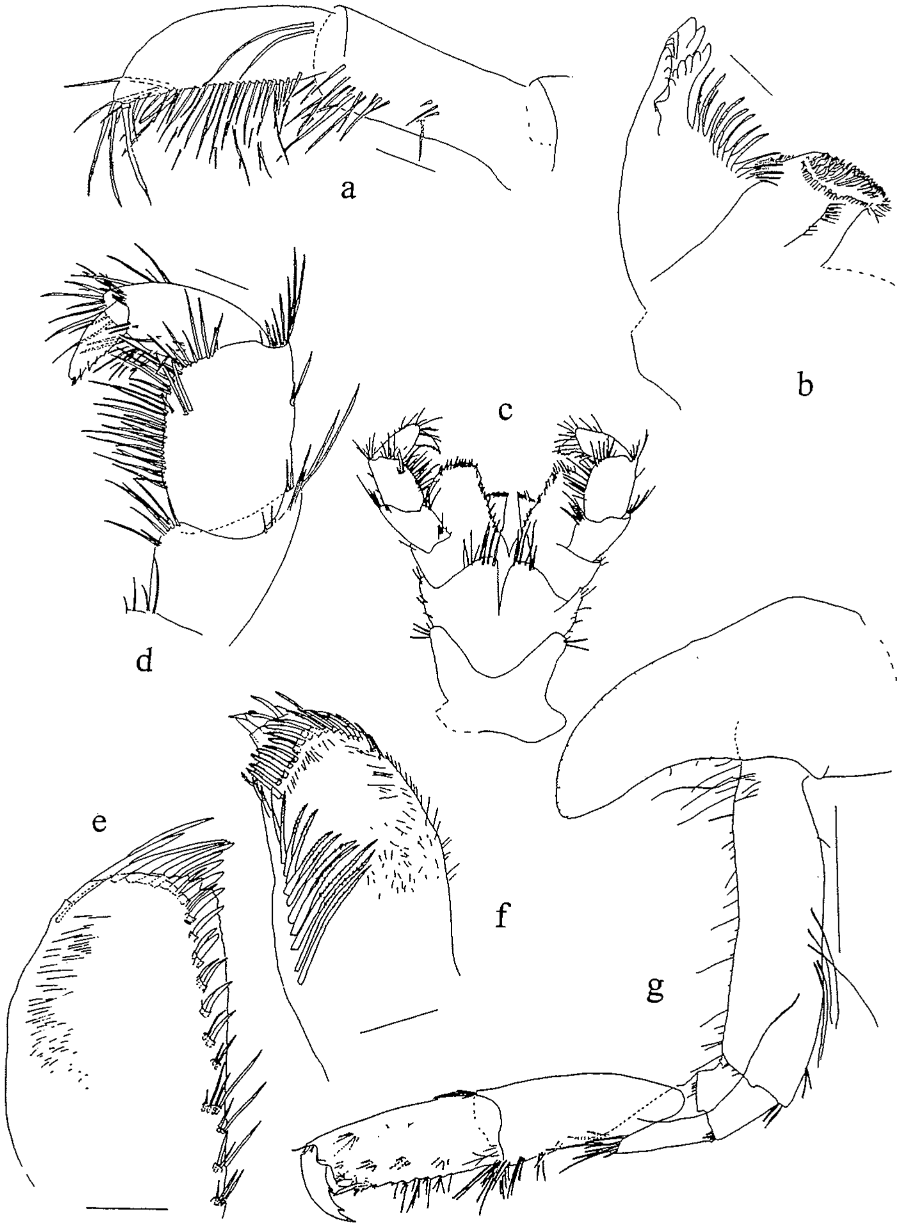

Fig. 2. *Epimeria reoproi* n. sp., holotype, 20 mm. a, mandibular palp; b, mandibular body; c, maxillipeds; d, right maxilliped palp, anterior aspect; e, left outer maxilliped plate, anterior aspect; f, left inner maxilliped plate, anterior aspect; g, pereopod 2. Scale bars: a, b, d-f, 200 µm; g, 1 mm.

similar but larger teeth on pleonites 1-3 (fig. 1a). Epimeral plates with posterolateral rounded protrusion and posteroventral acutely produced angles. Urosomite 1 (fig. 1b) with shallow dorsal elevation; urosomites 2 shortest; urosomite 2 and 3 smooth.

Antenna 1 (fig. 3b): peduncular article 1 stout, with many plumose setae (see detail in fig. 3b), distal margin with 3 short processes; article 2 less than half the length of article 1, distal margin with 2 short processes (see detail); article 3 shortest with scale-like accessory flagellum distally; flagellum consisting of 26 articles.

Antenna 2 (fig. 3d) longer than antenna 1; peduncular article 1 scale-like; article 2 with short nephridial cone (see detail of peduncle) and acute distal margin; articles 4 and 5 subequal; flagellum with 37 articles.

Labrum (fig. 1c) with distal notch and short, hair-like setae on distal margin.

Mandible (fig. 2a, b): incisor and lacinia mobilis strongly dentate; molar produced and triturative; palp 3-articulate (fig. 2a), article 2 longest with group of setae on posterior margin; article 3 densely setose posteromarginally, with long, stout setae distally.

Lower lip (hypopharynx) (fig. 1e) with wide lobes and groups of setae on distomedial angles (see detail in fig. 1e), hypopharyngeal gap narrow.

Maxilla 1 (fig. 3c): inner lobe wide, tapering distally, with 10 stout setae; outer lobe with groups of setae proximolaterally, distal margin oblique with 13 medially serrate setae; palp 2-articulate, surpassing outer lobe, proximal article short; distal article slightly curved medially, with slender setae on distomedial margin and stout setae distally.

Maxilla 2 (fig. 1d) with long, distally serrate setae on outer plate; inner plate with shorter, plumose distal setae (see detail).

Maxilliped (fig. 2c-f) basis with long setae on distal margin; outer plate wide, with setation as in fig. 2e; inner plate with 3 nodular setae and a row of long, plumose setae on medial, anterior face (fig. 2f). Maxillipedal palp 4-articulate (fig. 2d) medial margin strongly setose; article 1 distally expanded; article 2 subrectangular, wide; article 3 subelliptical; article 4 with serrate inner margin.

Pereopod (gnathopod) 1 (fig. 4c, d): coxa tapering distally, anterior margin sinuous; basis with slightly convex posterior margin, anteriorly straight; ischium shortest; merus slightly tapering distally, with group of setae distally; carpus expanded distally, wider than propodus; palm (fig. 4d) shorter than dactylus length; inner curvature of dactylus with traces of serration.

Pereopod (gnathopod) 2 (fig. 2g) longer than pereopod 1; coxa convex anteromarginally, concave posteromarginally, slightly tapering distally, apex rounded; basis slightly

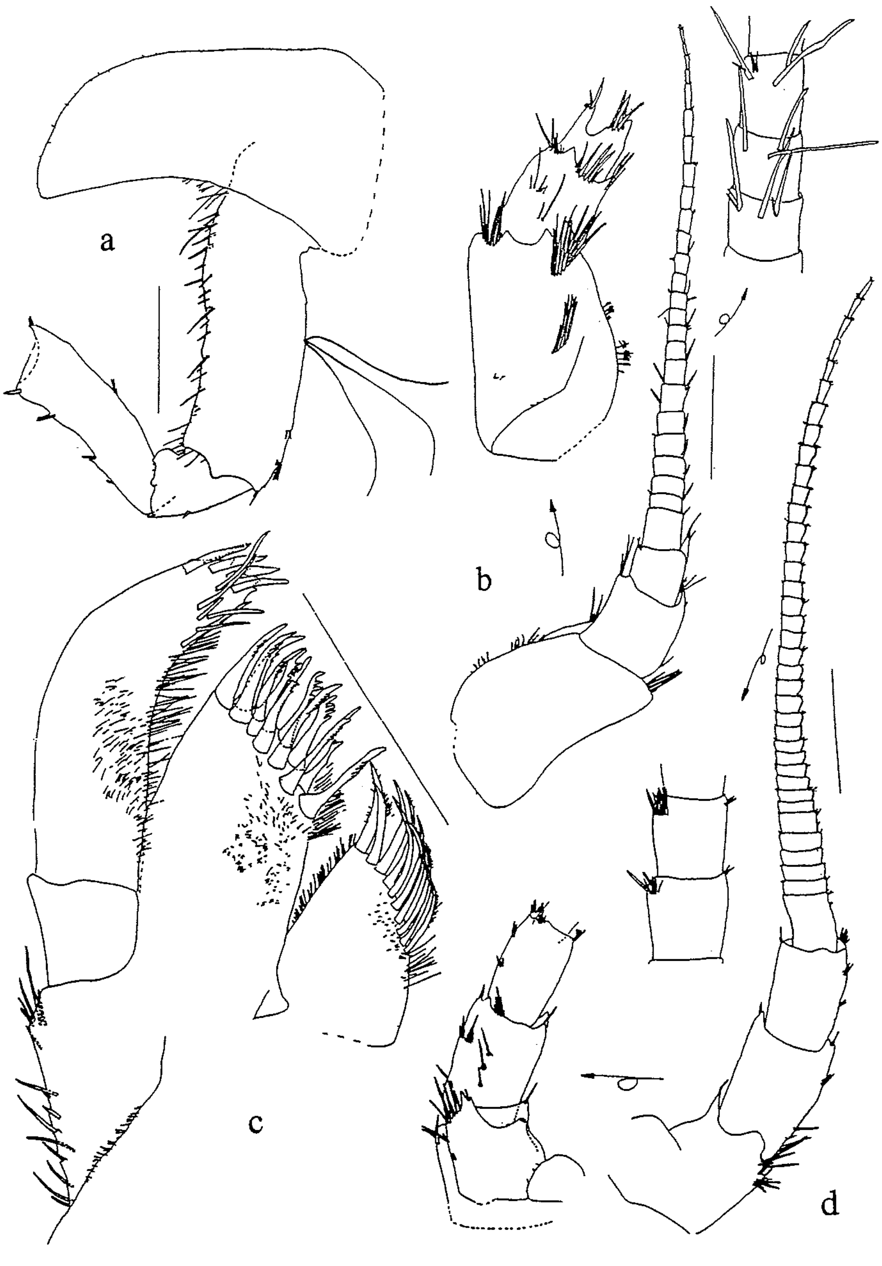

Fig. 3. *Epimeria reoproi* n. sp., holotype, 20 mm. a, pereopod 3, carpus to dactylus missing; **b**, antenna 1; c, maxilla 1, apical margin of outer plate hair-like setae omitted; d, antenna 2. Scale bars: a, b, d, 1 mm; c, 500 µm.

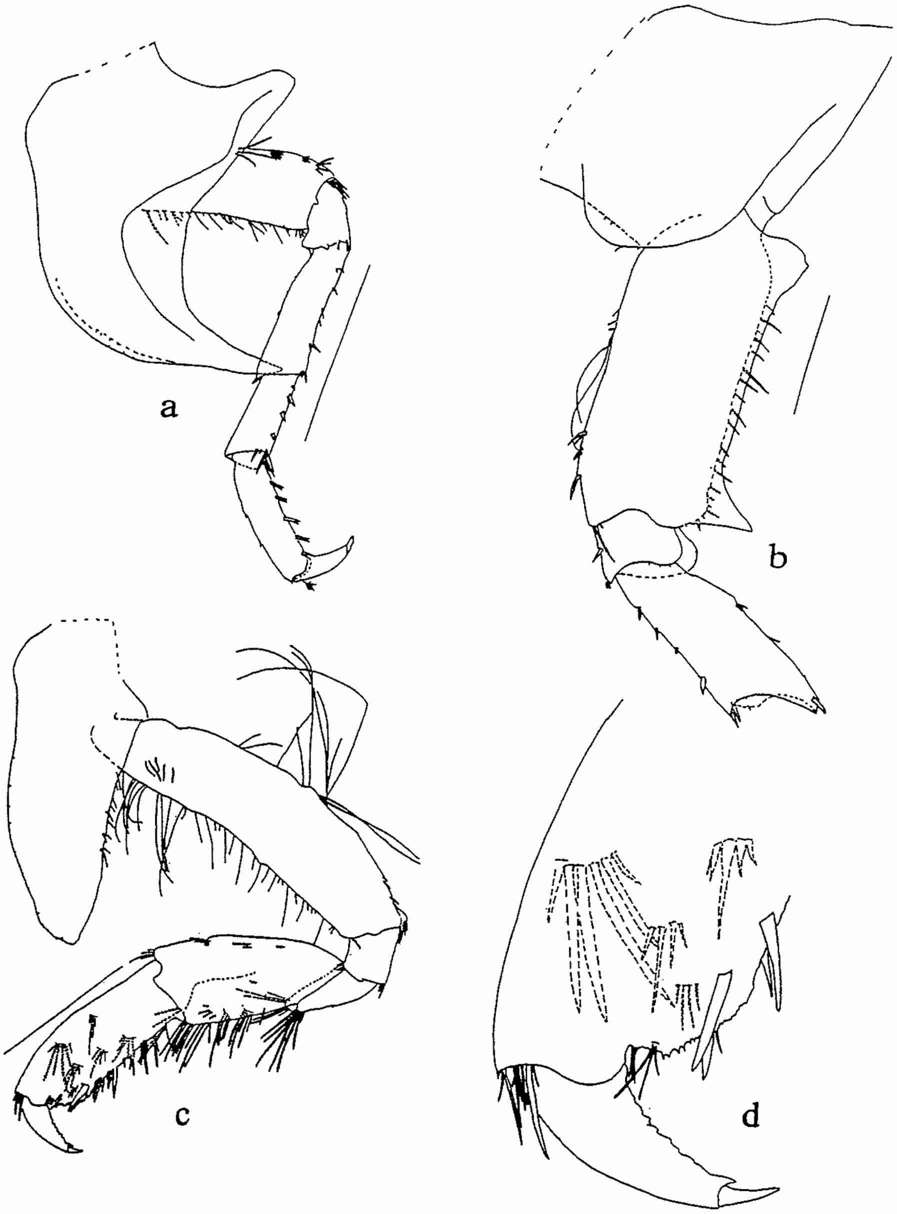

Fig. 4. *Epimeria reoproi* n. sp., holotype, 20 mm. a, pereopod 4; b, pereopod 5, carpus to dactylus missing; c, pereopod 1; d, detail of pereopod 1, palm and dactylus. Scale bars: a, 2 mm; b, c, 1 mm.

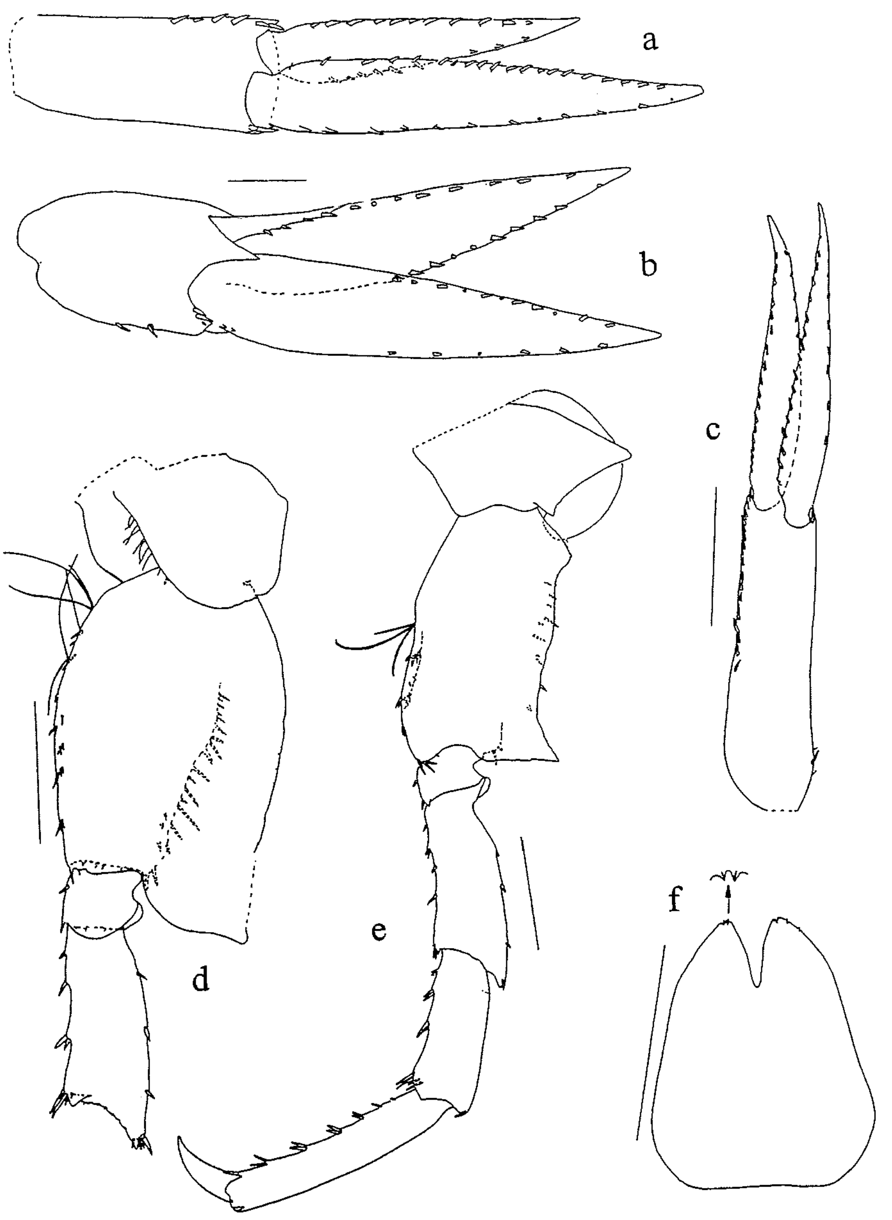

Fig. 5. *Epimeria reoproi* n. sp., holotype, 20 mm. a, uropod 2; b, uropod 3; c, uropod 1; d, pereopod 7; e, pereopod 6; f, telson. Scale bars: a, b, 500 µm; c-f, 1 mm.

expanded distally, apical margin oblique; ischium weakly excavate anteriorly, straight posteromarginally; merus tapering distally, with group of apical setae; carpus and propodus subequal in length and width; palm shorter than dactylus; inner curvature of dactylus with traces of serration.

Pereopod 3 (fig. 3a): coxa subequal in shape to that of pereopod 2, but wider; basis sinuous anteromarginally, setose, convex posteromarginally, with some very long, slender setae; ischium excavate anteriorly; merus slightly expanded distally and weakly drawn out anterodistally; carpus to dactylus missing.

Pereopod 4 (fig. 4a): coxa with ridge on lateral face, anteriorly strongly convex, apex drawn out into long, pointed, posteriorly curved process, proximomarginally on posterior side with rounded lobe; ischium and merus as in pereopod 3; carpus 60% of merus in length; propodus subequal to merus; dactylus weakly curved, stout.

Pereopod 5 (fig. 4b) coxa wider than long, drawn out into long, acute process, anteriorly rounded; basis weakly convex, posterior margin with proximal rounded process and distal pointed process, distal margin sinuous; ischium posteromarginally excavate; merus weakly expanded distally, drawn out into pointed process posterodistally, carpus to dactylus missing.

Pereopod 6 (fig. 5e) coxa truncate anteriorly, rounded posteriorly, large tooth on face of coxa; posterior margin similar to that of pereopod 5, but less deeply excavate, anterior margin sinuous; ischium and merus as in pereopod 5; carpus weakly expanded distally, length 92 % of merus; propodus length 134% of merus; dactylus weakly curved and stout.

Pereopod 7 (fig. 5d) coxa wider than long, truncate posteromarginally; basis convex anteromarginally, posterior margina weakly sinuous, posteroventrally subacutely lobate; ischium and merus as for pereopod 6; carpus to dactylus missing.

Uropod 1 (fig. 5c) peduncle subequal to outer ramus, outer ramus somewhat shorter than inner ramus.

Uropod 2 (fig. 5a) peduncle shorter than outer ramus.

Uropod 3 (fig. 5b) peduncle short, with pointed process on apical margin, rami subequal in length.

Telson (fig. 5 f) slightly tapering distally, notched at nearly ¼ of its length.

Discussion

The new species bears some superficial resemblance to *Metepimeria acanthurus*

Schellenberg, 1931, which has a similar dorsal armature. However, compared with the new species the maxillipedal palp of *M. acanthurus* is only 3-articulate (vs. 4-articulate), coxal plate 4 is truncate apically (vs. acutely pointed), and the rostrum is straight (vs strongly flexed).

Due to the 4-articulate maxillipedal palp the new species is classified as an *Epimeria,* however. Within this genus, several species are similarly smooth anterodorsally, and carinate on the posterior pereonites and/or pleonites. *Epimeria cora* J.L. Barnard, 1971, *E. cornigera* (Fabricius, 1779), *E. tuberculata* G.O. Sars, 1895, and *E. glaucosa* J.L. Barnard, 1961, have slender bases 5-7 which are not widened apically (vs. drawn out to posterodistal processes). None of these species, however, occur in the Antarctic ocean.

The new species has to be distinguished from previously described Antarctic species of *Epimeria* with a smooth anterior pereon: *Epimeria annabellae* Coleman, 1994, *E. heldi* Coleman, 1998, *E. monodon* Stephensen, 1947, *E. puncticulata* K.H. Barnard, 1930, *E. robusta* K.H. Barnard, 1930, and *E. vaderi* Coleman, 1998.

In *E. annabellae*, only pleonite 3 and urosomite 1 are carinate, coxa 4 is much wider and less pointed, coxae 5-6 are posteriorly rounded, and bases 5-6 are not cuspidate.

E. heldi has a rounded coxa 3 (vs. pointed) while coxa 4 is distally truncate (vs. pointed). In contrast to the new species *E. heldi* has slender bases 5-7.

E. monodon has a carina on pleonite 3 only.

E. puncticulata has inconspicuous carinae on the pleosome, while also additional teeth, accompanying the carinae on the pleon are wanting (vs. strong carina on pereonite 5 to urosomite 1 with lateral teeth on pleosome). *E. puncticulata* has coxa 4 apically rounded with a rather straight posterior margin (vs. strongly pointed and excavated), and coxae 5-6 rounded posterioly (vs. pointed).

E. robusta has a strongly widened coxa 4 with a convex posteroventral margin (vs. narrower, concave margin and strongly pointed apex) and the posterior margins of bases 5-6 are both deeply notched and have a pointed, ventrally directed lobe and narrow apices (vs. excavate with distal pointed process).

Epimeria vaderi and *Epimeria* sp. (cf. Andres, 1985) resemble the new species most closely. The differences between these three species are shown in table I. The result of this comparison is, that *Epimeria reoproi* n. sp. and *Epimeria* sp. (cf. Andres, 1985) are most similar. It is conceivable that *Epimeria* sp. (cf. Andres, 1985) is a subadult of *E. reoproi* n. sp. Although the male sex was determined in Andres′ (1985) specimen, it appeared to be impossible to sex the new species, although our specimens are about 3 times as large as Andres′ animal, considering their total length.

Tab. 1. Morphological differences between *Epimeria reoproi* n. sp., *Epimeria vaderi* Coleman, 1998 and *Epimeria* sp. (cf. Andres, 1985)

Characters	*Epimeria reoproi* n. sp.	*Epimeria vaderi*	*Epimeria* sp
Rostrum	Strongly flexed, reaching distal margin of 1st peduncular article of antenna 1	Straight, reaching distal margin of 1st peduncular article of antenna 1	Straight, surpassing distal margin of 1st peduncular article of antenna 1
Dorsolateral teeth on pleonites 1-2 (on both sides of carina)	Single tooth	Two teeth	Single tooth
Posteroventral angles of epimera1-3	Pointed and strongly produced	Pointed, but weakly produced	Pointed, but weakly produced
Coxa 1	Rounded	Pointed	Rounded
Coxa 3	Wide, with pointed apex	Wide with pointed apex	Narrow, angular apically
Coxa 4	Deeply excavate, apex acutely drawn out and curved posteriorly	Not deeply excavate apex moderately drawn out, angular	Deeply excavate, apex acutely drawn out and curved posteriorly
Posteroventral angle of basis 5-6	Strongly pointed	Strongly pointed	Less pointed
Posterior margin of basis 5-6	Deeply excavate	Deeply excavate	Rather straight
Telson	With v-shaped notch	With v-shaped notch	With u-shaped notch

Acknowledgements

The authors are grateful to Dr. Martin Rauschert who provided us with the material for this study. This work was supported by the Studienstiftung des deutschen Volkes and DFG grant Br 1121 / 18-1. This article is based on a doctoral study by Anne-Nina Lörz in the Faculty of Biology, University of Hamburg.

Veröffentlichung III

Description and ecology of a spongicolous lysianassoid amphipod (Crustacea) from Antarctica

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Abstract

In the canals of three species of Antarctic Demospongiae a new species of Lysianassoidea (Crustacea: Amphipoda) was found. The new species *Pseudokoroga spongiophila* is described, its ecology is briefly summarised. While the superfamily is represented in the Southern Ocean by 146 species, belonging to 54 genera, *Pseudokoroga spongiophila* n.sp. is one of the rare species symbiontically living in sponges. Up to 24 individuals were collected in 1000 cm^3 of tissue of the host Demospongiae *Jophon spatulatus* (Kirkpatrick, 1907).

Keywords: Amphipoda, Lysianassoidea, Antarctic, taxonomy, symbiosis, Demospongiae, *Pseudokoroga spongiophila* n. sp.

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Introduction

During the Antarctic autumn (May 2000) the benthic communities of the continental shelf of the Eastern Weddell Sea and the Antarctic Peninsula were investigated.

Within these ecosystems peracarid crustaceans are considered to be the most speciose taxon (De Broyer and Jazdzewski, 1996). Among crustaceans, amphipods represent the richest group, with 376 species of Amphipoda inhabiting the West Antarctic and 222 species in the East Antarctic region (De Broyer and Rauschert, 1999). Sponges, on the other hand, are also a major component of many Antarctic communities (e.g. Barthel and Gutt, 1992; Cattaneo-Vietti *et al.*, 1999). Only a few studies have focused on ecological or taxonomic aspects of Amphipoda associated with sponges in the Weddell Sea (Kunzmann, 1996; De Broyer *et al.*, 2001; Lörz, 2001).

The aim of this paper is to describe a spongicolous species of lysianassoid amphipod, *Pseudokoroga spongiophili* n. sp., which is new to science although it occurs in high numbers in the Demospongiae *Jophon spatulatus* (Kirkpatrick, 1907) and *Clathria pauper* (Broenstedt, 1926). In addition, an outline of its ecology is given.

Material and methods

During the RV *Polarstern* expedition ANT XVII-3 (EASIZ III) (Arntz and Brey, 2001) sponges and sponge pieces were collected by means of a bottom trawl. Commensal amphipods of Demospongiae were collected at three stations:
Sta. 119-1; 266 m; 70°50,40'S, 10°35,20'W; 7 April 2000
Sta. 124-1; 269 m; 70°50,40'S, 10°35,10'W; 9 April 2000
Sta. 166-1; 666 m; 63°01,90'S, 59°10,00'W; 28 April 2000.
The volume of sponges was calculated by multiplying length, height and width. Sponge tissue was dissected with a pair of tweezers and rinsed in sea water to collect the amphipod infauna. The small sponge pieces were examined under a stereoscope for remaining animals. The samples were sieved through a mesh of 300 µm. Specimens of *Pseudokoroga spongiophila* were fixed in buffered formalin (4%) and later transferred into ethanol (70%) or immediately transferred into pre-chilled 96 % ethanol for molecular studies.

For comparison of abundance in different sponge species the numbers of inhabiting individuals were calculated for 1 litre (= 1000 cm^3). Only amphipods living within the sponge tissue, not on the external surface, were considered.

All dissected appendages were mounted in polyvinyl-lactophenol, stained with rose-bengal. The appendages and the habitus drawings were made using a Leitz DIAPLAN microscope. Classification of setae follows Lowry and Stoddart (1995).

This taxonomic work takes place in the framework of a general revision of the Southern Ocean amphipod fauna, undertaken by the "Antarctic Amphipodologist Network" formed by G.M. Alonso (Buenos Aires), H. G. Andres (Hamburg), D. Bellan-Santini (Marseille), J. Berge (Tromsoe), C.O. Coleman (Berlin), K. E. Conlan (Ottawa), C. De Broyer, co-ordinator (Bruxelles), J. M. Guerra-Garcia (Sevilla), E. A. Hendrycks (Ottawa), T. Krapp-Schickel (Bonn), K. Jazdzewski (Lodz), M. Rauschert (Berlin), I. Takeuchi (Tokyo) and M.H. Thurston (Southampton). The taxonomic and distributional data of the new species will be recorded in the "Biodiversity Reference Centre for Antarctic Amphipoda ANT'PHIPODA" at the Royal Belgian Institute of Natural Sciences in Brussels (www.naturalsciences.be/amphi).

List of abbreviations used in figures:
A1: Antenna 1; G1: Gnathopod 1; G2: Gnathopod 2; LL: Labrum; lMd: left Mandible; rMd: right Mandible; Mx1: Maxilla 1; Mx2: Maxilla 2; Mxp: Maxilliped; P3: Pereopod 3; P4: Pereopod 4; P5: Pereopod 5; P6: Pereopod 6; P7: Pereopod 7; Pl: Pleopod; T: Telson; U1: Uropod 1; U2: Uropod 2; U3: Uropod3.

Description

Pseudokoroga spongiophila sp. nov.

(figures 1-5)

Holotype: ovigerous female 5.4 mm, Zoological Museum Hamburg (ZMH K 39943), *Polarstern* ANT XVII-3, St. 124-1, symbiotic in *Jophon spatulatus* (Kirkpatrick, 1907)
Paratypes: males (3.5 - 5.15 mm) and females (3.0- 5.16 mm) ZMH K39943-K 39946; IRScNB Brussels and ZMB Berlin

Distribution: eastern Weddell Sea and Bransfield Strait, 266-666m

Diagnosis: lateral cephalic lobe regularly rounded. Eyes suboval. Peduncle of antenna 1 elongated, first article of flagellum short. Dorsal length ratio head: pereonite 1 about 1:1. Epimeral plates posterodistal angle rounded. Gnathopod 1 with tubercle in the middle of the palm. Urosomite 1 with a prominent rounded dorsal hump.

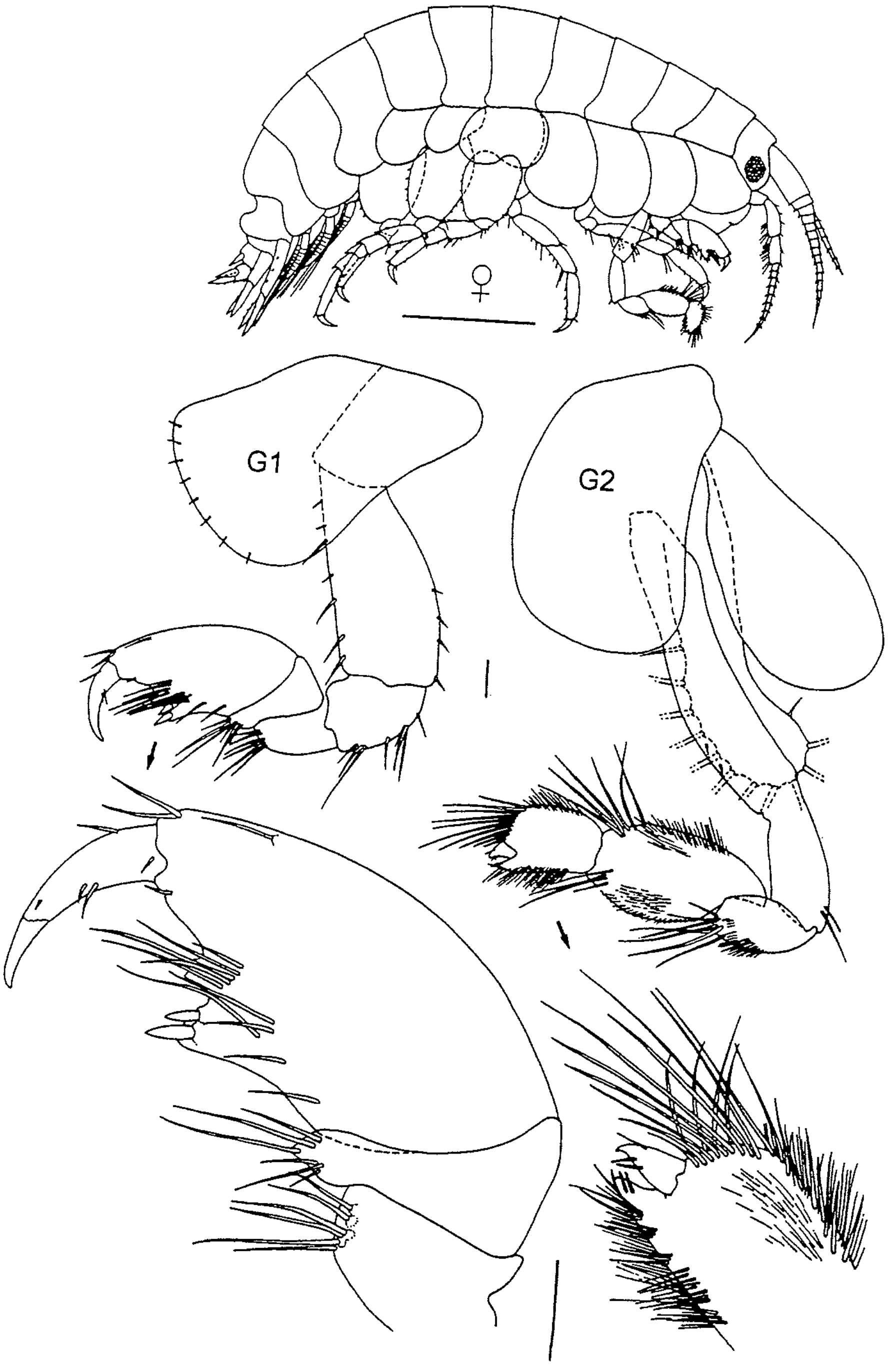

Fig. 1. *Pseudokoroga spongiophila* n. sp. Holotype female, 5.4 mm. Scale bars: habitus: 1 mm, gnathopods: 100 µm.

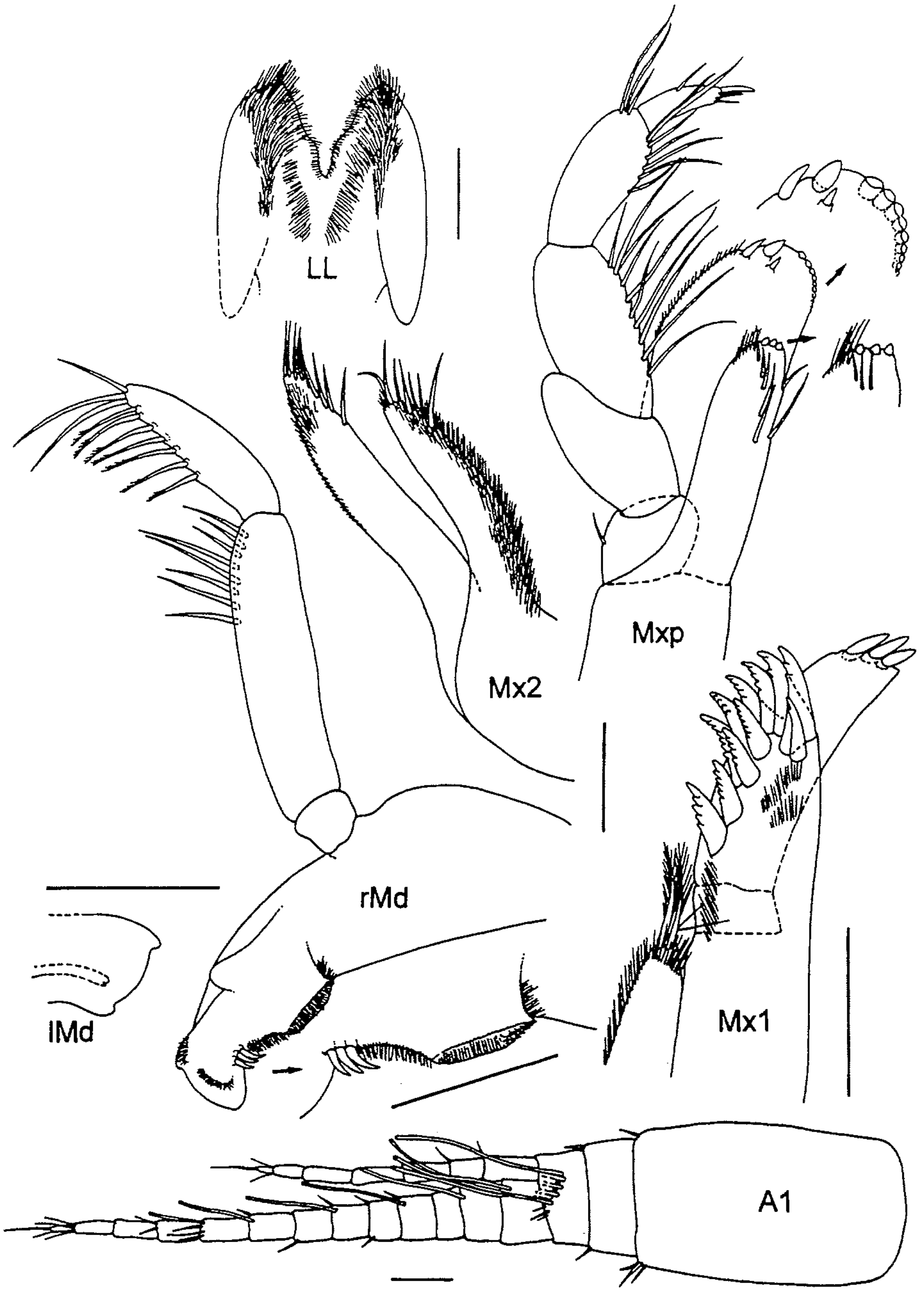

Fig. 2. *Pseudokoroga spongiophila* n. sp. Holotype female, 5.4 mm. Scale bars: 100 µm.

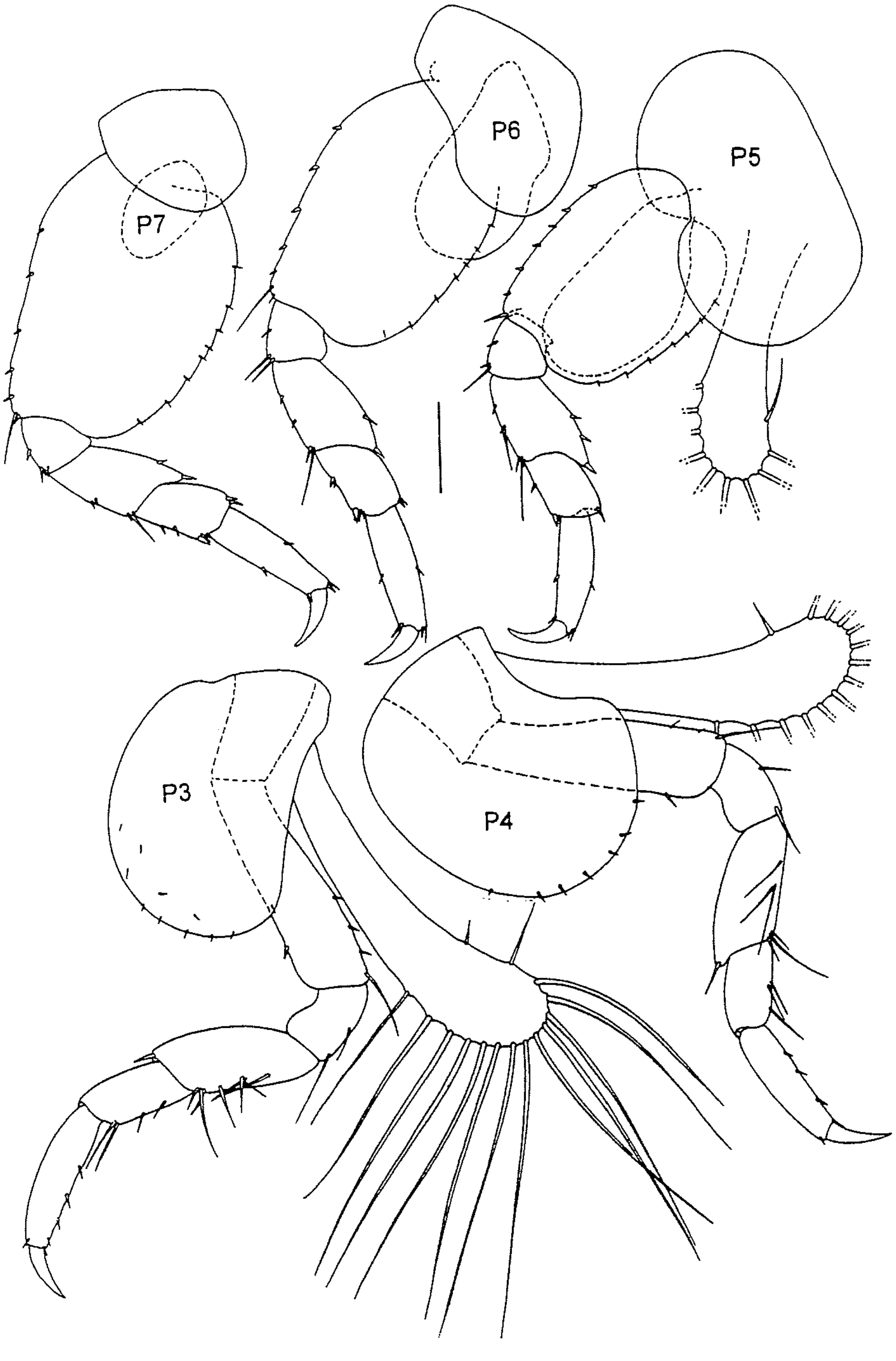

Fig. 3. *Pseudokoroga spongiophila* n. sp. Holotype female, 5.4 mm. Scale bars: 100 µm.

