

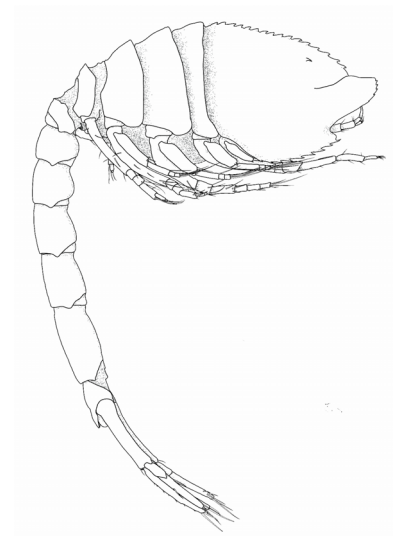
Cumacea (Crustacea; Peracarida)

of the Antarctic shelf – diversity,
biogeography, and phylogeny

Peter Rehm

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1. Examiner

Prof. Dr. Wolf E. Arntz
Alfred Wegener Institute
University of Bremen

2. Examiner

Dr. Sven Thatje
National Oceanography Centre
University of Southampton

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SUMMARY

The crustacean order Cumacea belongs to the Peracarida and comprises an evolutionary old group with conservative morphology. Predominantly bound to soft bottom habitats in benthic marine environments they show a cosmopolitan distribution. As other Peracarida they display brood protection; juvenile stages are carried in the marsupium. It is supposed that the marsupium plays a major role in the success of this abundant and specious group of Crustacea.

The Peracarida are a dominant group in Southern Ocean benthic communities. Quantitative investigations of the Ross Sea shelf fauna demonstrated that the Peracarida contribute 63% to abundance and 50% to biomass. Amphipods dominated clearly, while different sample sites yielded high dominances by Cumacea, Isopoda, and Tanaidacea. The recorded number of peracarid species from the Ross Sea is lower than in other high-Antarctic regions. The present study could show, that cumacean diversity with respect to species richness resembles that of the Weddell Sea or the East Antarctic. Species number has now increased from 13 to 34 for the Ross Sea, which highlights the requirement for choosing the appropriate sampling gear, and continued 'classical' taxonomical as well as biogeographical work. With the present study equal distribution of cumacean species with an affinity to the Magellan region in all high-Antarctic regions could be demonstrated.

A new species *Leucon rossi* (see front page) and the subspecies *Diastylis enigmatica rossensis* was described from the Ross Sea. Further species from the Ross Sea showed slight morphological differences to literature. In the context of the discussion about cryptic speciation these differences might indicate that diversity of Antarctic cumaceans is likely much higher as currently known. In the present study genetic differences in the 16S rRNA gene of populations of *Leucon antarcticus* from the Ross Sea and the Weddell Sea make clear that these have genetically separated for an extended period of time. According to the analysis of 16S rRNA data, populations of the species *Leucon intermedius* from the Ross Sea and the Weddell Sea belong to the same species. Genetic diversity of the cytochrome oxidase I (COI) gene of two caridean decapods supports the concept of circumantarctic species distribution in marine broadcasters. A broadcasting mode in reproduction seems to favour high gene flow and homogeneous populations around Antarctica. Contrarily, brooders with limited capability to disperse over long distances are more likely exposed to geographic isolation on the Antarctic continental shelf, i.e. in glacial periods, which favours cryptic speciation patterns and high diversity in these taxa.

The phylogenetic history of cumaceans is obscure as there is almost no fossil record and derived and primitive characters, which vary within and between families, distinguish families. Though assumptions about the succession of cumacean families exist, details are still ambiguous. The present molecular study of mitochondrial 16S rDNA

confirmed the Cumacea as a monophylum with respect to Tanaidacea and Isopoda with the monophyletic Diastylidae as a basal family. The hypothesis of a derived group of Cumacea bearing a fused pleotelson was confirmed as well. Furthermore this study demonstrated that within the family Leuconidae the genus *Leucon* is paraphyletic, whereas the subgenus *Crymoleucon* resolved monophyletic.

ZUSAMMENFASSUNG

Die Cumacea gehören zu den Peracariden und sind eine Ordnung der Crustacea. Diese evolutiv alte Gruppe zeichnet sich durch eine konservative Morphologie aus. Überwiegend an Weichböden in marinem Milieu gebunden, zeigen diese eine kosmopolitische Verbreitung auf. Wie andere Peracariden betreiben sie Brutpflege; junge Stadien, welche die Morphologie der ausgewachsenen Tiere widerspiegeln, werden im Marsupium getragen. Es wird vermutet, dass das Marsupium eine wichtige Rolle für den Erfolg dieser häufigen und artenreichen Gruppe der Crustacea spielt.