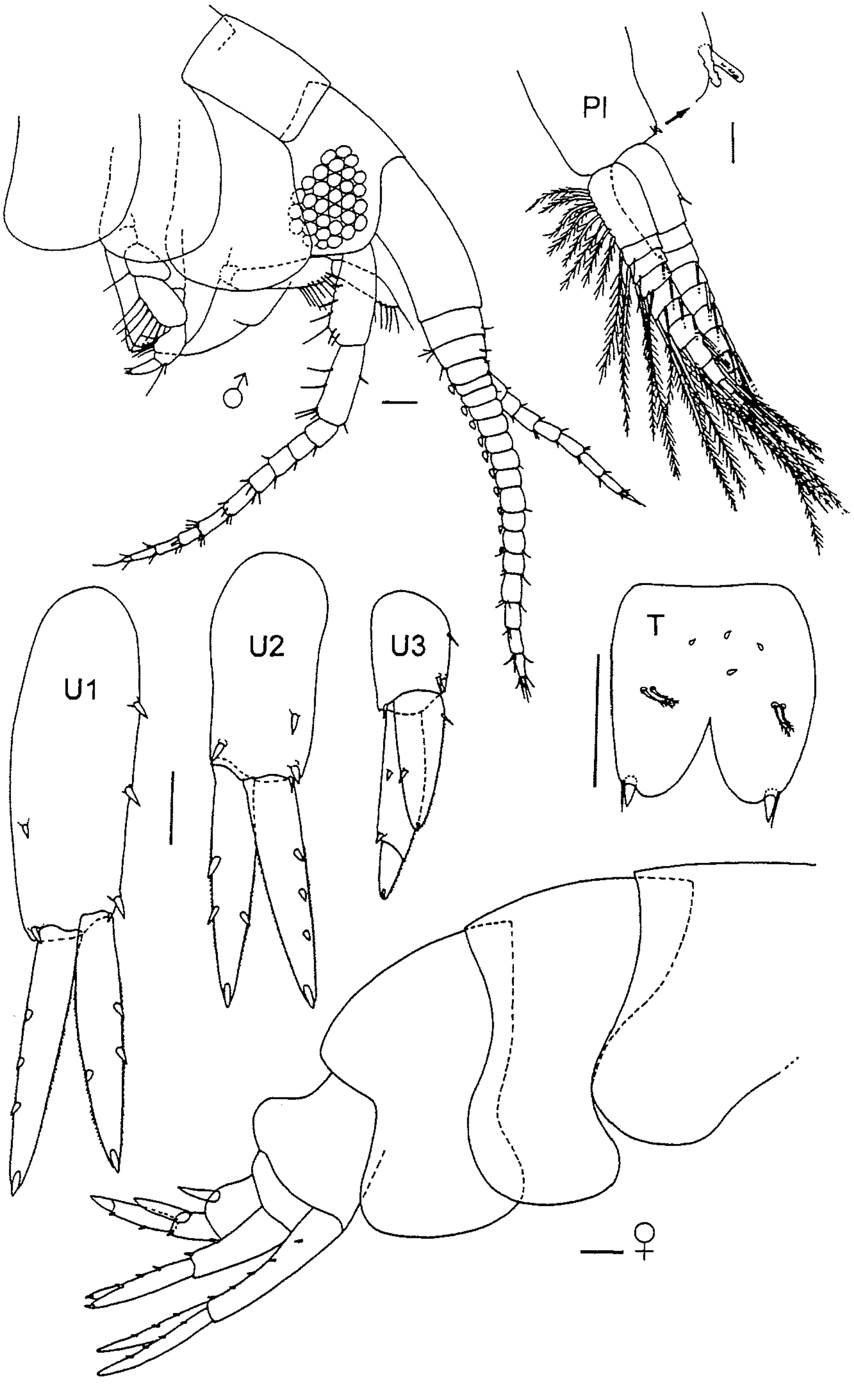

Fig. 4. *Pseudokoroga spongiophila* n. sp. Holotype female, 5.4 mm. Scale bars: 100 µm.

Description: Body: rather slender, dorsally smooth, except urosomite 1 bearing a rounded dorsal boss. Coxa 1-4 short, slightly longer than the corresponding pereonites, slightly longer than broad, slightly overlapping, broadly rounded distally. Antero- and posteroventral angles of epimeral plates 1-3 rounded. Colour white in live and preserved specimen.

Head (figure 1): half as long as deep, dorsally as long as first pereonite, rostrum small; lateral cephalic lobe short, rounded; eyes large, broadly oval.

Antenna 1 (figure 2): peduncle longer than head, article 1 elongated, article 2 and 3 ordinary. Callynophore poorly developed. Primary flagellum long, 1.5 times as long as peduncle, of 13 articles, first article short, calceoli absent in female, present in male. Simple setae and aesthetascs on peduncle and flagellum. Accessory flagellum with 7 articles, more than half as long as primary flagellum.

Antenna 2 (figures1, 4): only slightly longer than antenna 1. Peduncular article 4 slightly longer than article 5, flagellum subequal to peduncle.

Mouthparts forming subquadrate bundle. Epistome and upper lip separate, blunt, epistome slightly prominent.

Mandible (figure 2): incisor smooth; lacinia mobilis on left mandible, three raker spines present, molar triturative, of medium size, palp three-articulate attached strongly proximally to molar; article 1 shorter than wide, article 2 1.4 times as long as article 3, with a row of long D2 setae on distal third of posterior margin; lacina mobilis digitiform. Article 3 bearing D3 and E3 setae.

Maxilla 1 (figure 2): inner plate weakly setose, narrow, with two long, plumose setae at distal margin; outer plate with a 7/4 crown setal-tooth arrangement; ST A not reaching two thirds height of ST 1; palp two-articulate, distal article large, with three distal robust setae.

Maxilla 2 (figure 2): inner plate narrow with one setal row distally, consisting of six long setae; outer plate 1.3 times as long as inner plate. Both plates tapering apically.

Maxilliped (figure 2): inner and outer plate well developed, inner plate with three robust setae on distal margin; outer plate with two apical robust setae and one smaller seta just below, palp strongly exceeding outer plate, dactylus well developed.

Gnathopod 1 (figure 1): robust, smaller than gnathopod 2; coxa 1 slightly expanding anteroventrally, small setae on ventral margin; basis bearing setae anteriorly and posteriorly; carpus lobate; propodus 3.5 times as long as carpus, slightly widened proximally, strongly subchelate, palm oblique, excavate, with two setulated robust setae on produced posterior corner; dactylus large. Inner side of propodus with two pectinate setae as seen in figure 5a,b.

Dactylar article ventrally grooved, claw ornamented with longitudinal furrows as seen in figure 5c.

Gnathopod 2 (figure1): coxa subrectangular with anterior margin strongly convex; ischium elongated; carpus 1.9 times as long as wide, anterior and posterior margin convex, carpus nearly twice as long as propodus; propodus chelate and strongly setose; dactylus fitting palm, with a minutely dentate cutting margin as seen in figure 5d.

Pereopod 3 (figure 3): coxa 3 similar to coxa 2; propodus 1.5 times as long as carpus, posterior margin with a row of single and paired robust setae.

Pereopod 4 (figure 3): similar to pereopod 3; coxa 4 broader than coxa 3, posterior margin concave.

Pereopod 5 (figure 3): coxa 5 equilobate, each lobe semi-circular; basis broadly expanded, with a row of slender robust setae along anterior margin, weakly crenulate along posterior margin. Basis, ischium and merus with a long robust setae on anterodistal angle; merus slightly expanded, three robust setae on posterior margin; propodus 1.4 times as long as carpus; dactylus half as long as propodus.

Pereopod 6 (figure 3): coxa 6 small, slightly wider than long; basis almost 1.5 times as long as wide, almost oval, with a row of single robust setae on anterior margin. Basis, ischium and merus with long robust setae on anterodistal angle; merus similar to merus of pereopod 5, but with only two strong robust setae on posterior margin; propodus about twice as long as dactylus.

Pereopod 7 (figure 3): coxa 7 suboval; basis 1.2 times longer than wide, row of single robust setae on anterior margin, posterior margin strongly convex, posterior border slightly crenulated. Basis, ischium and merus with long robust setae on anterodistal angle; merus twice as long as wide, posterodistal angle of merus produced; carpus and propodus similar to those of pereopod 6.

Epimeral plates 1-3 (figure 4): with rounded posterodistal angle.

Pleopods (figure 4): well developed, rami subequal.

Gills (figures 1, 3): simple on pereopods 2 to 7.

Uropod 1 (figure 4): outer ramus about as long as inner ramus, reaching three quarters of the length of peduncle; both rami with serrated margins and one large apical robust setae.

Uropod 2 (figure 4): inner ramus without notch; rami equal in length, slightly longer than peduncle; both rami with large apical robust setae and serrated margins.

Uropod 3 (figure 5): peduncle short, rami lanceolate, without plumose setae, inner ramus slightly shortened, outer ramus two-articulate, twice as long as peduncle, article 2 short, reaching a third of the length of article 1. As in uropod 1 and 2 rami margins densely serrated. Telson (figure 4): as long as broad, 40 % cleft, with two apical robust setae.

Sexual dimorphism weakly developed. Compared to females the eyes in males are larger and closer to the head anterior margin. Only males have calceoli on their first antennae, located on the first five to 11 articles (figure 4). The first articles of the antennae 1 flagellum are thicker than those of females, the length / width ratio is about one half compared to nearly three quarters. Uropod 3 of males extends a little further and the second article of uropod 3 is relatively longer in males.

Etymology: Named after the habitat of the new species.

Ecology

The highest density of *Pseudokoroga spongiophila* was found in *Jophon spatulatus* (Kirkpatrick, 1907) at station 124-1 with up to 24 individuals per 1000 cm^3.

At the same station 15 specimens of *Pseudokoroga spongiophila* were found per 1000 cm^3 in *Clathria pauper* (Broenstedt, 1926). In contrast to *J. spatulatus* which is greyish white coloured *C. pauper* is bright yellow- orange. In the third species of Demospongiae: *Microxonia simplex* (Topsent, 1916), also greyish, only a single specimen of *Pseudokoroga spongiophila* was found. While the first two sponges were caught at Kapp Norvegia in the Weddell Sea the latter was collected in the Bransfield Strait at the Antarctic Peninsula.

The stomach contents of 60 specimens were checked. Among these 50 specimens were boiled in KOH for 2 hours, to detect the presence of sponge spicules. Most stomachs were empty, only very few specimens of *Pseudokoroga spongiophila* contained parts of sponge spicules as well as pieces of Copepoda.

No juveniles of *Pseudokoroga spongiophila* were found in the sponge tissue. The smallest ovigerous female reached a length of 4.7 mm, the largest 5.2 mm. The brood size varied from 9 to 14 eggs. All eggs belong to stage 1 following Bellan-Santini (1999). The mean egg size was 0.55 mm. The males showed a size range of 3.5 - 5.15 mm.

Discussion

The new species is attributed with some doubt to the genus *Pseudokoroga* Schellenberg, 1931, in the sub-family Tryphosinae Lowry and Stoddart, 1997. However, it differs from *Pseudokoroga* as defined by Barnard and Karaman (1991) by the epistome which is not prominent in size and projection, the inner plate of maxilla 2 distinctly shorter than the outer plate, the gnathopod 1 not strongly enlarged in male, the coxa 1 slightly expanded anteroventrally and the cleft telson. These differences may justify the erection of a new genus but in the present state of flux of Lysianassidae taxonomy it seems more appropriate to wait for the publication of the revision of the group.

The superfamily Lysianassoidea is presently represented in the Southern Ocean by 146 species in 54 genera (De Broyer and Jazdzewski, 1996). Seventy six species are endemic to the Antarctic region, south of the Polar Front. Among the Antarctic lysianassoids few species are considered associated with sponges such as *Abyssorchomene rossi* (Walker, 1903), *Uristes gigas* Dana, 1849 and *Waldeckia obesa* (Chevreux, 1905) (Dauby *et al.*, 2001b)

Lysianassoid amphipods are well known as dominant scavengers in cold water seas. Stomach content analysis did not allow unambiguous characterisation of the feeding regime of *Pseudokoroga spongiophila*, but indicated that it could be an opportunistic- and suspension feeder (see the trophic types defined by Dauby *et al.*, 2001a). Most likely *Pseudokoroga spongiophila* might feed on any potential food which passes into its host. Since *P. spongiophila* may occasionally feed on sponge tissue there is a reduced need to leave the sponge habitat for feeding. The absence of juveniles of *Pseudokoroga spongiophila* in the sponges could be explained by their possible inability to feed on sponge tissue.

The mouthparts of *Pseudokoroga spongiophila* do not show any special adaptation to the symbiotic lifestyle as found in other Antarctic amphipods. *Echiniphimedia hodgsoni* (Walker, 1906), Iphimediidae, for example, is known as a specialist sponge feeder. Its right mandible bears a lacina mobilis which works as an additional cutting edge, enabling *E. hodgsoni* to bite out tough sponge material (Coleman,1989b). According to Oshel and Steele (1985) *Paramphithoe hystrix* Ross, 1835 eats the tissue of it's host sponge *Haliclona* . The modifications of its mouthparts for swallowing the sponge's spicules as a whole are minimal, but the mandibular molar process are supposed to be modified to manipulate the spicules without breaking.

Further species of amphipods which were found in the same sponges belonged to four different families; *Colomastix fissilingua* (Schellenberg, 1926): Colomastigidae; *Andaniotes linearis* (K.H. Barnard, 1932) and *Stegosoladius ingens* (Chevreux, 1906): Stegocephalidae; *Leucothoe spinicarpa* (Abildgaard, 1789): Leucothoidae; *Polycheira antarctica* (Stebbing, 1875): Dexaminidae. At Kapp Norvegia *Colomastix fissilingua* and *Pseudokoroga spongiophila* were the dominant taxa living in the sponges, whereas the stegocephalids dominated at the Antarctic Peninsula (Lörz, 2001).

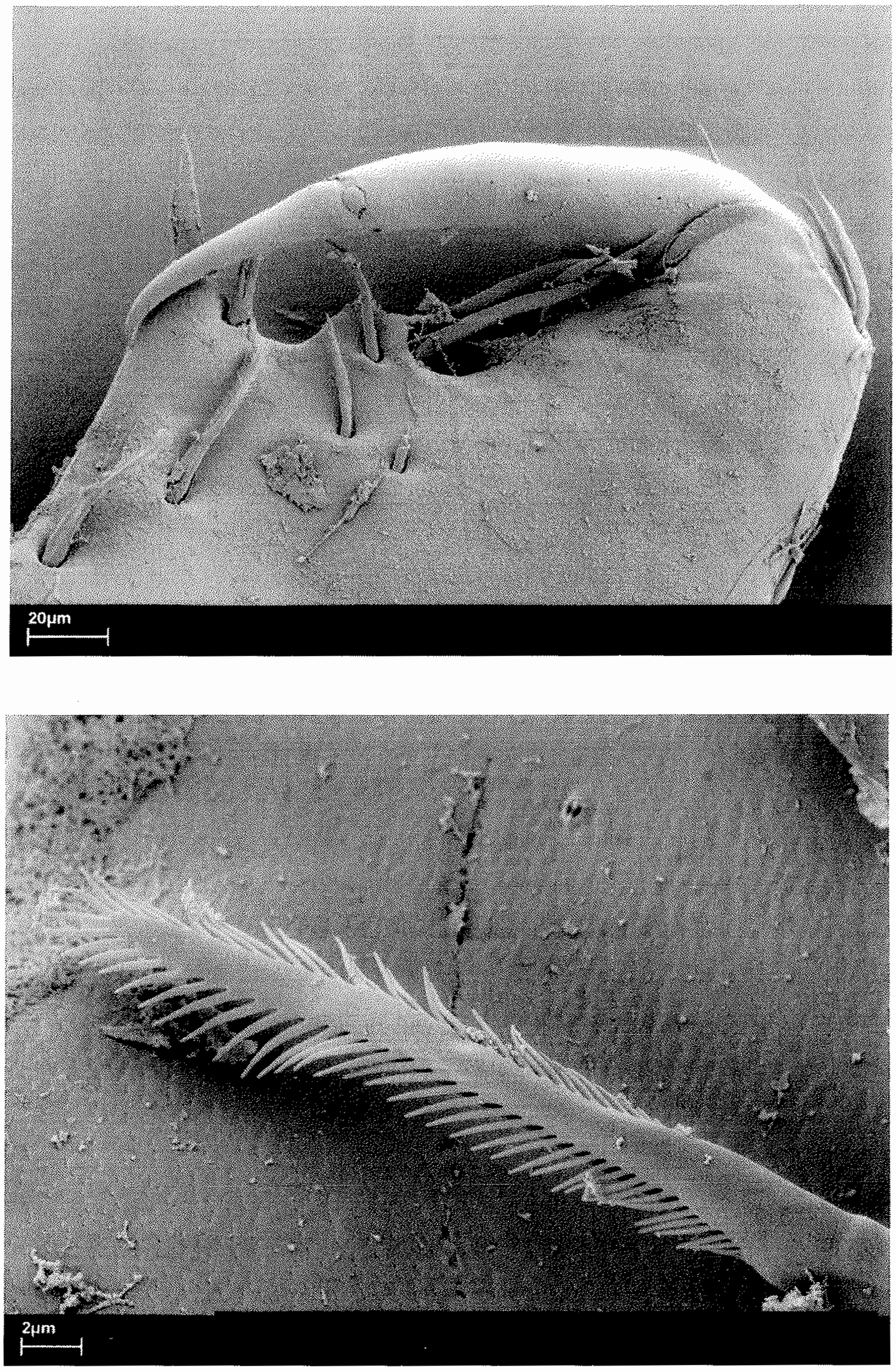

Fig. 5 A B. *Pseudokoroga spongiophila* n. sp. A) palm and dactylus of first gnathopod; B) pectinate setae on palm of first gnathopod;

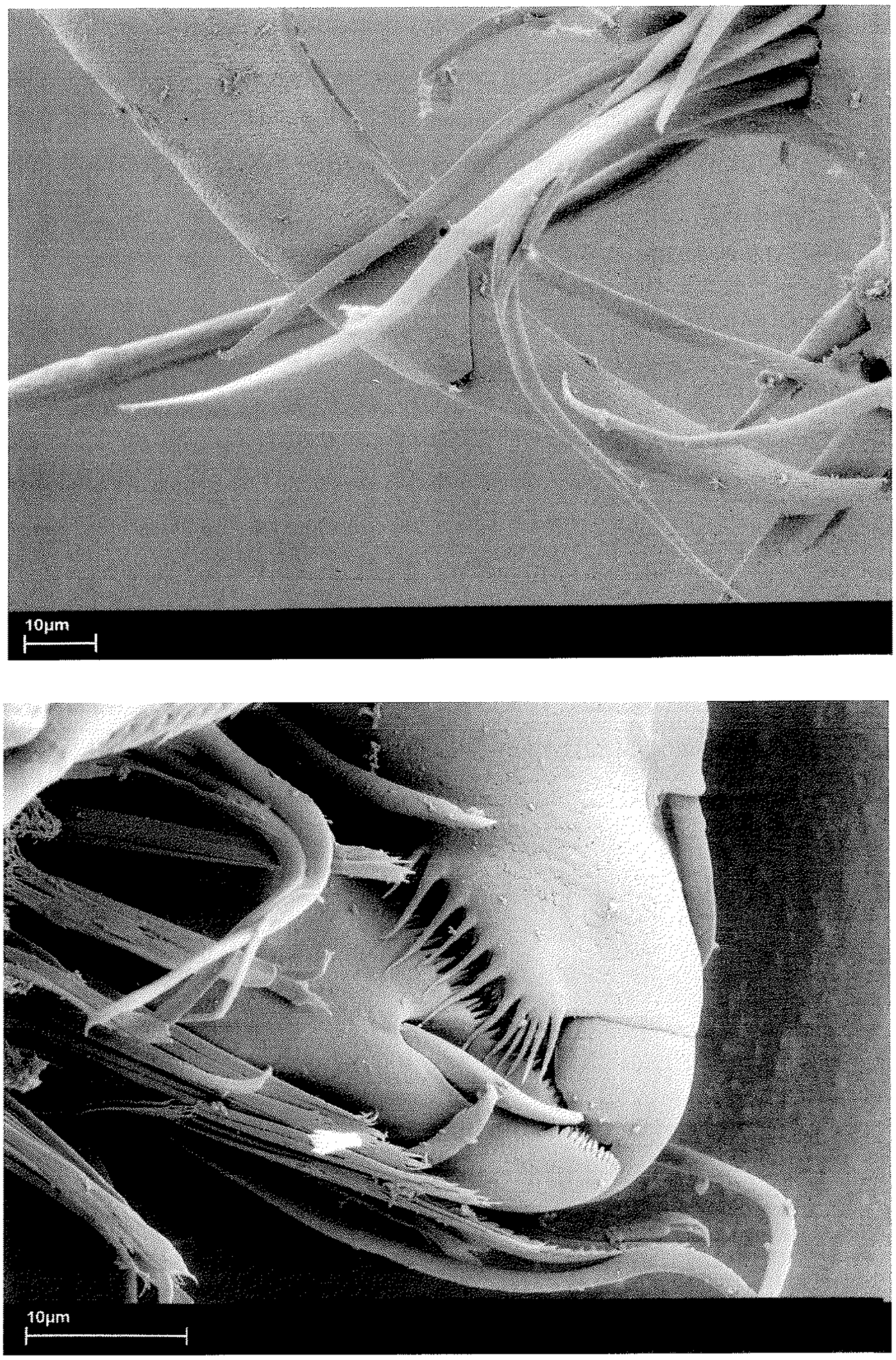

Fig. 5 C D. *Pseudokoroga spongiophila* n. sp: C) dactylus of first ganthopod; D) chela of second gnathopod.

Sponges were the third important item of the diet of 29 representative amphipod species in the eastern Weddell Sea shelf ecosystem, following by plankton-originating cells and crustaceans (Dauby *et al.*, 2001b). Among these amphipods three species of Lysianassoidea had ingested Porifera, which constituted less than 10 % of their food items. These species did not show any morphological adaptation to sponge feeding and were considered "opportunistic feeders" by Dauby *et al.* (2001a). The stomach contents as well as the basic mouthparts might indicate that *Pseudokoroga spongiophila* feeds unspecifically.

Acknowledgements

The authors are very grateful to Professor Wolf Arntz (Bremerhaven), ANT XVII-3 cruise leader, and the crew of RV *Polarstern*. Special thanks are due to Ole Ziemer who helped sorting the material. Claire Swartenbroeck (Brussels) contributed to the illustration. Renate Walter (Hamburg) helped with the REM pictures. We thank Ole Tendal (Copenhague) and Susanne Gatti (Kiel) for determining the sponge species. We are grateful to Angelika Brandt, Hans-Georg Andres (both Hamburg) and Charles-Oliver Coleman (Berlin) for helpful suggestions concerning the contents. This article is based on a doctoral study by Anne-Nina Lörz in the faculty of Biology, University of Hamburg, supported by the *Studienstiftung des deutschen Volkes*.

Veröffentlichung IV

A common but undescribed huge species of *Eusirus* from Antarctica (Crustacea, Amphipoda, Eusiridae)

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Abstract

A huge, common eusirid amphipod of the genus *Eusirus* recently recorded from the Weddell Sea and the region of South Shetland Islands but hitherto confused with the species *Eusirus perdentatus* CHEVREUX, 1912 is described, *Eusirus giganteus* sp. nov. Its systematic position within the genus *Eusirus* is discussed, and a key to the currently known species of *Eusirus* is presented.

Keywords: Taxonomy, Amphipoda, Eusirida, *Eusirus*, new species, key, Antarctica.

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Introduction

In austral autumn 2000 biological benthic surveys and fishery projects were carried out during «Polarstern» expedition ANT XVII/3 in the Weddell Sea and the vicinity of the South Shetland Islands (ARNTZ & BREY 2001). Material obtained by qualitative hauls made with a bottom trawl at depths of 316-690 m frequently yielded specimens of an unknown *Eusirus* species. Besides particular characters of peraeopods 3 and 4, antenna 2, and gnathopods the new taxon could easily be taken for the well known Antarctic *Eusirus perdentatus* CHEVREUX, 1912. For example, of 132 eusirid specimens collected at Sta. 166 off King George Island (South Shetland Islands) and formerly designated to *E. perdentatus,* only two are *E. perdentatus* while the bulk is attributable to the new species. The two most closely related taxa are *E. perdentatus* and *E. propeperdentatus* ANDRES, 1979, which form a species complex together with the new taxon. This complex is characterized by a disto-middorsal, conspicuously strong tooth on peraeonites 5-7 and pleonites 1-3.

It is remarkable that the new species has not been distinguished earlier with regard to the considerable number of samples already obtained, its high frequency, and large body size. Within the material studied the range of body length of males was 29-79 mm, of females 28->88 mm (*vs. E. perdentatus*: maximal body size of males 63 mm, of females 75 mm). Considering these differences of body length, the maximal size of 100 mm previously recorded for *E. perdentatus* (ARNTZ *et al.* 1992) hints that the specimen in question might be identical with the new species.

The reassessment of former records obtained from various RV «Polarstern» expeditions in the Weddell Sea and the region of the Antarctic Peninsula confirms the sympatric distribution of both species. However, from this study restricted to two Antarctic regions no conspicuous ecological preferences of the new taxon compared with *E. perdentatus* are evident, there is no difference in either the vertical or horizontal distribution, and the same state of development of the brood pouch observed suggests a synchronous reproduction.

The taxonomical analysis of the material used for the extensive investigations on population dynamics (KLAGES 1991, 1993) proves that the new species has been taken for *E. perdentatus*. The new species contributes 26 % to the material analysed (n=132 individuals; recorded during several RV «Polarstern» expeditions in the eastern Weddell Sea). Consequently the results and conclusions published by KLAGES on the population dynymics of *E. perdentatus* are erroneous.

The hitherto unknown *Eusirus* specimens are described and illustrated as a new taxon below. A key to the currently known 28 *Eusirus* species is presented.

Material and methods

The specimens of the new *Eusirus* taxon were caught off King George Island (South Shetland Islands) at Sta. 166, and in the eastern Weddell Sea at Sta. 102 and Sta. 109 during RV «Polarstern» expedition ANT XVII/3. Sampling was done by ANNE-NINA LÖRZ in the austral autumn 2000 (Table 1). The *Eusirus* specimens obtained were qualitatively collected from bottom-trawl hauls (ARNTZ & BREY 2001). The animals were fixed in 4 % buffered formalin and later transferred to 70 % ethanol in the laboratory.

The material is deposited at the Zoological Museum of the University Hamburg (ZMH).

Additional material studied was caught during various RV «Polarstern» expeditions. The animals formerly used for investigations on population dynamics (KLAGES 1991, 1993) were obtained during RV «Polarstern» expeditions ANT III/3, ANT VII/4, and ANT VIII/5 (see Table 1 for data of samplings).

A comparison with the holotype of *E. perdentatus* (Muséum National d'Histoire Naturelle, Paris; the specimen is in bad condition, damaged, and appendages dissected are missing: mouthparts and legs) was performed, additionally samples obtained during «Walther Herwig» expedition 1977/78 (ANDRES 1982), «Polarstern» expedition ANT I (VOSS 1988) as well as current Antarctic collections received from Drs C. DE BROYER and H. M. RAUSCHERT were compared.

Body length was measured from rostrum to tip of the telson on straightened animals, article length from articulation to articulation. Presence of genital papillae and oostegites was used to determine sex. Figures were drawn with the aid of a camera lucida.

The following abbreviations are used: **A1**, antenna 1; **A2**, antenna 2; **Art.**, article; **Ep**, epimeral plate (epimeron); **Fl**, flagellum; **Gp**, gnathopod; **Md**, mandible; **ovig.**, ovigerous; **P**, peraeopod; **Sta.**, station; **T**, telson; **U**, urosomite (urosome segment); **Up**, uropod.

Systematics

Eusirus giganteus sp. nov.

Eusirus perdentatus; – VOSS 1988 (part.); KLAGES 1991(part.), 1993 (part.); ARNTZ *et al.* 1992 (part.).

Tab. 1. *Eusirus giganteus* sp. nov. – Sampling data and composition of specimens studied from the eastern Weddell Sea and the region of the Antarctic Peninsula. (AGT = Agassiz trawl; BT = bottom trawl; BTs = bottom trawl, small).

Expedition	Station	Date	Position		Depth (m)	Gear	Number of specimens (size in mm)			Registration No. ZMH	Collector
			S	W			Females	Males	Juv./sex indet.		
ANT I/2	213	26 Feb. 1983	72°25'	16°21'	221	AGT			1 (specimen incomplete)		J. Voss
ANT III/3	248	22 Jan. 1985	73°10'	20°27'	409	BT	1 (48)	–	– / –	K 40 123	M. Klages
	273	27 Jan. 1985	72°35	18°07'	673	AGT	1 (45)	1 (46)	– / –	K 40 124	M. Klages
	286	01 Feb. 1985	73°15'	20°21'	403	BT	1 (47)	–	– / –	K 40 125	M. Klages
	288	02 Feb. 1985	74°39'	25°18'	602	AGT	2 (42,45)	3 (43-53)	– / –	K 40 126	M. Klages
	290	03 Feb. 1985	77°41'	35°24'	419	AGT	6 (41-60)	11 (29-65)	– / –	K 40 127	M. Klages
	299	05 Feb. 1985	77°31'	41°36'	664	BT	1 (69)	2 (46-67)	– / –	K 40 128	M. Klages
	300	05 Feb. 1985	77°29'	41°48'	627	BT	–	1 (70)	– / –	K 40 129	M. Klages
ANT VII/4	292	19 Feb. 1989	71°04'	12°42'	561	BT	–	2 (45-48)	– / –	K 40 130	M. Klages
ANT VIII/5	423	18 Jan. 1990	74°52'	27°40'	475	BTs	1 (28)	–	1 (23) / –	K 40 131	M. Klages
ANT XIII/3	39/29	28 Feb. 1996	71°31'	12°26'	600	BT	6 (49-54)	8 (49-60)	– / –	K 40 132	M. Rauschert
ANT XV/3	100	30 Jan. 1998	73°36'	22°07'	519	BT	1 (62)	1 (51)	– / –		M. Rauschert
	84	03 Feb. 1998	72°51'	19°09'	400	BT	1 (77)	1 (47)	– / –		M. Rauschert
	97	05 Feb. 1998	73°35'	22°13'	690	BT	1 (57)	3 (57-58)	– / –	K 40 133	M. Rauschert
ANT XVII/3	102	03 Apr. 2000	71°12'	12°22'	323	BT	8 (52-55)	8 (48-53)	– / –	K 33 519	A.-N. Lörz
	109	04 Apr. 2000	71°11'	12°21'	316	BT	1 (57)	–	– / –	K 33 520	A.-N. Lörz
	166	28 Apr. 2000	63°01'	59°09'	673	BT	75 (37->88)	50 (40-79)	– / 5 (38-45)	K 33 517 (Holotype) K 33 518	A.-N. Lörz
							(Paratypes				
							12 (45-83)	11 (37-77)	– / –	K 40 134	M. Rauschert

Holotype. – Male, 75 mm; ZMH - K 33 517; 28 April 2000; A.-N. LÖRZ leg.

Type locality. – Antarctica, South Shetland Islands, off King George Island; 63°09' S 59°10' W; RV «Polarstern» expedition ANT XVII/3, Sta. 166, depth 673 m; gear: bottom trawl.

Paratypes. – One female, > 82 mm, ovig.; six females, 70->88 mm, brood pouch present but empty; 68 females, 37-77 mm, oostegites small buds to long lamellae but without bristles; 49 males, 40-79 mm; five individuals, sex?, 38-45 mm. ZMH - K 33 518. Locality as for holotype.

Additional material examined. – For data see Table 1.

Etymology. – The name refers to the large body size of the specimens studied; allied to *giganteus* [*Lat.*, adj.] = gigantic, huge.

Diagnosis. – Peraeonites 5-7 and pleonites 1-3 with middorsal carina extending into a strong tooth. Antenna 1 reaching body length. Antenna 2 article 5 slender (linear), flagellum 2.6 to 4.3 times length of peduncular article 5 (depending on body size). Palp article 2 of maxilliped lacking distodorsal small, acute process; distolateral margin smoothly or dentately proceeding mediad; distal medial margin armed with few teeth. Carpus process of gnathopods linguiform, broad, slightly tapering distad, distally rounded, posterior margin convex. Peraeopod 3 and 4 propodus as long as merus. Dactyli anterior margins of peraeopods 3 to 4 armed with fine setules, and posterior margins of peraeopods 5 to 7 barely armed with fine spinules.

Description: – Peraeonites 5-7 and pleonites 1-3 with middorsal carina backwardly prolonged into strong tooth; the tip of pleonite 3 slightly vertically extended (Fig. 1). Epimera (Fig. 2B): first tapering distally and posterodistally pointed, posterior margin sinuous; second ventral margin rounded, armed with spines, posterodistal angle toothed, and posterior margin sinuous; third ventral margin slightly convex, small spines present, posterior margin gently convex, postero-inferior corner rectangular, finely serrate. Urosomite 1 with proximal depression followed by a middorsal, sinuous carina, roundly sloping distally.

Head (Fig. 2A) as long as peraeonites 1 and 2 combined. Rostrum short, downcurved, concave transversally near base. Lateral lobe produced, subrectangular, anterior margin slightly ventrally diminished. Postantennal sinus variable: narrowly v- to u-shaped or (sub)rectangular (Figs 1, 2A). Ventral margin slightly concave. Eyes large, prominent, reniform, pigmental portion often pyriform.

Antenna 1 (Figs 1, 2C, D) conspicuously longer than A 2, reaching (or even extending) body length, peduncle articles 1 and 2 projecting peduncle of A 2. Length ratios (measured laterally) of peduncular articles in male (72 mm) 1.0:0.9:0.1; in female (82 mm) 1.0:1.0:0.08 (in juveniles second article shorter than first). Peduncle article 1 with distoventral tooth laterally and two distal teeth medially; article 2 dentate distolaterally and -medially. Article 3 with dorsal and ventral process. Accessory flagellum of one article, short, thin (ratio length to basal breadth 1:0.17), apically setose (up to three setae). Flagellum more than 3.5 times of total peduncle length; first article about as long as accessory flagellum, incompletely aticulate; numerous articles short, all but distal ones stout; calceoli (Fig. 2G) ventrally present on peduncular articles 2, 3, and on distoventral surface of flagellar articles (proximal 40 per cent of flagellum length); fine aesthetascs present up to the terminal article. – Antenna 2 (Figs 2E-G) peduncular article 4 more robust than 5, flat, dorsally strongly serrate and weakly produced dorsodistad, distinctly produced distomedially and dentate; article 5 slender, linear; length ratios article 4 to 5 (ventral margin measured) 1:1 (article 5 incidentally slightly shorter). Flagellum 2.6 to 4.3 times length of peduncular article 5 (depending on body size); all but first (incompletely articulate) articles short, all but distal ones stout. Calceoli dorsally present along peduncular articles 4 (distally), 5, and on distodorsal surface of flagellum articles (proximal two thirds of flagellum length); aesthetascs lacking.

Mouthpart bundle subquadrate. Upper lip (labrum; Fig. 3A) entire, ventrally rounded, slightly more prominent than straight epistome, separeted by incision (Fig. 3B). – Mandible (Figs 3C, D) left incisor long, smooth, with blunt anterodistal process, right incisor smooth but antero- and posterodistally with small, blunt tooth; left lacinia mobilis broad, with irregular, blunt teeth, right peg-like and irregularly humped (finely toothed or notched). Accessory spine row with numerous spines. Molar process columnar but narrowing distad, triturative surface reduced. Palp three-articulate, attached midway, much longer than mandible body; article 1 short, with one anterodistal seta; length of article 2 about two-thirds of article 3, ventral margin expanded, heavily setose (D2-setae), distally constricted; article 3 falcate, ventral margin heavily setose (D3-setae), E3-setae short, A3-, B3- (proximally grouped in rows), and F3-setae present. – Lower lip (paragnath or hypopharynx; Fig. 3E) inner lobes small, outer lobes gaping, mandibular processes short, rounded. – Maxilla 1 (Figs 3F, G) inner plate slender, oblong, subapically bearing one short and one long plumose seta; outer plate with 12 (11) spines, partially dentate; palp two-articulate, length ratios 1.0:1.4;

article 1 with seta anterodistally; anterior margin of article 2 midward armed with setae, posterodistal margin obliquely truncate and heavily setose. – Maxilla 2 (Fig. 4A) plates subequal in length, apically rounded; outer plate about half width of inner plate, with stiff setae distally; apical margin of inner plate fringed with shorter stiff setae. – Maxilliped (Figs 4B-E) inner plate short (medially extending to end of palp article 1), distally and distolaterally densely armed with spines. Outer plate oblong (medially extending one-third to half length of palp article 2), laterally and apically armed with plumose setae, along medial margin with plumose setae and in addition with more robust, distally pectinate setae. Palp robust, four-articulate, articles 1 and 2 distally dilated; article 2 longest, article 1 sparsely setose. Dorsodistal corner of palp article 2 not acutely produced, bearing fringe of setae (Fig. 4D); distolateral margin smoothly or dentately proceeding ventrad (= mediad); ventrodistal margin armed with few teeth (dentition abundantly not pronounced, margin often weakly corrugate); distomedial and ventral margins more densely setose than dorsal. Palp article 3 laterally weakly extending base of article 4, densely setose. Palp article 4 about as long as article 3 (medially measured; or three-fourths of overall length of article three), claw-like, unguis very short, distal half of posterior margin armed with uniform, short spines.

Gnathopods subchelate, very similar to each other, articles of Gp 2 little longer. Basis anterior margin flat, laterally armed with few small spines, medially with long setae. Ischium laterally and medially roundly winged. Carpus lobe linguiform, broad, distally tapering, posterior margin regularly convex, clearly exceeding merus, distally setose. Propodus subrectangular (longest axis about 1.5 times length of anterior margin), posterior margin concave. – Gnathopod 1 (Fig. 5A) coxal plate about as deep as maximal height of corresponding peraeonite, wider than deep, anteroventral angle roundly produced, anterior margin concave, posterodistal angle irregularly, finely serrate. Basis weakly curved, proximally narrowed, distolaterally rounded angle in female armed with longer setae than in male. Ischium posterodistal margin setose. Merus about as long as ischium, posterodistal angle rounded; posterior margin sinuate, distally setose with simple and pectinate setae; laterally with oblique ridge directed towards posterodistal corner, distally clearly toothed, armed with long pectinate setae. Carpus about two-thirds length of basis; length ratios (anterior margins) carpus to propodus in male 1:0.7 to < 0.6 (ratio decreasing with increasing body size), in female about 1:0.7. Propodus palma convex, longer than anterior margin, bearing shorter and longer setae, defined by a hump armed with rows of short to long spines. Dactylus falcate, fitting up with the hump. – Gnathopod 2 (Figs 5B, C) coxal plate not as deep as maximal height of corresponding peraeonite, subrectangular, slightly tapering distad,

Tab. 2. External diagnostic characters descriminating *E. perdentatus, E. propeperdentaus,* and *E. giganteus* sp. nov.

Characters	*E. perdentatus*	*E. propeperdentaus*	*E. giganteus* sp. nov.
Head			
Dorsal interocular space	wide	very narrow	wide
Post-antennal sinus	narrow, v- to u-shaped or subrectangular	obtuse-angled	narrow, v- to u-shaped or subrectangular
Antennae			
Ratios of antenna 1 and 2	A 1 distincly longer than A 2, extending pleonite 2	A 1 only little longer than A 2, extending pleonite 2	A 1 distincly longer than A 2, length = body size (or longer)
Antenna 2			
Ratios of peduncular articles 4 to 5	subequal	4 distinctly longer than 5	subequal
Shape of peduncular article 5	slender, cylindrical	stout (flat)	slender, cylindrical
Ratios of peduncular article 5 to flagellum	1:1.6 (to 1.8)	1:9	1:2.6 (to 4.3)
Maxilliped			
Palp article 2			
Dorsal (= lateral) margin			
Distal corner	acutely produced and setose	smooth and setose	smooth and setose
Ventrodistal (= mediodistal) margin	toothed, setose	smooth (frequently crenated or corrugated, setose)	toothed, setose
Coxal plate 1	expanded distally and extending craniad	subquadrate, trapezoid	expanded distally and extending craniad
Gnathopods			
Carpus process	subtrapezoid, not exceeding merus	broadly linguiform, not exceeding merus	linguiform, exceeding merus
Propodus	subquadrate, posterior margin concave	oval, posterior margin strongly convex	subquadrate, posterior margin (slightly) concave
Peraeopods 3 and 4			
Ratios of merus to propodus	merus distinctly longer than propodus	merus and propodus subequal	merus as long as propodus
Peraeopod 7			
Basis	not lobate posterodistad (but acutely produced)	lobate posterodistad (lobe rounded or toothed)	not lobate posterodistad (but acutely produced)

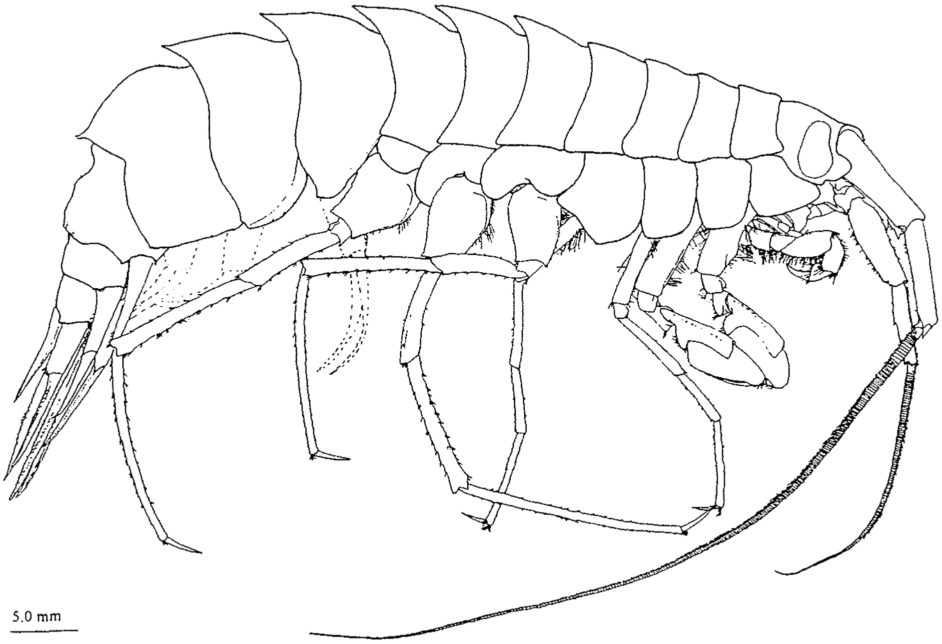

Fig. 1. *Eusirus giganteus* sp. nov. – Habitus, holotype, male, 75 mm (lateral view, not levelled).

deeper than wide, posterior margin with marginal spine midward, ventral margin, anterior-, and posteriordistal angle irregularly notched. Merus posterodistal angle nearly acute, oblique ridge more distinctive. Length ratios (anterior margins) carpus to propodus in male and female 1:0.6. Palma and dactylus as in Gp 1, armature of hump stronger.

Peraeopods 3 and 4 (Figs 6A, B) slender, similar to each other; bases subequal in length; articles merus, carpus, and propodus longer in P 4. Merus and propodus subequal in length; length ratios (posterior margins measured; examplary in male, 75 mm) of articles merus to propodus in P 3 1.0:0.6:1.0, in P 4 1.0:0.7:1.0. Dactyli straight, about one-fifth length of respective basis; overall length about 8 times its breadth (= maximal breadth of open proximal section). Armature of P 3 and P 4 alike: basis proximally setose (long setae), distally spinose; anterior and posterior margins of merus to propodus spinose; posterodistal edge of propodus armed with fringe of setae; dactyli anterior margins sparsely armed with fine setules (Fig. 6B). – Peraeopod 3 coxal plate not as deep as maximal height of corresponding peraeonite, subrectangular, slightly tapering distad, deeper than wide, posterior margin with marginal spine midward; ventral margin and anterior-, posteriordistal angles irregularly notched. – Peraeopod 4 coxal plate not as deep as maximal height of corresponding peraeonite, posteriorly emarginate, angle subacute, ventral margin irregularly notched.

Peraeopods 5 to 7 similar (Figs 6C-F), long, slender; P 5 shortest, P 6 and P 7 subequal. Basis increasing in length from P 5 to P 7, expanded, not lobate posterodistad, but postero-inferior corner acute (weak in P 5 and P 6, strongest in P 7), its inferior margin sinuate, running into a small, bifurcate tooth; anterior margins convex proximally, nearly straight distad, and slightly furrowed distally, extending into teeth; posterior margins concave (P 7 strongest), serrated. Merus slightly curved, posterodistally weakly produced. Carpus postorodistally weakly produced, distolaterally toothed. Propodus posterodistal edge armed with fringe of setae. Ratios of articles merus to propodus exemplary in male, 80 mm (anterior margins measured), P 5 1.0:1.6:2.6, P 6 1.0:1.6:2.4, P 7 1.0:1.5:2.6; ratios in female, 70 mm: P 5 1.0:1.6:2.5, P 6 1.0:1.6:2.4, P 7 1.0:1.5:2.2. Margins of merus to propodus spinose. Dactyli (Fig. 6F) thin, slightly curved, about one-fifth the length of corresponding propodus; overall length about 9 times its maximal breadth; posterior margins sparsely armed with fine spinules. Coxal plate of P 5 longer than deep, bilobed, lobes rounded, posterior lobe slightly deeper than proximal. Coxal plate of P 6 bilobed, lobes rounded; proximal lobe short, distal long, as deep as coxal length, distal lobe deeper than in P 5. Coxal plate of P 7 small, rounded.

Gills on peraeopods P 2 to P 7, proximally voluminous, sack-like (partially pleated), distally lammellate; with oblong accessory gill.

Oostegites weakly linguiform, on P 2 to P 5; oostegites present from body size of 28 mm, well developed pouch present from body size of 70 mm.

Pleopods without conspicuous characters.

Uropods (Figs 7A-C) biramous, Up 1 and 2 extending to subequal distances, Up 3 slightly shorter. Rami lanceolate, spinose. – Uropod 1 peduncle and short outer ramus subequal in length; inner ramus 1.5 times length of outer ramus. – Uropod 2 peduncle shorter than short outer ramus, length ratios 0.8:1.0; inner ramus 2.3 times as long as outer. – Uropod 3 inner ramus weakly exceeding outer ramus. Peduncle 0.5 times as long as rami. – Telson (Fig. 7C) long, slender tapering distad, cleft; exceeding rami of Up 3 one-third to > half of their lengths. Telson length about three times its breadth. Cleft 18 % of length, distally gaping, lobes apically acute.

No sexual dimorphism has been noted.

Remarks. –*Eusirus giganteus* spec. nov. belongs to the Antarctic species complex constitutively characterized by a distomiddorsal, strong tooth on peraeonites 5-7 and pleonites 1-3. Until now, this complex only comprised two taxa: *E. perdentatus* and *E. propeperdentatus*. The following characters distinguish *E. giganteus* sp. nov. just as well as *E. perdentatus* from *E. propeperdentatus*: antenna 2, peduncular article 4 and 5 subequal in length, article 5 slender and linear; flagellum short [*vs.* peduncular article 5 shorter than 4, stout; flagellum nearly as long as flagellum of antenna 1]; maxillipedal palp article 2, transition section between distolateral and medial margins toothed (but in *E. giganteus* dentition less developed), setose [*vs.* transition section lacking teeth, however, distomedial margin frequently crenated or corrugated, indentations with setae]; propodus of gnathopods subrectangular, anterior margin shorter than carpus (anterior margins measured), posterior margin concave [*vs.* oval, longer than carpus, posterior margin strongly convex]; peraeopod 7 basis not lobate posterodistad, similar to P 5 and 6, acutely produced, but with stronger process, inferior margin sinuate, extending into a small, bifurcate tooth [*vs.* posterodistally lobate, lobe rounded or toothed]. Further distinctive characters emphasized by DE BROYER (1983) and DE BROYER & JAZDZEWSKI (manuscript) are: dorsal interocular space wide, postantennal sinus narrow, v- to u-shaped or (sub)rectangular, coxal plate 1 expanded distad and extending craniad [*vs.* dorsal interocular space very narrow, postantennal sinus obtuse-angled, coxal plate 1 subquadrate to trapezoid]. The similarity of the character states mentioned shows a close relationship of *E. giganteus* to *E. perdentatus*.

In general the outward appearence of *E. perdentatus* is more compact. Moreover, *Eusirus giganteus* particularly contrasts with *E. perdentatus* in following characters: (1) antenna 1 about as long as body size (or even longer) [*vs.* somewhat extending pleonite segment 2]; (2) merus and propodus in peraeopods 3 and 4 of subequal length, as an example, ratios (posterior margins measured) of articles merus:carpus:propodus in P 4 of female 1.0:0.7:1.0 [*vs.* holotype, female (Fig. 8A) 1.0:0.6:0.7]; (3) length of flagellum in antenna 2, ratios of peduncular article 5 (ventral margin) to flagellum 1.0:2.6 (to 4.3) [*vs.* 1:1.6 (to 1.8)]; (4) carpus process of gnathopods linguiform, distally tapering and rounded, posterior margin

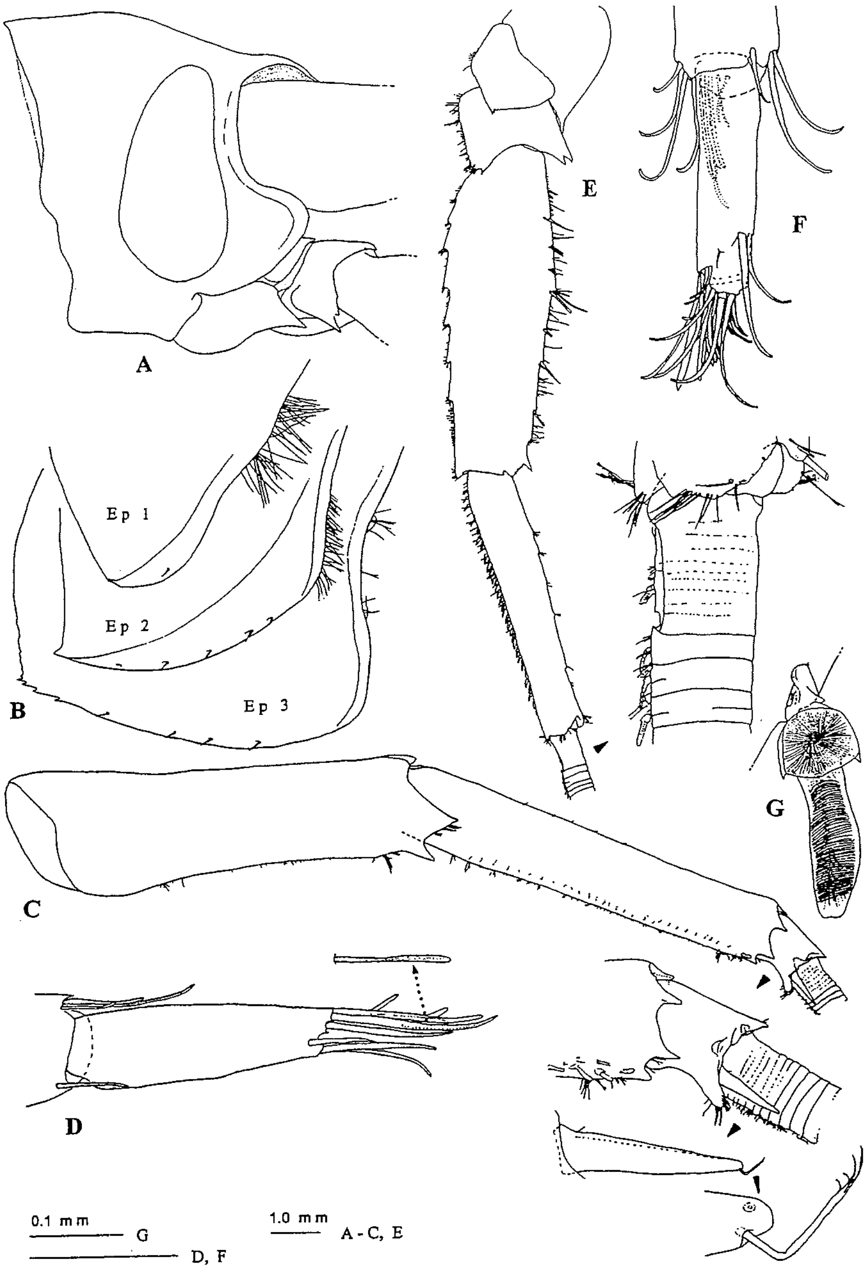

Fig. 2. *Eusirus giganteus* sp. nov. – A-C, E and G, paratype, male, 72 mm. D, male, 52 mm, Sta. 102. F, female, 57 mm, Sta. 109. – **A**, head (lateral). **B**, epimera 1-3: **C** and **D**, antenna 1; peduncle (median, C), terminal article of flagellum (D, detail: concealed aesthetasc). **E-G**, antenna 2; peduncle (median, E), terminal article of flagellum (F), calceolus (G).

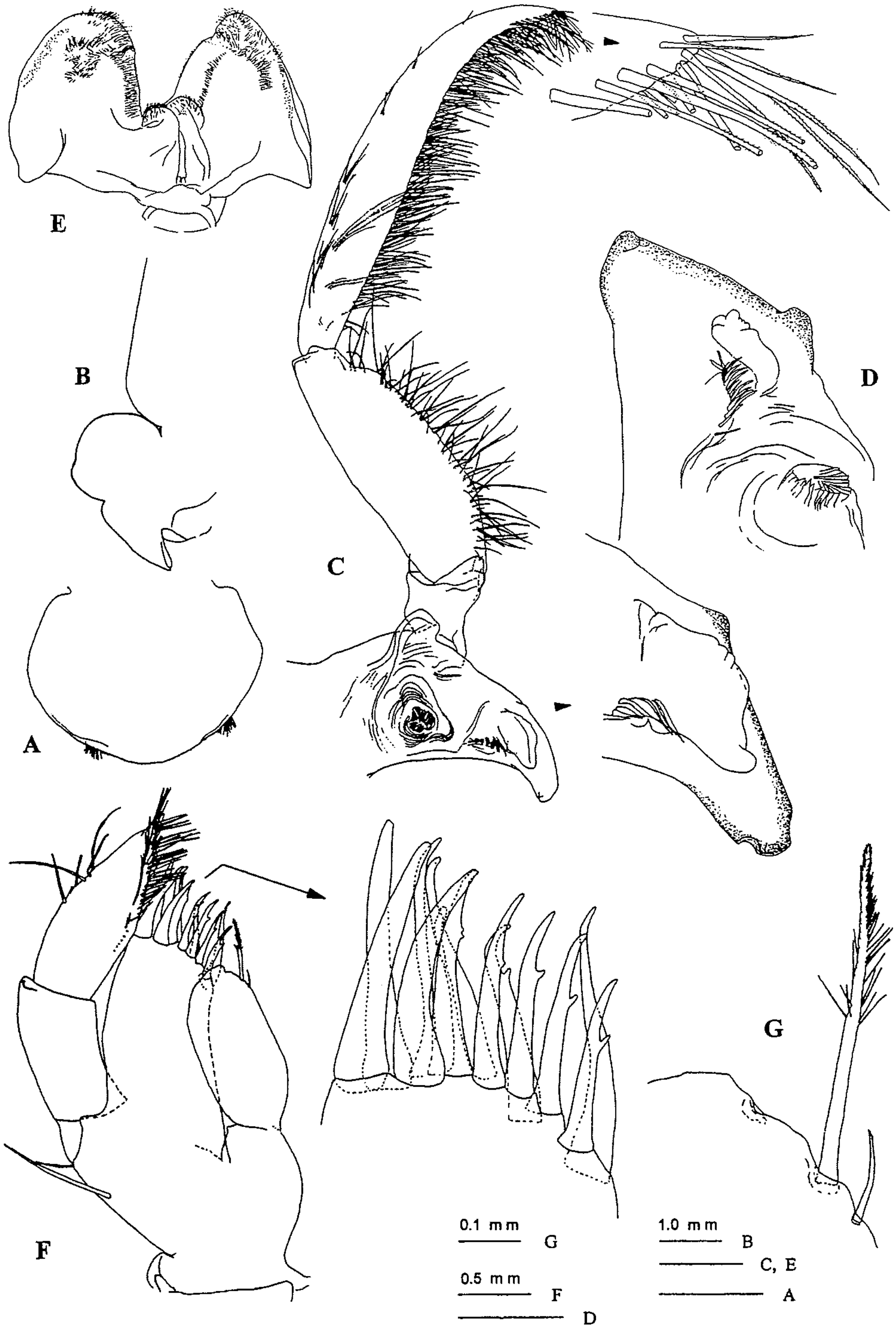

Fig. 3. *Eusirus giganteus* sp. nov. – A, C-G, paratype, male, 72 mm. B, paratype, female, 73 mm. – **A**, labrum (upper lip). **B**, labrum-epistome complex (lateral). **C** and **D**, mandible; left Md (C), right Md (D). **E**, lower lip. **F** and **G**, maxilla 1; apical setae of inner plate (G).

regularly convex, exceeding merus [*vs.* lobe subtrapezoid, blunt, not exceeding merus (Figs 8I, J)]; (5) dactyli of peraeopods 3-7 longer; in P 3 and P 4 about 8, in P 5 to P 7 about 9 times of respective breadth; anterior margins in P 3 and P 4 sparsely armed with setules, posterior margins in P 5 to P 7 barely armed with fine spinules [*vs.* dactylus length in P 3 and P 4 about 4.5 -, in P 5 to P 7 about 7 times of corresponding breadth; dactyli armed with small spines in P 3 and P 4, with conspicuously stronger spines in P 5 to P 7; Figs 8B, F], (6) accessory flagellum longer and more slender, ratios length to basal breadth 1.0:0.17 [*vs.* 1.0:0.23 (to 0.36)]; (7) distodorsal margin of article 2 of maxillipedal palp not produced (small, acute process lacking), but setose [*vs.* process present: dorsodistal margin produced, apically toothed, incisions with setae (Figs 8G, H)]; (8) articles merus, carpus, and propodus of peraeopods 5 to 7 longer, ratios (anterior margins) in P 5 1.0:1.4 (to 1.6):2.2 (to 2.6), in P 6 1.0:1.6:2.3 (to 2.6), in P 7 1.0:1.5 (to 1.6):2.0 (to 2.6) [*vs.* in P 5 1.0:1.4:2.0 (to2.2), in P 6 1.0:1.3 (to 1.4):2.0 (2.1), in P 7 1.0:1.2 (to 1.4):1.7 (to 2.1)].

Essential characters of *E. giganteus* – *e.g.*, (1) to (4) and (7) – are consistent for all body sizes of both sexes.

Biology. – Oostegites not fully developed (small buds to long lamellae but without bristles) are present over the body size of 28 to 77 mm. Within 118 females ten have a brood pouch (over the body size of 70 to >88 mm) but only two are gravid; number of eggs carried: 365 (> 82 mm), 181 (83 mm).

Eusirus giganteus is the giant within the Antarctic *Eusirus* complex considering the data of body size noticed by DE BROYER (1983) and DE BROYER & JAZDZEWSKI (manuscript). In the material studied, females reach a maximal length of >88 mm, and males of 79 mm; details for *E. perdentatus*: female 75 mm, male 62 mm. The maximal length in *E. propeperdentatus* for females is 63 mm, males 57 mm (DE BROYER & JAZDZEWSKI; manuscript).

Distribution (present study). – Eastern Weddell Sea and region of South Shetland Islands; depth range: 221-690 m.

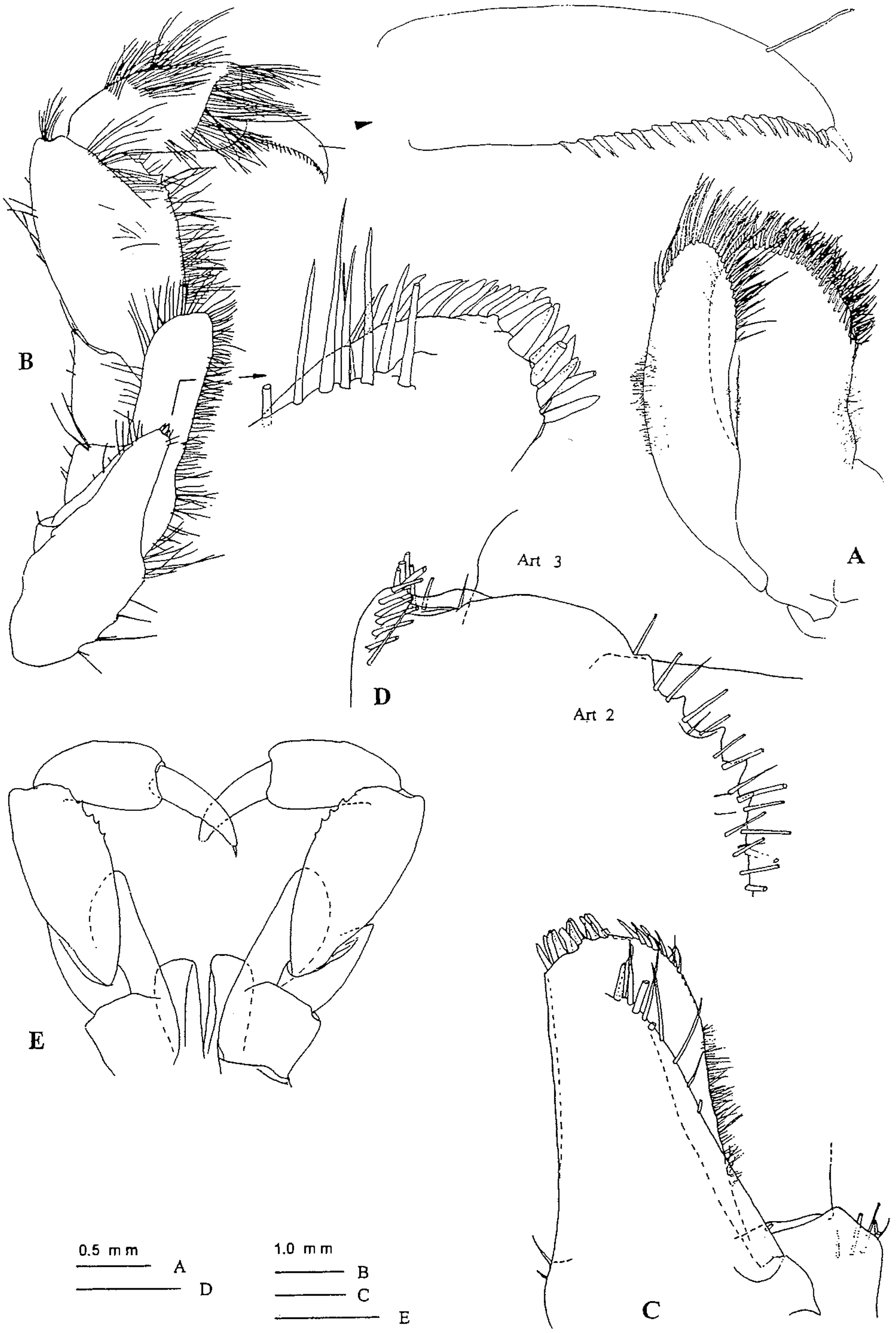

Fig. 4. *Eusirus giganteus* sp. nov. – A-D, paratype, male, 72 mm. E, paratype, sex?, 40 mm. – **A**, maxilla 2. **B-E**, maxilliped; inner plate, right (C), distolateral margin of palp article 2 (D), maxilliped (setation not drawn, E).

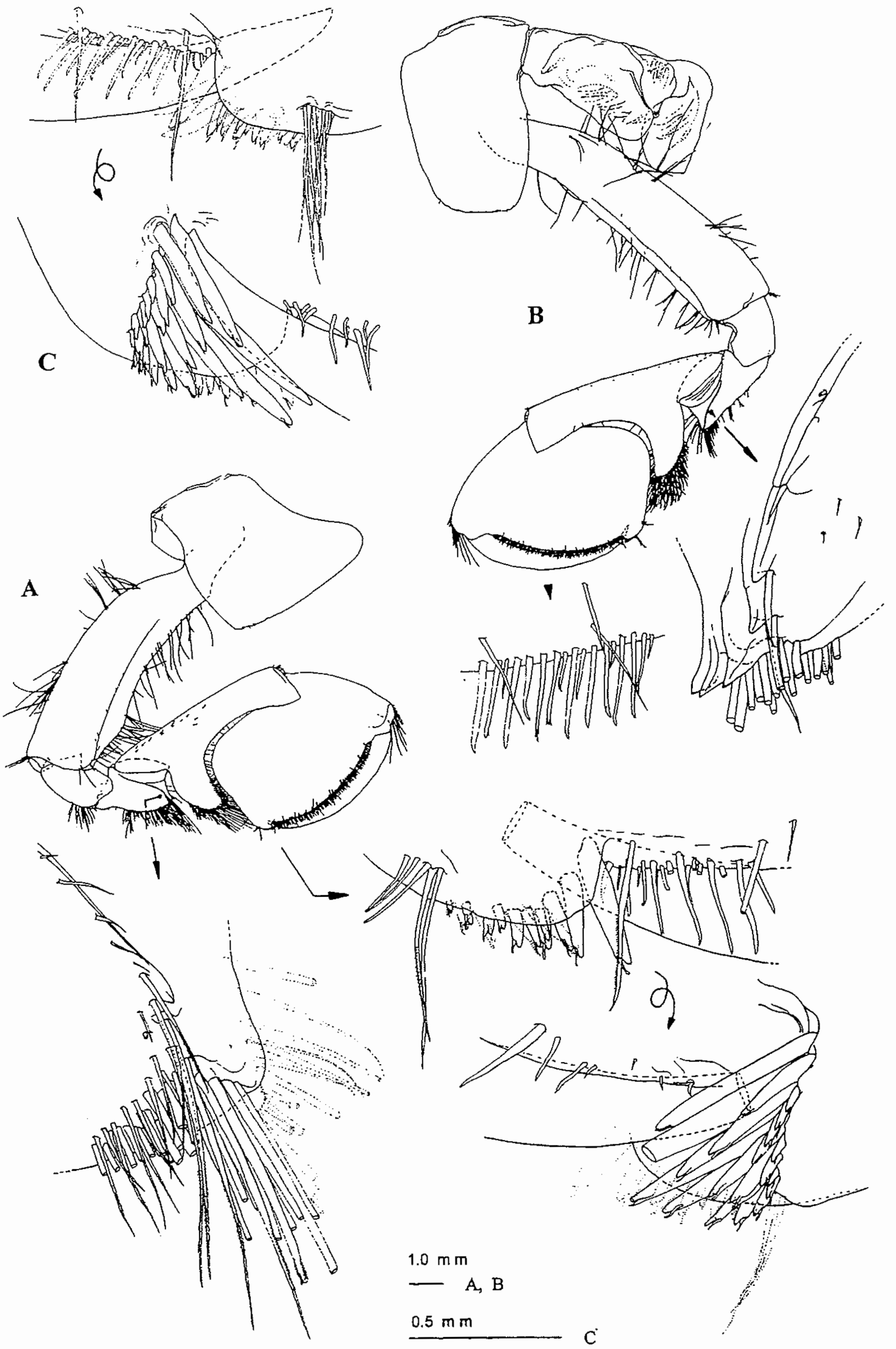

Fig. 5. *Eusirus giganteus* sp. nov., paratype, male, 72 mm. – **A**, gnathopod 1 (right). **B** and **C**, gnathopod 2 (left); armament of palm defining hump (**C**).

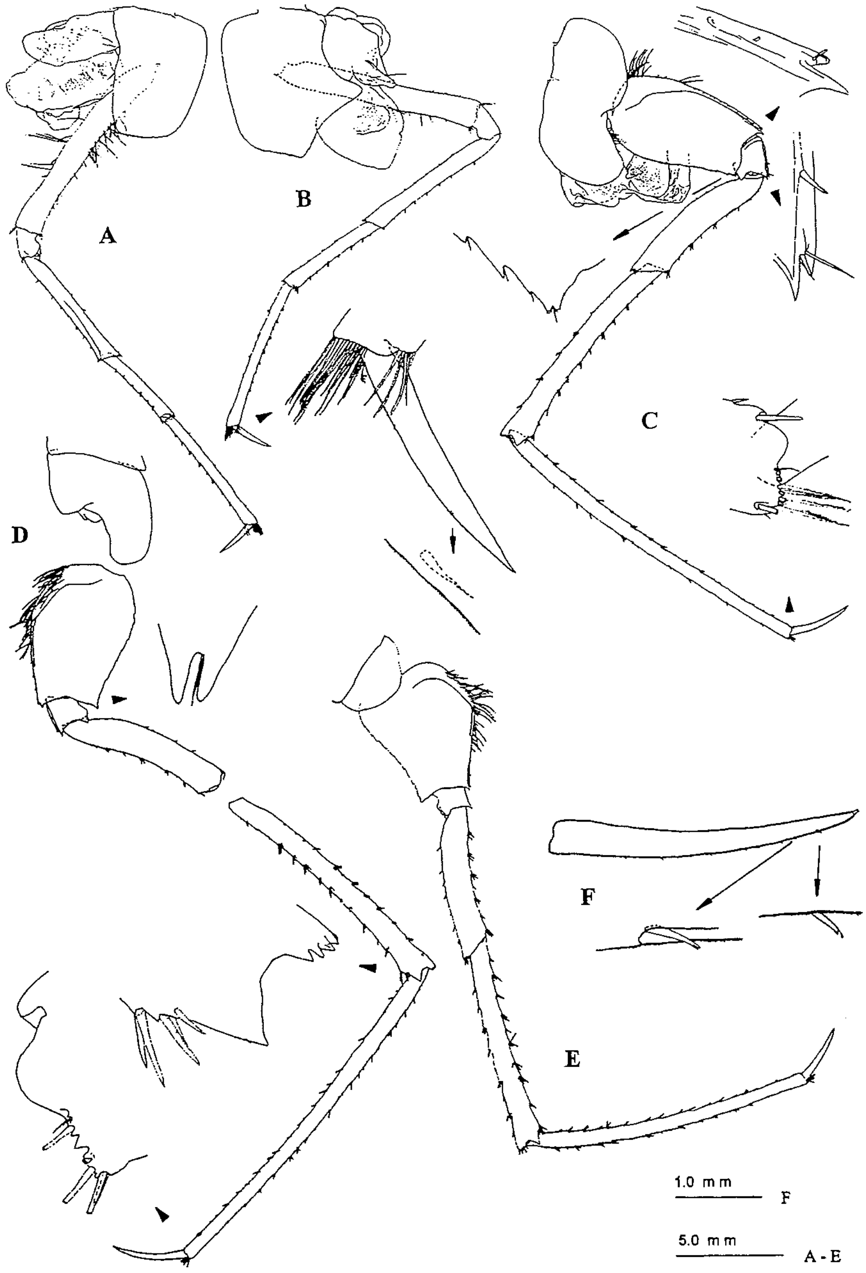

Fig. 6. *Eusirus giganteus* sp. nov. – A-D, paratype, male, 72 mm. E, holotype, male, 75 mm. F, paratype, male, 75 mm. – **A**, peraeopod 3. **B**, peraeopod 4. **C**, peraeopod 5. **D**, peraeopod 6. **E** and **F**, peraeopod 7; dactylus (F), armament of posterior margin: fine spinules.

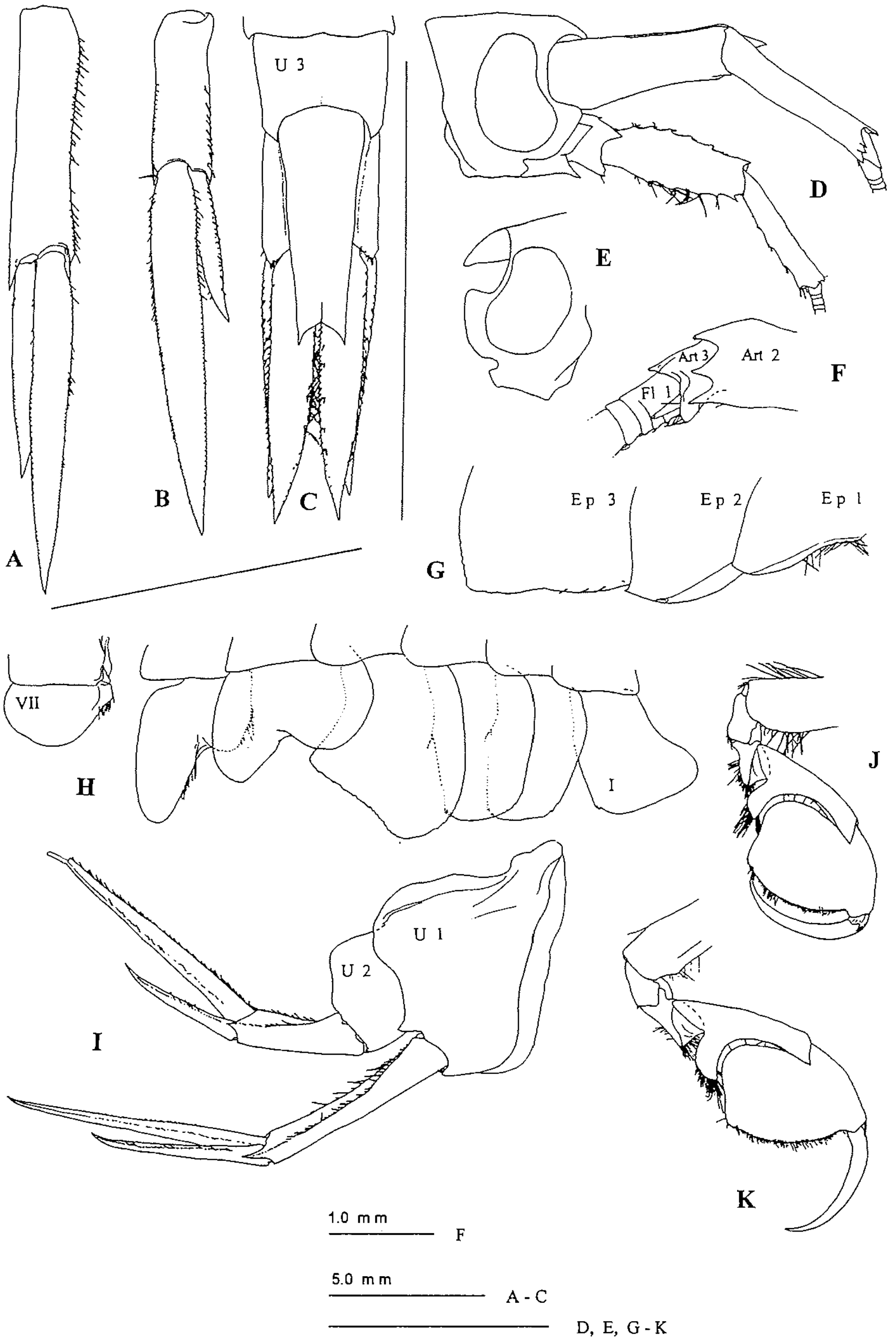

Fig. 7. *Eusirus giganteus* sp. nov., paratype, male, 72 mm. – **A** and **B**, uropods 1 and 2. **C**, telson and uropod 3. – *Eusirus perdentatus* CHEVREUX, 1912; holotype, female. **D** and **E**, head (lateral); head and peduncles of antennae 1 and 2, right (D), left side (E). **F**, antenna 1 (median); peduncular articles 2 (distal part) and 3, and proximal articles of flagellum. **H**, coxal plates 1-7. **I**, urosomites 1 and 2 (lateral) with respective uropods. **J** and **K**, gnathopods 1 and 2 (lateral view, not levelled).

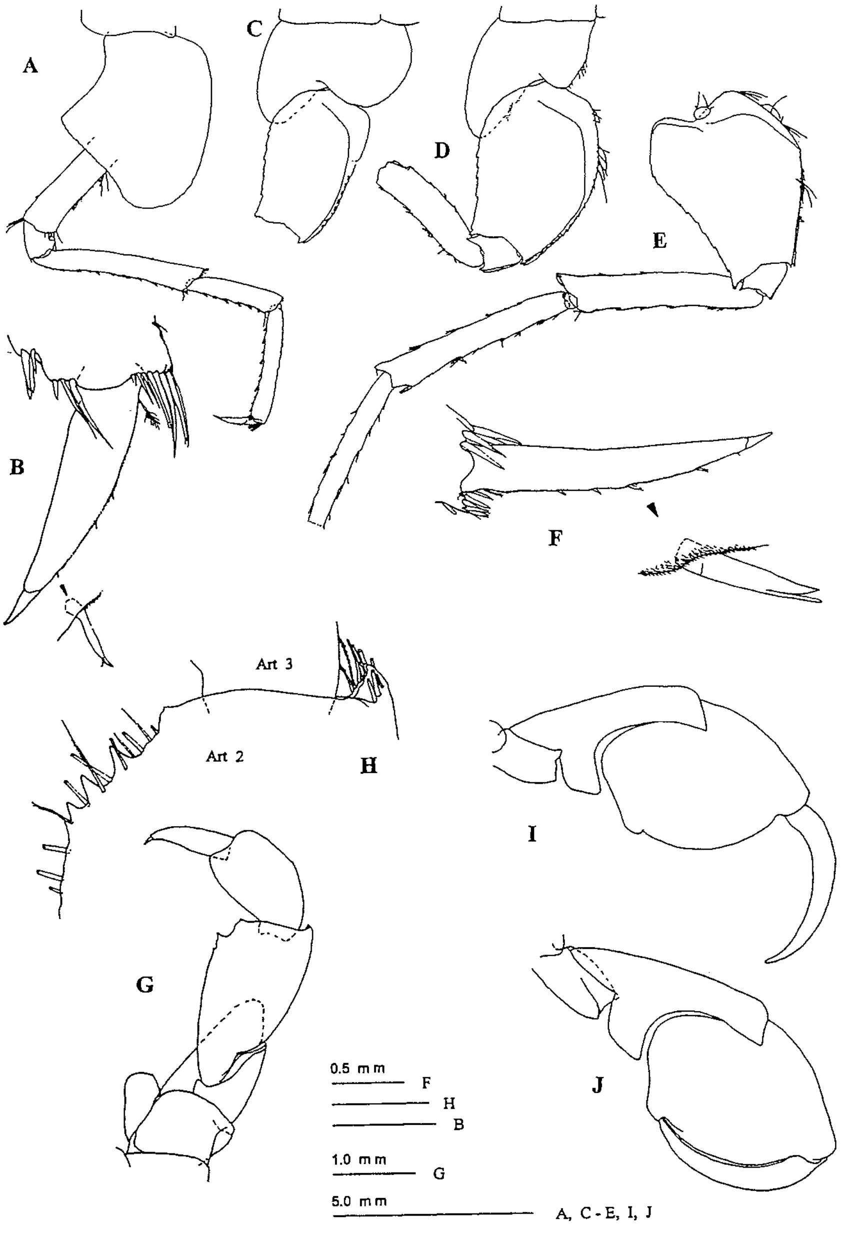

Fig. 8. *Eusirus perdentatus* CHEVREUX, 1912. – A and C-E, holotype, female. B, F, H-J, male, 61 mm, C. DE BROYER leg. G, male, 38 mm, ZMH K 32 183. – **A** and **B**, peraeopod 4; dactylus (B), armament of anterior margin: small spines. **C**, peraeopod 5. **D**, peraeopod 6. **E** and **F**, peraeopod 7; dactylus (F), armament of posterior margin: strong spines. **G** and **H**, maxilliped (setation not drawn, G), distolateral margin of palp article 2 (H). **I** and **J**, gnathopods 1 and 2 (levelled, setation not drawn).

Key to *Eusirus* species

This key is based on DE BROYER 1983. Characters used are restricted to those that can be observed without dissection. According to DE BROYER 1983 and DE BROYER & JAZDZEWSKI 1993, *E. laticarpus* CHEVREUX, 1906 has been re-established. (A thorough, critical analysis of type species characters would be necessary for the preparation of a key to all currently known 28 *Eusirus* species.)

1 Pleonite 3 with distodorsal tooth (distomiddorsal teeh present on pleonites 1-2 and
peraeonites 5-7) 2
– Pleonite 3 lacking distodorsal tooth (pleonites 1-2 and peraeonites 5-7 of different denition). 4

2 Antenna 1 and 2 flagella nearly subequal in length. Propodus of gnathopods oval, posterior margin
convex .... *E. propeperdentatus*
– Antenna 2 flagellum distinctly shorter than in antenna 1. Propodus of gnathopods subrectangular,
posterior margin concavce 3

3 Antenna 1 extending somewhat pleonite 2. Antenna 2 flagellum 1.6 to 1.8 times length of peduncular
article 5. Maxillipedal palp article 2, distodorsal corner with small, acute process. Carpus lobe of
gnathopods trapezoid, not exceeding merus. Peraeopod 3 and 4 propodus conspicuously shorter than merus.
.... *E. perdentatus*
– Antenna 1 as long as body length. Antenna 2 flagellum 2.6 to 4.3 times length of peduncular article 5
Maxillipedal palp article 2, distodorsally lacking small, acute process. Carpus lobe of gnathopods
linguiform, distally tapering, exceeding merus. Peraeopod 3 and 4 merus and propodus subequal in length
.... *E. giganteus* sp. nov.

4 Peraeonite 7 with distomiddorsal tooth. 5
– Peraeonite 7 lacking distomiddorsal tooth. 6

5 Pleonites 1 and 2 with distal, middorsal tooth. Rpimeron 3 posterior margin rather convex, crenulated;
posterior angle actually produced. Coxal plate 1 not expanded ventrad, subquadrate. Antenna 1
peduncular article 1 about three-fourth of article 2. Maxilliped palp article 2 dentate. Gnathopod 1
carpus and propodus anterior margin equal in length. Peraeopods 5-7 dactyli slightly curved, point blunt
with curved tooth. ....*E. micrps*
– Pleonite 1 and 2 with distal, middorsal tooth. Epimeron 3 posterior margin smooth, inferior angle
and distoventral margin lightly serrate. Antenna 1 peduncular article 1 and 2 subequal in ength.
Maxillipedal palp article 2 smooth. Peraeopods 5-7 dactyli not toothed. ....*E. tridentatus*

6 Pleonites 1 and 2 with middrsal teeth 7
– Pleonites 1 and 2 lacking middorsal teeth. Epimeron 3 posterior margin rounded, smooth. Peraeopods
5-7 basis posterior margins smooth. Carpus process of gnathopods short, blunt, stout............ *E. laevis*

7 Maxilliped palp article 2 dentate. Coxal plate 1 clearly expanded craniad. Epimeral plates 1 and 2 posterodistally toothed, epimeron 3 posterior margin and inferior angle serrate. Propodus of gnathopods oval, posterior margin convex. .... *E. bouvieri*

– Maxilliped palp article 2 smooth...8

8 Posterior and distoventral margins of epimeron 3 serrate. Peraeopod 7 basis weakly lobate, lobe subrectangular, it margin smooth. ....*E. antarcticus*

– Posterior margin of epimeron 3 smooth, inferior angle slightly crenulated. Peraeopod 7 basis not lobate, its inferior margin serrate. ....*E. laticarpus*

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Veröffentlichung V

A preliminary molecular and morphological phylogeny of the Antarctic Epimeriidae and Iphimediidae (Crustacea, Amphipoda)

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Abstract

The phylogenetic relationships of 14 species of the Antarctic amphipod families Epimeriidae and Iphimediidae were investigated using 558 bp of the gene for the mitochondrial cytochrome oxidase subunit I (COI) and 98 morphological characters. Both families are dominant members of the Antarctic benthic amphipod community. In contrast to previous studies, our molecular and morphological data suggest that the families Epimeriidae and Iphimediidae may not be sister taxa. Our study suggest that Iphimediidae is more closely related to *Eusirus* (Eusiridae) than to *Epimeria* (Epimeriidae). Phylogenetic analyses based on maximum parsimony (MP) and maximum likelihood (ML) indicate that the genera *Iphimediella* and *Gnathiphimedia* are not monophyletic.