Die Peracariden sind eine dominante Gruppe in den benthischen Gemeinschaften des Südozeans. Quantitative Studien der Fauna des Rossmeer Schelfs haben gezeigt, dass die Peracariden 63% zur Abundanz und 50% zur Biomasse beitragen. Amphipoden dominierten deutlich, obwohl verschiedene beprobte Stellen durch hohe Abundanzen von Cumaceen, Isopoden und Tanaidaceen dominiert waren. Die Zahl der bekannten Peracariden Arten aus dem Rossmeer ist geringer als in anderen hochantarktischen Gebieten. In der vorliegenden Studie konnte gezeigt werden, dass die Diversität der Cumaceen im Bezug auf deren Artenreichtum dem des Weddellmeeres oder der Ostantarktis entspricht. Bisher waren nur 13 Arten aus dem Rossmeer bekannt. Diese Artenzahl im Rossmeer hat sich nun von 13 auf 34 erhöht. Dies verdeutlicht die Notwendigkeit der Wahl geeigneter Geräte zur Probennahme und fortgeführter „klassischer“ taxonomischer und biogeographischer Arbeit. Vollständige Artenlisten und grundlegendes Verständnis von Artengemeinschaften sind nötig, um die Beziehungen zwischen verschiedenen Habitaten zu verstehen. Mit der vorliegenden Studie konnte die konstante Verbreitung von Cumaceenarten, welche auch in der Magellan Region anzutreffen sind, in allen hochantarktischen Regionen gezeigt werden.

Die neue Art *Leucon antarcticus* und die Unterart *Diastylis enigmatica rossensis* aus dem Rossmeer wurden beschrieben. Weitere Arten des Rossmeeres zeigten morphologische Unterschiede zu ursprünglichen Beschreibungen. Vor dem Hintergrund der Diskussion über kryptische Artbildung scheinen diese Unterschiede darauf hinzuweisen, dass die Diversität der antarktischen Cumaceen größer ist als bisher angenommen. Die in der gegenwärtigen Untersuchung angezeigten genetischen Unterschiede des 16S rRNA Gens in Populationen von *Leucon antarcticus* aus dem Ross- und dem Weddellmeer verdeutlichen, dass diese seit einer ausgedehnten Zeitspanne genetisch voneinander getrennt sind, während die untersuchten Fragmente des 16S rRNA Gens von Populationen von *Leucon intermedius* aus den gleichen Gebieten keine Unterschiede aufwiesen, die auf eine genetische Trennung hindeuten. Die genetische Diversität des Cytochromoxidase I Gens (COI) von zwei Decapodenarten unterstützte das Konzept der zirkumantarktischen Verbreitung von Arten mit Driftstadien. Die Reproduktion über planktische Larven scheint zu höherem Genfluß und zu homogenen

Populationen rund um die Antarktis beizutragen. Für Populationen von Arten mit Brutpflege, die ein verringertes Ausbreitungspotential über lange Distanzen besitzen, bestand dagegen während glazialer Perioden eine erhöhte Wahrscheinlichkeit von geographischer Isolation auf dem antarktischen Schelf. Diese spielt eine wichtige Rolle bei der Bildung von kryptischen Arten.

Die Phylogenie der Cumaceen ist unklar, weil es nur wenige fossile Funde gibt und die Familien anhand von ursprünglichen und abgeleiteten Merkmalen unterschieden werden, die innerhalb und zwischen den Familien variieren. Obwohl Annahmen über die Abfolge der Cumaceen Familien existieren, sind die Details noch mehrdeutig. In dieser Studie konnte anhand von mitochondrialer 16S rDNA die Monophylie der Cumaceen gegenüber den Tanaidaceen und Isopoden bestätigt werden. Die Diastyliden traten als monophyletische und basale Familie auf. Die Hypothese einer abgeleiteten Gruppe der Cumaceen mit einem fusionierten Pleotelson wurde ebenfalls bestärkt. Überdies hat sich erwiesen, dass innerhalb der Familie Leuconidae die Gattung *Leucon* paraphyletisch ist, während die Untergattung *Crymoleucon* als Monophylum zu erkennen war.

1 INTRODUCTION

1.1 Antarctic peracarid crustaceans

Systematics and morphology — The supraorder Peracarida (Malacostraca, Eumalacostraca) is subdivided into eight orders; five of these are represented in the Southern Ocean (Tab.1) Systematics of this group has been subject to controversial discussion, and as a result it was suggested to discard or revise the taxon fundamentally (Dahl 1983). A recent classification (Martin & Davis 2001) includes the Thermosbaenacea as a peracarid order. In the classical organization of the Peracarida Thermosbaenacea were not included, as they are lacking the marsupium found in female specimens, which is an autapomorphic character shared by all other peracarids (Westheide & Rieger 1996). The marsupium is a brood pouch on the ventral side of the carapace of the mature female. Eggs are laid into the marsupium and undergo direct development without planktonic larvae in contrast to most other marine invertebrate species, which follow a complex life cycle including larval stages. The brood chamber consists of overlapping lamella (oostegites), which are interpreted as epipodites that have moved from the lateral to the medial side (Claus 1885). This movement was achieved by a special hinge of the thoracopods between coxa and basis, which is also an autapomorphy of the classic Peracarida (Westheide & Rieger 1996). Still, Thermosbaenacea have a brood pouch consisting of the swollen

Table 1 Orders of the supraorder Peracarida (estimated worldwide numbers after Brandt 1999; Sieg 1986; Westheide & Rieger 1996; Antarctic and Magellan regions after De Broyer & Jazdzewski 1996; Brandt et al. 1998; Brandt 1999, Schmidt & Brandt 2001; Haye et al. 2004; De Broyer et al 2003; publication II, IV).

peracarid order	species number		
	worldwide	Antarctic	
Amphipoda	>7000	531	(821)
Cumacea	1400	67	(98)
Isopoda	>10000	356	(427)
Mysidacea	780	37	(59)
Tanaidacea	2000	74	(127)
Mictacea	3	-	(-)
Spelaeogriphacea	2	-	(-)
Thermosbaenacea	20	-	(-)

Numbers in brackets including Magellan region

dorsal carapace cavity. Undoubtedly, peracarid crustaceans owe their evolutionary success to the marsupium and brood protection. This comes true especially for terrestrial isopods as the marsupium was a prerequisite for the radiation of this group (Westheide & Rieger 1996).

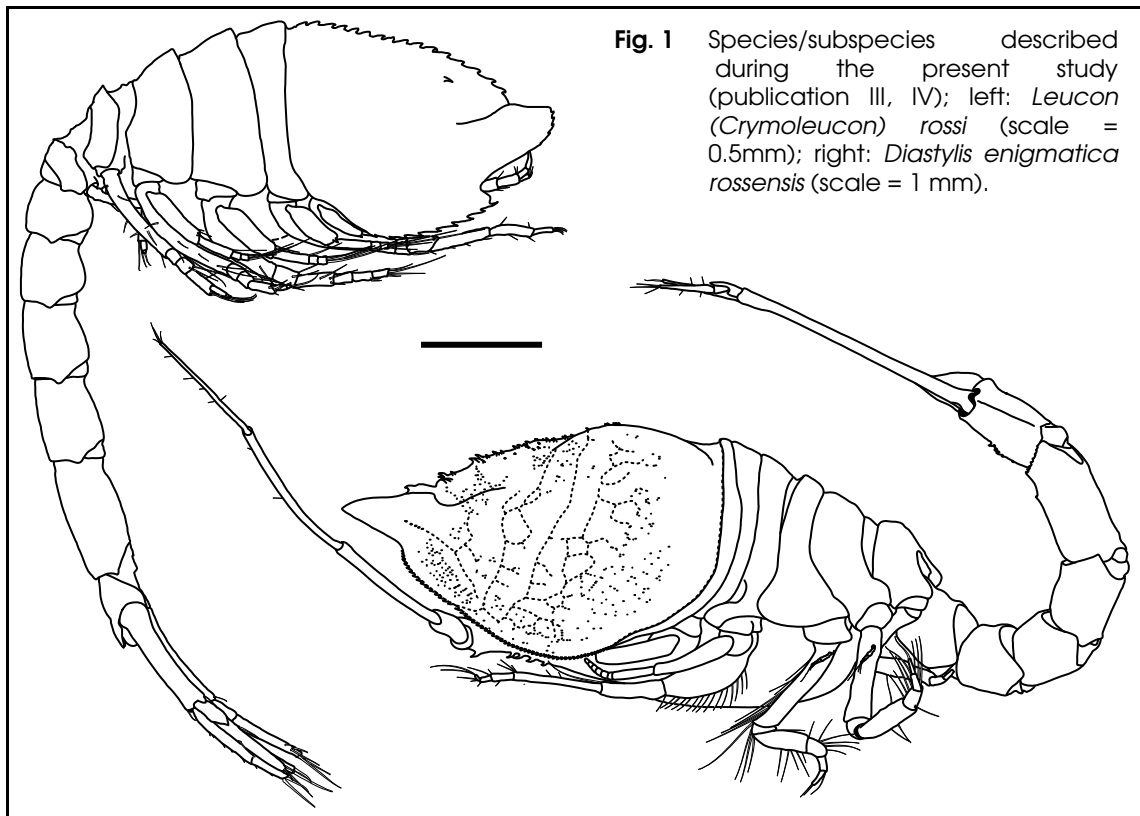
Ecological importance and evolution — Although some isopods conquered firm land and inhabit most arid areas, the majority of the Peracarida populate aquatic, mainly marine, environments. Also, some amphipods and an abundance of isopods are parasitic, the latter, as the exception from the rule, including few forms with a complex life cycle (e.g. Raupach & Thatje 2006). In the marine environment the dominant mode of life is benthic though several peracarids display to some extent affinity to the water column (Westheide & Rieger 1996). Antarctic peracarid crustaceans constitute an important element of the benthos both in diversity and abundance (Jazdzewski et al. 1992; De Broyer & Jazdzewski 1996; De Broyer et al. 2003; publication I). After more than a century of Antarctic research species numbers are still increasing every year (De Broyer & Jazdzewski 1996; De Broyer et al. 2003). High diversity of Antarctic Peracarida is elucidated with the long evolutionary history of the isolated Antarctic environment, habitat heterogeneity partly caused by iceberg scouring and drop stones (compare chapter 2.1), low dispersal potential due to the brooding reproduction mode, limited mobility of bottom dwelling peracarids, and finally the extinction of most benthic predators including decapods, particularly brachyuran crabs, owing to the tertiary cooling of the Southern Ocean, which left ecological niches vacant for peracarid crustaceans (De Broyer & Jazdzewski 1996; Aronson & Blake 2001; De Broyer et al. 2003; Thatje et al. 2005a). Actual diversity of Southern Ocean Peracarida might be even higher than observed today, if it turns out that cryptic speciation recently revealed within the isopod species *Ceratoserolis trilobitoides* and *Glyptonotus antarcticus* (Held 2003; Held & Wägele 2005) is a general feature of Antarctic Peracarida, a pattern that might be the result of the evolutionary history of the Southern Ocean (for discussion see Thatje et al. 2005b).