Keywords: Antarctica, benthic amphipods, cytochrome oxidase I (COI), cladistics, Eusiridae, Epimeriidae, Iphimediidae

Introduction

The families Epimeriidae and Iphimediidae are dominant members of the Antarctic benthic amphipod community (Coleman, 1996; De Broyer et al., 2001a). Currently 25 species in 6 genera of Epimeriidae are known from the Southern Ocean, 17 of them from the genus *Epimeria*. The Iphimediidae consist of 48 species belonging to 13 genera. Both families are found throughout the Antarctic.

Very little is known about the evolution and phylogeny of these two families. Watling and Thurston (1989) considered the Epimeriidae (former Paramphithoidae Stebbing 1906) as the sister taxon to the Iphimediidae, but the cladistic biogeography of Antarctic Iphimediidae was based on only six morphological characters. In addition the relativly small phylogenetic analysis, which was carried out before programs such as PAUP were readily available, has proved to be a powerful tool for biogeography. These authors suggested that the retraction of species from a former cosmopolitan distribution occurred before the thermal isolation of Antarctica.

This present study, presents the first molecular analysis of phylogeny of a subset of Antarctic Epimeriidae and Iphimediidae. It is not intended to represent a complete phylogeny of the two families because the number of species was limited due to formaldehyde fixation of specimens from previous expeditions. The Epimeriidae are represented by six species of *Epimeria*, while the Iphimediidae genera *Echiniphimedia*, *Gnathiphimedia* and *Iphimediella* are represented by a total of eight species.

For molecular study a mitochondrial DNA region was chosen to provide resolution at the intergeneric level. Among the mitochondrial genes investigated in Crustacea, the cytochrome oxidase I subunit (COI) gene has proved to be a very useful taxonomic and phylogenetic marker at the intergeneric level (e.g. Meyran et al.,1997; Wares, 2001).

The molecular study is compared with a phylogenetic approach based on morphological characters.

Material and Methods

Amphipods were collected during the cruise ANT XVII-3 by the RV "Polarstern" (Arntz and Brey, 2001). The animals were hand-sorted from towed gear (bottom trawl and Rauschert dredge). In order to minimize degradation of DNA, live animals were briefly rinsed with pre-chilled freshwater and preserved in 96% ethanol at minus 30°C as in Held (2000). Muscle tissue of the first pleopods was isolated while keeping the animals on ice. The tissue was kept refrigerated in 96% ethanol until DNA extraction took place. Species names, sampling locality and depth, as well as accession numbers and collection numbers in the Zoological Institute and Zoological Museum Hamburg are listed in Table 1.

Eusirus cf. *perdentatus* (Eusiridae) and *Monoculodes* sp. (Oedicerotidae) were chosen as outgroups. While *Eusirus* is considered to be closely related to Epimeriidae and Iphimediidae (Englisch, 2001), the Oedicerotidae are believed to be distantly related to Epimeriidae or Iphimediidae (Berge et al., 2001). Two outgroup taxa were chosen because multiple outgroup taxa can increase resolution and support for basal ingroup nodes (Maddison et al., 1984). Specimens of the outgroup species were collected on the same cruise and treated the same way as the epimeriid and iphimediid specimens.

DNA amplification and sequencing

Genomic DNA was isolated using the method of Held (2000) from small pieces of muscle tissue using a QIAamp DNA Mini Kit. PCRs were carried out in 50-µl volumes; with 2 units Qiagen *Taq* polymerase, 5 µl 10xPCR buffer including 1.5mM $MgCl_2$, 250µM of each dNTP, 60 pmol of each amplification primer, 0.5 - 1.2 µl DNA template. Sterile water was added to a total of 50 µl. The COI fragment was amplified using primer sequences developed by Folmer et al. (1994). For amplification modified versions of the primers carrying a sequence tag on their 5' tails were used (Held submitted): HCO 5'- AGC GGA TAA CAA TTT CAC ACA GGT AAA CTT CAG GGT GAC CAA AAA ATC-3' and LCO 5'- CCC AGT CAC GAC GTT GTA AAA CGG TCA ACA AAT CAT AAA GAT ATT GG-3', both primers were provided by MWG-Biotech GmBH. The amplification profile was 3 min at 94°C for denaturation, 36 cycles of 1 min at 94°C, 1 min at 42°C, 1.5 min at 72°C, and last 7 min at 72°C for final extension.

PCR products were purified with Qiagen spin columns (PCR purification kit) and run on an 1% ethidium bromide stained agarose minigel to evaluate purity and DNA content. 1-3 µl of purified PCR product was used for dideoxy cycle sequencing using the manufacturer's protocols (Amersham and Biozym). The sequencing amplification protocol was 94°C for 2 min, 30 cycles of 94°C for 25 s, 52°C for 25 s, and 70°C for 35 s and stored at 4°C.

For sequencing the COI amplification products the fluorescent labelled primers PFS: 5'-CCC AGT CAC GAC GTT GTA AAA C-3' PRS: 5'-AGC GGA TAA CAA TTT CAC ACA GG-3' were used. Depending on their concentration 0.5 – 3 µl of the cycle sequencing reaction were loaded onto an automated sequencer (Li-Cor, models 4000 and 4200).

Gels were proofread using the image analysis software of the automated sequencer. Double stranded sequences were assembled with AlignIR v1.1.

Phylogenetic analysis

The proof-read sequences of the 16 species were aligned with Clustal W version 1.4 (Thompson et al.,1994) as included in BioEdit (Hall, 1999). Using default parameters, minor corrections of the alignment were carried out in order to preserve a contiguous reading frame. Phylogenetic trees were inferred by using maximum parsimony (MP) and maximum likelihood (ML) as optimality criteria. All analyses of the sequences were carried out using PAUP version 4.8 and 4.10 beta (Swofford, 2001, 2002). Chi-square tests of homogeneity of base frequencies and uncorrected pairwise sequence differences were also calculated in PAUP 4.8 beta. Models of sequence change over time were chosen based on a hierarchical likelihood ratio test (Huelsenbeck and Crandall, 1997) as implemented in Modeltest version 3.06 (Posada and Crandall, 1998). This model was then used to calculate pairwise genetic distances and the ML tree (data not shown).

The effect of different transition/transversion rates and weighting schemes of codon positions on the inferred tree topology was tested. Bootstrap tests with 100 and 1000 replicates were used to assess support of various phylogenetic groups.

All morphological characters coded in the matrix were examined on several individuals of each species deposited in the Zoological Museum Hamburg and through descriptions in the literature. One specimen of *Iphimediella georgei* Watling and Holman, 1980 was borrowed from the Museum für Naturkunde in Berlin, Germany. A database of 98 morphological characters was assembled using the software DELTA (Dallwitz et al., 1997). We primarily used binary rather than multistate characters (Table 2). A data matrix (nexus file) was generated for input in PAUP 4.10. beta. All characters were unordered and treated as having equal weight. The list of characters is presented in Table 2, the matrix is shown in Table 3.

Results

Analysis of the nucleotide sequences

Within the 558 aligned nucleotide sites in the mitochondrial COI gene, 271 are constant and 23 variable bases are parsimony-uninformative (including the outgroup species). The majority of variable sites occurred in the third codon position. An indel of the aminoacid

Serine took place at the nucleotid sites 376-378 in five species: *Iphimediella rigida, I. cyclogena, Echiniphimedia hodgsoni, E. waegeli* and *E. echinata*. A heuristic search found a single most parsimonious tree when transitions and transversions are weighted equally (length 1012 steps, CI = 0.51, RI = 0.579, RC = 0.29) (Fig.1a).

Downweighting transitions by a factor of 3-5 resulted in slightly different bootstrap values but in the same tree topology, indicating a robust phylogenetic signal (data not shown). Excluding *Monoculodes* and choosing *Eusirus* cf. *perdentatus* as the only outgroup as well as excluding the third codon position (data not shown) did not change the general topology of *Epimeria* or the Iphimediidae. The Likelihood Ratio Test (LRT) revealed the HKY85 with a transition/transversion ratio of 2.8964, invariant sites (pinvar = 0.4343) and gamma distributed rates (alpha=1.1017) as the model with the best fit to the data. The MP and the ML tree are compatible. The weakly supported node of *Epimeria reoproi, E. similis* and *E. macrodonta* in the MP collapses in the ML tree. The only further difference is the grouping of *Gnathiphimedia sexdentata* and *Iphimediella cyclogena* with *G. mandibularis* in the MP analysis.

Analysis of the amino acids sequences

The phylogenetic analyses based on amino acid sequences yield results congruent to those of the nucleotide sequence analyses. Of 184 Amino acids 53 were parsimony informative (tree length = 159, CI = 0.824, RI = 0.885, RC = 0.729). A heuristic search resulted in four most parsimonious trees, these differ mainly in the position of *Gnathiphimedia mandibularis*, and the relationships of the species of *Epimeria* to each other, although the two clades of the same three species were always retained.

Analysis of the morphological characters

The branch-and-bound search using unweighted characters resulted in one tree (tree length = 205, CI = 0.532, RI = 0.713, RC = 0.379), Fig. 1b. Of 98 unordered characters 9 are constant and 6 are parsimony-uninformative, 83 characters are parsimony-informative. The tree based on morphological characters differs only slightly from those based on the COI fragment.

All analyses indicated the monophyly of *Epimeria,* supported by a bootstrap value of 98 at the basal branch. The analyses suggest that the studied species of Iphimediidae are more closely related to the eusirid *Eusirus* cf. *perdentatus,* originally chosen as an outgroup, than to *Epimeria*. The monophyly of the genus *Echiniphimedia* is supported by all analyses except the amino acid analysis. The varying positions of species of the genera *Iphimediella* and *Gnathiphimedia* indicate clearly that these genera are paraphyletic.

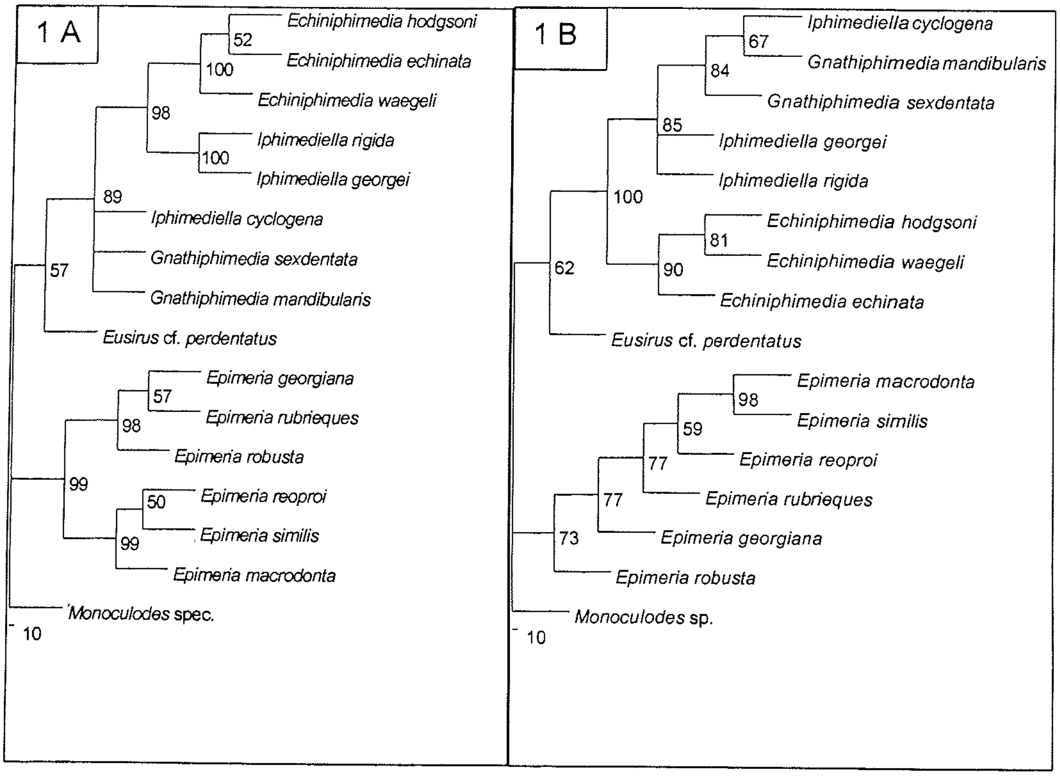

Fig. 1: Phylogenetic trees of 16 Antarctic Amphipoda, bootstrap values of 1000 replicates higher than 50 % shown

A) maximum parsimony phylogram based on a 558 -bp sequence of cyctochrome oxidase subunit 1 (tree length: 1012, CI = 0.51, RI = 0.579)

B) phylogram based on 83 phylogenetic informative morphological characters, (tree length: 205, CI: 0.532, RI: 0.713).

Discussion

Although only a relative small number of taxa were used in this study, our results show that analysis of the COI sequence is suitable for revealing differences at the interspecific level and family level for two Antarctic amphipod families. The higher classification of iphimedioid amphipods has frequently been revised in recent years (Watling and Thurston, 1989; Coleman and Barnard, 1991; Berge et al., 1998). The magnitude of the genetic differences observed between species of *Epimeria* and between species of Iphimediidae is not correlated with spatial differentiation. According to the zoogeographical zonation of the Southern Ocean (De Broyer and Jazdewski, 1993), the outgroup taxa used in this analysis (*Eusirus* cf. *perdentatus*, *Monoculodes* sp.) and *Epimeria georgiana* and *E. reoproi* are from West-Antarctica, while all the other species are from the East Antarctic. Since the two West Antarctic species showed the highest nucleotide divergence within the species of *Epimeria*, the geographic distance apparently does not influence the genetic differentiation.

For *Epimerias* the mean genetic distance for a pairwise sequence comparison for COI calculated with the Kimura 2 parameter test is 20%. Wares (2001) estimated the substitution rate of the same region of COI for Cirripedia 3.1 percent divergence per million years. Referring to this rate the split between the *Epimeria* complex can be dated about 6 million years ago. Since the cooling of Antarctica took place about 40 million years ago, the divergence between *Epimerias* occurred long after the cooling of the Southern Ocean.

One of our aims was to gain an independent assessment of morphological and molecular characteristics that are thought to be of phylogenetic importance. Our molecular and morphological analyses result in very similar phylogenies of the tested species and provide some new insights into character evolution that partly contradict previous interpretations (e.g. Watling and Thurston, 1989). Some characters and difficulties are discussed in more detail below.

Coleman and Barnard (1991) defined two characters for differentiation between the families Epimeriidae and Iphimediidae; the Iphimediidae do not have raker spines, but possess at least one pair of chelate gnathopods. Upon examination of 14 species of these families only certain characters turned out to be restricted to the family Iphimediidae or the genus *Epimeria*. Only *Epimeria* bear spines on the inner curvature of the dactyli of their gnathopods. The examined iphimediids as well as *Eusirus* cf. *perdentatus* have pointed posteroventral corners of pereonite 5 and 6 while those of the examined *Epimeria* are rounded. The posteroventral corner of pereopod 7 is also pointed in *Epimeria*, except in *E. robusta*.

Morphological characters which might support the monophyly of the genus *Echiniphimedia* are, in addition to the body surface covered with processes, spines on the posterolateral margin of pereonite 7 and produced posteroventral corners of pereonites 1-4. The monophyly of *Iphimediella* is questionable because characters such as the incisor show both toothed (*I. georgiana*, *I. rigida*) and smooth states (*I. cyclogena*). *I. cyclogena*, which bears a smooth incisor, clades with the genus *Gnathiphimedia,* which also bears a smooth incisor. In addition *Gnathiphimedia* and *Iphimediella* both have paired teeth on pereonite 7.

One main character used in species keys of *Epimeria* is the presence of dorsal carinae on the pereon (e.g. Wakabara and Serejo, 1999). This obvious character is not phylogenetically supported by our molecular analyses, since *E. robusta*, with all pereon segments lacking dorsal carinae, appears to be closely related to *E. rubrieques* (Fig 1a), a species with carinae on all pereon segments. A morphological character shared by *E. robusta* and *E. georgiana* is the sharply notched basis of pereopod 5.

Conclusion

The Antarctic amphipod families Epimeriidae and Iphimediidae are unlikely to be sister taxa. The results of our molecular and morphological phylogenetic analyses agree closely. Iphimediidae were found to be more closely related to the supposed outgroup *Eusirus* cf. *perdentatus* than to the epimeriids. Very surprisingly, the oedicerotid *Monoculodes* sp. shows a relatively close relationship to *Epimerias*. These results underline the importance of the choice of outgroup for phylogenetic analyses. We suggest the genera *Iphimediella* and *Gnathiphimedia* are paraphyletic, not monophyletic. Potential conclusions from this study are limited by sample size, but further molecular and morphological studies of these and other taxa of Epimeriidae and Iphimediidae from wider geographic areas will test the monophyly of other genera and increase our knowledge of relationships among amphipod families.

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Tab. 1. Species, availability of sequences, collection localities and specimen-deposition number of the Zoological Institute and Zoological Museum Hamburg (ZIM)

Taxa	Sequence acc. no.	Depth (m)	Latitude	Longitude	ZIM collection number
Epimeriidae					
Epimeria georgiana Schellenberg, 1931	AF451341	202	62°49.50' S	060°49.30' W	39888
Epimeria reoproi Lörz and Coleman, 2001	AF451342	48	63°00.10' S	060°31.00' W	39876
Epimeria robusta K.H. Barnard, 1930	AF451344	323	71°11.90' S	012°21.70' W	39902
Epimeria macrodonta Walker, 1906	AF451343	316	71°11.90' S	012°20.70' W	39889
Epimeria rubrieques De Broyer and Klages, 1991	AF451345	648	71°16.67' S	013°45.79' W	39890
Epimeria similis Chevreux, 1912	AF451346	648	71°16.67' S	013°45.79' W	39891
Iphimediidae					
Iphimediella georgei Watling and Holman, 1980	AF451349	316	71°11.90' S	012°20.70' W	39892
Iphimediella rigida K.H. Barnard, 1930	AF451347	323	71°11.90' S	012°21.70' W	39893
Iphimediella cyclogena K.H. Barnard, 1930	AF451348	323	71°11.90' S	012°21.70' W	39894
Eciniphimedia echinata Walker, 1906	AF451352	266	70°50.40' S	010°35.20' W	39895
Echiniphimedia hodgsoni Walker, 1906	AF451350	323	71°11.90' S	012°21.70' W	39896
Echiniphimedia waegeli Coleman and Andres, 1988	AF451351	266	70°50.40' S	010°35.20' W	39897
Gnathiphimedia mandibularis K.H. Barnard, 1930	AF451353	269	70°50.20' S	010°34.89' W	39898
Gnathiphimedia sexdentata (Schellenberg, 1926)	AF451354	318	71°12.19' S	012°19.01' W	39899
Eusiridae					
Eusirus cf. perdentatus Chevreux, 1912	AF451355	673	63°01.20' S	059°09.20' W	39900
Oedicerotidae					
Monoculodes sp.	AF451356	48	63°00.10's	060°31.00' W	39901

Tab. 2. Character list for the morphological analysis of 16 Antarctic Amphipoda.

The data set was prepared in DELTA, which labels the characters in binary states 1 and 2, therefore 0 is not used. The order of states does not reflect any assumptions on which state is plesiomorphic and apomorphic.

1. Telson apically:(1) rounded;(2) pointed
2. Telson, setae on lobe: (1) absent ; (2) present
3. Telson excavation: (1) wide, shallow or absent; (2) narrow
4. Telson:(1) entire or cleft u-shaped; (2) cleft v-shaped
5. Telson elongation: (1) absent; (2) present (clearly longer than broad) Uropod 3 outer ramus: (1) at least twice the length of peduncle; (2) less than twice the length of peduncle
7. Uropod 3 pointed process on apical margin:(1) absent; (2) present
8. Uropod 2 outer ramus: (1) same length or longer than peduncle; (2) shorter than peduncle
9. Uropod 1outer ramus: (1) same length or longer than peduncle; (2) shorter than peduncle
10. Urosomit 1dorsally: (1) smooth; (2) small projection; (3) long pointed projection;(4) multidentate carinae
11. Urosomite 1: (1) longer than urosomites 2 and 3 comined; (2) shorter than urosomites 2 and 3 combined
12. Urosomites 2 and 3 dorsally: (1) smooth; (2) articulated
13. Urosomite 1 posterolateral margin pointed process: (1) absent; (2) present
14. Urosomite 2 posterolateral margin pointed process: (1) absent; (2) present
15. Urosomite 3 posterolateral margin pointed process: (1) absent; (2) present
16. Urosomite 1 middorsal keel: (1) absent; (2) present
17. Urosomite 2 middorsal keel: (1) absent; (2) present
18. Urosomite 3 middorsal keel: (1) absent; (2) present
19. Pleon spinose cuticula:(1) absent; (2) present
20. Epimeral plate 3 posteroventral corner: (1) not produced; (2) slightly produced (3) strongly produced and pointed
21. Epimeral plate 2 posteroventral corner: (1) not produced; (2) slightly produced (3) strongly produced and pointed
22. Epimeral plate 1 posteroventral corner: (1) not produced; (2) slightly produced (3) strongly produced
23. Epimeral plates 1-3 midlaterally: (1) not produced; (2) strongly produced
24. Epimeral plate 3 posterolateral margin: (1) not produced; (2) slightly produced (3) strongly produced and pointed
25. Epimeral plate 2 posterolateral margin: (1) not produced; (2) produced
26. Epimeral plate 1 posterolateral margin: (1) not produced; (2) produced
27. Epimeral plates 1, 2 and 3 middorsally: (1) projection absent; (2) small projection; (3) long pointed projection
28. Epimeral plate 3 paired teeth on dorsal amature: (1) absent; (2) present
29. Epimeral plates 1 and 2 paired teeth on dorsal amature: (1) absent; (2) present
30. Epimeral plate 1 carinae: (1) absent; (2) present
31. Epimeral plates 2 and 3 carinae: (1) absent; (2) present
32. Pereon 1 carina: (1) absent; (2) small; (3) long and pointed
33. Pereon 2 carina: (1) absent; (2) small; (3) long and pointed
34. Pereon 3 carina: (1) absent; (2) small; (3) long and pointed
35. Pereon 4 carina: (1) absent; (2) small; (3) long and pointed
36. Pereon 5- 7 carina: (1) absent; (2) small;(3) long and pointed
37. Pereon 1dominant midlateral protrusion: (1) absent; (2) present
38. Pereon 3and 4 dominant midlateral protrusion: (1) absent; (2) present
39. Pereon 5-7 dominant midlateral protrusion: (1) absent; (2) small; (3) long and pointed
40. Pereonite 6 spines on posterolateral margin: (1) absent; (2) present
41. Pereonite 7 spines on posterolateral margin: (1) absent; (2) present
42. Pereonites 1-4 posteroventral corner: (1) rounded; (2) pointed
43. Pereonite 5 posteroventral corner: (1) rounded; (2) pointed
44. Pereonite 6 posteroventral corner: (1) rounded; (2) pointed
45. Pereonite 7 posteroventral corner: (1) rounded; (2) pointed
46. Pereonite 2: (1) shorter than pereonite 1; (2) same lenght or longer than pereonite 1
47. Pereonite 7 paired teeth: (1) absent; (2) present
48. Coxal plate 1-3 dorsoventral ridge on lateral surface:(1) absent; (2) present
49. Coxa 4 dorsoventral ridge on lateral surface:(1) absent; (2) present
50. Coxal plates 5 and 6 anteriodorsal ridge on lateral surface: (1) absent; (2) present
51. Coxa 7 ateriposterior ridge on lateral surface: (1) absent; (2) present
52. Coxa 5 posteroventral angle:(1) rounded; (2) pointed not produced; (3) produced and pointed
53. Coxa 6 posteroventral angle: (1) rounded; (2) pointed not produced; (3) produced and pointed

54. Coxa 7 posteroventral angle: (1) rounded; (2) pointed
55. Basis 5 posteroventral angle: (1) rounded; (2) pointed not produced; (3) pointed and produced
56. Basis 6 and 7 posteroventral angles: (1) rounded; (2) pointed not produced; (3) produced and pointed
57. Basis 5-7 posterior margin: (1) smooth; (2) sinous
58. Coxa 5 winglike acute process: (1) absent; (2) present
59. Coxal plates 1-3 lateral face: (1) smooth; (2) acute teeth present
60. Coxa 4 laterally: (1) smooth; (2) acute teeth present
61. Coxa 5 and 6 lateral face: (1) smooth; (2) with acute teeth
62. Coxa 7 laterally: (1) smooth; (2) with acute teeth
63. Coxa 4 anteroventrally: (1) not produced; (2) produced
64. Coxa 4 margin midventrally: (1) rounded; (2) pointed
65. Coxa 4 posteroventral margin: (1) concav; (2) straight or convex
66. Coxa 4 posterolateral corner: (1) rounded; (2) pointed
67. Rostrum: (1) shorter than first article of Antenna 1; (2) at least reaching distal margin of first article of Antenna 1
68. Rostrum shape: (1) straight; (2) flexed
69. Antenna 1 peduncle article 1 number of processes: (1) 0; (2) 1; (3) 2;(4) 3; (5) 4; (6) 5
70. Antenna 1 peduncle article 2 number of processes: (1) 0; (2) 1; (3) 2;(4) 3; (5) 4
71. Antenna 2 peduncle article 3 number of processes: (1) 0 or 1; (2) 2 or more
72. Antenna 2 peduncle article 4 number of processes: (1) 0 or 1; (2) at least 2
73. Antenna 2 peduncle article 5 number of processes: (1) 0 or 1; (2) at least 2
74. Labrum: (1) entire; (2) incised
75. Mandible molar: (1) absent or reduced; (2) well developed
76. Mandibular rakers: (1) absent; (2) present
77. Mandibular body: (1) bulky; (2) elongate
78. Mandible incisor: (1) smooth; (2) toothed
79. Maxilla 1 palp: (1) two articulate; (2) three articulate
80. Maxilla 1 palp short robust setae: (1) absent; (2) present
81. Maxilla 1 palp long setae: (1) absent; (2) present
82. Maxilliped palp article 2 distally: (1) not produced; (2) produced
83. Maxille 1 palp: (1) larger than outer plate; (2) smaller than outer plate
84. Maxilla 2 outer plate: (1) broad; (2) narrow, less than1 2 of inner plate
85. Maxilliped palp article 4: (1) absent or weakly developed; (2) well developed
86. Gnathopod 1 palm shape: (1) narrow; (2) wide
87. Gnathopod 2 palm shape: (1) narrow; (2) wide
88. Gnathopod 1 palm length: (1) shorter than dactylus; (2) same or longer than dactylus
89. Gnathopod 2 palm length: (1) shorter than dactylus; (2) same or longer than dactylus
90. Gnathopod 1 spines on inner curvature of dactylus: (1) absent; (2) present
91. Gnathopod 2 spines on inner curvature of dactylus: (1) absent; (2) present
92. Gnathopod 1: (1) simple or subchelat; (2) chelat
93. Gnathopod 2: (1) simple or subchelat; (2) chelat
94. Pereopod 3 and 4 merus:(1) not produced; (2) produced
95. Pereopod 5 merus: (1) not produced; (2) produced
96. Pereopod 6 merus: (1) not produced; (2) produced
97. Pereopod 7 merus: (1) not produced; (2) produced
98. Subantennal sinus: (1) absent; (2) present

Tab. 3. Character matrix of 16 Antarctic Amphipoda and 98 characters, character states shaded are variable.

Character:	10	20	30	40	50	60
Epimeria georgia	1 2 2 2 1 1 2 1 1 2	1 1 1 1 2 1 1 2 1 3	2 1 1 1 1 1 2 1 1 2	2 1 1 1 2 2 1 1 1 1	1 1 1 1 1 1 1 1 2 1	1 1 1 1 1 1 1 1 1 1
Epimeria reoproi	2 2 2 2 1 2 2 1 1 2	1 1 1 1 2 1 1 2 1 3	2 2 2 1 1 1 2 1 1 2	2 1 1 1 1 2 1 1 2 1	1 1 1 1 1 1 1 1 2 1	1 1 1 1 3 3 1 1 1 1
Epimeria robusta	1 2 1 2 1 2 2 1 1 3	1 1 1 2 2 1 1 2 1 1	3 3 1 1 1 1 2 1 1 2	2 1 1 1 1 1 1 1 1 1	1 1 1 1 2 1 1 1 1 1	1 3 3 1 1 1 1 1 1 1
Epimeria macrodonta	2 1 2 2 1 2 2 1 1 3	2 1 1 2 2 1 1 2 1 3	3 3 2 1 1 1 3 1 1 2	2 2 1 2 3 3 2 2 3 1	1 1 1 1 1 1 1 2 2 1	1 1 1 1 3 3 1 2 1 2
Epimeria rubrieques	2 1 2 2 1 1 2 1 1 2	1 1 1 1 2 1 1 2 1 3	2 1 1 1 1 1 3 1 1 2	2 3 3 3 3 3 1 1 2 1	1 1 1 1 1 1 1 2 2 2	2 3 1 1 1 1 1 2 1 1
Epimeria similis	2 1 2 2 1 2 2 1 1 3	1 1 1 ■ 2 1 1 2 1 3	3 3 2 1 1 1 3 1 1 2	2 1 1 2 3 3 1 2 3 1	1 1 1 1 1 1 1 2 2 1	1 3 1 1 3 3 1 2 1 2
Iphimediella georgia	2 1 1 2 2 1 2 2 2 2	1 1 1 1 2 2 1 1 1 2	2 1 1 3 2 2 1 1 2 1	2 1 1 1 1 1 1 1 1 1	1 1 2 2 2 1 2 1 1 1	1 2 2 2 2 2 1 1 1 1
Iphimediella rigida	2 1 1 1 2 1 2 2 2 2	1 1 1 1 2 2 1 1 1 3	2 1 1 3 2 2 1 2 2 2	2 1 1 1 1 1 1 1 1 1	1 1 2 2 2 1 2 1 1 1	1 2 2 2 1 2 1 1 1 1
Iphimediella cyclgena	1 2 2 1 2 2 2 2 2 1	1 1 1 1 2 1 2 2 1 3	3 1 1 3 2 1 1 2 2 1	1 1 1 1 1 1 1 1 1 1	1 1 2 2 2 1 2 1 1 1	1 2 2 2 2 2 1 1 1 1
Echiniphimedia echinata	1 1 1 1 1 1 2 2 2 4	1 1 1 1 2 2 1 1 1 3	2 1 2 3 1 1 1 1 1 2	2 1 1 1 1 1 1 1 1 1	2 2 2 2 2 1 1 1 1 2	1 3 3 1 2 2 2 1 1 1
Echiniphimedia hodgsoni	2 1 1 1 2 1 2 2 2 4	1 1 1 2 2 2 1 2 1 3	3 1 2 3 1 1 1 1 1 2	2 1 1 1 1 1 1 1 1 2	2 2 2 2 2 1 1 1 2 1	1 1 1 1 2 2 2 1 2 2
Echiniphimedia waegeli	1 1 1 1 1 1 2 2 2 4	1 1 1 1 2 2 1 2 1 3	3 1 2 3 1 1 1 1 1 2	2 1 1 1 1 1 1 1 1 2	2 2 2 2 2 1 1 2 1 2	2 2 2 2 2 2 2 1 2 2
Gnathiphimedia mandibularis	2 2 1 1 2 2 2 2 2 1	1 1 1 1 2 1 2 2 1 3	2 1 1 3 2 2 1 2 2 1	1 1 1 1 1 1 1 1 1 1	1 1 2 2 2 1 2 1 1 1	1 2 2 2 2 2 1 1 1 1
Gnathiphimedia sexdentata	2 2 2 1 2 1 2 2 2 1	2 1 1 1 2 1 1 1 1 3	2 2 1 3 2 1 1 1 2 1	1 1 1 1 1 1 1 1 1 1	1 1 2 2 2 1 2 1 1 1	1 2 2 2 2 2 1 1 1 1
Eusirus cf. *perdentatus*	2 1 1 2 2 1 1 1 1 2	1 1 1 1 1 1 1 1 1 1	2 1 1 1 1 1 3 1 1 2	2 1 1 1 1 3 1 1 1 1	1 1 2 2 2 2 1 1 1 1	1 1 1 1 2 2 1 1 1 1
Monoculodes sp.	1 2 1 1 1 2 1 1 2 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 2	2 1 1 1 1 1 1 1 1 1	1 1 1 1 1 2 1 1 1 1	1 1 1 1 1 1 1 1 1 1

Character:	70	80	90	
Epimeria georgia	2 1 2 1 2 2 2 2 3 1	1 1 1 2 2 2 2 2 1 2	2 1 1 1 2 2 2 1 1 2	2 1 1 2 2 2 2 1
Epimeria reoproi	2 1 2 2 1 2 2 2 4 3	2 2 1 2 2 2 2 2 1 2	2 1 1 1 2 1 1 1 1 2	2 1 1 2 2 2 2 1
Epimeria robusta	1 1 2 1 2 2 2 1 1 1	1 1 1 2 2 2 2 2 1 2	2 1 1 1 2 2 2 2 1 2	2 1 1 2 2 2 2 1
Epimeria macrodonta	2 1 2 2 1 2 2 2 4 4	1 2 1 2 2 2 2 2 1 2	2 1 1 1 2 1 1 1 1 2	2 1 1 2 2 2 2 1
Epimeria rubrieques	2 1 2 2 1 2 2 2 3 3	1 1 1 2 2 2 2 2 1 2	2 1 1 1 2 2 2 1 1 2	2 1 1 2 2 2 2 1
Epimeria similis	2 1 2 2 1 2 ■ 2 4 3	1 2 1 2 2 2 2 2 1 2	2 1 1 1 2 1 1 1 1 2	2 1 1 2 2 2 2 1
Iphimediella georgia	1 1 1 2 1 1 1 2 4 3	1 2 1 2 1 1 2 2 1 1	2 1 1 1 1 1 1 2 2 1	1 2 2 2 2 2 2 2
Iphimediella rigida	1 1 1 2 1 2 2 2 3 2	1 2 1 2 1 1 2 2 1 1	2 1 1 1 1 1 1 1 2 1	1 2 2 2 2 2 2 2
Iphimediella cyclogena	1 1 1 2 1 1 1 2 3 3	1 2 1 2 1 1 2 1 1 1	2 1 1 1 1 1 1 2 2 1	1 2 2 2 2 2 2 2
Echiniphimedia echinata	1 1 1 2 1 2 2 2 4 3	1 1 1 1 1 1 2 1/2 1 1	2 1 1 1 1 1 1 2 2 1	1 2 2 2 2 2 2 2
Echiniphimedia hodgsoni	2 2 1 2 2 1 1 2 6 4	2 2 2 1 1 1 2 2 1 1	2 1 1 1 1 1 1 2 2 1	1 2 2 2 2 2 2 2
Echiniphimedia waegeli	2 2 1 2 1 2 2 2 4 3	1 2 1 1 1 1 2 2 1 2	1 1 1 1 1 1 1 2 2 1	1 2 2 2 2 2 2 2
Gnathiphimedia mandibularis	1 1 1 2 1 2 2 2 3 3	1 1 1 1 1 1 1 1 1 2	2 1 1 1 1 1 1 2 2 1	1 2 2 2 2 2 2 2
Gnathiphimedia sexdentata	1 1 1 2 1 2 1 2 4 2	1 1 1 1 1 1 1 1 1 1	2 1 1 1 1 1 1 2 2 1	1 2 2 2 2 2 2 2
Eusirus cf. *perdentatus*	1 1 2 1 2 1 1 1 4 5	2 2 1 1 2 2 2 2 1 2	2 ■ 1 1 2 2 2 2 2 1	1 1 1 1 2 2 2 2
Monoculodes sp.	1 1 1 1 2 1 1 1 1 1	1 1 1 1 2 2 2 2 1 2	2 1 1 1 2 2 2 1 2 1	1 1 1 1 1 2 2 1

Veröffentlichung VI

Phylogeny of Antarctic *Epimeria* (Epimeriidae, Amphipoda)

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Abstract

Amphipoda belong to the most abundant benthic organisms of Antarctica. Among those Epimeriidae belong to the most dominant families. Morphological characters are used to explore relationships between the species of all Antarctic *Epimeria*, 70% of Antarctic epimeriid species belong to this genus. Additionally some *Epimeria* from the deep sea of Brazil and the Tasman Sea, as well as from shallow Norwegian waters are analysed. Species of *Epimeriella* and *Metepimeria* as well as iphimedoid taxa are considered.

An extremely high intraspecific variation was observed, while studying several specimen of each species when possible. This intraspecific variation was neither related to size, nor sex, nor locality and may indicate a recent speciation of some taxa of Antarctic epimeriid Amphipoda.

The small amount of taxa studied from the deep-sea and the Northern Hemisphere and the difficulty to define apomorphic and plesiomrphic conditions does not allow to present final conclusions about the origin of Antarctic *Epimeria* living on the shelf. Nonetheless, deep-sea species from the mid Atlantic clade with deep-sea species from the west Pacific and two of the three studied north Atlantic species. This chains the idea of Watling and Thurston (1989) of Antarctica acting as an evolutionary incubator.

Introduction

In the Southern Ocean benthic ecosystem, crustaceans are by far the most speciose taxon (Arntz et al. 1997). Among the crustaceans amphipods are the most numerous group with more than 820 recorded species (De Broyer & Jazdezewski 1996. The amphipod family Epimeriidae Boeck, 1871 (formerly Paramphithoidae) belongs to the dominant members of Antarctic benthos (Coleman 1990). Even though recent studies have addressed the feeding behaviour or the potential impact of several species of *Epimeria* (Dauby et al. 2001 a, b) their phylogeny has not been seriously approached. Of 26 species of Antarctic Epimeridae 18 belong to the genus *Epimeria*. With the exception of the *Epimeria* sp., Andres 1985, the phylogeny of all species of Antarctic *Epimeria* is investigated in the present study.

Very few cladistic studies based on morphological characters of closely related taxa of amphipods, and also of other peracarid crustaceans exist (e.g. Berge 2001, Leistikow & Schmidt 2002). An obvious problem is the difficulty to define phylogenetic informative characters while dealing with morphologically similar species. Especially among amphipods the characters separating families are often very small. For example, Iphimediidae only differ from Epimeriidae in having at least on pair of chelat gnathopods and lack the mandibular raker spines (Coleman & Barnard 1991); Iphimediidae differ from Eusiridae by having at least one of coxae 1-4 being pointed (Barnard & Karaman 1991).

Epimeriidae, former Paramphithoidae Stebbing, 1906, are among other things characterised by a compressed body, a well developed rostrum, elongate antenna, strong mandibular raker row and a large molar. The genus *Epimeriella* differs from *Epimeria* mainly in the shape of their molar, which is not triturative, and the wide gap of the hypopharynx. A separation of genera based on the shape of mouthparts is common within amphipod taxonomy, e.g. *Gnathiphimedia* and *Iphimediella* have a differently shaped mandible and a different width of their epistome. Coleman (1989b) described the functional morphology of the mouthparts of two iphimediid amphipods. An adaptation of the structure of the mandibles to the presumed food was investigated, unique in each case of the genera.

Material & Methods

A database of 106 morphological characters was assembled using the software DELTA (Dallwitz et al. 1997). Most of the characters are binary rather than multistate (Tab. 1), 22 characters have three states, three characters have four or more conditions. A data matrix (nexus file) was generated for input in PAUP 4.10. beta version. All characters were unordered and treated as having equal weight in the first analysis.

Improved resolution was received by "reweighting" the characters based on rescaled consistency indices (CI). Stability of trees was assessed using bootstrap (Felsenstein 1985), based on 1000 replicates. Trees were drawn using TreeView 1.6.5. The list of characters is presented in table 1, the matrix is shown in table 2, the apomorphies according to figure 2 are listed in table 3. The order of states does not reflect any assumptions on which state is plesiomorphic.

In total 37 taxa were phylogenetically approached.

The main object of this study, the phylogeny of the genus *Epimeria* of the Southern Ocean is delineated by 17 of the 18 known Antarctic species; *Epimeria* sp. Andres, 1985 was not considered. Further three species of *Epimeria* of the deep sea of Brazil were included as well as four species of the northern Atlantic, in order to resolve a better resolution of the Antarctic species. Further genera of Antarctic Epimeriidae are used in the analysis: *Epimeriella*, represented by two species and the monotypic genus *Metepimeria*.

The Iphimediidae, of which Watling & Thurston (1989) thought they would be the sister family of the Epimeriidae (formerly Parampithoidae) are represented by eight species belonging to the three genera *Gnathiphimedia*, *Iphimediella* and *Echiniphimedia*.

Outgroups were originally chosen from non-iphimedioid amphipods, *Eusirus* cf. *perdentatus* (Eusiridae) and *Monoculodes* sp. (Oedicerotidae).

All 106 characters were studied using several individuals of each species if possible. Specimens not deposited in the Zoological Museum Hamburg were borrowed from the Museum für Naturkunde in Berlin, Germany; Zoological Museum Copenhagen, Denmark; Museum of Victoria, Melbourne, Australia; Muséé Histoire Naturelle, Paris, France and Museum Tromsø, Norway.

Results

The analysis using 106 unweighted, unordered characters resulted in one single most-parsimonous tree with a tree length of 452 steps, consistency index (CI) 0.29 and retention index (RI) 0.65, illustrated in Fig.1. *Eusirus* cf. *perdentatus*, originally chosen as an outgroup, is grouped closely to the Iphimediidae.

Automatic reweighting of characters changed the weights of 83 parsimony informative characters. After reweighting twice, 6 characters were given weight zero so effectively excluded from the analysis, 41 were given a weight less than 0.2 leaving 59 with a weight between 0.2 and 1.0 (table 2). Again only one most parsimonious tree was received, CI= 0.52, RI=0.83. (Bootstrap values of 100 replicates are included). While studying several specimens of the single species –when possible - different states of one character were examined, e.g. the mandibular incisor being smooth and toothed (*Echiniphimedia echinata*), coxa 4 midventrally pointed and rounded (*Epimeria parasitica*), posterolateral margin of urosomit 2 being smooth and bearing a pointed process (Fig. 3a, b). The length of the rostrum varied e.g. between same sized females of *Epimeria rubriques* (Fig. 3 e, f).

The tree based on the reweighted characters (Fig. 2) differs slightly from the one with unweighted characters (Fig. 1), both differences take place in crown groups. While in Fig. 1 *E. oxicarinata* and *E. pulchra* are grouped, these are lined in fig. 2. The second difference is the ingrouping of *E. georgiana*, *E. robusta* and *E. heldi* after reweighting. The tree topology does not change from reweighting once to further reweighting, the consistency indices stay identical after reweighting twice.

Some clades are discussed in more detail: Next to characters with less weight, such as an incised labrum or urosomit 1 bearing a long pointed projection, the spines on the dactyli of both gnathopods characterise all species of Epimeriidae, clade 71. The genus *Epimeriella* (clade 69) is characterised by a mandibular molar being reduced and, with less support, the merus of pereopods 3 and 4 not being produced and the outer ramus of uropod 1 being shorter than the peduncle.

Clade 49 shows the single deep-sea species from the Tasmanian sea (*E. glaucosa*) with two species from Norway (*E. cornigera* and *E. parasitica*), their most important synapomorphy is the produced posterolateral margin of all epimal plates. The three Brazilian deep-sea species form clade 47, characterised mainly by their epimeral plates being smooth middorsally.

With the exception of *E. loricata,* the species occurring outside of Antarctic waters, from the northern and middle Atlantic as well as from the south-west Pacific group form clade 50. Their synapomorphies are a produced and pointed posteroventral angle of coxa 5, a midventrally pointed coxa 4, the lateral surface of coxa 5 bearing an acute tooth or bump and –with most weight- the merus of pereopods 5-7 not being produced. The third species from the northern hemisphere *E. loricata* groups with *E. grandirostris* from Antarctica and further spiny species from the Southern Ocean bearing for example a dominant midlateral protrusion on the first pereon.

Discussion

A main character used in determination keys to species of *Epimeria* is the presence or absence of a carina on the pereon segments (Wakabara & Serejo, 1999). This character is also used in our phylogeny. The carina on the pereonites is coded by the characters 20-26,

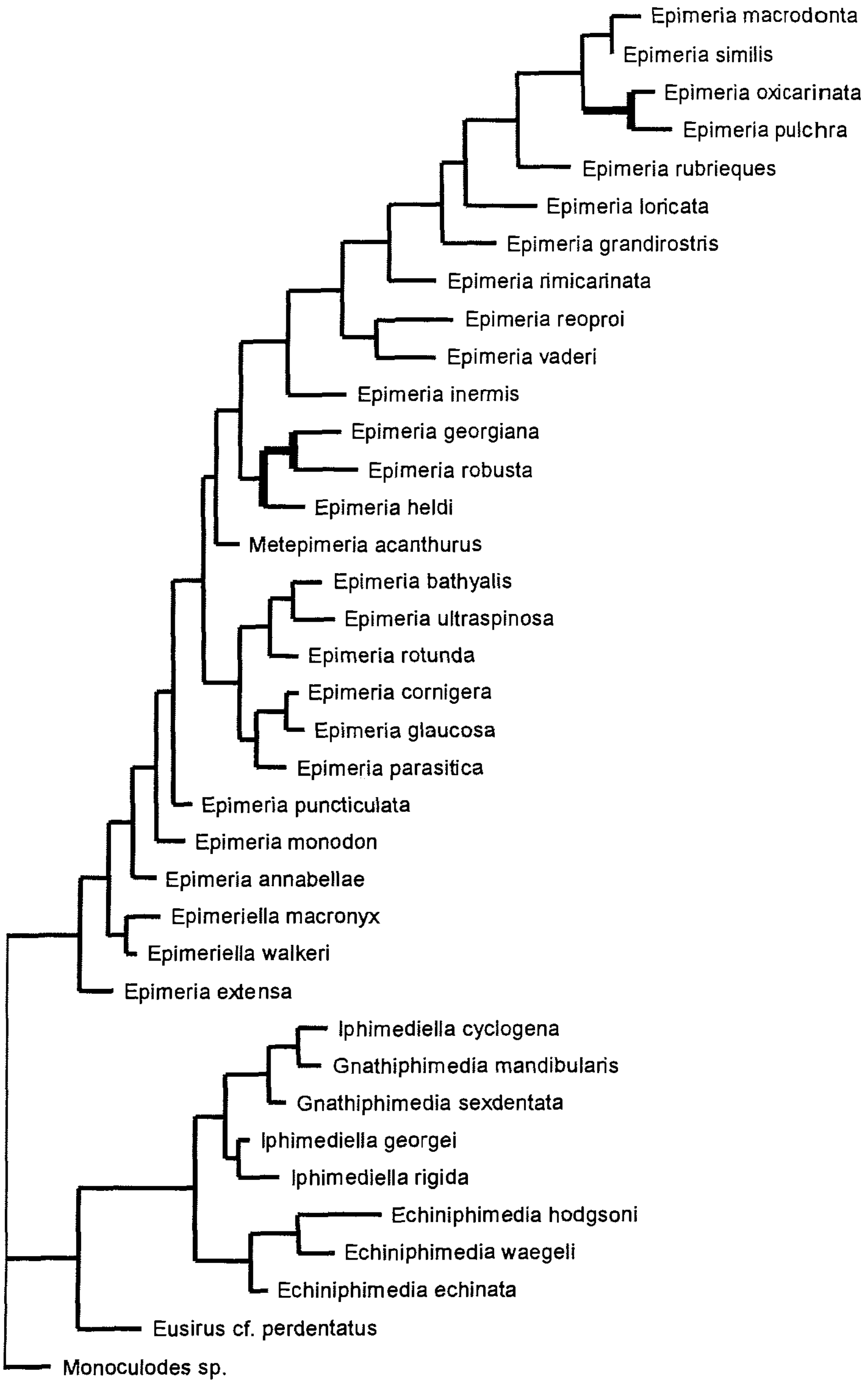

Fig. 1. Single most parsimonious tree of 106 unweighted characters. The differences to the tree resulting after reweighting are indicated by thicked lines.

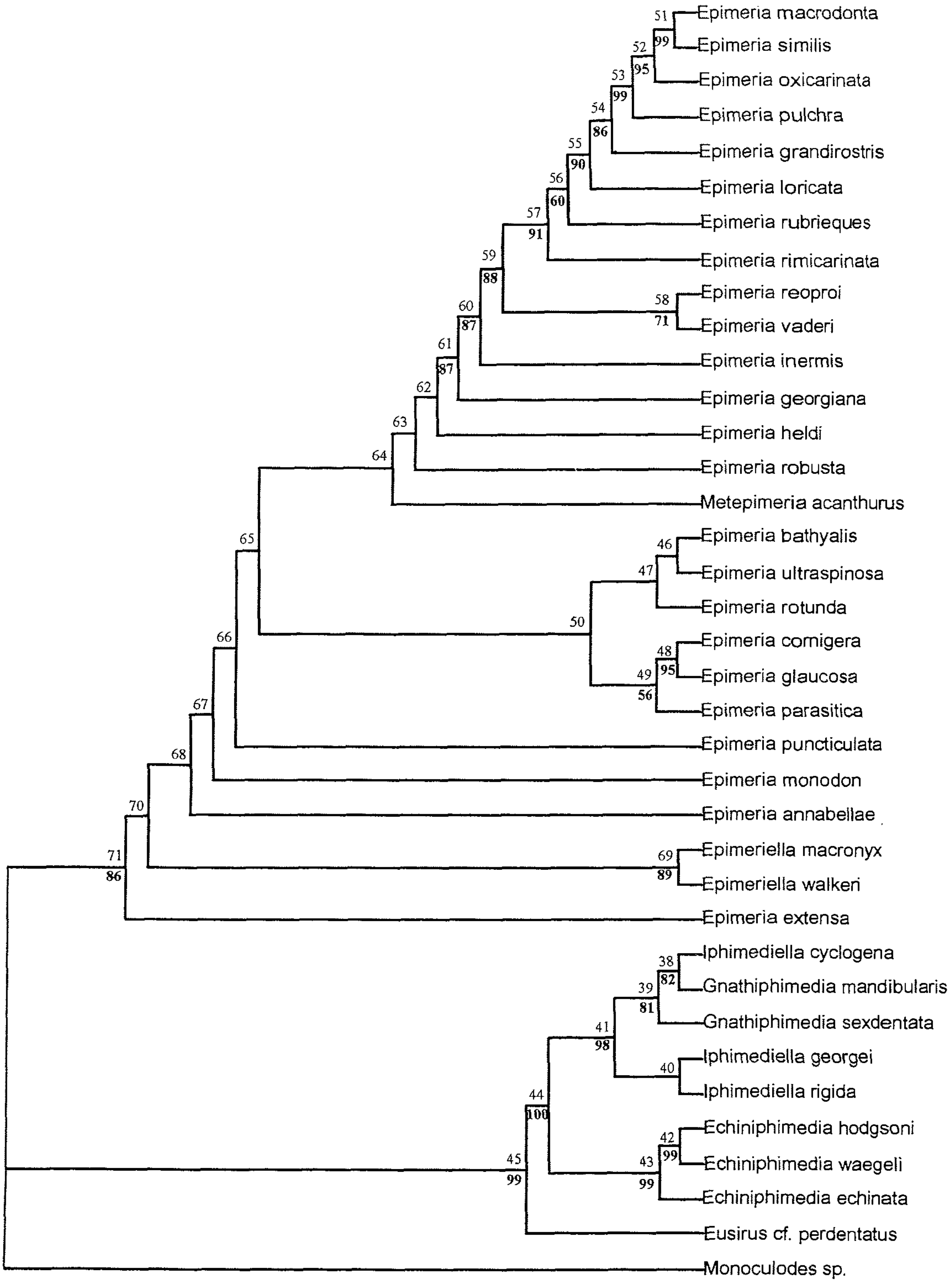

Fig. 2. Single most parsimonous tree resulting after automatic reweighting of characters in Paup; bootstrap values of 1000 replicates below the banches, numbers of clades above the branches, referring to table3.

these show highly variable weights, the carina on pereon 3 is scored highest (CI: 1.00), Tab. 1.

All characters were treated as unordered, the authors cannot say which states are apomorphic and which are plesiomorphic. Juveniles of several *Epimeria* species were studied to get hints about plesiomorphic conditions of characters. An example of changing morphological proportions with age is the length of the rostrum in proportion to the articles of the peduncle of the first antenna. The juveniles of *Epimeria robusta* showed to have a significant longer rostum than the adults, its length extended the second article of the peduncle of the first antenna, while the rostrum of the adults of *E. robusta* just reached the length of the first article, Fig. 3 c and d. Unfortunately a long rostrum cannot be interpreted as a plesiomorphic condition, since this character condition is irregularly expressed among species of Antarctic *Epimeria*. Coleman (1990) showed the rostra of juveniles of *E. oxicarinata* and *E. pulchra* to be shorter than those of their adults.

Coleman (1990) also mentioned the reduction of acute body processes of juveniles as an adaptation of the life in the marsupium, we clearly agree.

While the monophyly of the family Epimeriidae, Boeck 1871, is supported by our data, the monophyly of the genera *Epimeria, Epimeriella* and *Metepimeria* has to be questioned. The main apomorphy of *Metepimeria*, only containing the single species *Metepimeria acanthurus*, among the family Epimeriidae is the absence of the fourth article of the maxillipedal palp. This is a character also presented by the studied species of Iphimediidae. An apomorphy of the genus *Epimeriella* is the drawn out pars molaris without a triturative surface. If *Epimeria extensa* would not have been included in this analysis, the monophyly of *Epimeriella* would have been shown. Even though the holotype of *Epimeria extensa*, described by Andres 1985, is considered a male, it might be a juvenile of another Antarctic epimeriid amphipod (Coleman, pers. com.). With a length of 11 mm the species belongs to the smallest *Epimeria* described from the Southern Ocean. It might well be that *Epimeria* and *Epimeriella* are paraphyletic. A further character which is supposed to be an apomorphy for *Epimeriella* (Coleman pers. com.) is the width of the hypopharyngeal gap. Our measurements showed no significant difference for example between *Epimeria macrodonta* and *Epimeriella truncata.* We assume that species of *Epimeriella* show plesiomorphic characters of Antarctic Epimeriidae and should therefore be synonymised with *Epimeria.*

A main difficulty of this analysis was to find morphological distinct characters on the generic level. Many characters considered were not expressed as discrete states and could not be translated in phylogenetic information, such as the width of the rostrum, spines on the epimeral plates or on the lobes of the telson, the shape of the posteroventral angle of the bases 5-7, the shape of the second article of the maxillipedal palp and shape and size of the eye. There is a tendency of the species of *Epimeriella* and their closely related species of *Epimeria* to have large eyes. *Epimeria robusta* has clearly kidney-shaped eyes while those of *E. grandirostris* are round, and those of *E. vaderi* are oval, but too many stages amid occurred, such as from *E. ultraspinosa* or *E. rubrieques*. Other characters which could not be included due to high variability are the number of spines on different parts of the body, e.g. on every uropod ramus, on the uropodal peduncle, on the bases of pereopds 5–7 or on mouthparts such as the mandibular incisor. The amount of spines varied intraspecifically as well as related to size. Further characters not included in the matrix were all kind of length ratios, such as articles of the antenna or pereopods. After checking for a normal distribution of data for the single species a T-Test was conducted. Often the character states did not differ significantly between a first group of species and a second group, but did differ significantly between the first and a third group. Unfortunately, the third group would not differ significantly from the second group. This problem was often found with ratio calculations, for example the length to width of the telson, the length of the peduncle of uropod 3 to the length of the telson, and the ratios of certain epimeral plates and pereonites. The ratio of the outer rami to the inner rami of uropod 2 seemed to be relatively constant within species. The rami ratio varied between 0.5 and 0.69 in E*pimeria*, while the outer rami of the second uropod of iphimediids were generally longer, with a ratio of 0.63-0.73. Future phylogenetic analyses of closely related taxa based on morphological characters could include multivariate tests to extract the relationships of characters.

Some characters varied intraspecifically, but were related neither to sex, size, nor location. Examples are the incision of the labrum, which was differently developed among species of *Iphimediella*, especially among individuals of *I. cyclogena*; or the length of the rostrum of *Epimeria rubrieques* which sometimes reaches the second article of the first antenna, but often extends only to the first article. Not all studied specimens of *Epimeria similis* had a pointed, posterolateral process on the second urosomite. Coleman (1994) pointed out the variability of the dorsal armature of *E. robusta*.

The relatively high morphological variability of single species of *Epimeria,* especially of *E. similis*, may indicate a recent speciation in the Southern Ocean, Lörz & Held, pers. com., calculated the speciation of *Epimeria* about 4-6 million years ago. The observed high intraspecific variation supports the assumption that the speciation of Epimeriidae happened

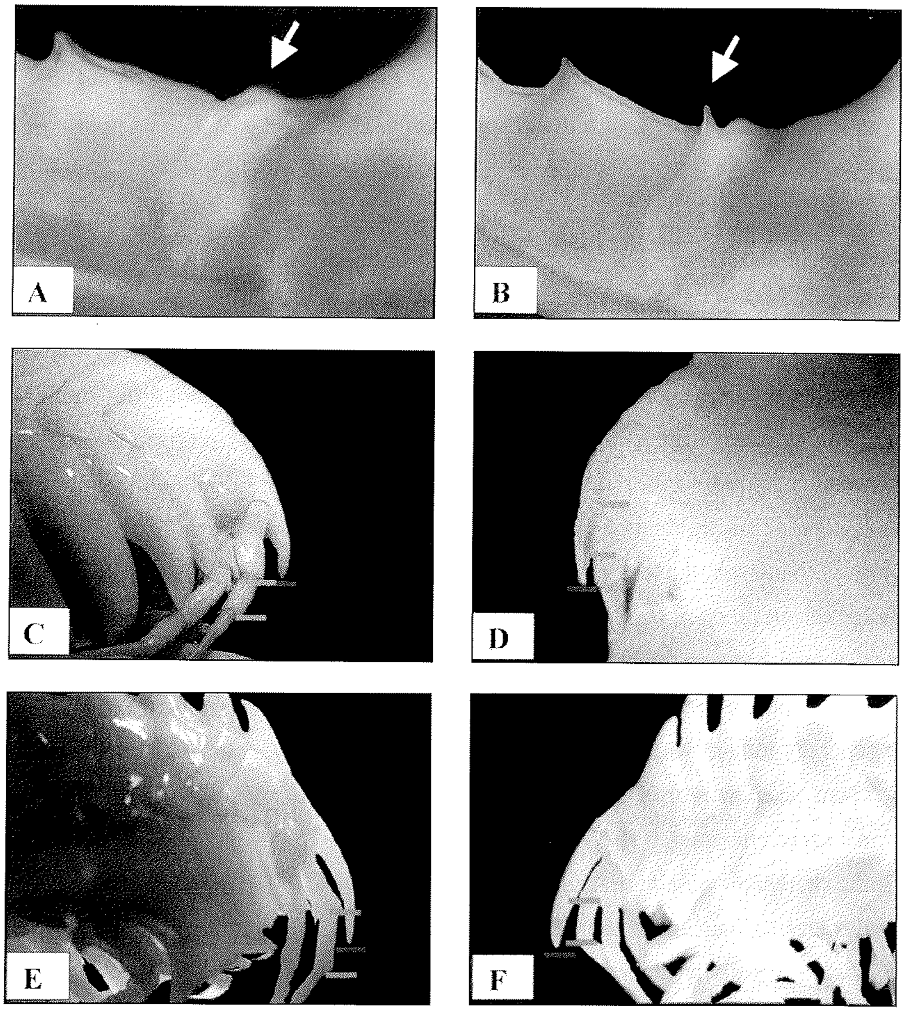

Fig. 3. Examples of intraspecific variation among Antarctic *Epimeria*

a), b) *Epimeria similis*, females, same size: a) dorsally smooth second urosomit, b) second urosomit with dorsal projection.

c), d) *Epimeria robusta*, female (c) and juvenile of its marsupium (d), the length of the rostrum is indicated by a red line, the beginning and end of the second article of the peduncle of the first antenna is pointed out by green lines.

e), f) *Epimeria rubrieques*, females, same sized, coloured lines as in c and d.

after the cooling of Antarctica about 40 MYA, and even after the establishment of the Drake Passage, which successively led to a deep water current with high velocity about 17 MYA. The relatively young dating of speciation in Antarctica, placed after it's cooling, was already proposed by Watling & Thurston (1989) for iphimediid amphipods, by Page & Linse (2002) for the bivalve *Limatula* and by Bargeloni et al. (2000) for the crustacean *Euphausia*. But not only invertebrates undergo a recent speciation in the Southern Ocean, Stankovic et al. (2001) dated the split between the nothothenoid fish genera *Patagonothen* and *Lepidonotothen* about 6.6-7.1 MYA.

The phylogenetic trees based on morphological and molecular characters to 6 species of *Epimeria* and 9 species of Iphimediidae was compared by Lörz & Held (pers. com). The matrix of Lörz & Held (pers. com.) consists of 98 characters and 16 taxa. The characters used could not be transferred to those extended present morphological phylogeny of the Antarctic *Epimeria*. A further analysis of characters revealed that some had to be separated and transferred into different character states. Some of these characters are: Urosom 2 and 3 are different in *Epimeria inermis*, *E. rimicarinata* and *E. vaderi*; the epimeral plates differ middorsally in *E. annabellae*, *E. monodon* and *E. puncticulata*; the carinae of pereon 5-7 differed in 5 species; the midlateral protusion of pereon 3 and 4 differed in *E. rimicarinata*, the bases of pereopod 6 and 7 had different posteroventral angles in *E. annabellae* and *E. grandirostris*. These examples underline the importance of the study of a high number of species most likely belonging to a monophyletic group.

The sampling depth of the analysed specimens varied from 48 m (*E. reoproi*, Antarctic Peninsula) to 3710 m (*E. glaucosa*, Tasmanian Sea). All Antarctic specimens were caught above 700 meters. Most of the studied species have a depth range of several hundred metres. No correlation between intraspecific variation among single species and depth was found. The Antarctic continental shelf extends to a depth of more than 1000 metres (Clarke, pers. com.). Therefore, it is not surprising that the intraspecific variation is not influenced by depth. No species of *Epimeria*, nor any species of the family Epimeriidae is known to occur in the Antarctic deep-sea, below 2000 m. The deep-sea species from Brazil *Epimeria bathyalis*, *E. rotunda* and *E. ultraspinosa* as well as *E. glaucosa* from the Tasmanian Sea could only be studied with a single individual, therefore no intraspecific variation is known for these deep-sea species of *Epimeria*. The three Brazilian species of *Epimeria* were caught in a depth above 1600 meter (Wakabara & Serejo, 1999) and have not been recorded from any other location yet. Therefore it is not known whether these species also occur in shallow waters. Even though the studied specimens of *E. cornigera* are from the north Atlantic (North Norway) this species also occurs in South Africa. The family Epimeriidae (formerly Paramphithoidae) is represented in South Africa only by the genus *Epimeria*. Species of *Epimeria* have not been recorded from the Antarctic deep sea. This might be due to the fact that this region belongs to the most unexplored of the world. The three deep-water species from Brazil, *E. bathyalis*, *E. rotunda* and *E. ultraspinosa* are closely related with the deep-water species from the Tasmanean Sea, *E.glaucosa*, and two species from shallow waters of the Northern hemisphere, *E. cornigera* and *E. parasitica.*

Dauby et al. (2001a) distinguished eight feeding types of amphipods in the Weddell Sea: suspension-feeding, deposit-feeding, deposit-feeding coupled with predation, opportunistic predation, micropredatory browsing, macropredation coupled with scavenging, opportunistic necrophagy and true necrophagy. The studied species are distributed among four trophic types, their lifestyle is not reflected by our phylogeny. *Epimeria macrodonta*, an opportunistic predator, is morphologically most similar to *E. similis*, a micropredatory browser that grazes on cnidarian colonies. These two morphologically very similar species have been synomised by K.H. Barnard (1930), but were separated by Andres 1985
The three species *Epimeria macrodonta*, *E. robusta* and *E. rubrieques* are opportunistic predators, they feed on small material that they detect using their antennae and capture it with the gnathopods. They are weakly motile but can walk on the seafloor in search of food (Dauby et al. 2001b). Surprisingly *Epimeriella walkeri* is considered as a macropredatory/opportunistic scavenger, from stomach contents it seems to be a predator of brittle stars, while *Epimeria georgiana* is a deposit-feeder (Dauby et al. 2001a).

Even though the three species of *Epimeria* belonging to the opportunistic predatory type are not very closely related, we believe that most *Epimerias*, if studied carefully, belong to this feeding type.
Echiniphimedia hodgsoni, feeds on sponges, and *Gnathiphimedia mandibularis* on bryozoans, are also considered to be micropredatory browsers. Traditionally, the morphology of mouthparts plays an important role in phylogenenetic reconstructions of the Crustacea (e.g. Berge et al., 1998). Three of the six characters used by Watling & Thurston (1989) are from the mouthparts. Watling & Thurston (1989) also based their frequently cited cladistic biogeography of the family Iphimediidae on the shape of these mouthparts. The present phylogenetic analysis is based on morphological characters from several body parts It suggests the conclusion that the phylogenetic relationships among *Epimeria* do not seem to be

influenced by their feeding type. The topology of the resulting tree only shows minor changes if the characters coding the mouthparts (# 9-19, Table 2) are excluded.

The small amount of taxa studied from the deep sea and the Northern Hemisphere and the difficulty to define apomorphic and plesiomrphic conditions does not allow to present final conclusions about the origin of Antarctic *Epimeria* living on the shelf. Nevertheless the deep sea species from the mid Atlantic clade with the deep sea species from the west pacific and two of the three north Atlantic species. This supports the idea of Watling and Thurston (1989) of Antarctica acting as an evolutionary incubator.

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Tab. 1. Character list for the analysis of Antarctic *Epimeria.* The order of states does not reflect any assumptions on which state is plesiomorphic. Character weights applied in the final heuristic search (the consistency indices after reweighting twice) follow in cornered parentheses. All characters are unordered.

1. Subantennal sinus: (1) absent; (2) present. [1.00]
2. Rostrum:(1) shorter than first article of Antenna 1; (2) at least reaching distal margin of first article Antenna 1. [0.07]
3. Rostrum shape: (1) straight; (2) flexed. [0.04]
4. Antenna 1 peduncle article 1 number of processes: (1) 0; (2) 1; (3) 2; (4) 3;(5) 4; (6) 5. [0.19]
5. Antenna 1 peduncle article 2 number of processes:(1) 0; (2) 1; (3) 2; (4) 3; (5) 4. [0.16]
6. Antenna 2 peduncle article 3 number of processes: (1) 0 or 1; (2) 2 or more. [0.11]
7. Antenna 2 peduncle article 4 number of processes: (1) 0 or 1; (2) at least 2. [0.07]
8. Antenna 2 peduncle article 5 number of processes: (1) 0 or 1; (2) at least 2. [1.0]
9. Labrum: (1) entire; (2) incised. [0.17]
10. Mandible molar: (1) absent or reduced; (2) well developed. [0.44]
11. Mandibular rakers: (1) absent; (2) present. [1.00]
12. Mandible incisor:(1) smooth; (2) toothed. [1.00]
13. Maxilla 1 palp: (1) two articulate; (2) three articulate. [1.00]
14. Maxille 1 palp:(1) larger than outer plate; (2) smaller than outer plate. [1.00]
15. Maxilla 1 palp short robust setae: (1) absent; (2) present. [0.20]
16. Maxilla 1 palp long setae: (1) absent; (2) present. [0.00]
17. Maxilla 2 outer plate: (1) broad; (2) narrow, less than1: 2 of inner plate. [1.00]
18. Maxilliped palp article 2 distally: (1) not produced; (2) produced. [1.00]
19. Maxilliped palp article 4: (1) absent or weakly developed; (2) well developed. [0.44]
20. Pereon 1 carina :(1) absent; (2) small; (3) long and pointed. [0.10]
21. Pereon 2 carina: (1) absent; (2) small; (3) long and pointed. [0.50]
22. Pereon 3 carina: (1) absent; (2) small; (3) long and pointed. [1.00]
23. Pereon 4 carina: (1) absent; (2) small; (3) long and pointed. [0.59]
24. Pereon 5 carina: (1) absent; (2) small; (3) long and pointed. [0.42]
25. Pereon 6 carina: (1) absent; (2) small; (3) long and pointed. [0.42]
26. Pereon 7 carina: (1) absent; (2) small; (3) long and pointed. [0.20]
27. Pereon 1dominant midlateral protrusion: (1) absent; (2) present. [1.00]
28. Pereon 2 dominant midlateral protrusion: (1) absent; (2) present. [0.20]
29. Pereon 3 dominant midlateral protrusion: (1) absent; (2) present. [0.42]
30. Pereon 4 dominant midlateral protrusion: (1) absent; (2) present. [0.24]
31. Pereon 5 dominant midlateral protrusion: (1) absent; (2) small; (3) long and pointed. [1.00]
32. Pereon 6 dominant midlateral protrusion: (1) absent; (2) small; (3) long and pointed. [1.00]
33. Pereon 7 dominant midlateral protrusion: (1) absent; (2) small; (3) long and pointed. [1.00]
34. Pereonite 6 spines on posterolateral margin:(1) absent; (2) present. [0.25]
35. Pereonite 7 spines on posterolateral margin: (1) absent; (2) present. [0.33]
36. Pereonites 1-4 posteroventral corner: (1) rounded; (2) pointed . [1.00]
37. Pereonite 5 posteroventral corner: (1) rounded; (2) pointed. [0.27]
38. Pereonite 6 posteroventral corner: (1) rounded; (2) pointed. [0.27]

39. Pereonite 7 posteroventral corner: (1) rounded; (2) pointed. [0.18]
40. Pereonite 2: (1) shorter than pereonite 1; (2) same length or longer than pereonite 1. [0.00]
41. Pereonite 7 paired teeth: (1) absent; (2) present. [1.00]
42. Coxal plate 1 dorsoventral ridge on lateral surface: (1) absent; (2) present. [0.11]
43. Coxal plate 2 dorsoventral ridge on lateral surface: (1) absent; (2) present. [0.14]
44. Coxal plate 3 dorsoventral ridge on lateral surface: (1) absent; (2) present. [0.14]
45. Coxa 4 dorsoventral ridge on lateral surface: (1) absent; (2) present. [0.15]
46. Coxa 5 posteroventral angle: (1) rounded; (2) pointed not produced; (3) produced and pointed. [0.11]
47. Coxa 6 posteroventral angle: (1) rounded; (2) pointed not produced; (3) produced and pointed. [0.08]
48. Coxa 7 posteroventral angle: (1) rounded; (2) pointed. [0.40]
49. Basis 5 posteroventral angle: (1) rounded; (2) pointed not produced; (3) pointed and produced. [0.24]
50. Basis 6 posteroventral angles: (1) rounded; (2) pointed not produced; (3) produced and pointed. [0.62]
51. Basis 7 posteroventral angle: (1) rounded; (2) pointed not produced; (3) produced and pointed. [0.24]
52. Coxal plates 1-3 lateral face: (1) smooth; (2) acute teeth present. [1.00]
53. Coxa 4 margin midventrally : (1) rounded; (2) pointed. [0.09]
54. Coxa 4 anteroventrally: (1) not produced; (2) produced. [0.06]
55. Coxa 4 posteroventral margin: (1) concave; (2) straight or convex. [0.05]
56. Coxa 4 laterally: (1) smooth; (2) acutee teeth present . [0.42]
57. Coxa 4 posterolateral corner: (1) rounded; (2) pointed. [0.00]
58. Coxa 5 lateral surface: (1) smooth; (2) with acute teeth or bump. [0.15]
59. Coxa 5 winglike acute process: (1) absent; (2) present. [0.14]
60. Coxa 6 lateral surface: (1) smooth; (2) with acute teeth or bump. [0.11]
61. Coxa 7 laterally: (1) smooth; (2) with acute teeth. [0.17]
62. Gnathopod 1 palm length: (1) shorter than dactylus; (2) same or longer than dactylus. [0.25]
63. Gnathopod 2 palm length: (1) shorter than dactylus; (2) same or longer than dactylus. [0.27]
64. Gnathopod 1 spines on inner curvature of dactylus: (1) absent; (2) present. [1.00]
65. Gnathopod 2 spines on inner curvature of dactylus: (1) absent; (2) present. [1.00]
66. Gnathopod 1: (1) simple or subchelat; (2) chelat. [1.00]
67. Gnathopod 2: (1) simple or subchelat; (2) chelat. [1.00]
68. Pereopod 3 and 4 merus: (1) not produced; (2) produced. [0.04]
69. Pereopod 5 merus: (1) not produced; (2) produced. [0.16]
70. Pereopod 6 merus: (1) not produced; (2) produced. [0.22]
71. Pereopod 7 merus: (1) not produced; (2) produced. [0.24]
72. Pleon spinose cuticula: (1) absent; (2) present. [0.17]
73. Epimeral plate 1 carinae: (1) absent; (2) present. [0.12]
74. Epimeral plates 2 carinae: (1) absent; (2) present. [0.16]
75. Epimeral plate 3 carinae: (1) absent; (2) present. [0.13]
76. Epimeral plate 1 middorsally: (1) projection absent; (2) small projection; (3) long pointed projection. [0.21]
77. Epimeral plate 2 middorsally: (1) projection absent; (2) small projection; (3) long pointed projection. [0.21]
78. Epimeral plate 3 middorsally: (1) projection absent; (2) small projection; (3) long pointed projection. [0.22]

79. Epimeral plates 1 and 2 paired teeth on dorsal amature: (1) absent: (2) present. [1.00]
80. Epimeral plate 3 paired teeth on dorsal amature: (1) absent; (2) present. [0.25]
81. Epimeral plate 1 midlaterally: (1) not produced; (2) strongly produced. [0.27]
82. Epimeral plate 2 midlaterally: (1) not produced; (2) produced. [0.27]
83. Epimeral plate 3 midlaterally: (1) not produced; (2) produced. [0.27]
84. Epimeral plate 1 posterolateral margin: (1) not produced; (2) produced. [0.20]
85. Epimeral plate 2 posterolateral margin: (1) not produced; (2) produced. [0.43]
86. Epimeral plate 3 posterolateral margin: (1) not produced; (2) slightly produced: (3) strongly produced and pointed. [0.40]
87. Epimeral plate 1 posteroventral corner: (1) not produced; (2) slightly produced; (3) strongly produced. [0.05]
88. Epimeral plate 2 posteroventral corner: (1) not produced; (2) slightly produced; (3) strongly produced and pointed. [0.03]
89. Epimeral plate 3 posteroventral corner: (1) not produced; (2) slightly produced; (3) strongly produced and pointed. [0.17]
90. Urosomite 1: (1) longer than urosomites 2 and 3 combined; (2) shorter than urosomites 2 and 3 combined. [0.00]
91. Urosomite 1 middorsal keel: (1) absent; (2) present. [0.03]
92. Urosomite 2 middorsal keel: (1) absent; (2) present. [0.06]
93. Urosomite 3 middorsal keel: (1) absent; (2) present. [0.03]
94. Urosomite 1 posterolateral margin pointed process: (1) absent; (2) present. [0.00]
95. Urosomite 2 posterolateral margin pointed process: (1) absent; (2) present. [0.17]
96. Urosomit 3 posterolateral margin pointed process: (1) absent; (2) present. [0.06]
97. Urosomit 1dorsally: (1) smooth; (2) small projection; (3) long pointed projection; (4) multidentate carinae. [0.21]
98. Urosomite 2 dorsally: (1) smooth; (2) articulated. [1.00]
99. Urosomite 3 dorsally: (1) smooth; (2) articulated. [1.00]
100. Uropod 1outer ramus: (1) same length or longer than peduncle; (2) shorter than peduncle. [0.13]
101. Uropod 2 outer ramus: (1) same length or longer than peduncle; (2) shorter than peduncle. [0.13]
102. Uropod 3 outer ramus: (1) at least twice the length of peduncle; (2) less than twice the length of peduncle. [0.07]
103. Uropod 3 pointed process on apical margin: (1) absent; (2) present. [0.00]
104. Telson apically:(1) rounded; (2) pointed. [0.07]
105. Telson excavation: (1) wide, shallow or absent; (2) narrow. [0.04]
106. Telson elongation: (1) absent; (2) present, clearly longer than broad. [0.01]

Tab. 2. Character matrix of 36 taxa and 106 characters, the shaded numbers indicate highly variable character states.