Furthermore, peracarid crustaceans are an important food source for many Antarctic benthic invertebrates, demersal fishes, sea birds, and marine mammals (e.g. Dearborn 1965, 1977; Ainley et al. 1992; Jazdzewski & Konopacka 1999; Olaso et al. 2000, De Broyer et al. 2004). In total about 60 million tons of amphipods are estimated to be consumed every year within the Antarctic food web (Dauby et al. 2002).

1.2 Antarctic Cumacea

After Băcescu and Petrescu (1999), Swammerdam was the first to mention a cumacean species in 1680 (published 1737). The first description of that species according to Linnean nomenclature dates back to 1780, when Le Lepechin described *Oniscus scorpioides*, which today is known as *Diastylis scorpioides* (Zimmer 1941; Băcescu & Petrescu 1999). Only 1804, the second cumacean *Cancer scorpioides* (*Bodotria scorpioides*) was described by Montagu. Synonym to this species is *Cuma audouinii* (Milne-Edwards 1828), after which this peracarid order was named. In 1841, four further species were described by Krøyer (Zimmer 1941). The first description of an Antarctic cumacean was published by Sars in 1873. He described five additional species from the Antarctic in the following years (Sars 1887). During that time about 130 species have been described worldwide. Today eight families are recognized (Bodotriidae, Ceratocumatidae, Diastylidae, Gynodiastylidae, Lampropidae, Leuconidae, Nannastacidae, and Pseudocumatidae) and are all known to occur in Southern Ocean waters, although Ceratocumatidae and Pseudocumatidae were recorded from the Subantarctic only.

General cumacean morphology is conservative throughout all families and comprises a widened and raised carapace and a slender pleon ending in two uropods (compare Fig. 1). The size of the average cumaceans is 0.5 to 1 cm, the largest species, *Diastylis goodsir*, is recorded from the Arctic and reaches 3.5 cm in total length. Polar species tend to be larger in general (Chapelle & Peck 1999). Whereas Palaeozoic forms were lacking a pseudorostrum and still possessed well-developed eyelobes (Schram 1986), the present form was reached in the early Jurassic (Băcescu & Petrescu 1999). Monophyly of the Cumacea is supported by numerous synapomorphies: the carapace covers the first three thoracic somites and is forming the pseudorostrum anteriorly; the first thoracic appendage is bearing a branchial epipod which extends to a siphon; the second thoracic appendage carries a modified oostegite in females; and the pleopods are lacking from the second to the fifth abdominal somite in females (Haye et al. 2004). Only little is known about cumacean phylogeny. Until now, no satisfying phylogenetic hypotheses have been proposed. Latest molecular work indicated that the most derived group of cumacean families (Bodotriidae, Nannastacidae, and Leuconidae) without articulated telson is a monophylum. Still, within this group Bodotriidae are paraphyletic. The Pseudocumatidae is the most basic family and leads via Gynodiastylidae and Diastylidae to more derived forms (Haye et al. 2004).



Cumaceans exhibit a cosmopolitan distribution and live most of their life buried in the sediment. Therefore, they are not found on rocky bottom. Several studies revealed that nocturnal vertical migrations are common for cumaceans with species specific and seasonal variations (e.g. Granger 1969; Steams & Dardeau 1990; Akiyama & Yoshida 1990; Macquart-Moulin 1991; Wang & Dauvin 1994). Occurrence in the plankton is connected to moulting, courtship, and reproduction and was interpreted as avoidance of predation during sensible phases of life as well as important for dispersion of an animal which is almost immotile most of its life cycle (Anger & Valentin 1976; Yoda & Aoki 2002).

Most species feed on sediment by grazing on grains of varying size or filtering microorganisms or organic substances from the sediment. They inhabit mainly marine habitats, but few species are adapted to brackish water. Cumaceans are an essential component of the benthic fauna (e.g. Hessler & Sanders 1967; Brandt et al. 1999) and are important as food source for demersal fish and other macrofauna (e.g. Kühl 1964; Arntz 1971, 1974; Arntz & Finger 1981; Cartes 1993; Schlacher & Wooldridge 1996).

1.3 Hypotheses and aims of the study

Cumacean phylogeny — Cumacean phylogeny has been studied recently (Haye et al. 2004); before assumptions about family relationships were proposed by Zimmer (1941) and Lomakina (1968). Though information indicates two major groups within the Cumacea, still most of the relationships within and between families remain obscure. Whereas monophyly is strongly suggested by morphology (Zimmer 1941), recent molecular studies failed to prove monophyly (Haye et al. 2004).

Hypothesis

The peracarid order Cumacea is a monophyletic taxon. Also, the family Leuconidae is monophyletic within the higher cumacean taxa.

Diversity of the Ross Sea — Although it is known that diversity of Antarctic peracarid crustaceans is high the reported species numbers for the Ross Sea is comparatively low (e. g. Brandt 1991; Mühlenhardt-Siegel 1999; Corbera 2000). Most of the research characterizing habitats of the Ross Sea has been done around McMurdo Sound (Waterhouse 2001). Information about macrozoobenthic community structure and diversity along the Victoria-Land coast (Ross Sea) is limited to only few restricted shallow water areas such as Terra Nova Bay.

Hypothesis

The low peracarid species numbers reported from the Ross Sea area are reported due to under-sampling of the region with inappropriate gear. True diversity of the Ross Sea region is as high as in other high-Antarctic regions (e.g. Weddell Sea, East Antarctic).

Diversity and speciation of Antarctic Cumacea — Morphological data from the Antarctic often show small differences within species, which are attributed to geographical variation. Nevertheless, recent studies showed cryptic speciation is common in Antarctic isopods (Held 2003; Held & Wägele 2005; Raupach & Wägele 2006).

Hypothesis

Cryptic speciation in Peracarida is not restricted to the order Isopoda. Direct reproduction mode and brood protection result in limited dispersal potential, and thus genetic diversity might be higher than expected from circum-Antarctic cumaceans species.

Aims of the study — The aims of this study are to:

- investigate macrozoobenthic community structure and cumacean diversity of the Ross Sea in order to evaluate the status of this region in comparison with diversity and faunal composition of other high Antarctic oceans.
- revamp the cumacean species inventory of the Ross Sea.
- study biogeographic affinities between Antarctic cumaceans and areas, to elucidate the origin of the Ross Sea cumacean fauna and connection to other (sub-)Antarctic regions.
- to examine genetic relationships of cumaceans in order to elucidate phylogeny within the Cumacea.
- and to analyse genetic diversity within Antarctic cumacean species to reveal speciation processes in the context of the evolutionary history of the Southern Ocean.

2 MATERIALS AND METHODS

2.1 Study areas

The results of this work are mainly based on fieldwork carried out in the Ross Sea, the world's southernmost ocean (Fig. 2). The Ross Sea is a glacially deepened continental shelf basin that is fringed by Victoria Land and Marie Byrd Island. As a consequence of glacial abrasion in glacial-interglacial ice extent and retreat, the depth of the shelf break lies at about 800 m and is much greater than in any other place on earth (Russo et al. 1999). Typically, the sea floor is covered with glacial sediments of silt, sand, gravel, and scattered erratic boulders (Kennet 1968). During winter, the sea ice extends to cover up to 86 percent of the Ross Sea. This corresponds to over 4 million km² or one fifth of the total extent of Antarctic winter sea ice (Jacobs & Comiso 1989). The shelf ice of the Ross Sea is the largest in the world. Large polynya (areas of combined open water and thin ice surrounded by sea and/or land and ice) are a feature of the Ross Sea and play an important role in many natural processes, including heat transfer from ocean to atmosphere, and phytoplankton production and is driving the Ross Sea food web. The Ross Sea polynya contains the most productive and spatially extensive phytoplankton bloom in the entire Southern Ocean and in mid-winter covers an area of 27,000 km² (Zwally et al. 1985; Bromwich et al. 1998). It extends along the Victoria-Land Coast from Ross Island to Coulman Island and probably persists throughout winter. Minor polynyas also occur off Cape Royds, Ross Island, and a larger one in Terra Nova Bay (Kurtz & Bromwich 1985; Van Woert 1999). The Ross Sea is one of the most biologically productive regions of the Southern Ocean (Sullivan et al. 1993; Arrigo & McClain 1994; Walker et al. 1995; Carrada et al. 2000; Innamorati et al. 2000; Saggiomo et al. 2000) with estimated annual production four-fold higher than the average global ocean production (Saggiomo et al. 2000).

Additional sampling was carried out in the Weddell Sea (Fig. 2) for a genetic comparison of species from two geographically separated high Antarctic regions. The Weddell Sea is a part of the Southern Ocean: its boundaries are defined by the coasts of Coats Land and the Antarctic Peninsula and comprises an area as much as 2.3 mio km². As a high Antarctic ocean water temperature of the shelf (to 500 m) varies between -1.6 and -2.2°C. The shelf break – in contrast to the Ross Sea - lies at about 600 m (Carmack & Foster 1977). Vast areas of the shelf are covered by soft bottom with varying components of silt, sand, gravel, and stones up to the size of dropstones (Voß 1988; Gutt 1991a). The northern part of the Weddell Sea is in the seasonal sea ice zone, whereas the southern part lies in the permanent sea ice zone (Hempel 1985). During summer, polynyas develop regularly at the eastern and southern shelf-ice coast (Hellmer & Bersch 1985).