Character:	**10**	**20**	**30**	**40**	**50**
Monoculodes sp.	1 1 1 1 1 1 1 1 1 2	2 2 1 1 2 2 1 1 2 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 2	1 1 1 1 1 1 1 1 1 1
Eusirus cf. *perdentatus*	2 1 1 4 5 2 2 1 1 2	2 2 1 1 2 2 1 2 2 1	1 1 1 3 3 3 1 1 1 1	1 1 1 1 1 1 2 2 2 2	1 1 1 1 1 1 1 1 2 2
Iphimediella cyclogena	2 1 2 3 3 1 2 1 2 1	1 1 1 1 1 2 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 2 2 2 1	2 1 1 1 1 2 2 2 2 2
Iphimediella georgiana	2 1 2 4 3 1 2 1 2 1	1 2 1 1 1 2 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 2 2 2 1	2 1 1 1 1 2 2 2 2 2
Iphimediella rigida	2 2 2 3 2 1 2 1 2 1	1 2 1 1 1 2 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 2 2 2 1	2 1 1 1 1 2 2 2 1 2
Echiniphimedia echinata	2 2 2 4 3 1 1 1 1 1	1 2 1 1 1 2 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 2 2 2 2 2 1	1 1 1 1 1 3 3 1 2 2
Echiniphimedia hodgsoni	2 1 2 6 4 2 2 2 1 1	1 2 1 1 1 2 1 1 1 1	1 1 1 1 1 1 1 2 1 1	1 1 1 2 2 2 2 2 2 1	1 1 1 1 2 1 1 1 2 2
Echiniphimedia waegei	2 2 2 4 3 1 2 1 1 1	1 2 1 1 2 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 2 2 2 2 2 2 1	1 2 2 2 1 2 2 2 2 2
Gnathiphimedia mandibularis	2 2 2 3 3 1 1 1 1 1	1 1 1 1 2 2 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 2 2 2 1	2 1 1 1 1 2 2 2 2 2
Gnathiphimedia sexdentata	2 1 2 4 2 1 1 1 1 1	1 1 1 1 1 2 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 2 2 2 1	2 1 1 1 1 2 2 2 2 2
Epimeria annabella	1 1 1 3 1 1 1 1 2 2	2 2 1 1 2 2 1 1 2 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 2 2 2 1 1 1 1 1 1
Epimeria bathyalis	1 1 2 1 1 1 1 1 2 2	2 2 1 1 2 1 1 1 2 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 2	1 2 2 2 1 3 1 1 1 1
Epimeria cornigera	1 2 2 1 1 1 1 1 1 2	2 2 1 1 2 2 1 1 2 1	1 1 1 1 1 2 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 2 2 2 2 3 2 1 1 1
Epimeria extensa	1 1 1 4 2 1 1 1 2 2	2 2 1 1 2 2 1 1 2 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 2 2 2 1	1 1 1 1 1 1 1 1 1 1
Epimeria georgiana	1 2 2 3 1 1 1 1 2 2	2 2 1 1 2 2 1 1 2 1	1 1 2 2 2 2 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 2 1 1 1 1 1
Epimeria glaucosa	1 2 2 1 1 1 1 1 1 2	2 2 1 1 2 1 1 1 2 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 2 2 2 2 3 1 1 1 1
Epimeria grandirostris	1 2 1 3 2 1 1 1 2 2	2 2 1 1 2 2 1 1 2 2	2 3 3 3 3 3 2 2 2 2	2 2 2 2 2 1 1 1 1 1	1 2 2 2 2 1 1 1 3 3
Epimeria heldi	1 2 1 1 1 1 1 1 2 2	2 2 1 1 2 1 1 1 2 1	1 1 1 1 2 2 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 2 1 1 1 1 1
Epimeria inermis	1 2 2 4 1 1 1 1 2 2	2 2 1 1 2 2 1 1 2 1	1 1 2 2 2 2 1 1 2 2	2 2 1 1 1 1 1 1 1 1	1 2 2 2 1 1 1 1 1 1
Epimeria loricata	1 2 2 1 1 1 1 1 2 2	2 2 1 1 2 2 1 1 2 2	2 3 3 3 3 3 2 2 2 2	2 2 2 1 1 1 1 1 1 1	1 2 2 2 2 3 3 1 1 1
Epimeria macrodonta	1 2 2 4 4 1 2 1 2 2	2 2 1 1 2 2 1 1 2 2	1 2 3 3 3 3 2 1 2 2	3 3 3 1 1 1 1 1 1 1	1 2 2 2 2 1 1 1 3 3
Epimeria monodon	1 2 2 1 1 1 2 1 2 2	2 2 1 1 2 2 1 1 2 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 2 2 1 1 1 1 1 1
Epimeria oxicarinata	1 2 1 4 2 1 2 1 2 2	2 2 1 1 2 1 1 2 2 3	2 3 3 3 3 3 2 2 2 2	3 3 3 1 1 1 1 1 1 1	1 2 2 2 2 3 2 1 3 3
Epimeria parasitica	1 1 2 1 1 1 1 1 1 2	2 2 1 1 2 2 1 1 2 1	1 1 1 2 2 2 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 2 2 2 2 3 3 1 1 1
Epimeria pulchra	1 2 1 4 3 1 2 1 2 2	2 2 1 1 2 2 1 1 2 3	2 3 3 3 3 3 2 2 2 2	2 2 2 1 1 1 2 2 2 1	1 2 2 2 2 3 2 1 3 3
Epimeria puncticulata	1 1 2 1 1 1 1 1 2 2	2 2 1 1 2 2 1 1 2 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 2 2 2 1 1 1 1 2 1
Epimeria reoproi	1 2 2 4 3 2 2 1 2 2	2 2 1 1 2 2 1 1 2 1	1 1 1 2 2 2 1 1 1 1	2 2 2 1 1 1 1 1 1 1	1 1 1 1 2 1 1 1 3 3
Epimeria rimicarinata	1 2 2 3 3 1 1 1 2 2	2 2 1 1 2 2 1 1 2 1	2 3 3 3 3 3 1 1 1 2	2 2 2 1 1 1 1 1 1 1	1 2 2 2 2 2 1 1 1 1
Epimeria robusta	1 2 1 1 1 1 1 1 2 2	2 2 1 1 2 2 1 1 2 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 2 1	1 1 1 1 1 3 3 1 1 1
Epimeria rotunda	1 1 2 1 1 1 1 1 2 2	2 2 1 1 2 2 1 1 2 1	1 1 1 1 1 2 1 1 1 1	1 1 1 1 1 1 1 1 1 2	1 2 2 2 2 1 1 1 1 1
Epimeria rubrieques	1 2 2 3 3 1 1 1 2 2	2 2 1 1 2 2 1 1 2 3	3 3 3 3 3 3 1 1 1 1	2 2 2 1 1 1 1 1 1 1	1 2 2 2 2 3 1 1 1 1
Epimeria similis	1 2 2 4 3 1 2 1 2 2	2 2 1 1 2 2 1 1 2 1	1 2 3 3 3 3 2 2 2 2	3 3 3 1 1 1 1 1 1 1	1 2 2 2 2 3 1 1 3 3
Epimeria ultraspinosa	1 2 1 1 1 1 1 1 2 2	2 2 1 1 2 2 1 1 2 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 2 2 2 1 3 1 1 1 1
Epimeria vaderi	1 2 2 5 5 2 2 1 2 2	2 2 1 1 2 2 1 1 2 1	1 1 2 2 2 3 1 1 1 1	2 2 2 1 1 1 1 1 1 1	1 2 2 2 2 1 1 1 3 3
Epimeriella macronyx	1 1 1 1 1 1 1 1 2 1	2 2 1 1 2 1 1 1 2 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 2 2 2 1 1 1 1 1 1
Epimeriella walkeri	1 1 2 1 1 1 1 1 2 1	2 2 1 1 2 2 1 1 2 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 2 2 2 1 1 1 1 2 1
Metepimeria acanthurus	1 2 2 1 1 1 1 1 2 2	2 2 1 1 2 2 1 1 1 1	1 1 1 1 1 2 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 2 2 2 2 1 1 1 1 1

Character:	60	70	80
Monoculodes sp.	1 1 1 1 2 1 1 1 1 1	1 1 2 1 1 1 1 1 1 2	2 1 2 2 2 1 1 1 1 1
Eusirus cf. *perdentatus*	2 1 1 2 2 1 1 1 1 1	1 2 2 1 1 1 1 1 2 2	2 1 2 2 2 3 3 3 1 1
Iphimediella cyclogena	2 1 2 1 1 1 1 1 1 1	1 2 2 1 1 2 2 2 2 2	2 1 1 1 1 1 1 1 2 2
Iphimediella georgei	2 1 2 1 1 1 1 1 1 1	1 2 2 1 1 2 2 2 2 2	2 1 1 2 2 1 1 1 2 1
Iphimediella rigida	2 1 2 1 1 1 2 1 1 1	1 1 2 1 1 2 2 2 2 2	2 1 2 2 2 1 1 1 2 2
Echiniphimedia echinata	2 1 2 1 1 1 2 1 1 1	1 2 2 1 1 2 2 2 2 2	2 1 2 2 2 1 1 1 1 1
Echiniphimedia hodgsoni	2 2 2 1 2 2 1 2 1 2	2 2 2 1 1 2 2 2 2 2	2 1 2 2 2 1 1 1 1 1
Echiniphimedia waegeli	2 2 2 1 1 2 2 2 1 2	2 2 2 1 1 2 2 2 2 2	2 1 2 2 2 1 1 1 1 1
Gnathiphimedia mandibularis	2 1 2 1 1 1 2 1 1 1	1 2 2 1 1 2 2 2 2 2	2 1 1 1 1 1 1 1 2 2
Gnathiphimedia sexdentata	2 1 2 1 1 1 2 1 1 1	1 2 2 1 1 2 2 2 2 2	2 1 1 1 1 1 1 1 2 1
Epimeria annabella	2 1 1 1 1 1 2 1 1 1	1 1 1 2 2 1 1 2 2 2	2 1 1 1 2 1 1 2 1 1
Epimeria bathyalis	1 1 2 1 1 1 2 1 1 2	1 1 1 2 2 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1
Epimeria cornigera	1 1 2 1 1 1 2 2 2 2	1 1 1 2 2 1 1 1 1 1	1 1 2 2 2 2 2 2 1 1
Epimeria extensa	1 1 1 1 2 1 2 1 1 1	1 1 1 2 2 1 1 2 2 2	2 1 1 1 1 1 1 1 1 1
Epimeria georgiana	1 1 1 2 2 1 2 2 1 2	1 1 1 2 2 1 1 2 2 2	2 1 2 2 2 2 2 2 1 1
Epimeria glaucosa	1 1 2 1 1 1 2 2 2 2	1 1 1 2 2 1 1 1 1 1	1 1 2 2 2 2 2 2 1 1
Epimeria grandirostris	2 1 1 1 1 2 2 2 1 2	2 1 1 2 2 1 1 1 2 2	2 2 2 2 2 2 2 2 1 1
Epimeria heldi	1 1 1 1 1 1 2 1 1 1	1 1 1 2 2 1 1 1 1 1	1 1 2 2 2 2 2 2 1 1
Epimeria inermis	1 1 1 1 2 1 1 2 1 1	1 1 2 2 2 1 1 1 2 2	2 1 2 2 2 2 2 2 1 1
Epimeria loricata	1 1 1 1 2 1 1 2 1 2	1 1 1 2 2 1 1 1 1 1	1 2 2 2 2 3 3 3 1 1
Epimeria macrodonata	3 1 2 2 1 2 2 2 2 2	1 1 1 2 2 1 1 2 2 2	2 1 2 2 2 3 3 3 1 1
Epimeria monodon	1 1 1 1 1 1 2 1 1 1	1 1 1 2 2 1 1 2 2 2	2 1 1 1 2 1 1 2 1 1
Epimeria oxicarinata	3 1 2 2 1 2 2 2 2 2	2 1 1 2 2 1 1 2 2 2	2 2 2 2 2 3 3 3 1 1
Epimeria parasitica	1 1 ▨ 1 1 1 2 2 1 1	1 1 1 2 2 1 1 1 1 1	1 1 2 2 2 2 2 2 1 1
Epimeria pulchra	3 1 2 2 1 2 2 2 2 2	2 1 1 2 2 1 1 2 2 2	2 2 2 2 2 3 3 3 1 1
Epimeria puncticulata	1 1 1 1 1 1 2 1 1 1	1 1 1 2 2 1 1 2 2 2	2 1 1 2 2 1 2 2 1 1
Epimeria reoproi	3 1 2 2 1 1 2 2 1 2	1 1 1 2 2 1 1 2 2 2	2 1 2 2 2 2 2 2 1 1
Epimeria rimicarinata	1 1 2 1 1 1 2 2 1 2	1 1 2 2 2 1 1 2 2 2	2 2 2 2 2 2 2 2 1 1
Epimeria robusta	1 1 1 2 2 1 2 1 1 1	1 2 1 2 2 1 1 2 2 2	2 1 2 2 2 2 2 2 1 1
Epimeria rotunda	1 1 1 1 1 1 2 2 1 1	1 1 1 2 2 1 1 ?1 ?	1 1 2 2 2 1 1 1 1 1
Epimeria rubrieques	1 1 2 2 1 1 2 2 2 2	1 1 1 2 2 1 1 2 2 2	2 1 2 2 2 3 3 3 1 1
Epimeria similis	3 1 2 2 1 2 2 2 2 2	1 1 1 2 2 1 1 2 2 2	2 1 2 2 2 3 3 3 1 1
Epimeria ultraspinosa	1 1 2 1 1 1 2 1 2 1	1 1 1 2 2 1 1 1 1 1	1 1 2 2 2 3 3 3 1 1
Epimeria vaderi	2 1 1 1 1 1 1 1 1 1	1 1 1 2 2 1 1 2 2 2	2 1 2 2 2 3 3 3 1 1
Epimeriella macrodonta	1 1 1 1 2 1 2 1 1 1	1 1 1 2 2 1 1 1 2 2	2 1 1 1 1 1 1 1 1 1
Epimeriella walkeri	1 1 1 1 2 1 2 1 1 1	1 1 1 2 2 1 1 1 2 2	2 1 1 1 1 1 1 1 1 1
Metepimeria acanthanthurus	1 1 1 1 1 1 2 1 1 1	1 1 1 2 2 1 1 1 2 2	2 1 2 2 2 2 2 2 1 1

Character:	90	100	
Monoculodes sp.	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 2	1 2 1 1 1 1
Eusirus cf. *perdentatus*	1 1 1 1 1 1 2 2 2 1	1 1 1 1 1 1 2 1 1 1	1 1 1 2 1 2
Iphimediella cyclogena	1 1 1 1 2 3 1 3 3 1	1 2 2 1 1 2 1 1 1 2	2 2 2 1 2 2
Iphimediella georgei	1 1 1 2 2 3 1 2 2 1	2 1 1 1 1 2 2 1 1 2	2 1 2 2 1 2
Iphimediella rigida	1 1 1 2 2 3 1 2 3 1	2 1 1 1 1 2 2 1 1 2	2 1 2 2 1 2
Echiniphimedia echinata	2 2 2 1 1 3 1 2 3 1	2 1 1 1 1 2 4 1 1 2	2 1 2 1 1 1
Echiniphimedia hodgsoni	2 2 2 1 1 3 1 3 3 1	2 1 2 1 2 2 4 1 1 2	2 1 2 2 1 2
Echiniphimedia waegeli	2 2 2 1 1 3 1 3 3 1	2 1 2 1 1 2 4 1 1 2	2 1 2 1 1 1
Gnathiphimedia mandibularis	1 1 1 2 2 3 1 2 3 1	1 2 2 1 1 2 1 1 1 2	2 2 2 2 1 2
Gnathiphimedia sexdentata	1 1 1 1 2 3 2 2 3 2	1 1 1 1 1 2 1 1 1 2	2 1 2 2 2 2
Epimeria annabella	1 1 1 1 1 1 1 3 3 1	2 1 1 1 1 1 3 1 1 1	1 2 2 2 2 2
Epimeria bathyalis	1 1 1 1 1 1 1 2 2 1	1 1 1 1 1 1 3 1 1 1	1 1 2 1 1 2
Epimeria cornigera	1 1 1 2 2 2 1 2 2 1	2 1 1 1 1 1 1 1 1 1	1 1 2 1 1 2
Epimeria extensa	1 1 1 1 1 1 1 2 2 1	2 1 2 1 1 2 2 1 1 1	1 2 2 2 1 2
Epimeria georgiana	1 1 1 1 1 1 1 2 3 1	1 1 2 1 1 2 2 1 1 1	1 1 2 1 2 1
Epimeria glaucosa	1 1 1 2 2 2 1 2 2 1	2 1 1 1 1 1 3 1 1 1	1 1 2 1 1 1
Epimeria grandirostris	2 2 2 1 1 1 1 2 3 1	2 1 2 1 1 1 3 1 1 1	1 1 2 2 2 2
Epimeria heldi	1 1 1 1 1 1 1 1 3 1	2 1 1 1 1 2 2 1 1 1	1 2 1 1 1 2
Epimeria inermis	1 1 1 1 1 1 1 2 3 1	1 1 1 1 1 1 2 1 1 2	2 1 2 1 1 2
Epimeria loricata	2 2 2 1 1 1 2 3 3 1	2 1 1 2 1 1 3 1 1 1	1 1 2 2 2 2
Epimeria macrodonata	2 2 2 1 1 1 3 3 3 2	1 1 2 1 2 2 3 1 1 1	1 2 2 2 2 1
Epimeria monodon	1 1 1 1 1 1 1 2 2 1	1 1 1 1 1 2 2 1 1 1	1 1 2 1 1 2
Epimeria oxicarinata	2 2 2 1 1 1 1 2 3 1	2 1 1 2 2 2 3 1 1 1	1 2 2 2 1 2
Epimeria parasitica	1 1 1 2 2 1 1 2 3 1	2 1 2 1 1 1 3 1 2 1	1 1 2 1 1 2
Epimeria pulchra	2 2 2 1 1 3 1 2 3 1	2 1 1 2 2 2 3 1 1 1	1 2 2 2 2 2
Epimeria puncticulata	1 1 1 1 1 1 1 2 2 1	2 2 2 1 1 1 3 1 1 1	1 1 2 1 2 2
Epimeria reoproi	2 2 2 1 1 1 2 2 3 1	1 1 2 1 1 2 2 1 1 1	1 2 2 2 2 1
Epimeria rimicarinata	2 2 2 1 1 1 1 3 3 2	2 2 2 1 1 2 3 1 1 2	2 2 2 1 1 2
Epimeria robusta	1 1 1 1 1 1 2 3 3 1	1 1 2 1 2 2 3 1 1 1	1 2 2 1 1 1
Epimeria rotunda	1 1 1 1 1 1 1 1 1 2	1 1 2 1 1 1 3 1 1 1	1 1 2 1 1 2
Epimeria rubrieques	1 1 1 1 1 1 1 2 3 1	1 1 2 1 1 2 2 1 1 1	1 1 2 2 2 1
Epimeria similis	2 2 2 1 1 1 3 3 3 1	1 1 2 1 2 2 3 1 1 1	1 2 2 2 2 1
Epimeria ultraspinosa	1 1 1 1 1 1 1 2 2 1	1 1 1 1 1 1 3 1 1 1	1 1 2 1 1 2
Epimeria vaderi	2 2 2 1 1 1 1 2 3 2	2 2 2 1 1 2 2 1 1 1	2 2 2 2 1 2
Epimeriella macrodonta	1 1 1 1 1 1 2 2 2 2	2 1 2 1 1 2 3 1 1 2	2 2 1 2 2 2
Epimeriella walkeri	1 1 1 1 1 1 1 2 2 1	2 1 2 1 1 1 3 1 1 2	1 2 2 2 2 2
Metepimeria acanthanthurus	1 1 1 1 1 2 1 1 2 1	2 1 2 1 1 2 3 1 1 1	1 1 2 2 1 2

Tab. 3. Synapomorphies of each clade and taxon in the reweighted phylogram, figure 2

node 72 -> *Monoculodes* sp.
40: 1->2; 69: 2->1; 88: 2->1; 89: 2->1; 97: 2->1; 100: 1->2; 104: 2 ->1; 106: 2 ->1;
node 72 -> node 45
1: 1->2; 4: 1->4; 5: 1 ->3; 7: 1 ->2; 37: 1->2; 38: 1 ->2 ; 39: 1->2 ; 49: 1->2; 50: 1->2; 51: 1->2; 62: 1->2; 102: 2->1
node 45 -> *Eusirus* cf. *perdentatus*
5: 3->5; 6: 1->2; 24: 1->3; 25: 1->3; 26: 1->3; 40: 1->2; 54: 1->2; 76: 1->3; 77: 1->3; 78: 1->3; ; 87: 1->2
node 45 -> node 44
3: 1->2; 10: 2->1; 11: 2->1; 15: 2->1; 19: 2->1; 46: 1->2; 47: 1->2; 53: 1->2; 55: 2->1; 57: 1->2;; 66: 1->2; 67: 1->2; 68: 1->2; 86: 1->3; 89: 2 ->3; 91: 1 ->2; 96: 1 ->2; 100: 1->2;; 101: 1->2; ; 103: 1->2
node 44 -> node 41
41: 1->2; 48: 1->2; 73: 2->1; 79: 1->2; 85: 1->2
node 41 -> node 39
7: 2->1; 12: 2->1; 74: 2->1; 75: 2->1; 91: 2->1; 97: 2->1; 105: 1->2
node 39 -> node 38
4: 4->3; 80: 1->2; 92: 1->2; 93: 1->2; 102: 1->2
node 38 -> *Iphimediella cyclogena*
7: 1->2; 9: 1->2; 57: 2->1; 88: 2->3; 104: 2->1
node 38 -> *Gnathiphimedia mandibularis*
2: 1->2; 15: 1->2; 84: 1->2; 105: 2->1
node 39 -> *Gnathiphimedia sexdentata*
5: 3->2; 87: 1->2; 90: 1->2
node 41 -> node 40
9: 1->2;84: 1->2
node 40 -> *Iphimediella geogei*
57: 2->1; 89: 3->2
node 40 -> *Iphimediella rigida*
2: 1->2; 4: 4->3; 5: 3->2; 49: 2->1; 62: 2->1; 73: 1->2; 80: 1->2
node 44 -> node 43
2: 1->2; 35: 1->2; 36: 1->2; 81: 1->2; 82: 1->2; 83: 1->2; 97: 2->4; 104: 2->1; 106: 2->1
node 43 -> *Echiniphimedia echinata*
7: 2->1; 46: 2->3; 47: 2->3
node 43 -> node 42
34: 1->2; 52: 1->2; 56: 1->2; 58: 1->2; 60: 1->2; 61: 1->2; 88: 2->3; 93: 1->2
node 42 -> *Echiniphimedia hodgsoni*
2: 2->1; 4: 4->6; 5: 3->4; 6: 1->2; 8: 1->2; 28: 1->2; 45: 1->2; 46: 2->1; 47: 2->1; 55: 1->2; 57: 2->1; 95: 1->2; 104: 1->2; 106: 1->2
node 42 -> *Echiniphimedia waegeli*
15: 1->2; 16: 2->1; 42: 1->2; 43: 1->2; 44: 1->2; 48: 1->2
node 72 -> node 71
9: 1->2; 57: 1->2; 63: 2->1; 64: 1->2; 65: 1->2; 68:1->2; 73: 2->1; 74: 2->1; 75: 2->1; 91: 1->2; 93: 1->2; 103: 1->2
node 71 -> node 70
42: 1->2; 43: 1->2; 44: 1->2; 97: 2->3; 105: 1->2
node 70 -> node 68
55: 2->1; 75: 1->2; 78: 1->2; 93: 2->1
node 68 -> *Epimeria annabella*
4: 1->3; 51: 1->2; 88: 2->3; 89: 2->3
node 68 -> node 67
3: 1->2; 102: 2->1; 104: 2->1; 105: 2->1
node 67 -> node 66
74: 1->2; 77: 1->2; 93: 1->2
node 66 -> node 65
26: 1->2; 45: 1->2; 68: 2->1; 73: 1->2; 76: 1->2
node 65 -> node 50
46: 1->3; 53: 1->2; 58: 1->2; 69: 2->1; 70: 2->1; 71: 2->1
node 50 -> node 47
40: 1->2; 76: 2->1; 77: 2->1; 78: 2->1; 91: 2->1
node 47 -> node 46
26: 2->1; 45: 2->1; 58: 2->1; 93: 2->1

node 46 -> *Epimeria bathyalis*
16: 2->1; 60: 1->2; 73: 2->1; 74: 2->1; 75: 2->1
node 46 -> *Epimeria ultraspinosa*
2: 1->2; 3: 2->1; 40: 2->1; 59: 1->2; 76: 1->3; 77: 1->3; 78: 1->3
node 47 -> *Epimeria rotunda*
46: 3->1; 53: 2->1; 88: 2->1; 89: 2->1; 90: 1->2
node 50 -> node 49
9: 2->1; 84: 1->2; 85: 1->2
node 49 -> node 48
2: 1->2; 59: 1->2; 60: 1->2; 86: 1->2; 93: 2->1
node 48 -> *Epimeria cornigera*
47: 1->2; 97: 3->1
node 48 -> *Epimeria glaucosa*
15: 2->1; 26: 2->1; 106: 2->1
node 49 -> *Epimeria parasitica*
24: 1->2; 25: 1->2; 47: 1->3; 89: 2->3; 99: 1->2
node 65 -> node 64
2: 1->2; 88: 2->1; 96: 1->2
node 64 -> node 63
3: 5 2->1; 42: 2->1; 43: 2->1; 44: 2->1; 55: 1->2; 68: 1->2; 89: 2->3; 91: 2->1; 102: 1->2
node 63 -> node 62
25: 1->2; 97: 3->2
node 62 -> node 61
3: 1->2; 4: 1->3; 23: 1->2; 24: 1->2; 58: 1->2; 60: 1->2; 88: 1->2; 102: 2->1
node 61 -> *Epimeria georgiana*
54: 1->2; 105: 1->2; 106: 2->1
node 61 -> node 60
4: 3->4; 30: 1->2; 31: 1->2; 32: 1->2; 42: 1->2; 43: 1->2; 44: 1->2; 101: 1->2
node 60 -> node 59
5: 1->3; 26: 2->3; 33: 1->2; 53: 1->2; 55: 2->1; 81: 1->2; 82: 1->2; 83: 1->2; 91: 1->2; 102: 1->2; 104: 1->2
node 59 -> node 57
4: 4->3; 21: 1->2; 22: 1->3; 23: 2->3; 24: 2->3; 25: 2->3; 46: 1->2; 72: 1->2; 97: 2->3
node 57 -> node 56
20: 1->2; 46: 2->3; 76: 2->3; 77: 2->3; 78: 2->3; 101: 2->1; 102: 2->1; 105: 1->2
node 56 -> node 55
27: 1->2; 28: 1->2; 29: 1->2; 53: 2->1; 68: 2->1; 93: 2->1; 94: 1->2; 96: 2->1
node 55 -> node 54
3: 2->1; 49: 1->3; 50: 1->3; 51: 1->2; 56: 1->2; 61: 1->2
node 54 -> *Epimeria grandirostris*
5: 3->2; 34: 1->2; 35: 1->2; 4:6 3->1; 76: 3->2; 77: 3->2; 78: 3->2; 93: 1->2; 94: 2->1
node 54 -> node 53
4: 3->4; 7: 1->2; 20: 2->3; 47: 1->2; 51: 2->3; 53: 1->2; 54: 1->2; 59: 1->2; 68: 1->2; 95: 1->2; 96: 1->2; 102: 1->2
node 53 -> node 52
32: 2->3; 32: 2->3; 33: 2->3
node 52 -> node 51
3: 1->2; 20: 3->1; 21: 2->1; 22: 3->2; 47: 2->1; 61: 2->1; 72: 2->1; 87: 1->3; 88: 2->3; 91: 2->1; 93: 1->2; 94: 2->1; 106: 2->1
node 51 -> *Epimeria macrodonta*
5: 3->4; 20: 1->2; 28: 2->1; 46: 3->1; 90: 1->2
node 52 -> *Epimeria oxicaricarinata*
5: 3->2; 16: 2->1; 18: 1->2; 105: 2->1
node 53 -> *Epimeria pulchra*
37: 1->2; 38: 1->2; 39: 1->2; 86: 1->3
node 55 -> *Epimeria loricata*
4: 3->1; 5: 3->1; 47: 1->3; 55: 1->2; 57: 2->1; 69: 2->1; 70: 2->1; 71: 2->1; 87: 1->2; 88: 2->3
node 56 -> *Epimeria rubrieques*
20: 2->3; 21: 2->3; 30: 2->1; 54: 1->2; 59: 1->2; 72: 2->1; 81: 2->1; 82: 2->1; 83: 2->1; 91: 2->1; 97: 3->2; 106: 2->1
node 57 -> *Epimeria rimicarinata*
63: 1->2; 88: 2->3; 90: 1->2; 92: 1->2; 100: 1->2; 104: 2->1
node 59 -> node 58

6: 1->2; 7: 1->2; 30: 2->1; 49: 1->3; 50: 1->3; 51: 1->2
node 58 -> ***Epimeria reoproi***
23: 2->1; 26: 3->2; 42: 2->1; 43: 2->1; 44: 2->1; 51: 2->3; 54: 1->2; 87: 1->2; 91: 2->1; 101: 2->1; 105: 1->2; 106: 2->1
node 58 -> ***Epimeria vaderi***
4: 4->5; 5: 3->5; 53: 2->1; 57: 2->1; 58: 2->1; 60: 2->1; 76: 2->3; 77: 2->3; 78: 2->3; 90: 1->2; 92: 1->2
node 60 -> ***Epimeria inermis***
29: 1->2; 45: 2->1; 57: 2->1; 60: 2->1; 63: 1->2; 68: 2->1; 93: 2->1; 96: 2->1; 100: 1->2
node 62 -> **Epimeria heldi**
16: 2->1; 55: 2->1; 68: 2->1; 69: 2->1; 70: 2->1; 71: 2->1; 91: 1->2; 93: 2->1; 103: 2->1
node 63 -> ***Epimeria robusta***
26: 2->1; 39: 1->2; 45: 2->1; 46: 1->3; 47: 1->3; 54: 1->2; 62: 1->2; 87: 1->2; 88: 1->3; 95: 1->2; 106: 2->1
node 64 -> ***Metepimeria acanthurus***
19: 2->1; 86: 1->2; 104: 1->2
node 66 -> ***Epimeria puncticulata***
49: 1->2; 92: 1->2; 105 1->2
node 67->***Epimeria monodon***
7: 1->2; 42: 2->1; 91: 2->1; 96: 1->2; 97: 3->2
node 70 -> **node 69**
10: 2->1; 68: 2->1; 100: 1->2
node 69 -> ***Epimeriella macronyx***
17: 2->1; 87: 1->2; 90: 1->2; 96: 1->2; 101: 1->2; 103: 2->1
node 69 -> ***Epimeriella walkeri***
3: 1->2; 49: 1->2
node 71 -> ***Epimeria extensa***
4: 1->4; 5: 1->2; 37: 1->2; 38: 1->2; 39: 1->2; 96: 1->2

Veröffentlichung VII

Dikwa andresi, a new amphipod crustacean (Diwidae) from the Scotia Arc

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Abstract

The new amphipod crustacean species *Dikwa andresi* from the Scotia Arc is described in detail. This is the first record of the family Dikwidae in the Southern Ocean. The white species was caught in water depth of 270- 290 meter during the Antarctic autumn, living on the red hydrocoral (Hydrozoa) *Errinopsis reticulum*. It has a carinate pereon and pleon, no eyes and the head is telescoped into the first pereon segment. The first gnathopod is propodochelate, the second gnathopod is simple.

The only known species of the family is *Dikwa acrania* from Southern Africa. The new species mainly differs from *D. acrania* in having dorsal processes on all pereonites and the first coxa being twice as long as the second. An intraspecific variation of the shape of the telson was observed.

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Introduction

During the expedition of the R/V 'Polarstern', cruise ANT XIX-5 to the Scotia Arc amphipods were collected by different gear types. Compared to previous expeditions members of Iphimedoidea were not the dominant families of gammaridean Amphipoda. Anyway, in two of the dredged samples a fascinating new dikwiid amphipod species was collected, living on a red hydrocoral.

Material and Methods

The animals were fixed in prechilled 96 % ethanol, transferred into glycerol for the study and drawn with a camera lucida on a Leica Wild M8 dissecting microscope. The specimens were dissected and appendages and mouthparts transferred onto slides in glycerol and drawn under a Leica DMLB and a Dialux Leitz Wetzlar light microscope using a camera lucida.

The type material of the new species is deposited in the Zoological Institute and Zoological Museum of Hamburg.

SYSTEMATICS

Order Amphipoda Latreille, 1816
Suborder Gammaridea Latreille, 1802
Family Diwidae Coleman & Barnard, 1991
Dikwa andresi n. sp.
(Figures 1- 5)

Type material

(south of Falkland Islands, South Atlantik, Scotia Arc)

Holotype male 5.3 mm (without expressed female of male sexual characters), right side and mouthparts dissected and mounted on 24 slides, body preserved in 76% ethanol. (ANT XIX-5, LAMPOS, station 150- 1, coordinates: 54°30.22'S- 54°29. 64`S, 56°8.2'W- 56°8.13'W; water depth 290 m) [ZMH K 40223]. Collected by A.-N. Lörz, 6 April 2002.

Paratypes 'A' 7.3 mm, 'B': 5.0 mm, partially dissected, bodies preserved in 76% ethanol. (ANT XIX-5, LAMPOS, station 150-1, coordinates: 54°30.22'S- 54°29. 64`S, 56°8.2'W- 56°8.13'W; water depth 290 m) [ZMH K 40224]. Collected by A.-N. Lörz, 6 April 2002.

Paratype 'C': 3,2 mm partially dissected, body preserved in 76% ethanol. (ANT XIX-5, LAMPOS, station 145-1, coordinates: 54°1.36`S- 54°1.11`S, 62°1.3`W- 62°1.63`W; water depth 272 m) [ZMH K 40224]. Collected by A.-N. Lörz, 5 April 2002.

Etymology. The species is dedicated to Hans-Georg Andres who kindly introduced both authors into the secrets of amphipod taxonomy.

Description. Head (Figure 1A, D) telescoped into the first pereonite, shorter than first pereon segment, directed ventrally; eyes absent; pereonites, pleonites (Figure 1B, E) and coxae complex, sculptured and acuminate; pereonites and pleonites in lateral view with wide, blunt dorsal processes, apart from pereonite 1 with weak depression (Figure1A, D); epimeral plate 1 (Figure 1E) pointed ventrally, epimeral plates 2 posteroventrally angular and plate 3 posteroventrally rounded; urosomite 1 longer than urosomite 2 and 3 combined (Figure 1B); entire integument composed of small plates.

Antenna 1 (Figure 2B): peduncular article 1 stout with three plumose setae, distal margin drawn out into rounded projection reaching distal margin of article 2, second article less than half the length of article 1; article 3 longer than second, with scale-like accessory flagellum.

Antenna 2 (Figure 2C) slightly longer than 1; flagellum with 6 articles.

Labrum (Figure 2A) wider than long, with distal notch and short hair-like setae on distal margin, with short, triangular proximal protrusion.

Mandible (Figure 3E): left mandible; incisor strongly dentate; 15 raker spines; molar produced and triturative; palp 3-articulate, article 3 longest densely setose posteromarginally.

Lower lip (hypopharynx) (Figure 2g) with wide lobes and groups of setae distomedially; hypopharyngeal gap narrow.

Maxilla 1 (Figure 3D): inner lobe small, with 3 apical setae; distal margin of outer lobe oblique with 9 medially serrate setae; palp 2-articulate, surpassing outer lobe, proximal article short; distal article, slightly curved medially, with slender setae on distomedial margin and 3 apical stout, laterally serrate setae.

Maxilla 2 (Figure 3C) with long, distally setulated setae on outer and inner plate, plates of similar length.

Maxillipeds (Figure 2D-F) basis with 2 setae on distal margin; outer plate reaching distal margin of first palp article, with setation as in 2f; inner plate with 11 setulated setae on apical and medial, anterior margin (Figure 2E). Maxilliped palp 4-articulate (Figure 2D) medial margin with setation as in Figure 2d; article 1 distally slightly expanded; article 4 small.

Pereopod (gnathopod) 1 (Figure 1D, 3B): slender; coxa (Figure 1D) twice as long as coxa 2, produced laterally, complexely sculptured, bearing two apical tips; merus strongly tapering distally with a group of apical setae; propodus more than twice the length of carpus; chelate, dactylus longer

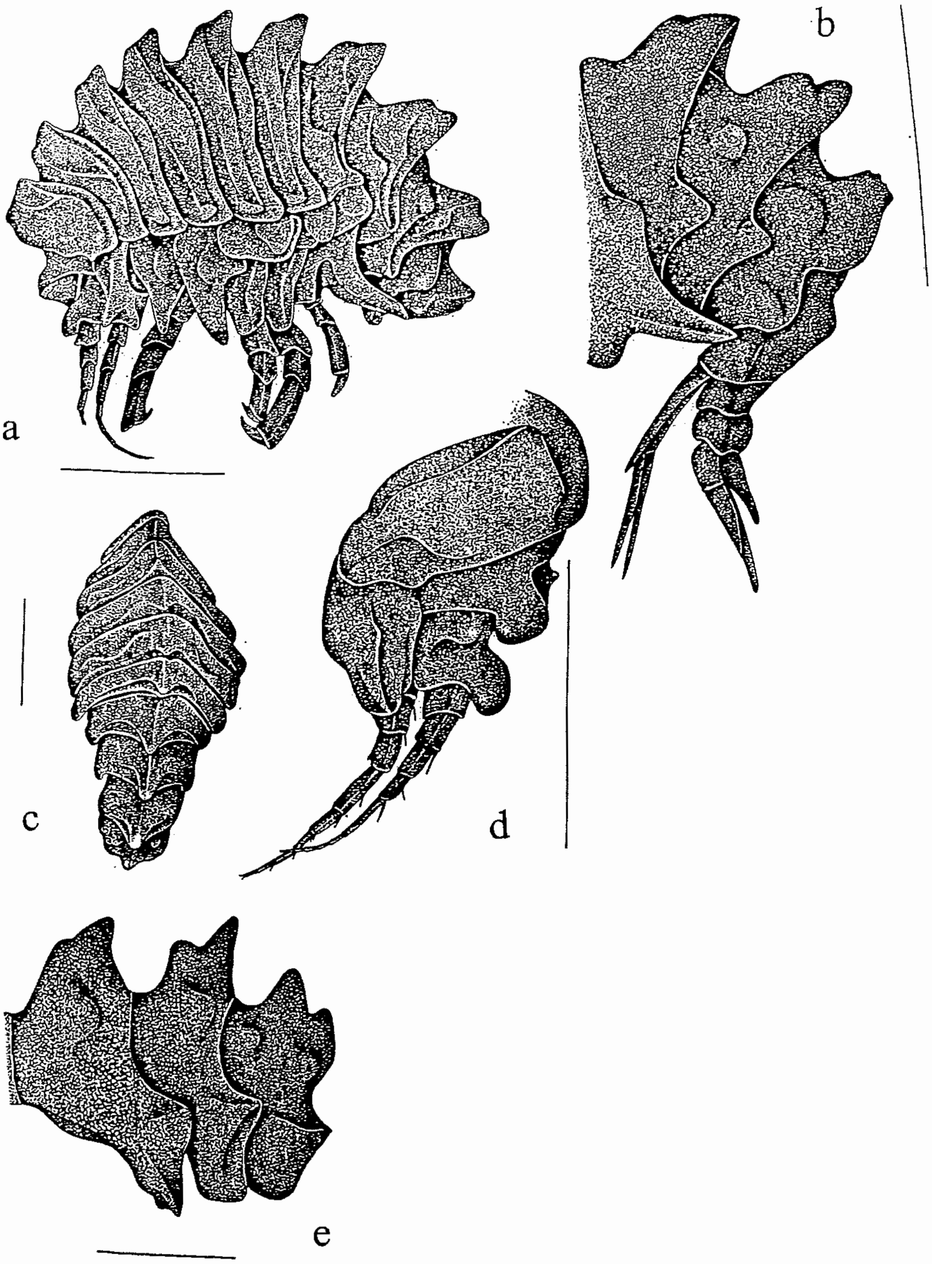

Fig. 1 A-E. *Dikwa andresi* n. sp., holotype, 5.3 mm, (A) lateral habitus without urosome; (B) epimeron and urosom, without uropod 2, left lateral aspect; (C) dorsal habitus; (D) head with first coxa, right side; (E) epimeral plates. Scale bars: a-e: 1mm.

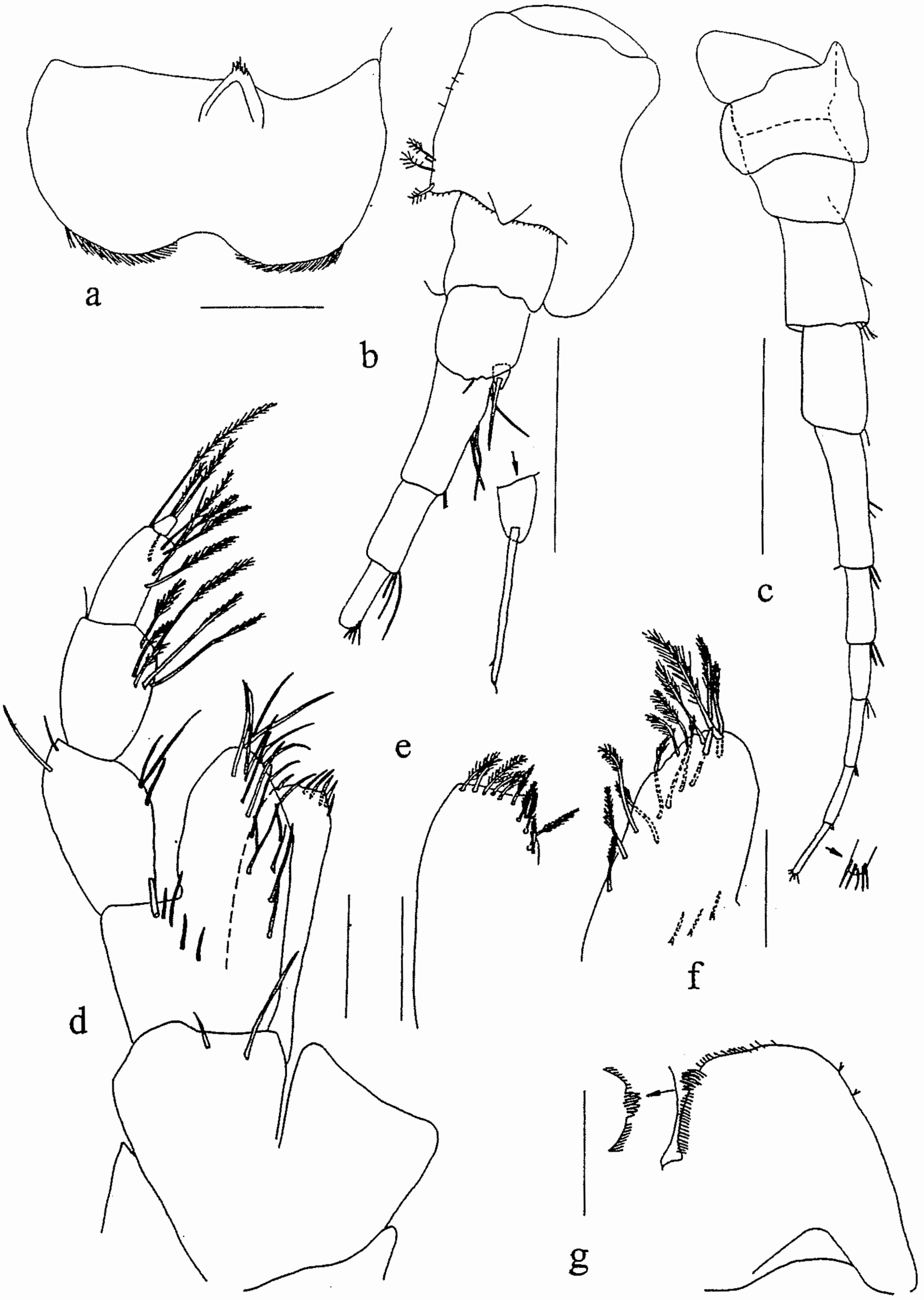

Fig. 2 A-G. *Dikwa andresi* n. sp., holotype, 5.3 mm, (A) labrum; (B) antenna 1; (C) antenna 2; (D) maxilliped; (E) inner maxilliped plate, anterior aspect; (F) outer maxilliped plate, anterior aspect; (G) lower lip. Scale bars: A,D-F: 100 µm; B,C: 300µm.

than fixed finger, setose.

Pereopod (gnathopod) 2 (Figure 3A): slender, longer than pereopod; simple; basis elongate and curved; propodus and dactylus extremely elongated, tapering, setae on distal end (see detail of Figure 3A).

Pereopod 3 (Figure 4A): coxa tapering distally, dorsoventrally ridged; merus widened distally, drawn out anteriorly; carpus anterior margin elongate and pointed; propodus and dactylus 2 stout spine-like setae on posterior margin.

Pereopod 4 (Figure 4B, 4C): coxa (4C) with ridges on lateral face, posteriorly concav, apex drawn out into pointed process, posteroproximomarginally with rounded lobe; merus expanded anteromarginally and drawn out distally; carpus anteriorly produced, 2 spines on posteroventral margin; dactylus of similar shape as that of pereopod 3, 2 spines on posterior margin.

Pereopod 5 (Figure 4D): coxa wider than long, complexely sculptured; basis anterior and posterior margins parallel, posterior margin with ventrodistally rounded process; merus distally widened, posterior angle produced; carpus with similar lobe as merus, anteroventrally with 2 spine-like setae; propodus longer than merus and carpus combined; dactylus stout, slightly curved, with 3 spines on inner curvature.

Pereopod 6 (Figure 5A): coxa ridged (Figure 1A), basis wider than that of pereopod 5, with ventrodistal rounded process; merus and carpus drawn out ventrodistally; carpus with 2 spines anteroventrally; propodus longer than merus and carpus combined; dactylus stout, slightly curved, 3 spines on inner curvature.

Pereopod 7 (Figure 5B): coxa wider than long, with extremely elongate protrusion, curved posteriorly; merus widened, not elongated; carpus posteroventral corner slightly produced and pointed; propodus longer than merus and carpus combined; dactylus stout, slightly curved, 1 spine on inner curvature.

Uropod 1 (Figure 5C): missing, take from paratype ‘C’: peduncle same length as outer ramus; rami narrow-lanceolate; subequal in length.

Uropod 2 (Figure 5D): rami and peduncle about same length; rami narrow-lanceolate.

Uropod 3 (Figure 5E): peduncle less than half the length of rami; outer ramus slightly shorter than inner.

Telson (Figure 5F): slightly longer than broad, one plumose seta, emarginated; that of paratype ‘B’ tapering distally, apically rounded (Figure 5G).