Ice is a major disturbance factor through anchor-ice formation and subsequent rafting, and through scour and disturbance by sea ice and icebergs. Ice scouring usually is an important factor in structuring benthic assemblages in the Weddell Sea as well as in the Ross Sea (Oliver & Slattery 1985; Picken 1985a; Dayton 1990; Gutt et al. 1996; Gutt & Starmans 1998; Arntz & Gallardo 1994; Arntz et al. 1997; Gutt & Piepenburg 2003; Knust et al. 2003). Differences in the intensity of ice disturbance varying by an order of magnitude over Milankovitch timescale are discussed as major driving forces in the evolution of Antarctica shelf communities (Thatje et al. 2005a).

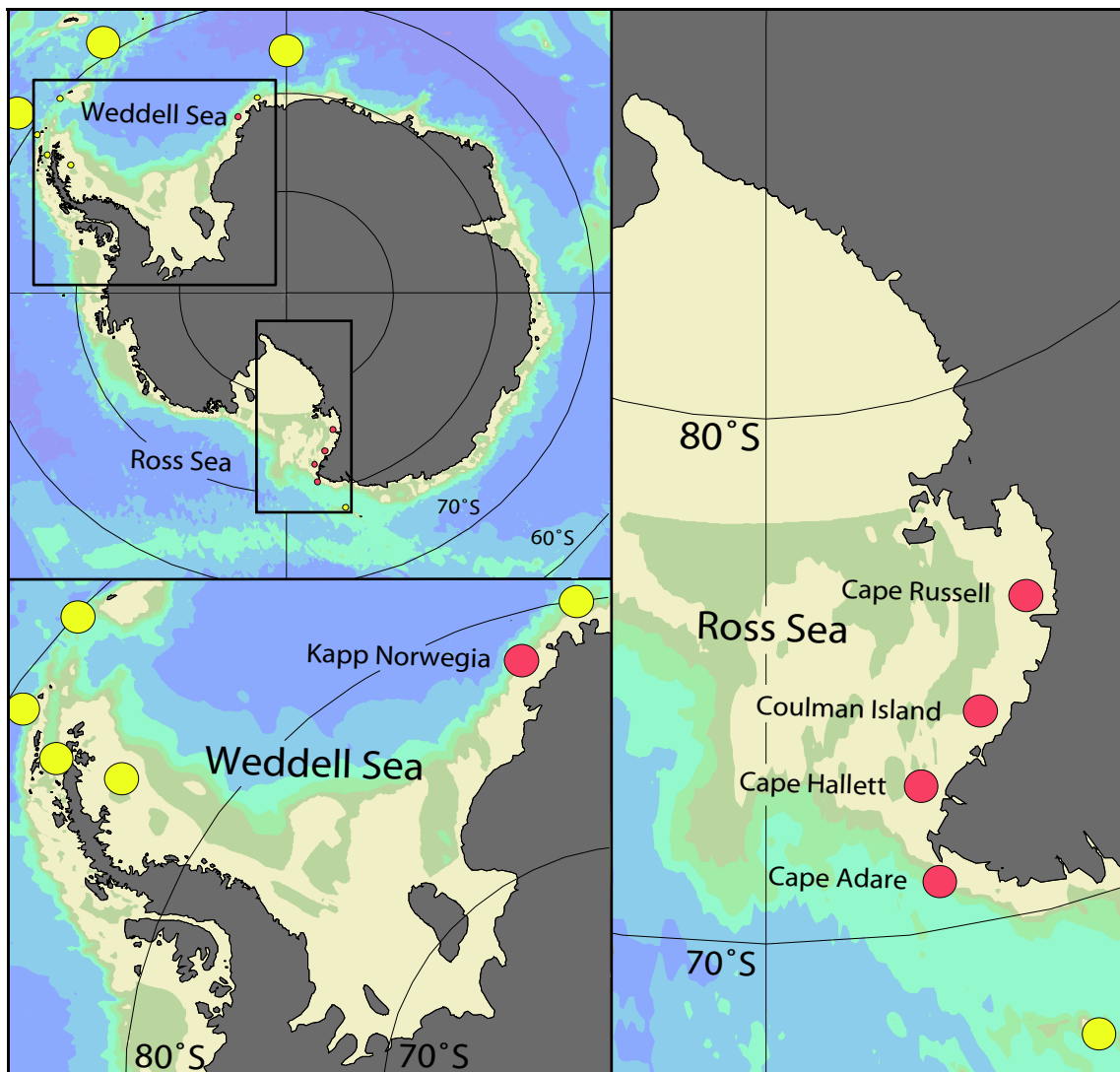


Fig. 2 Study sites and sample areas. Main sample areas red; additional sample areas yellow (compare publication III).