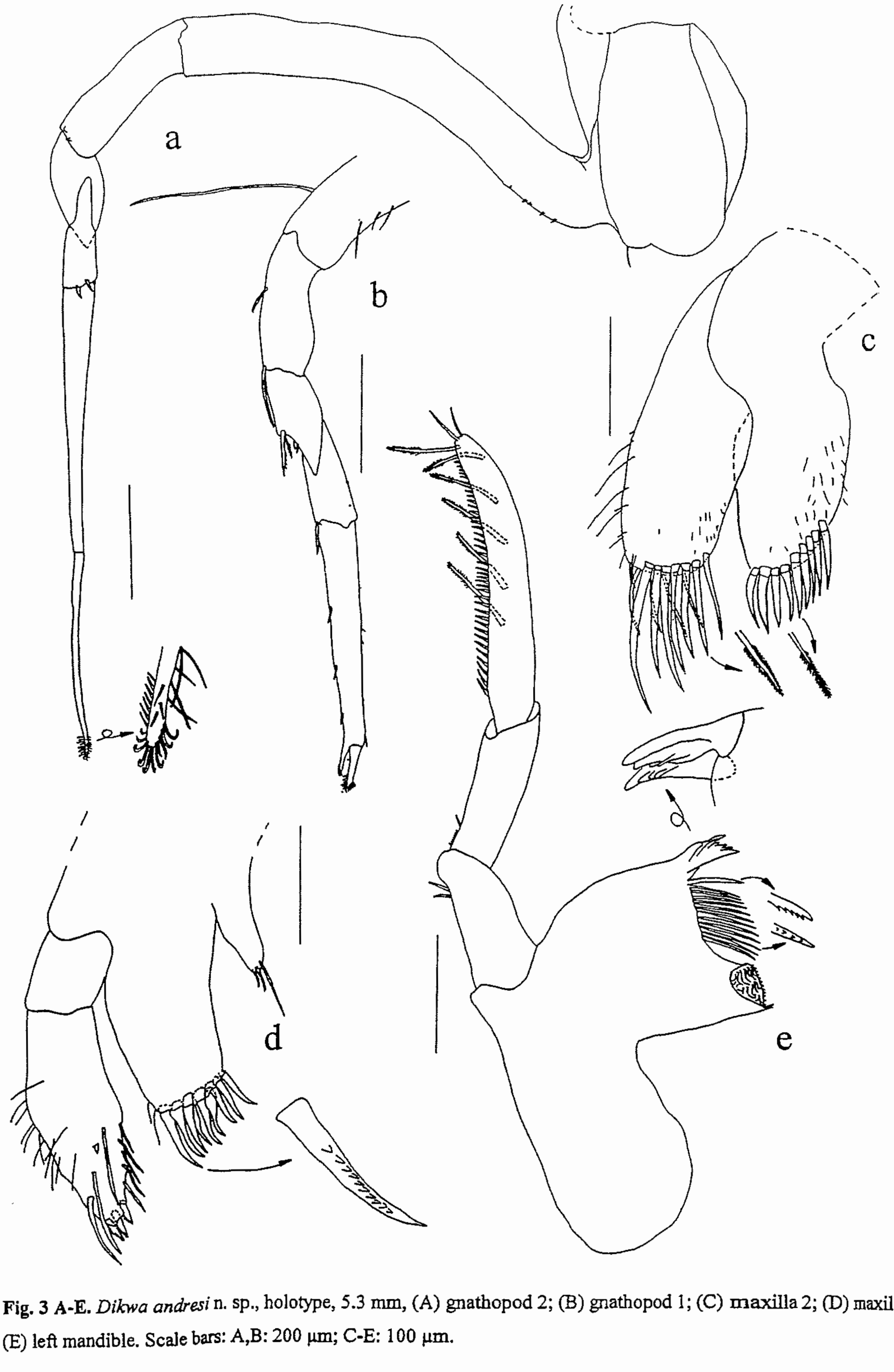

Fig. 3 A-E. *Dikwa andresi* n. sp., holotype, 5.3 mm, (A) gnathopod 2; (B) gnathopod 1; (C) maxilla 2; (D) maxilla 1; (E) left mandible. Scale bars: A,B: 200 µm; C-E: 100 µm.

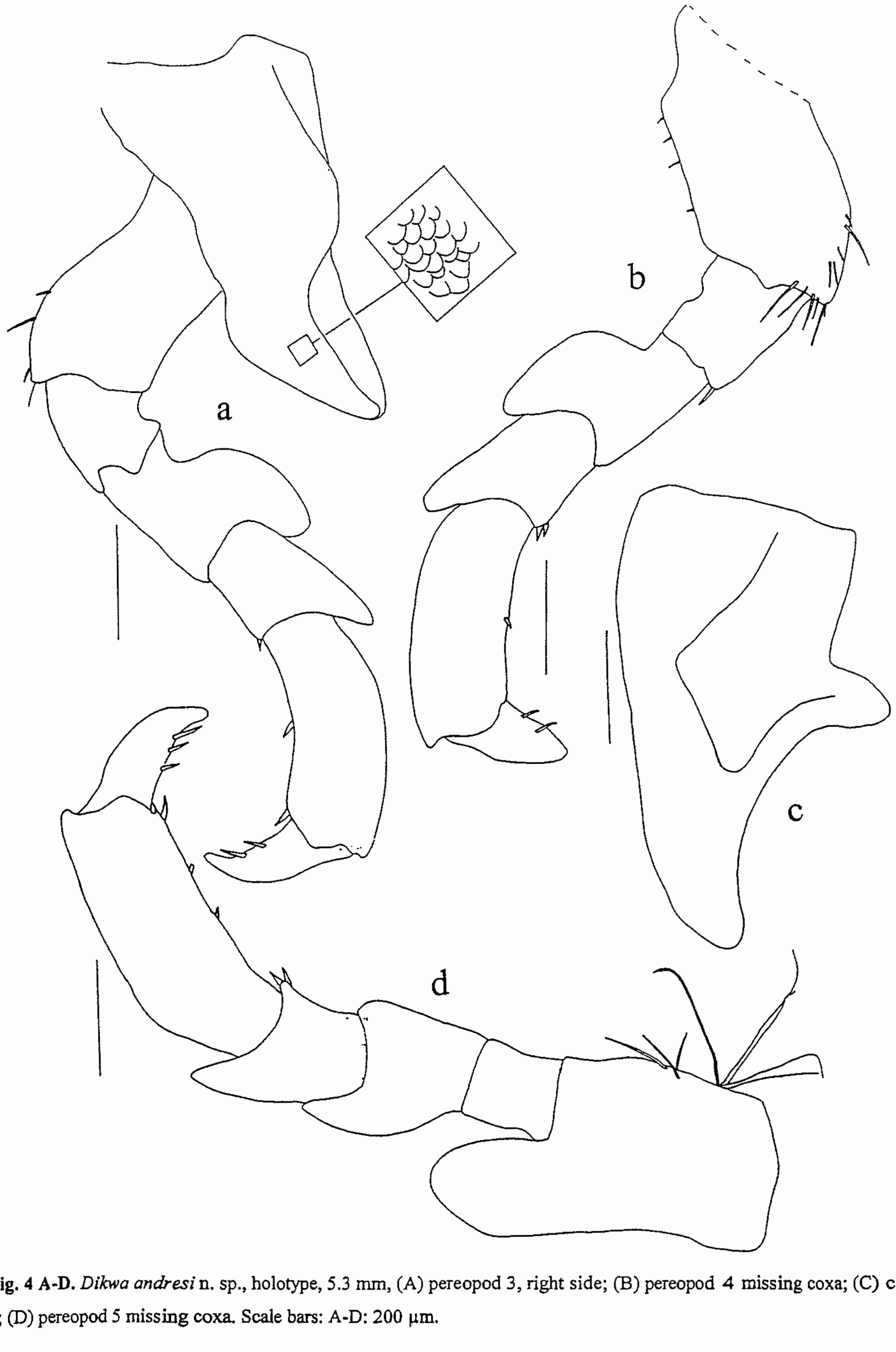

Fig. 4 A-D. *Dikwa andresi* n. sp., holotype, 5.3 mm, (A) pereopod 3, right side; (B) pereopod 4 missing coxa; (C) coxa 4; (D) pereopod 5 missing coxa. Scale bars: A-D: 200 µm.

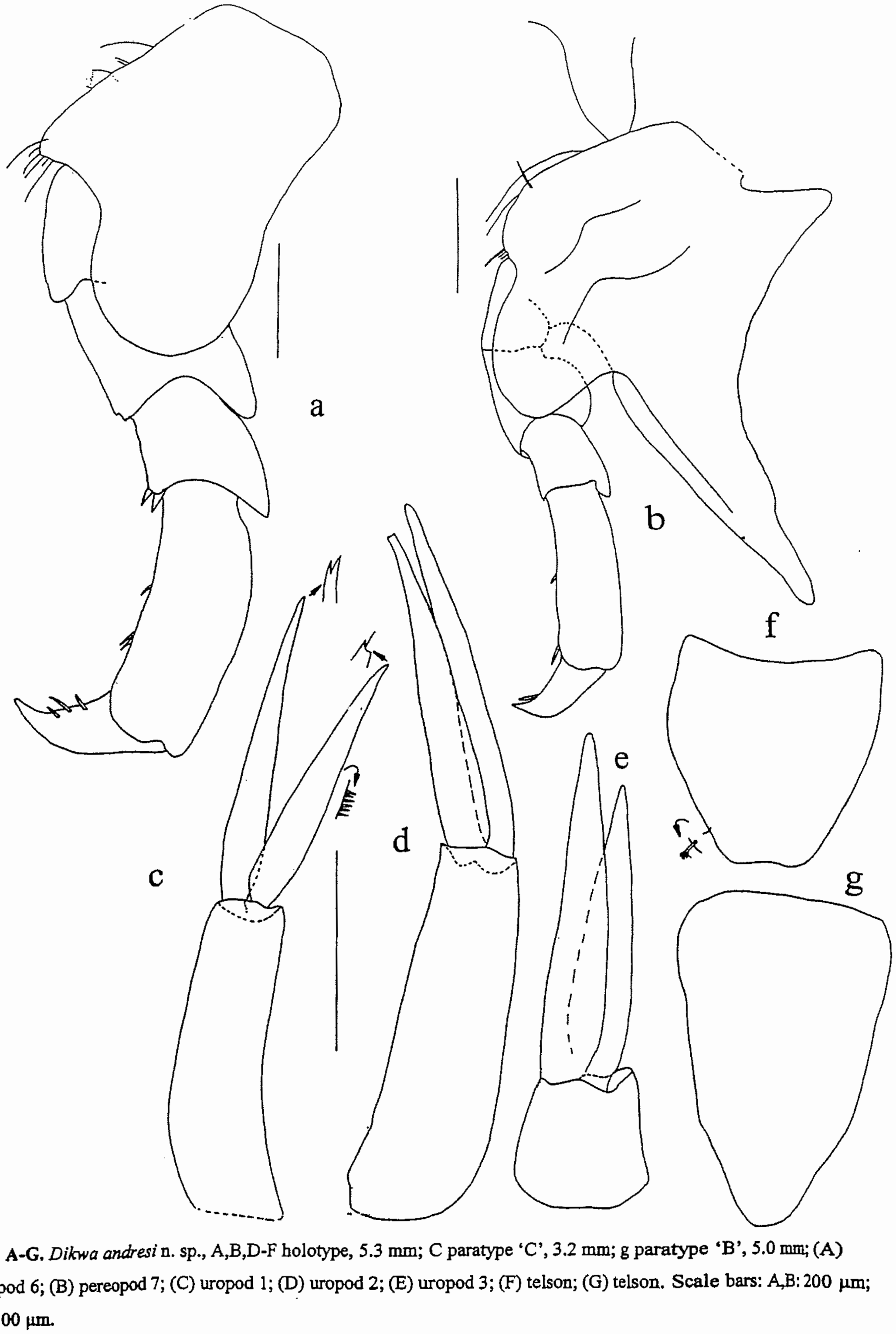

Fig. 5 A-G. *Dikwa andresi* n. sp., A,B,D-F holotype, 5.3 mm; C paratype 'C', 3.2 mm; g paratype 'B', 5.0 mm; (A) pereopod 6; (B) pereopod 7; (C) uropod 1; (D) uropod 2; (E) uropod 3; (F) telson; (G) telson. Scale bars: A,B: 200 µm; C-G 300 µm.

Discussion

The family Diwidae only consists of one genus *Dikwa*. Formerly the genus *Dikwa* was classified as Acanthonotozomatidae, but now differs from this family in having a mandibular molar, chelate first gnathopod, flagellar second gnathopod and a reduced head (Coleman & Barnard, 1991).

The new species is the first record of the genus *Dikwa* in the Southern Ocean and the second species described. *Dikwa acrania* (Griffiths, 1974) is known from Southern Africa, the Cape Province east of Cape Agulhas. The two species differ mainly in the dorsal armature and the shape of coxa 1. The differences are summarized in Table 1.

Tab. 1. Morphological differences between *Dikwa andresi* n. sp. and *Dikwa acrania* Griffith, 1974.

Characters	*Dikwa andresi* n. sp.	*Dikwa acrania*
Accessory flagellum	present	absent
Pereonites 1-5	with blunt elevated processes	with continuous dorsal keel
Pereonites laterally	produced	smooth
Coxa 1	twice the length of coxa 2	one third longer than coxa 2
Coxa 7	projection strongly turned backwards	projection slightly turned backwards
Pereon segments dorsally produced	all	6 and 7
Epimeral plate 1 ventral margin	pointed	rounded
Epimeral plates 2 and 3 postero-ventrally	rounded	produced

Even though only three paratypes exist of *Dikwa andresi* n. sp., some intraspecific variation was observed among the four individuals. The main difference is the shape and relative length of the telson (Figure 5G, 5F). While the telson of the holotype is about as long as broad and emarginate (Figure 5F), the telson of paratype 'B' (Figure 5G) is far longer than broad, with rounded apex. The telsa of the other paratype have intermediate stages of elongation (not drawn).

The individuals of *Dikwa andresi* n. sp., were collected south of the Falkland Islands, in depths of 270- 290 meter. Therefore it is not surprising that eyes of the living animals are absent and the animals lack pigments, are bright white. *Dikwa acrania* occurs in 200 meter depth, also without eyes and pigments. While *Dikwa acrania* was living on coarse khaki sand (Griffiths, 1974), *Dikwa andresi* n.sp. was caught clinging to the bright red hydrocoral (Hydrozoa) *Errinopsis reticulum* Broch, 1951. From the strong triturative molar and toothed incisor it can be speculated that *Dikwa andresi* n. sp. is able to bite out tough material of the coral.

Griffiths (1974) mentioned the integument of *D. acrania* to be composed of small plates resembling scales of a fish. The new species of *Dikwa* shows a similar cuticular structure (see detail of Figure 3A).

Acknowledgements

The authors are grateful to Professor Wolf Arntz (Bremerhaven), ANT XIX-5 cruise leader and the crew of RV Polarstern. Miss Monika Hänel kindly inked the habitus drawing (Figure 1). The hydrocoral *Dikwa andresi* n. sp. was found on was identified by Pablo Lopez-Gonzalez (Sevilla). This article is based on a doctoral study by Anne-Nina Lörz in the Faculty of Biology, University of Hamburg, supported by the Studienstiftung des deutschen Volkes.

Veröffentlichung VIII

Composition of suprabenthic Peracarida (Crustacea, Malacostraca) during the Antarctic autumn

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Abstract

The composition of suprabenthic Peracarida from a depth between 1 and 1.33 m above the seafloor was investigated. In order to study the abundance and diversity semi-quantitatively, the samples were taken by means of the supranet of an epibenthic sledge off Kapp Norvegia and off the South Shetland Islands. The samples were taken during ANT XVII-3 with RV *Polarsten* in April and May 2000.These samples of EASIZ III received during the Antarctic autumn are compared with those of EASIZ II taken during the austral summer. While the present study shows far less abundance of all taxa, the diversity is about twice as high as during summer. In total 115 species of peracarid crustaceans were sampled at six stations yielding 1336 individuals standardized to 1000m³ hauls. Amphipoda dominated in abundance and diversity at all stations.

Keywords: Antarctica, Peracarida, Suprabenthos

Introduction

In the present only few studies have been conducted on Antarctic suprabenthic peracarids, however none have yet treated samples collected during the Antarctic autumn. Linse et al. (2002) analysed the composition and distribution of suprabenthic fauna in the south-eastern Weddell Sea and off King George Island. Siegel & Mühlenhardt-Siegel (1988) published on the occurrence of mysids in the region of the Antarctic Peninsula and San Vincente et al. (1997) described first results on composition and vertical distribution of suprabenthic assemblages from the South Shetland Island and the Bransfield Strait. A comparison between the peracarid density of the Arctic and Antarctic has been conducted by Brandt (2001). All literature dealing with Antarctic suprabenthic peracarid crustaceans relies on material taken during the Antarctic summer.

The present study is based on material collected by means of an epibenthic sledge (Brandt & Barthel 1995) during the EASIZ III programme of the RV Polarstern ANT XVII-3 expedition to the Weddell Sea and the Antarctic Peninsula. Samples were taken from March-May 2000, during the Antarctic autumn.

The main aspects of this study were:

1. to analyse the abundance and diversity of the suprabenthic Peracarida off the South Shetland Islands and off Kapp Norvegia
2. to compare these data collected during the Antarctic autumn with data of abundance and diversity of suprabenthic peracarids taken with the same gear during the Antarctic summer (Linse et al. 2002).

Material & Methods

The exact station locations on the Antarctic shelf are listed in Tab. 1. The samples were taken by means of an epibenthic sledge (EBS). The sledge was originally designed by Rothlishberg & Pearcy 1977, modified by Brattegard & Fosså (1991) and extended by Brandt & Barthel (1995) in order to catch suprabenthic and epibenthic fauna. The suprabenthic sampler collects the layer 1-1.33 m above the bottom. Both samplers have a opening of 100 cm width and 33 cm height. A plankton net is attached to the sampler with a mesh size of 0.3 mm. For more details see Brandt & Barthel (1995). The sledge was hauled over the ground for 10 minutes at a mean of one knot (= 0.5 m/s). The distance hauled were calculated on the basis of the GPS-derived positions of the ship at the start and end of each haul (after Brandt & Barthel 1995, Linse et a. 2002):

Distance in m= $1852 \times \sqrt{}(\Delta lat`)^2+(\cos lat` \times \Delta long`)^2$.

The length of hauls varied from 124 –554 m (see Tab. 1), therefore the abundance data were standardized to 1000 m hauls. To compare the data to Linse et al. (2002) the area of 1 m x 0.33 m wide net opening was calculated to an 1m² area, resulting in 1000 m³sampled area. On the deepest station, 138-1, the supranet was twisted, therefore the lack of animals on this station is not considered in the present analysis.

After the samples were washed through a 250 µm screen, they were fixed in 4 % buffered formalin and transferred into 70 % ethanol after a few days.

Tab. 1. Station list of the epibenthic sledge samples (EBS) taken during ANT XVII-3 (EASIZ 3) of RV *Polarstern*.KN= KappNorvegia, W/D= west of Deception Island

Station	Date	Time	Area	Latitude		Longitude		Depth	Length of haul
				S beg.	S end	W beg.	W end	(m)	(m)
97-1	03.04.00		KN	71°06.30`	71°06.20`	12°50.50`	12°49.90`	743	406
138-1	11.04.00	8:10	KN	71°08.90`	71°08.80`	13°12.80`	13°13.20`	840	
174-1	30.04.00	18.52	W/D	63°01.10`	63°01.30`	61°09.10`	61°08.60`	365	554
175-1	30.04.00	19.56	W/D	63°01.00`	63°00.88`	61°08.80`	61°09.34`	305	505
177-2	01.05.00	20.17	W/D	62°50.13`	62°50.16`	60°50.39`	60°50.39`	206	124
180-2	02.05.00	22.08	W/D	62°07.20`	62°07.40`	60°22.80`	60°23.00`	201	409
184-2	03.05.00	20.05	W/D	62°.00.09`	62°00.26`	60°19.33`	60°19.54`	399	364

Results

In total 688 suprabenthic peracarid crustaceans were collected, representing 115 taxa. For comparison between stations and with the suprabenthic data of Linse et al. (2002) the individuals were standardized to 1000 m trawled distance. Amphipoda were by far the most abundant peracarids in the supranet with 2334 individuals per 1000 m³, followed by Cumacea (644 inds/1000m³) and Isopoda (561 inds/1000m³) (Tab. 2).

The highest species richness was also shown by amphipods with 56 species, comprising 50 percent of the total peracarid species found. While the suprabenthic Isopoda consisted of 30 species, the cumaceans beared 15 and the tanaids 13 species (Tab. 3). Mysidacea were only represented at one station with only one species. Since several animals, including the mysids, were damaged, the number of species was calculated very conservatively.

Tab. 2. Abundance of the suprabenthic peracarid crustacean taxa, standardized to 1000 m³ hauls during the Antarctic autumn.

Station	97-1	174-1	175-1	177-2	180-1	184-2
Depth (m)	743	365	305	206	201	399
Mysidacea	0	0	0	0	0	33
Amphipoda	66	662	463	193	315	635
Cumacea	30	15	48	24	24	503
Tanaidacea	7	11	18	242	37	33
Isopoda	45	153	171	24	36	132
Sum	148	841	700	483	412	1336

Tab. 3. Number of species per station for the peracarid taxa caught with the supranet of the EBS during the Antarctic autumn.

Station	97-1	174-1	175-1	177-2	180-1	184-2
Depth (m)	743	365	305	206	201	399
Mysidacea						1
Amphipoda	9	22	23	7	15	20
Cumacea	3	6	4	1	4	10
Tanaidacea	1	3	3	10	3	2
Isopoda	6	11	12	1	3	7
Sum	19	42	42	19	25	40

Amongst the occurring 17 amphipod families individuals of Podoceridae were most frequent, followed by Lysianassidae and Photidae. The highest species richness was shown by the gammarid families Lysianassidae, Oedicerotidae and Synopiidae. Other families like Amphilochidae, Melphidippidae and Caprellidae were only represented by a single species (Appendix 1). The 561 inds/1000m^3 individuals of Isopoda were distributed among 12 families, 27 genera and 30 species. Antarcturidae, Munnopsididae and Paramunnidae were the dominating families. The 348 inds/1000m^3 of tanaidaceans represent seven families, of which Typlotanaidae was most speciose with four species while Psedotanaidae had most individuals. The cumaceans distributed their 15 species among five families. While Nannastacidae were most speciose, most individuals belong to Diastylidae (Appendix 1). Only one species of Mysidacea was caught, *Boreomysis brucei* Tattersall, 1913.

The supranet catches yielded highly varying abundances for the peracarid taxa at the six stations (Tab. 2). The single station at Kapp Novegia, 97-1, which was also the deepest, showed the lowest abundance and species richness, while station 184-2, the northernmost station, showed the by far highest abundance.

Discussion

Not many investigations on suprabenthic peracarid crustaceans have been conducted yet, especially rare are results from polar regions. When Sirenko et al. (1996) investigated suprabenthic invertebrates in the Laptev Sea, Siberian Arctic, they used a benthopelagic sampler attached to an Agassiz trawl. Brandt (1993) and Brandt et al. (1996) published on Arctic suprabenthic crustaceans caught by the epibenthic sledge modified by Brandt & Barthel (1995). Sampling with the type of modified epibenthic sledge Linse et al. (2002) provided the first suprabenthic community analysis from Antarctic waters. We used the same sledge in order to get data best comparable to those provided by Linse et al. (2002) from the suprabenthic fauna in the Weddell and Scotia Seas.

Slight mistakes may occur because of turbulence in front of the gear (Buhl-Jensen 1986). This results in sampling of water below the opening. Therefore not all peracarid crustaceans determined in this analysis only occur 1-1.33 meters above the ground, it may happen, that epifauna is whirled up.

While the results of suprabenthic communities of Linse et al. (2002) rely on animals caught during February and the first part of March, our sampling took place in April and May, the latter considered as Antarctic autumn. Therefore changes in abundance and diversity shall be judged with a seasonal background. Even though most peracarids are known to live for several years (e.g. Klages 1993, Wägele 1987), it is a general assumption, that abundance and diversity is highest during the Antarctic summer. Pasternak & Schiel (2001) compared the

seasonal feeding pattern of two Antarctic copepods. Only one of the two species of copepods underwent diapause at depth and was never found feeding in winter. Even though many of the amphipods caught are suspension feeders (Dauby et al. 2001a) and the resuspension during the Antarctic autumn is less produced than during the austral summer, we assume that the suprabenthic peracarids caught do not undergo a winter diapause.
While Linse et al. (2002) caught Mysiadacea at most stations, resulting in an average of more than 1000 individuals/1000m³, we only caught 6 individuls/1000m³ at one station belonging to one species. Until now this species, *Boreomysis brucei* Tattersall 1913, was not known to occur suprabenthically (Brandt et al. 1998). Additionally, its bathymetric distribution known from 750-4300 m has now increased to a depth of 364 m.

Comparing the abundance with the data of Linse et al. (2002) the present data show far less individuals standardized to 1000m³ per station. Linse et al. sampled 16 station during the austral summer and we had six successful stations. The following table compares the average of the five peracarid taxa per 1000m³:

	Linse et al. (2002) EASIZ II	Lörz & Brandt EASIZ III
Mysidacea	1034	6
Amphipoda	1052	389
Cumacea	1458	107
Tanaidacea	92	58
Isopoda	678	94

Surprisingly it is noted, that the species diversity among peracarid crustacean taxa is far higher in the present study. While Linse et al. (2002) found an average of 16 species of Peracarida per station, we have an average of 31 species per station. The diversity of suprabenthic peracarid crustaceans is therefore twice as high in the Antarctic autumn as during the Antarctic summer. The only two stations where Linse et al. (2002) caught more than 30 peracarid species per station were off Vestkapp in more than 900 m depth. The depth of the present studied stations varied from 201-399 m off the South Shetland Islands, with the exception of the single station off Kapp Norvegia with 743 m. The authors believe in the amount of stations taken with the modified EBS being too small to allow interpretation referring to depth. The Antarctic shelf extends to a depth of 1000 m (Clarke & Johnston in press), therefore other factors as current directions or velocities or sediment structure are responsible for in charge of the patchy distribution of the suprabenthic peracarid crustaceans. The EBS has proved again to be an efficient sampler for suprabenthos. Further studies on the communities one meter above the ground may contribute to a better understanding of bentho-pelagic coupling.

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Appendix 1: Species list of Peracarida caught in the supranet of the Epibenthic sledge (EBS) during ANT XII-3 (EASIZ III), Amtz & Brey (2001).

Family	Genus	Species	Author	Stations ANT XVII-3					
				97-1	174-1	175-1	177-2	180-2	184-2
MYSIDACEA									
Mysidae	Boreomysis	brucei	Tattersall, 1913						4
AMPHIPODA									
Ampeliscidae	Amplelisca	cf. dallenei	Bellan-Santini, 1985		4	7			
Ampeliscidae	Amplelisca	sp.				1			
Ampeliscidae	Byblis	cf. securiger	(K.H. Bamard, 1931)		1			8	
Amphilochidae	sp.							2	
Corophioidea	Pseudericthonius	sp.			5	3	1	1	
Dexaminidae	Lepechinella	cf. cetrata	K.H. Barnard, 1932		2	1			
Dexaminidae	Lepechinella	drygalski	Schellenberg, 1926	1					
Eusiridae	Djerboa	cf. furcipes	Chevreux, 1906				1		3
Eusiridae	Eusirus	antarcticus	Thomson, 1880	1					
Eusiridae	Prostebbingia	sp. A				2		3	
Eusiridae	Prostebbingia	sp. B				1			4
Eusiridae	sp.						1		
Photidae	Gammaropsis sensu lato				2	25		2	1
Photidae	Photis	sp.				1			
Ischyroceridae	Jassa	sp.				1			
Ischyroceridae	Pseudischyrocerus	sp. A			1	2		3	
Ischyroceridae	Pseudischyrocerus	sp. B				1			
Ischyroceridae	Pseudischyrocerus	cf. distichon	(K.H. Barnard, 1930)	1					
Ischyroceridae	sp.				2	1			1
Leucothoidae	Leucothoe	cf. spinicarpa	(Abildgaard, 1789)	1					
Lilljeborgidae	Lilljeborgia	sp. A							1
Lilljeborgidae	Lilljeborgia	sp. B					1		
Lilljeborgidae	Lilljeborgia	cf. macrodon	Schellenberg, 1931					2	1
Lilljeborgidae	Lilljeborgia	quinquedentata	Schellenberg, 1931		3	4			
Lysianassidae	sp. A			1					
Lysianassidae	sp. B			1	1				2
Lysianassidae	sp. C				1				
Lysianassidae	sp. D				3				

				97-1	174-1	175-1	177-2	180-2	184-2
Lysianassidae	sp. E				1				3
Lysianassidae	sp. F				1	2		1	
Lysianassidae	sp. G					3		5	
Lysianassidae	sp. H								24
Lysianassidae	sp. J								23
Lysianassidae	Lepidepcreoides	cf. xenops				1			
Melphidippidae	Melphidippa	Antarctica		1					
Oedicerotidae	sp. A				3				
Oedicerotidae	sp. B				1	1			
Oedicerotidae	sp. C ?								2
Oedicerotidae	sp. D								2
Oedicerotidae	Monoculodes	Scabriculosus	K.H. Barnard, 1932	1					
Oedicerotidae	Oediceroides	sp.				2			1
Oedicerotidae	Oediceroides	Calmani	Walker, 1906					4	1
Phoxocephalidae	sp.				2	6		1	1
Podoceridae	Neoxenodice	sp.						2	
Podoceridae	Neoxenodice	cf. cryophile	Lowry, 1976		146	10			
Podoceridae	Podocerus	cf. septemcarinatus	Schellenberg, 1926		1				1
Stenothoidae	sp.A				3	1	2	2	2
Stenothoidae	sp. B				1		1		1
Stenothoidae	sp.C								1
Synopiidae	sp.							3	
Synopiidae	Syrrhoe	sp. A		1					
Synopiidae	Syrrhoe	sp. B			2				
Synopiidae	Syrrhoe	Nodulosa	K.H. Barnard, 1932		1	1			
Synopiidae	Syrrhoites	Anaticauda	K.H. Barnard, 1930						2
Synopiidae	Tiron	Antarcticus	K.H.Barnard, 1932			1			
Caprellidae	Aeginoides	Gaussi	Schellenberg, 1926				1	4	
CUMACEA									
Bodotriidae	Cyclaspis	Cristulata	Gamo, 1987		12	3		1	8
Bodotriidae	Cyclaspis	sp. A							21
Bodotriidae	Cyclaspis	sp. B		1	2				
Diastylidae	Leptostylis	sp. A			20	3	1	1	11
Diastylidae	Diastylis	sp. A			3	1			2

				97-1	174-1	175-1	177-2	180-2	184-2
Diastylidae	Diastylis	sp. B				1			
Diastylidae	Diastylis	sp. C			1				
Lampropidae		sp. A			3			8	1
Leuconidae	Leucon	sp. A							1
Leuconidae	Leucon	sp. B		1					
Nannastacidae	Campylaspis	maculata	Zimmer 1909						4
Nannastacidae	Campylaspis	maculata (?) manca 1	Zimmer 1909	2				1	
Nannastacidae	Procampylaspis	sp. A							1
Nannastacidae	Procampylaspis	sp. B							1
Nannastacidae	Campylaspis								11
TANAIDACEA									
Typhlotanaidae	sp. A			1		1			
Typhlotanaidae	sp. B						5	3	
Typhlotanaidae	sp. C				1	1	4		
Typhlotanaidae	sp. D						5		
Pseudotanaidae	sp. A				1				3
Pseudotanaidae	sp. B						23		1
Pseudotanaidae	sp. C						1		
Tanaidae	sp.							1	
Nototanaidae	Nototanais	antarcticus	(Hodgson 1902)				1	1	
Colletteidae	Collettea	arnaudi	(Shiino 1978)			1			
Agathotanaididae	Paranarthrura	fortispina	Sieg 1986		1		1		
Anarthruridae	Araphuroides	parabreviremis	Sieg 1986				1		
Anarthruridae	Araphura	cf. elongata	(Shiino 1970)				1		
Anarthruridae	Akanthophoreus	sp.					1		
ISOPODA									
Antarcturidae	sp. A					2			
Antarcturidae	sp. B					1			
Antarcturidae	Fissarcturus	hirticornis	Monod, 1926			2			
Idoteidae	Edotia	oculopetiolata	Sheppard, 1957			8			
Munnopsidae	Eurycope	sp. (cf. antarctica)				1			
Munnopsididae	Echinozone	spicata	(Hodgson, 1910)			1			
Munnidae	Munna	spicata	Teoderczyk & Wägele, 1994			6			
Paramunnidae	Pleurosignum	elongatum	Vanhöffen, 1914			1			
Paramunnidae	Paramunna	antarctica	Richardson, 1906			1			

				97-1	174-1	175-1	177-2	180-2	184-2
Santidae	Santia	charcoti	Richardson, 1906			1			
Paramunidae	Coulmannia	frigida	Hodgson, 1910		2				
Antarcturidae	Chaetarcturus	cf. sp. nov. ?				1			
Munnidae	Munna	spicata	Teoderczyk & Wägele, 1994			2			
Antarcturidae	Fissarcturus	hirticornis	(Monod, 1926b)		1				
Idoteidae	Edotia	oculoptiolata	Sheppard, 1957		1				
Paramunnidae	Coulmannia	frigida	Hodgson, 1910		3				
Munnidae	Munna	spicata	Teoderczyk & Wägele, 1994		7				
Munnidae	Munna	antarctica	(Pfeffer, 1887)		9				
Paramunnidae	Notoxenus	spinifer	Hodgson, 1910		4				
Paramunnidae	Notoxenus	cf. sp. nov. ?			2				
Paramunnidae	Paramunna	cf. antarctica	(Richardson, 1906)		1				
Paranthuridae	Leptanthura	glacialis	Hodgson, 1910			2			
Antarcturidae	Dolichiscus	pfefferi	Richardson, 1913		1				
Paranthuridae	Leptanthura	glacialis	Hodgson, 1910		2				
Antarcturidae	Antarcturus	furcatus	Studer, 1882						
Paramunnidae	Paramunna	cf. antarctica	(Richardson, 1906)				1		
Serolidae	Serolis	sp.						2	
Acanthaspidiidae	Acanthaspida	drygalski	Vanhöffen, 1914	1					
Munnopsididae	Eurycope	cf. antarctica	?	1					
Paramunnidae	Austrosignum	glaciale	Hodgson, 1910	1					
Paramunnidae	Pleurogonium	cf. serratum	Beddard, 1886	1					
Paramunnidae	Paramunna	rostrata	(Hodgson, 1910)	1					
Munnopsidae	Munna	cf. antarctica	(Pfeffer, 1887)	1					
Munnopsididae	Echinozone	spicata	(Hodgson, 1910)					2	
Paramunnidae	Notoxenus	spinifer	Hodgson, 1910					1	
Paranthuridae	Paranthura	antarctica	Kussakin, 1967		1				
Paranthuridae	Leptanthura	glacialis	Hodgson, 1910		9				
Cirolanidae	Natatolana	intermedia	(Vanhöffen, 1914)						3
Munnopsididae	Coperonus	frigida	(Vanhöffen, 1914)						2
Munnopsididae	Eurycope	cf. acutiperaeons	Schulz, 1978						1
Munnopsididae	Eurycope	sp. cf. gaussi	Vanhöffen, 1914						3
Munnidae	Munna	spicata	Teoderczyk & Wägele, 1994						4
Cryptoniscidae	Cryptoniscium	sp.							2
Desmosomatidae	Torwolia	sp. nov.							1

4. Diskussion

Die Diskussion der vorliegenden Arbeit ist nach den Fragestellungen (Kap. 1.4.) in 1. Taxonomie und Systematik, 2. Abundanz und Diversität sowie 3. Phylogenie gegliedert. Diese Einteilung dient einer vereinfachten Lesbarkeit und soll auf keinen Fall implizieren, dass diese Bereiche voneinander abzugrenzen sind, die Disziplinen sind vielmehr eng miteinander verwoben. Besonders deutlich tritt diese thematische Verflechtung bei den Abundanz- und Biodiversitätsstudien hervor, die ohne taxonomische Kenntnisse des untersuchten Materials nicht möglich sind. Die phylogenetischen Arbeiten setzen ebenfalls gute Kenntnisse der Taxonomie und Systematik voraus. Die Untersuchungen verwandtschaftlicher Beziehungen dienen wiederum der Verbesserung der systematischen Kenntnisse.

4.1. Taxonomie und Systematik

Systematik beschäftigt sich mit der Beschreibung natürlich gewachsener Systeme, also mit materiellen Strukturen oder natürlichen Einheiten, die sich aus historischen Tatsachen ergeben (Wiesemüller et al. 2003). Taxonomie befasst sich mit den formalen Regeln und Vorschriften für die Klassifikation und Benennung von Organismengruppen.
Da die vorliegenden Veröffentlichungen bisher unbekannter Arten und ihre Abgrenzung zu bereits beschriebenen Vertretern beiden Themen zugeordnet werden, sind Taxonomie und Systematik im folgenden Kapitel gemeinsam behandelt.

Die Entdeckungen und Beschreibungen neuer Arten aus dem Südozean sind in den letzten Jahren rapide angestiegen. Sowohl für verschiedene Ordnungen des Makrobenthos, z.B. Gastropoda, Bivalvia, Cephalopoda, Crinoidea, Holothuroidea, Polychaeta und Isopoda, als auch der Meiofauna wurden zahlreiche neue Arten und Gattungen beschrieben. Allein während ANT XVII-3 wurden z.B. drei neue Cephalopodenarten der Gattung *Megaleledone* , zwei neue Arten des Holothurientaxons Apodida und mindestens fünf neue Arten verschiedener Mollusken gesammelt (Allcock 2001, Bohn 2001, Sirenko & Schrödl 2001). Während der EASIZ Fahrten I-III wurden mehr als 10 % der jeweils gefangenen Amphipoda Arten als unbeschrieben eingestuft (De Broyer et al. 1997, De Broyer et al. 1999, Lörz et al. 2001). Die hohe Anzahl der noch unbeschriebenen Amphipoda während der *Polarstern*-Expeditionen ist dadurch bedingt, dass die entsprechenden Sammler zum Teil ihre Ergebnisse nicht publizieren. Sehr wahrscheinlich handelt es sich oft um Fänge der gleichen neuen Arten, die zwar mehrfach gefangen wurden, aber noch nicht beschrieben sind.

In der vorliegenden Arbeit werden vier neue Arten beschrieben (Veröffentlichung zwei, drei, vier und sieben). Bei *Epimeria reoproi* Lörz & Coleman 2001 handelt es sich um eine weitere Art zu den bisher 20 bekannten Arten der Gattung *Epimeria*, Epimeriidae. Die Epimeriidae zählen zu den dominantesten Amphipodenfamilien des antarktischen Benthos (Coleman 1990), dies ist u.a. auf ihre Körpergröße zurückzuführen. Tiere von mehreren Zentimeter Länge werden auch von Fischereigerät wie Grundschleppnetz und Aggassiztrawl mit relativ großen Maschenweiten gefangen. Zudem bewirkt die primär epibenthische Lebensweise epimeriider Amphipoda (De Broyer et al. 2001a), dass sie häufig von geschleppten Fanggeräten gesammelt werden. Bei der Beschreibung von *Epimeria reoproi* handelt es sich um den „klassischen Fall" einer neuen Art. Eine Bestimmung nach Barnard & Karaman (1991) führte eindeutig zu der Familie Epimeriidae. Obwohl der Habitus, insbesondere die dorsale Bezahnung der Art *Metepimeria acanthurus* Schellenberg 1931 ähnelt, handelt es sich aufgrund des viergliedrigen Maxillipeden Palpus um einen Vertreter der Gattung *Epimeria*. Die Gattung *Metepimeria* zeichnet sich dagegen durch einen dreigliedrigen Palpus aus. Die bearbeitete Art entspricht keiner der bereits 18 beschriebenen *Epimeria*-Arten. *Epimeria reoproi* unterscheidet sich von den zwei ähnlichsten Vertretern der Gattung, *E. vaderi* Coleman 1998 und *Epimeria* sp. Andres 1985 in mehreren eindeutigen Merkmalen, z.B. Form der ersten, dritten und vierten Coxalplatte, Form und Länge des Rostrums oder Anzahl der dorsolateralen Zähnchen auf den ersten beiden Pleoniten (s. S. 29). Aufgrund des Vorhandenseins zweier Paratypen mit entsprechenden Merkmalen lassen sich potentielle Varianzen bekannter Arten ausschließen.