2.2 Sampling methods

The benthic macrofauna was sampled in the setting of the Victoria Land Transect project during the 19th Italian Antarctic expedition with RV 'Italica'. Macrozoobenthic samples were obtained along a latitudinal transect off the Victoria Land coast in February 2004. A depth gradient was sampled at each of the four sampling sites (Cape Adare, Cape Hallett, Coulman Island, and Cape Russell; Fig. 2) ranging from 84 to 515 m (publication I, II). A modified Rauschert dredge with a mesh size of 500 μ m was used (for detailed descriptions of sampling compare publication I, II). Further material was obtained from the parallel cruise to the Ross Sea with RV 'Tangaroa' (publication II), from the expeditions ANT XXI-2 (BENDEX) to the Weddell Sea in austral summer 2004 (Arntz & Brey 2005; publication III) and the ANDEEP (ANT XIX3/4) cruises I and II (Fütterer et al. 2003) to the Scotia-Arc region and the Weddell Sea in 2002 (all with RV 'Polarstern'), and several sites sampled at the Antarctic Peninsula, South Shetland Islands, South Sandwich Islands, Balleny Islands etc. during various cruises (publication III) (Fig. 2). Sampling was carried out using a variety of gears, such as epibenthic sledges, bottom trawls, or Agassiz trawls (for more details see Brandt & Barthel 1995; Brenke 2005; publication III) in depths ranging from the shelf to the deep sea.

Macrozoobenthic samples were directly preserved in 90% pre-cooled ethanol and were stored at -25°C during the following 4 months. Alcohol was changed after that period and samples were sorted into major taxonomic groups using a dissecting microscope. For the following 6 months samples were kept at 5°C.

2.3 Morphological studies

Material for morphological studies was examined with a dissecting microscope. Dissected appendages were mounted on slides in glycerine prior to microscopical work. Digital photographs were taken with an attached camera (Olympus DP70) and used for scientific drawings that were created with a digital drawing tablet (Wacom Intuos3 9x12) as described by Coleman (2003, 2006). Body length of cumaceans was measured from the tip of the pseudorostrum to the posterior margin of the telson. Length of articles was measured as proposed by Mühlenhardt-Siegel (2005) and given as relative length of peduncle (RLP) articles 1 to 3 of antenna 1 compared to total peduncle length. The ratio basis to rest of appendage (B/R) is given for maxillipeds and paraeopods, which is the proportion of the basis to the combined length from ischium to dactylus, not including terminal setae. RLA refers to the relative length of each article

from the ischium to dactylus, excluding terminal setae. All lengths were measured from the digital drawings (publications IV, V).

2.4 Molecular genetic methods

Tissue dissection and DNA extraction — DNA was extracted from the dissected pleon of the cumaceans. The remaining parts of the animals were kept in 80% ethanol for later identification or repeated analysis. The specimens were dissected using a dissecting microscope and sterile tweezers. In some cases whole animals were used for DNA extraction. To avoid DNA contamination the extraction was carried out in sterile conditions. The following alterations were applied to the protocol of the *QIAamp DNA Mini Kit* (Qiagen), which was used for DNA extraction:

- Before elution of the DNA from the spin column, the column loaded with elution buffer was incubated for 5 min at 70°C.
- The volume of the elution buffer was decreased from 200 to 50 µl in order to increase the concentration of DNA.

After the extraction, quality and quantity of the DNA was determined by a *ND-1000* Spectrophotometer (*NanoDrop Technologies*). DNA was stored at 4°C for further processing.

Polymerase chain reaction (PCR) — The method of the polymerase chain reaction (Mullis 1986; Saiki et al. 1986; Mullis & Fallona 1987; Saiki et al. 1988) is used to amplify DNA from template DNA. A single molecule may be multiplied to millions of copies, which then can be further processed to analyse the sequence of the DNA. The processes of nucleic acid duplication during PCR are similar to the processes of natural replication. A new strand of DNA is synthesized by the polymerase along a single strand of nucleic acid beginning with a starter molecule (primer). Primers are synthetic DNA oligonucleotides, which hybridize with the single strand DNA matrix. In the next step a heat resistant DNA polymerase synthesizes a new DNA double strand from the 3' end. With two primers oriented to the opposite directions an intermediate DNA sequence can be copied. During a PCR run the single steps of the reaction (denaturation, primer annealing, and primer extension) are cyclically repeated. As the matrix DNA is doubled with each cycle it is multiplied exponentially (detailed reaction profiles used are given in Table 2).

Table 2 PCR reaction profiles according to primer combinations.

primer pair	temperature (°C)	Time (min.s)	No. of cycles	reaction profile
16a/16b	94	2.00	1	initial denaturation
	94	0.20	38	denaturation
	52	0.10		annealing
	65	1.00		extension
	65	8.00	1	final extension
16a/craR	94	2.00	1	initial denaturation
	94	0.20	38	denaturation
	42	0.20		annealing
	65	1.00		extension
	65	8.00	1	final extension
ALh/CLr	94	2.00	1	initial denaturation
	94	0.20	38	denaturation
	46	0.10		annealing
	65	1.00		extension
	65	8.00	1	final extension

The PCR was used to amplify a homologous region of the mitochondrial 16S rRNA gene. Amplifications were performed on an *Eppendorf Master Cycler* in 25 µl reactions using the *HotMaster Taq*-polymerase and reaction buffer of *Eppendorf*. According to the protocol provided by the manufacturer the following concentrations were used:

- 2.5 µl 10x PCR buffer
- 0.5 µl dNTPs (2 mmol/µl)
- 0.125 µl of each primer both 100 pmol/µl
- 3 µl of DNA template
- 0.25 µl BSA
- 0.15 µl Taq (5 U/µl)
- filled up to 25 µl with sterile H₂O.