Arten der Überfamilie Lysianassoidea sind sehr häufige Vertreter des antarktischen Benthos. Die Lysianassoidea werden im Südozean von 146 Arten aus 54 Gattungen repräsentiert (De Broyer & Jazdzewski 1996). Von diesen sind 76 Arten in antarktischen Gebieten südlich der Konvergenz endemisch. Da es sich bei den Lysianassidae vorwiegend um Aasfresser handelt, können Tausende von Individuen in beköderten Fallen gefangen werden (z.B. De Broyer et al. 1997). Es gibt jedoch auch Lysianassidae, die mit Schwämmen assoziiert leben , z. B. *Abyssorchomene rossi* (Walker 1903), *Uristes gigas* Dana 1849 und *Waldeckia obesa* (Chevreux 1905) (Dauby et al. 2001b). Der Lysianassidae *Pseudokoroga spongiophila* Lörz & De Broyer im Druck wurde, wie der Name impliziert, ebenfalls in Schwämmen gefunden (s. S. 33). Die Zuordnung der neuen Art zu der Amphipodengruppe Lysianassidae war ohne Zweifel möglich. Die weitere Klassifizierung der Gattung

Pseudokoroga Schellenberg 1931 der Unterfamilie Tryphosinae Lowry & Stoddart 1997 erfolgte mit gewissen Vorbehalten. Von der Gattung *Pseudokoroga* unterscheiden sich die beschriebenen Tiere der neuen Art u. a. in einem Epistom, welches nicht prominent und ausgezogen ist, einer inneren Platte der zweiten Maxille, die deutlich kürzer ist als die äußere und einem eingeschnittenen Telson. Diese Merkmale, sowie der nicht vergrößerte erste Gnathopod der Männchen und die anteroventral verbreiterte erste Coxalplatte, könnten jedoch auch die Einführung einer neuen Gattung rechtfertigen. Da sich die Taxonomie der Lysianassidae derzeit in starker Bewegung befindet (Lowry pers. Mitt., De Broyer pers. Mitt.), schien es adäquat, die neue Lysianassidenart zunächst in einer bekannten Gattung zu publizieren und die Unterschiede herauszuarbeiten. Selbstverständlich weist *Pseudokoroga spongiophila* von den bekannten Gattungen der Lysianassidae die größten Ähnlichkeiten mit *Pseudokoroga* auf. Der glückliche Umstand 300 Paratypen zur Verfügung zu haben, ermöglichte Untersuchungen zu Größenverteilung, Reproduktionsraten bzw. Anzahl und Größe der Eier, Länge der Oostegiten und Magenanalysen (s. S. 40). Auf die Ökologie dieser bisher unbekannten lysianassiden Amphipoda wird im folgenden Kapitel (4.2) näher eingegangen.

Der ebenfalls neu beschriebene Amphipode der Familie Eusiridae, *Eusirus giganteus* Andres et al. 2002, sieht seinem Schwestertaxon *Eusirus perdentatus* Chevreux 1912 sehr ähnlich (s. vierte Veröffentlichung). Die Unterschiede, die von Andres et al. (2002) herausgearbeitet wurden, lassen diese Art jedoch klar von *E. perdentatus* und *E. properperdentus* Andres 1979 unterscheiden (s. S. 52). Dieser antarktische *Eusirus*- Komplex besteht nun aus drei Arten, die sich durch einen distalen, middorsalen deutlichen Zahn auf den fünften bis siebten Peraeoniten sowie auf den drei Pleoniten auszeichnen. Den weiteren sechs bekannten antarktischen, sowie 19 anderen weltweit verbreiteten, Vertretern der Gattung *Eusirus* fehlt ein disterodorsaler Zahn auf dem dritten Pleoniten. Während es sich bei den oben erwähnten neuen Arten von Epimeriidae und Lysianassidae meist um relativ einfache Merkmale zur Abgrenzung bereits bekannter Taxa handelt („Zähnchen vorhanden oder fehlend“), sind die Merkmale zur Unterscheidung der Arten innerhalb des *Eusirus*-Komplexes wesentlich schwieriger. Die Längenverhältnisse von z.B. Merus zu Propodus des dritten und vierten Peraeopoden oder des vierten zu fünften Grundgliedes der zweiten Antenne sind morphologische Merkmale, die zur Unterscheidung dienen. Um solche proportionalen Unterschiede nicht als intraspezifische Varianz zu verkennen, war die Vermessung zahlreicher Tiere nötig. Es wurden zahlreiche Merkmale mehrerer hundert Tiere geprüft, von denen sich 13 Merkmale zur Aufspaltung des antarktischen Eusiriden-Komplexes in *Eusirus perdentatus*, *E. properperdentatus* und *E. giganteus* eignen (s. vierte Veröffentlichung). Im Rahmen dieser umfangreichen Untersuchungen wurde neben den Fängen von ANT XVII-3 auf Material von den *Polarstern*-Expeditionen ANT III-3, ANT VII-4 und ANT VIII-5 zurückgegriffen. Dabei stellte sich heraus, dass die neue Art *Eusirus giganteus* fälschlicherweise als *E. perdentatus* bearbeitet wurde. Die neue Art stellte 26 % des untersuchten Materials. Beide Arten weisen eine sympatrische Verbreitung auf. Ähnliche Entwicklungen von Oostegiten von *E. perdentatus* und *E. giganteus* von Fängen aus derselben Jahreszeit, sogar des selben Hauls, lassen auf eine vermutlich synchrone Reproduktion schließen. Dennoch müssen die Ergebnisse von Klages (1991, 1993) über die Verbreitung, Reproduktion und Populationsdynamik von *Eusirus perdentatus* angezweifelt werden, da es sich hier um Untersuchungen an zwei Arten handelt.

Bei der Beschreibung von *Dikwa andresi* Lörz & Coleman im Druck (s. siebte Veröffentlichung) handelt es sich um den zweiten Vertreter der Familie Dikwidae Coleman 1991. Zudem wird diese Familie erstmals aus antarktischen Gewässern beschrieben. Die einzige bisher bekannte Art, *Dikwa acrania* Griffith 1974, wurde bisher nur in Gewässern vor Südafrika gefunden. Merkmale, die die Familienzugehörigkeit von *Dikwa andresi* bestimmen, sind u.a. der reduzierte Kopf, der Molar der Mandibel und der chelate erste Gnathopod. Für die Unterscheidung von *Dikwa andresi* und *Dikwa acrania* kann insbesondere die Länge der zweiten Coxalplatte und die Form der siebten Coxalplatte beachtet werden, für detaillierte Unterschiede s. S. 108.

Zwei Individuen von *Dikwa andresi* wurden auf der roten Hartkoralle *Errinopsis reticulum* Broch 1951 gefangen. Wegen der geringen Anzahl von drei Paratypen wurde auf die Analyse des Mageninhaltes verzichtet. Bei diesen kleinen Tieren mit einer sehr harten, d.h. brüchigen, Cuticula kann eine starke Beschädigung des Individuums bei Magen-/ Darmpräparationen nicht ausgeschlossen werden. Ein kräftiger, triturativer Molar und ein gezähnter Incisor lassen vermuten, dass *D. andresi* in der Lage ist, Stückchen der harten Hydrozoe herauszubeißen. Die südafrikanische Schwesternart *D. acrania* wurde auf grobem Sand gefangen, ihr Nahrungsspektrum ist unbekannt. Vermutlich gibt es innerhalb der antarktischen Amphipoda viele Arten, deren epizooische Lebensweise noch unbekannt ist. Da die untersuchten Fänge von Proben mit geschlepptem Gerät stammen, ist eine Trennung von Symbionten während des Fanges nicht auszuschließen. Es könnte ebenfalls der umgekehrte Fall vorliegen, dass eine augenscheinliche Vergesellschaftung erst während des Fanges eintrat. Im Falle von *D. andresi* wird davon ausgegangen, dass diese Art sich in ihrem natürlichen Lebensraum ebenfalls auf der Hartkoralle aufhält. Erstens wurden zwei Individuen auf getrennten Stücken der Hydrozoe gefangen und zweitens kletterte *D. andresi* bei Aquarienhälterung auf die Hartkoralle; dieses Verhalten wurde bei keiner anderen Amphipodenart beobachtet.

Es sei hier darauf hingewiesen, dass es sich bei *Dikwa andresi* um Material handelt, das nicht während der Expedition EASIZ III gesammelt wurde, sondern während der Expedition LAMPOS (Latin American Polarstern Studies), die im antarktischen Herbst 2002 ebenfalls mit PFS *Polarstern* stattfand. Der Fundort liegt am nördlichen Beginn des Scotia Bogens, s. S. 100. Ein Hauptziel der LAMPOS Expedition war das Benthos des Scotia Bogens in Beziehung zu Südamerika und der Antarktis zu untersuchen. Da bisher erst ein Vertreter der Amphipodenfamilie Dikwidae von Südafrika bekannt ist, kann *Dikwa andresi* diesem Ziel nicht dienen. Der Fundort der neuen *Dikwa* gehört dem nördlichen Scotia Bogen an und befindet sich im Bereich der westwärts fließenden zirkumantarktischen Strömung. Es ist nicht auszuschließen, dass sich die Verbreitung im Südatlantik durch diese Ringströmung vollzog. Auf der Grundlage morphologischer Betrachtungen ist es nicht möglich, plesiomorphe Merkmale zu definieren und einer Art zuzuordnen. Die Farbe der Körper von *D. andresi* und *D. acrania* war auch im lebenden Zustand rein weiß. Beide wurden in 200 -300 m Wassertiefe gefangen. Die Abwesenheit von Pigmenten bei beiden Arten könnte eine Verbreitung in größeren Tiefen vermuten lassen. Die Tiefsee des Südatlantiks wurde bisher sehr wenig beprobt, dazu kaum mit kleinmaschigen Netzen. So ist zu vermuten, dass bei weiteren Probennahmen mit adäquaten Geräten noch mehr Vertreter der Familie Dikwidae gefangen werden. Andererseits könnte die bathymetrische Verbreitung von *D. andresi* durch das Vorkommen des potentiellen Wirtes, der Hartkoralle *Errinopsis reticulum,* beschränkt sein.

Clarke und Johnston (im Druck) stellen heraus, dass es für den Ursprung und die Diversifikation des antarktischen Benthos keine einheitliche Antwort gibt. Vielmehr geben Gruppen wie Pycnogonida, Amphipoda, Isopoda und Osteichtyes eine unterschiedliche Antwort auf tektonische, klimatische und ozeanische Veränderungen. Die vorangegangenen Beschreibungen und Diskussion der vier neuen Arten aus vier verschiedenen Familien antarktischer Amphipoda zeigen, dass sehr verschiedene Merkmale zu Abgrenzungen neuer Arten führen. Die Arten tragen auf unterschiedlichem Niveau zum Kenntnisstand der vertikalen und horizontalen Verbreitung des jeweiligen Taxons bei. Vor diesem Hintergrund wird angenommen, dass es auch auf die Frage nach dem Ursprung und der Diversifikation antarktischer Amphipoda keine einheitliche Antwort geben wird, sondern Flohkrebse innerhalb kleinerer taxonomischer Einheiten bearbeitet werden müssen. Da es zur Zeit noch sehr wenige molekulare Arbeiten an antarktischen Amphipoda gibt (Englisch 2001), sind künftige molekularbiologische Untersuchungen wertvolle Beiträge zur Klärung vieler taxonomischer und systematischer Fragen.

Die Entscheidung, ob es sich bei untersuchten Individuen um neue Arten handelt oder um bekannte Arten, die morphologische und / oder molekulare Varianz zeigen, liegt letztlich bei den Systematikern. In welchem Fall es sich um eine „neue Art" handelt ist nicht festgelegt. Zudem ist es nicht abschließend geklärt, was „eine Art" auszeichnet. Es werden biologische, evolutionäre und phylogenetische Artbegriffe unterschieden. Der kontrovers diskutierte Artbegriff wird z.B. in den Lehrbüchern von Wägele (2000) und Wiesemüller et al. (2003) behandelt.

4.2. Abundanz und Diversität

Das vorliegende Kapitel über Abundanz und Diversität wird in zwei Bereiche, entsprechend der ersten und achten Veröffentlichung, gegliedert. Der erste Teil behandelt die Amphipoda, die in verschiedenen Demospongia gefunden wurden, der zweite peracaride Krebse, die 1.00 bis 1.33 m über dem Boden gefangen wurden.

Schwämme stellen einen wichtigen Bestandteil der antarktischen Benthosgemeinschaft dar (z.B. Cattaneo-Vietti et al. 1999). Aus antarktischen Gewässern sind bisher ca. 300 Schwammarten beschrieben, von diesen sind 50 % endemisch. Der Großteil der Arten zählt zu den Demospongiae (Hornkieselschwämmen). Weiterhin gibt es einige wenige Arten von Calcarea (Kalkschwämme) und Hexactinellida (Glasschwämme) (Barthel 1995). Allerdings kommen die Glasschwämme in so hohen Abundanzen vor, dass sie einen beträchtlichen Teil der benthischen Biomasse stellen. Zahlreiche Arten von Hexactinellidae und Demospongiae werden von anderen Organismen als Wirt benutzt, u.a. mehrere Vertreter von Amphipoda (Costello & Myers 1987, Serejo 1998). Studien an Amphipoden, die kommensalistisch in Schwämmen der Antarktis leben, sind sehr rar und wurden nur teilweise auf Artniveau durchgeführt (Kunzmann 1996). Um die Abundanz, im Sinne von Häufigkeit, in verschiedenen Schwammgeweben abschätzen zu können, wurden die im Netz gefundenen Schwammstücke auf 1000 cm³ standardisiert (s. S. 12). Über 40 Individuen von Amphipoda wurden z.B. in 1000 cm³ Gewebe des Hornkieselschwammes *Jophon spatulatus* (Kirkpatrick

1907) gezählt. Ein anderer Hornkieselschwamm, *Clathria pauper* Broenstedt 1926, der ebenfalls bei Kapp Norvegia gefangen wurde, beinhaltete ebenfalls über 35 Amphipoda pro 1000 cm^3. Amphipoda wurden in drei Arten von Demospongiae gefunden. Die 1193 im Schwammgewebe lebenden Amphipoda verteilen sich auf sechs Arten aus fünf Familien.

Leider kann abschließend nicht beurteilt werden, ob es sich bei dem vorliegenden Datensatz wirklich um hohe Abundanzen und niedrige Diversitäten der kommensalistischen Amphipoda handelt, da Vergleichswerte fehlen. Bei den vorliegenden Daten wurden ausschließlich Flohkrebse aufgenommen, welche sich definitiv im Schwammgewebe aufgehalten haben. Costello & Myers (1987) bezeichnen diese als „inquiline" und stellen sie denen auf der Außenseite der Schwämme hausenden Amphipoda gegenüber. Da die Schwammstücke aus Fängen des Grundschleppnetzes geborgen wurden, ist es sehr wahrscheinlich, dass Organismen während des Fangvorganges an den Schwämmen bzw. ihren Teilstücken haften blieben, obwohl sie zuvor nicht vergesellschaftet waren. Um diese mögliche Fehlerquelle auszuschließen, wurden nur diejenigen Amphipoden als symbiontische Bewohner der untersuchten Hornkieselschwämme gewertet, die aus deren Kanälchen präpariert wurden. Da die herausgearbeiteten Abundanz- und Diversitätswerte antarktischer Amphipoda in Schwämmen auf einer sehr konservativen Berechnung basieren, liegen die tatsächlichen Werte vermutlich ein wenig höher. Auf jeden Fall liefern die qualitativen und quantitativen Untersuchungen gute Vergleichswerte für weitere Arbeiten an schwammbewohnenden Amphipoda. Vermutlich werden Abundanz und Diversität der Flohkrebse in anderen Jahreszeiten andere Werte ergeben als die während des antarktischen Herbstes aufgenommenen. Andererseits könnte das Habitat Schwamm gerade einen Schutz / Vorteil bei starken saisonalen Schwankungen bedeuten. Bezüglich der Verfügbarkeit von Nahrung ist diese These insbesondere für die Amphipoda zu vertreten, die sich von Schwammgewebe ernähren. Coleman (1989b) stellt fest, dass *Echiniphimedia hodgsoni* Walker 1906 darauf spezialisiert ist, Schwämme zu fressen. Die Lacina mobilis der rechten Mandibel fungiert als zusätzliche Schneidekante und diese ermöglicht es *E. hodgsoni*, Schwammgewebe herauszubeißen. Nach Oshel & Steele (1985) frisst *Paramphithoe hystrix* Ross 1835 seinen Wirt, den Schwamm *Haliclona ventilabrum* (Fristedt 1887). Die morphologischen Modifizierungen sind im Vergleich zu *E. hodgsoni* zwar minimal, aber der Molar der Mandibel scheint so konzipiert zu sein, dass er Schwammnadeln aufnehmen kann, ohne sie zu brechen. Bei dem Lysianassiden *Pseudokoroga spongiophila* konnten keine morphologischen Adaptionen an das Leben im Schwammgewebe festgestellt werden. Untersuchungen der Mageninhalte von 60 Paratypen haben nur vereinzelt Schwammnadeln gezeigt. In den meisten Fällen waren die Mägen leer, z.T. enthielten sie auch Stückchen von Copepoda (s. S. 40). Vermutlich handelt es sich bei *P. spongiophila* um einen unspezifisch fressenden Opportunisten. Vor diesem Hintergrund ist anzunehmen, dass der Schwamm dem Lysianassiden Schutz vor Räubern bietet.

Symbiose wird in der vorliegenden Arbeit im „amerikanischen Sinne" gebraucht: Die Vergesellschaftung muss nicht für beide Partner einen Vorteil darstellen (Herder 1988). Während mehrere Vorteile für die im Schwammgewebe lebenden Amphipoden ersichtlich sind (allen voran bei Nahrung und Fraßschutz), bleibt ein Vor- bzw. Nachteil für den Schwamm höchst spekulativ. Offensichtlich nachteilig ist es für den Schwamm, wenn seine Biomasse abnimmt, d.h. wenn er von den Amphipoda gefressen wird. Die potentielle Nahrungskonkurrenz von Filtrierern ist ebenfalls als Nachteil zu sehen. Allerdings könnten Flohkrebse die Kanälchen von feinem Sediment reinigen, indem sie durch ihren Pleopodenschlag und ihre Schwimm- bzw. Fortbewegungen Wasserströmungen erzeugen, die kräftiger sind als die von den Schwämmen durch ihre Choanocyten hervorgerufenen. In flachen, lichtdurchfluteten Schelfbereichen könnten epizooische, herbivore Weidegänger den Schwamm von Algenbewuchs befreien. Eventuell wird die Lebensqualität des Schwammes weder positiv noch negativ von kommensalistischen Amphipoda beeinflusst.

Interessanterweise wurden keine juvenilen Amphipoda innerhalb des Schwammgewebes gefunden. Die erste Vermutung, dass sich diese kommensalistischen Flohkrebse nicht während des antarktischen Herbstes reproduzieren, wurde durch Vermessungen der Oostegiten- und Embryonen wiederlegt. Eine Längenhäufigkeitsverteilung wurde an der häufigsten Amphipodenart *Colomastix fissilingua* (Schellenberg 1926) durchgeführt (s. S. 15). Diese Art zeigt einen deutlichen Sexualdimorphismus. Die Männchen besitzen stark vergrößerte zweite Gnathopoden. Bis auf zwei Individuen hatten alle 149 untersuchten Weibchen Oostegiten ausgebildet. Es konnte eine positive Korrelation zwischen Körpergröße und Oostegitenlänge festgestellt werden. Bei einer Oostegitenlänge von 0.49 mm beginnen die Borsten daran zu wachsen. Von sich gerade bildenden Oostegiten über Marsupia mit Embryonen bis zum leeren, voll ausgebildeten Marsupium fanden sich alle Entwicklungsstufen. Die leeren Marsupia mit großen, gewölbten Oostegiten mit langen Borsten zeigten deutlich, das die Juvenilen kurz zuvor entlassen worden waren. Es fanden sich trotz intensiver Suche keine juvenilen Amphipoda im Schwammgewebe. Die Abwesenheit der Juvenilen wurde ebenfalls bei dem Lysianassiden *Pseudokoroga spongiophila* und dem Stegocephaliden *Andaniotes linearis* festgestellt. Keine juvenilen Amphipoda jeglicher Art wurden in den verschiedenen Demospongiae gefunden. Eventuell sind die Juvenilen auf ein anderes Nahrungsspektrum angewiesen als die Adulten, welches ihnen innerhalb des Schwammgewebes nicht zur Verfügung steht. Dieses Ergebnis der schwammbewohnenden antarktischen Amphipoda darf jedoch nicht auf andere peracaride Taxa übertragen werden. Bei dem Isopoden *Gnathia calva* Vanhöffen 1914, einem Fischparasiten, finden drei larvale Entwicklungsstadien (Pranizae) statt. Das dritte Pranizastadium sucht hexactinellidae Schwämme auf, in denen die Häutung und Metamorphose zum geschlechtsreifen Tier stattfindet. Innerhalb des Schwammes werden „Harems“ gebildet (Wägele 1988).

Der zweite Teil des Kapitels „Abundanz und Diversität“ behandelt suprabenthische Peracarida, die im östlichen Weddell-Meer sowie an den Süd Shetland Inseln mittels eines Epibenthosschlittens (EBS) gefangen wurden (s. achte Veröffentlichung). Die Stationen sind in Abbildung 3 (S. 10) zu sehen. Den auf Seite 1 angesprochenen Schwierigkeiten, Biodiversität in definiertem Raum und Zeit zu messen, wurde abermals mit einer Standardisierung der Proben auf ein Volumen begegnet. Die Öffnung des Supranetzes des EBS ist genau 1.00 m breit und 0.33 m hoch, die Schleppzeit beträgt bei 1 Knoten 10 Minuten und die geschleppte Strecke kann über den Cosinus berechnet werden (Brandt & Barthel 1995). Vor diesem Hintergrund der einheitlichen Berechnungsfaktoren und des standardisierten Geräteeinsatzes wird angenommen, dass es sich bei den Fängen zumindest um semiquantitative Proben, auf jeden Fall aber um vergleichbare Proben, handelt. Fehler hinsichtlich der Proben könnten z.B. von Turbulenzen vor dem Gerät herrühren, die epibenthische Fauna aufwirbeln. Weiterhin muss berücksichtigt werden, dass der Schlitten in weichem Sediment tiefer einsinkt und bei großen Unebenheiten, z.B. Steinen, nicht gleichmäßig über den Boden gleitet. Bei den in der achten Veröffentlichung bearbeiteten Stationen handelt es sich allerdings um sehr homogene Sedimente, grober Sand mit Ton. Bei der Station 138-2, die ebenfalls mit dem EBS beprobt wurde, fand sich feiner Schlamm im Epinetz, jedoch hatte sich an dieser Station das Supranetz verdreht. Daher wurden die Station bei der Auswertung nicht berücksichtigt.

Ähnlich wie bei den Untersuchungen zu Abundanz und Diversität von Amphipoda in Schwämmen stehen bei den Studien der suprabenthischen Peracarida relativ wenig quantitative Vergleichsdaten zur Verfügung. Eine große Ausnahme stellt die Veröffentlichung von Linse et al. (2002) dar. Sie behandelt die Zusammensetzung und Verteilung suprabenthischer Fauna im südöstlichem Weddell-Meer und bei der Insel King George (zu den Süd Shetland Inseln gehörend). Da Linse et al. (2002) ebenfalls den ursprünglich von

Rothlishberg & Pearcy (1977) konzipierten und von Brandt & Barthel (1995) modifizierten EBS für die Probennahme einsetzten, können die Daten verglichen werden. Allerdings muss berücksichtigt werden, dass es sich bei den 16 Stationen von Linse et al. (2002) als auch bei den sechs Stationen, die in der achten Veröffentlichung vorgestellt wurden, um eine zu kleine Anzahl handelt, um generelle Aussagen über die suprabenthischen Peracarida der Antarktis treffen zu können. Die Anzahl der während EASIZ III genutzten EBS-Stationen ist nicht ausreichend, um eine ursprünglich geplante Clusteranalyse durchzuführen. Die geringe Anzahl an Stationen war teilweise durch die schwierigen Witterungsbedingungen begründet, zudem zwang starke Eisbedeckung das FS *Polarstern* auf geplante Stationen im Drescher Inlet zu verzichten und nordwärts zu fahren (Arntz & Brey 2001). Außerdem lagen die beprobten Stationen nicht in gleicher Tiefe und waren vermutlich anderen Strömungsverhältnissen ausgesetzt. Vermutlich spielt der Tiefenunterschied zwischen 200 und 800 Meter eine geringere Rolle, da sich die abiotischen Faktoren sehr ähneln und der antarktische Schelf z.T. bis 1000 m hinabreicht (Clarke & Johnston im Druck).

Ein wichtiger Unterschied der suprabenthischen Proben von EASIZ II und III ist die Saisonalität. Während die Probennahme von Linse et al. (2002) im Februar / März stattfand, dem antarktischen Sommer, wurde der EBS während EASIZ III im April / Mai geschleppt, dem antarktischen Herbst. Im antarktischen Sommer lagen die Abundanzen peracarider Krebse um ein Vielfaches über den im Herbst genommenen Proben (s. S. 115). Leider waren von Linse et al. (2002) keine Artenzahlen pro Taxon, z.B. Ordnung Amphipoda, erhältlich. Somit mussten beim Vergleich der Diversitäten die jeweiligen Anzahlen an Arten pro Station genügen. Die Peracarida wurden im Sommer und Herbst durch die fünf Ordnungen Mysidacea, Amphipoda, Cumacea, Tanaidcea und Isopoda präsentiert. Die durchschnittliche Anzahl an Arten der suprabenthischen Peracarida pro Station betrug bei EASIZ II (Sommer) 16, bei EASIZ III (Herbst) hingegen 31.

Im Gegensatz zu den schwammbewohnenden Amphipoda wurden bei den suprabenthischen Amphipoda (bzw. Peracarida) während des antarktischen Herbstes relativ niedrige Abundanzen und hohe Diversitäten festgestellt.

4.3. Phylogenie

Untersuchungen zu verwandtschaftlichen Beziehungen bei Amphipoda wurden an den Familien Epimeriidae und Iphimediidae durchgeführt, mit einem Schwerpunkt auf der

Gattung *Epimeria* (s. fünfte und sechste Veröffentlichung). Ein weiterer Schwerpunkt lag auf dem Vergleich der auf molekularen und morphologischen Merkmalen basierenden Analysen.

Molekulare Untersuchungen sind nur bei geeignet fixiertem Material möglich. Zahlreiche Arten und Individuen der Familien Epimeriidae und Iphimediidae wurden während vergangener Expeditionen mit Formol fixiert. Da diese Chemikalie die DNS denaturiert, ist damit fixiertes Material für Sequenzvergleiche ungeeignet. Sowohl Epimeriidae als auch Iphimediidae sind als dominante Vertreter der antarktischen Benthosgemeinschaft bekannt (Coleman 1990, De Broyer et al. 2001a). Allerdings wurden während ANT XVII-3 nur 14 Arten dieser Amphipoda aus zwei Regionen (s. S. 74) gefangen – und adäquat fixiert. Diese Arten, von denen Sequenzen der ersten Untereinheit der Cytochromoxidase verglichen werden konnten, sind anhand 98 morphologischer Merkmale phylogenetisch adressiert worden. Die resultierenden Bäume der verschiedenen methodischen Ansätze sind sich sehr ähnlich (s. S. 71). Zusätzlich zu dem abgebildeten Phylogram, das auf Nukleotiden beruht, wurden die resultierenden Aminosäure-Sequenzen der Cytochromoxidase für phylogenetische Untersuchungen genutzt. Indizien für die Qualität der Analysen geben z.B. der Konsistenzindex (CI), der Konservierungsindex (RI), Baumlänge und Anzahl der resultierenden „kürzesten Bäume“ (z.B. Riepel 1999). Diese Parameter sind in folgender Tabelle für eine auf „Maximum Parsimonie“ beruhenden Analyse der 16 selben Arten angegeben:

	Konsistenzindex (CI)	Konservierungsindex (RI)	Baumlänge	Anzahl Bäume
558 Nukleotide	0.51	0.58	1012	1
184 Aminosäuren	0.82	0.89	159	4
98 morph. Charak.	0.53	0.71	205	1

Sowohl die Sequenz der Cytochromoxidase I als auch die ausgewählten morphologischen Merkmale scheinen geeignet, um Verwandtschaftsanalysen auf interspezifischem Niveau durchzuführen. Sowohl bei morphologischen als auch bei molekularen Untersuchungen von 16 Taxa ist es relativ ungewöhnlich, nur einen sparsamsten Baum bei dieser Anzahl von Merkmalen zu erhalten. Die geringe Anzahl „kürzester Bäume“ (Topologien mit der geringsten Anzahl von Merkmalsänderungen) sowie die relativ geringe Baumlänge (die Summe der Merkmalsänderungen aller Merkmale des Datensatzes) sprechen für die Qualität der Daten. Allerdings werden die höchsten CI und RI Werte von der Analyse der Aminosäure-Sequenzen erzielt, die in vier sparsamsten Bäumen resultiert.

Das sogenannte Bootstrapverfahren wird von Wiesemüller et al. (2003) als ein Ansatz zur Beurteilung der Zuverlässigkeit der Ergebnisse aus Stammbaumanalysen genannt. Wägele (2000) weist darauf hin, dass keine allgemeingütigen Monophyliewahrscheinlichkeiten auf der Grundlage von Bootstrapwerten getroffen werden können. Vielmehr stelle dieses Verfahren einen Test für die Güte der Ergebnisse im Hinblick auf vorliegendes Datenmaterial und das gewählte Rekonstruktionsverfahren dar. Die Bootstrapwerte des molekularen wie morphologischen Datenmaterials liegen sowohl im Parsimonie- als auch im Likelihoodverfahren oftmals über 80 und implizieren somit zuverlässige Analysen.

Die Ergebnisse der phylogenetischen Arbeiten enthalten systematische Revisionsvorschläge, z.B. die Paraphylie der Gattungen *Iphimediella* und *Gnathiphimedia* aufzuheben und die Eusiridae den Iphimediidae näher zu stellen. Diese revidierenden Schritte wurden bisher nicht unternommen, da nur eine geringe Anzahl der Taxa und nur wenige Individuen pro Art molekular untersucht wurden. Im Rahmen der erweiterten, morphologisch phylogenetischen Untersuchung wurden viele Individuen pro Art bearbeitet, sofern Material zur Verfügung stand und präpariert werden durfte. Die Studie mehrerer Tiere der gleichen Art zeigt bei Vertretern der Epimeriidae und Iphimediidae hohe intraspezifische Varianz (s. S. 86, 87). Die intraspezifische Varianz wurde bei Tieren desselben Geschlechts, derselben Größe und oft desselben Fanges (Station) festgestellt. Geschlechtsdimorphismus ist weder bei Epimeriiden noch Iphimediiden stark ausgeprägt. Die Morphologie des Habitus und der Mundwerkzeuge ändern sich bei den untersuchten Tieren während des Wachstums erheblich. Der Versuch, anhand Merkmalsänderungen vom juvenilen zum adulten Tier, d.h. während dessen Ontogenese, Rückschlüsse auf die Phylogenese zu ziehen, führte zu keinem Ergebnis. Während Coleman (1990) für *Epimeria pulchra* Coleman 1990 und *E. oxicarinata* Coleman 1990 Änderungen von Merkmalen in eine „Lesrichtung" feststellt, verläuft diese z.B. bei *Epimeria robusta* K.H. Barnard 1930 genau entgegengesetzt. Viele während der Ontogenese veränderten Merkmale kommen a priori nicht für Hinweise auf plesiomorphe Zustände in Betracht, da sie eine Anpassung an das Leben im Marsupium darstellen, z.B. die Abwesenheit einer dorsalen Carina oder langer Fortsätze auf den Paereoniten oder Pleoniten. Fossilfunde kommen ebenfalls für die Findung potentieller plesiomopher Merkmale nicht in Betracht. Bisher sind keine Fossilien antarktischer Flohkrebse bekannt, weltweit gibt es auch keine Fossilfunde zu Vertretern der Überfamilie Iphimedoidea.

Die erweiterte morphologisch basierte phylogenetische Untersuchung der Gattung *Epimeria* beinhaltet alle Arten dieser Gattung aus der Antarktis, mit Ausnahme *Epimeria* sp. Andres 1985, Arten der Nordhemisphäre, der Tiefsee vor Brasilien und der Tasman-See. Die „Erweiterung" bezieht sich auf die erhöhte Anzahl untersuchter Taxa, im Vergleich zu den zuvor morphologisch und molekular analysierten Arten, und auf die erhöhte und veränderte Anzahl der berücksichtigten morphologischen Merkmale. Es sind bisher keine Vertreter der Familien Epimeriidae oder Iphimediidae aus der antarktischen Tiefsee bekannt, daher konnten sie nicht in diesen phylogenetischen Ansätzen integriert werden. Die nicht vorhandenen Funde müssen nicht auf Abwesenheit der Familien in der antarktischen Tiefsee schließen lassen, da es sich dabei um eines der am wenigsten beprobten Gebiete unserer Erde handelt (Brandt mündl. Mitt.). Die in die Analyse integrierten Arten der Tiefsee vor Brasilien und der Tasman-See gruppieren mit den Arten des Schelfs von Nord-Norwegen (s. S. 82, 83). Dies könnte eine Spezifizierung der antarktischen Arten unabhängig von den Taxa der Südhemisphäre oberhalb der zirkumantarktischen Strömung implizieren. Andererseits gruppiert sich eine *Epimeria*-Art des norwegischen Schelfs in einen aus antarktischen Arten bestehenden Verwandtschaftskreis (s. S. 83). Insgesamt können Fragen zur Geschichte der Besiedlung des antarktischen Schelfs mit diesen Datensätzen nicht zufriedenstellend beantwortet werden.

Bisher unveröffentlichte Berechnungen ergeben eine Aufspaltung der antarktischen Arten der *Epimeria* vor ca. 4-6 Millionen Jahren. Es wird eine konservative Substitutionsrate von 3.1 % Divergenz / 1 Millionen Jahren von Wares (2001) für die Sequenzen der ersten Untereinheit der Cytochromoxidase zugrunde gelegt. Die Analysen von Wares (2001) basieren auf der selben Region der Cytochromoxidase wie die hier diskutierten. Wares (2001) hat diese Rate zwar für Krebse, jedoch für nordamerikanische Balanidae (Seepocken) berechnet. Es soll an dieser Stelle nicht auf die begrenzten Möglichkeiten der sogenannten molekularen Uhr eingegangen werden. Wägele (2000) betont u.a., dass unregelmäßige Substitutionsraten zu Fehleinschätzungen der Divergenzzeiten führen. Jedoch bleibt festzustellen, dass selbst bei einer potentiell dreimal langsamer stattfindenden Speziation die *Epimeria*-Arten sich immer noch nach der Abkühlung der Antarktis vor 40 Millionen Jahren - sogar nach der Ausbildung des Zirkumpolarstroms vor 23.5 Millionen Jahren (Crame 1999) - aufgespalten haben. Diese relativ junge Speziation antarktischer Amphipoda wurde bereits von Watling & Thursten (1989) für Iphimediidae aufgrund weniger morphologischer Merkmale postuliert. Ebenfalls deutlich nach der Abkühlung fand die Speziation der Muschelgattung *Limatula* (Page & Linse 2002) und der in der Antarktis häufigen planktischen

Eucaridengattung *Euphausia* statt (Bargeloni et al. 2000). Es sind allerdings nicht nur Evertebraten von dieser erdgeschichtlich jungen Speziation betroffen. Die Gattungen der nothothenoiden Fische *Patagonothen* und *Lepidonotothen* trennten sich vor 6.6 –7.1 Millionen Jahren (Stankovic et al. 2002).

Die morphologischen und molekularen Methoden führen zu sehr ähnlichen Ergebnissen der Phylogenie bei den untersuchten Taxa (u.a. S. 71). Dennoch enthalten beide Methoden Vor- und Nachteile. Während die Analyse der Gensequenzen eine ungefähre zeitliche Trennung der Arten berechnen lässt, ist sie auf frisches, adäquat fixiertes Material angewiesen. Letzteres reduziert den Umfang der Proben erheblich. Zudem sind die molekularen Methoden sehr kostenintensiv. Die morphologischen Betrachtungen beweisen anhand der zahlreich untersuchten Individuen eine hohe intraspezifische Variation.

Die diskutierten Antworten auf die Frage „Kann die Phylogenie helfen, Fragen der Herkunft und des Alters ausgewählter Gruppen zu klären?“ sind im Folgenden zusammengefasst. Die Herkunft antarktischer *Epimeria* kann mit den eingesetzten Mitteln nicht abschließend geklärt werden. Die Anzahl molekular untersuchter Arten ist zu gering und die morphologischen Daten lassen keine „Lesrichtung“ der Merkmale zu, die plesiomorphe Zustände zeigen würden. Das junge Alter der *Epimeria*-Arten kann mit dem Vergleich der Cytochromoxidase Sequenzen festgestellt werden. Die hohe morphologische intraspezifische Variation und die lange nach der Abkühlung stattfindende Artaufspaltung lassen auf eine momentan stattfindende Speziation der Gattung *Epimeria* in der Antarktis schließen.

Bei einem Vergleich der Veröffentlichungen der vorliegenden Artbeschreibungen mit den phylogenetischen Untersuchungen sind die morphologischen Abgrenzungen bemerkenswert. Die intraspezifische Varianz bei Epimeriiden und Iphimediiden zeigt größere morphologische Unterschiede als sie z.B. interspezifisch bei dem aus drei Arten bestehenden *Eusirus*-Komplex festgestellt wurden. Bei einer Untersuchung der Gammaridea des östlichen Weddel-Meeres beschreiben De Broyer et al. (2001a) epibenthische Habitate von *Eusirus perdentatus*, *Epimeria rubrieques* und fünf Arten der Iphimediidae als „lower level“. Vier weitere *Epimeria*-Arten werden dem „upper level“ zugeordnet. Die Mobilität aller untersuchten Iphimediidae sowie der meisten Epimeriidae wird als „weakly motile“ beschrieben. Der etwas vagilere *Eusirus perdentatus* wird als „moderately motile“ eingeordnet, *Epimeriella walkeri* als „highly motile“. Der Fraßtyp der untersuchten Vertreter der drei Familien ist überwiegend räuberisch, eingeteilt in „opportunistic“, „macropredator“ und „micropredator“. Das Tiefenvorkommen zeigt keine deutlichen Unterschiede. Die Unterschiede in der Lebensweise können also nicht zu einer Erklärung der unterschiedlichen morphologischen Varianzen herangezogen werden.

Ausblick

Die vorliegende Arbeit unterstreicht den evolutionären und ökologischen Erfolg antarktischer Amphipoda. Es wurden u.a. die hohe Anpassung an verschiedene Nahrungsressourcen, Mechanismen der Brutpflege bzw. intraspezifisch unterschiedliche Habitatwahl zwischen Juvenilen und Adulten und die rasche, derzeit stattfindende Artaufspaltung diskutiert.

Um abschließend die Abundanz und Diversität kommensalistischer antarktischer schwammbewohnender Amphipoda beurteilen zu können, müssen standardisierte Untersuchungen innerhalb der Schwammgewebe während unterschiedlicher Jahreszeiten vorgenommen werden. Quantitative Ergebnisse können nur verglichen werden, wenn sowohl das Schwammvolumen berechnet wird als auch ausschließlich endozooische Amphipoda berücksichtigt werden. Der standardisierte Einsatz des EBS in verschiedenen Gebieten, in unterschiedlichen Tiefen und während verschiedener Jahreszeiten verspricht weitere Einblicke in die suprabenthische Fauna. Die Ergebnisse weiterer suprabenthischer Untersuchungen werden u.a. helfen, Zusammenhänge der benthopelagischen Kopplung zu verstehen.

Um abschließend phylogenetische Fragen nach Herkunft und Alter antarktischer Epimeriidae zu lösen, ist es notwendig, alle Arten des Südozeans sowie möglichst viele Arten der angrenzenden Gebiete molekularbiologisch zu untersuchen. Bisher sind keine Arten dieser Familie aus der antarktischen Tiefsee bekannt. Der Vergleich von Sequenzen der antarktischen Schelfbewohner mit potentiellen Bewohnern der antarktischen Tiefsee, der atlantischen und pazifischen Tiefsee und der Schelfregionen von Südamerika, Südafrika, Australien und Neuseeland können vor dem Hintergrund der Entstehungsgeschichte der Antarktis helfen, die Hypothesen der Sub– bzw. Emergenz zu klären. Zur phylogenetischen Bearbeitung innerhalb der Epimeriiden hat sich die mitochondriale Cytochromoxidase bewährt, allerdings sollten noch weitere schnell evolvierende Gensequenzen des Kerngenoms (z.B. 28S, ITS) oder der Mitochondrien (z.B. 16S, Kontrollregion) vergleichend untersucht werden. Eine weitere Verknüpfung morphologischer und molekularer Arbeiten wird unerlässlich sein.

Eine Untersuchung schnell evolvierender Gensequenzen der drei Arten des *Eusirus*-Komplexes ist in Vorbereitung. Die geplante genetische Populationsstudie der Eusiriden wird voraussichtlich Antworten auf den Ursprung und die Evolution dieser weiteren wichtigen Gruppe antarktischer Amphipoda geben können.

Während der Expedition LAMPOS mit PFS *Polarstern* im Jahre 2002 wurden bereits über 100 Individuen der zu untersuchenden Amphipoden gesammelt und ihre DNA extrahiert. Diese Proben sollen im Verlauf des Jahres 2003 molekular und phylogenetisch in Zusammenarbeit mit der Biodiversitätsgruppe am British Antarctic Survey in Cambridge, England, bearbeitet werden.

Die vorliegende Arbeit hat gezeigt, dass die ausgewählten Gebiete der Biodiversitätsforschung Systematik, Taxonomie, Biogeographie und Ökologie sich überschneiden und ergänzen. Ein weiterer wichtiger Aspekt für den Erfolg der Amphipoda liegt in ihrer ökophysiologischen Anpassung an die antarktischen Umweltbedingungen. Ökophysiologische Arbeitsgruppen beschäftigen sich z.B. mit enzymatischer Kälteanpassung, Magnesiumregulation und Sauerstoffbedarf antarktischer Invertebraten. Frederich et al. (2001) und Pörtner (2002) stellen u.a. Hypothesen auf, warum die Peracarida so weitaus häufigere Vertreter des antarktischen Benthos darstellen als reptante Krebse. Bisher wurden leider erst sehr wenige Untersuchungen zur Ökophysiologie antarktischer Amphipoda im Hinblick auf ihre erfolgreiche Anpassung an den antarktischen Lebensraum durchgeführt. Nur in Kooperation von Systematikern, Ökologen und Physiologen wird die hohe Biodiversität antarktischer Amphipoda zu erklären sein.

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