Primer design — The universal primers for the 16S rDNA (16a, 16b) (Table 3) were previously used with success for the study of several arthropod classes (Simon et al. 1994). Despite the general application of these primers on arthropod taxa amplification of cumacean DNA was weak. As primer 16b is less effective than primer 16a it was substituted with the reverse primer craR (Table 3) of Crandall & Fitzpatrick (1996), but no increase of DNA yield was achieved. Therefore, new primers were created from seven amplified sequences and three sequences obtained from the GenBank data base (National Center for Biotechnology Information). Conserved regions were identified using the program BioEdit (Hall 1999). Primers for these sites were constructed with the program Fast PCR (Kalender 2003) and the online java-applet netprimer

(<http://www.premierbiosoft.com/net-primer/index.html>) taking into account formation of hairpins and dimmers (Palumbi 1996). Primers ALh and CLr (Table 3) were constructed for the cumacean family Leuconidae at highly conserved regions of the 16S gene, the fragment length between ALh and CLr ranged from 255 to 256bp.

Table 3 Primers used for DNA amplification

primer	sequence	source
16a ¹	5'-CGC CTG TTT ATC AAA AAC AT-3'	Palumbi et al. 1991
16b ²	5'-CCG GTC TGA ACT CAG ATC ACG-3'	Palumbi et al. 1991
craR ²	5'-AGA TAG AAA CCA ACC TGG-3'	Crandall & Fitzpatrick 1996
ALh ¹	5'-GTACTAAGGTAGCATA-3'	publication VI
CLr ²	5'-ACGCTGTAYCCCTAAAGTAATT-3'	publication VI

¹ forward primer; ² reverse primer

Gel electrophoresis — During the present study, gel electrophoresis (Sambrook et al. 1989) was used for control of DNA amplification and purification. It is a common method used in every modern molecular laboratory to verify the quantity and purity of DNA. Electrophoresis separates charged biomolecules, which migrate in an electric field depending on molecule size and electric charge. From the migration rate and the number of different fragments, conclusions can be drawn about the purity of the PCR product. The amount of DNA can be estimated from the brightness of the signal.

A horizontal agarose gel (1.5%) was loaded with a mixture of 3 µl of amplified/purified DNA and 1 µl loading buffer (*peq/lab*). After a running time of 25 min (120 mV) the gel was removed from the electrophoresis chamber and stained for 1 min in an ethidiumbromide bath (0.1%) and subsequently destained in distilled water for 20 min. Ethidiumbromide binds with high affinity to the double-stranded DNA molecule and fluoresces under ultraviolet light. A 'ladder mix' (*Fermentas FastRuler DNA Ladder, Middle Range*) of DNA fragments with defined length was also applied onto the gel to characterize the sample DNA from photographs taken under an UV light source (observed bands from the samples are compared to the bands of the ladder mix to distinguish the length of the DNA molecule).

DNA purification — PCR products were purified of remaining primers, polymerase, nucleotides and salts, which might negatively influence the sequencing reaction (Hillis et al. 1996). The *QIAquick* PCR-purification kit of *Qiagen* was used according to the manufacturer's instructions. To achieve higher concentrations of purified DNA only 30 µl elution buffer were used. An aliquot of 3 µl of the purified DNA was again controlled by gel electrophoresis.

DNA sequencing — DNA sequencing is the final procedure to obtain nucleotide sequence of the examined genes. Therefore, the Thermal Cycle-Sequencing method was applied to the purified PCR products. Cycle sequencing (Sambrook et al. 1989) is a combination of two technologies: dideoxy-chain termination sequencing (Sanger et al. 1977) and the thermal cycling methodology as used in the PCR technique. The method is suitable for small amounts of template DNA. Dideoxyribonucleoside triphosphates (ddNTPs) are used as specific terminators of DNA chain elongation. In contrast to the common nucleotides (dNTPs) used in PCR, these ddNTPs lack the 3'-hydroxyl group necessary for incorporation of further dNTPs to the growing DNA chain. Thus, the growing chain is terminated whenever a ddNTP molecule is incorporated. Since the reaction mix contains dNTPs as well as ddNTPs; the latter are incorporated rarely and randomly under the particular conditions of the polymerase reaction. A number of dideoxy-terminated chains are synthesized from one template strand during the reaction cycles. Owing to the PCR-like character of the method a large amount of product copied from a single template strand is produced. Accordingly, this technique is far more sensitive than the standard sequencing method of Sanger et al. (1977).

In the present study cycle sequencing was performed according to the manufacturer's instructions of the *BigDye Terminator v3.1* kit of Applied Biosystems (ABI) using the *ABI 3130* sequencer. In general 1-3 µl of purified DNA was used for cycle sequencing with an *Eppendorf Master Cycler* (4 µl were used for samples with low DNA concentration). Excessive BigDye was removed with the *DyeEx 2.0 spin* kit (*Qiagen*) and the samples were denaturated 1:1 with formamide prior to sequencing. The BigDye mix, included in the kit, contains differently marked ddNTPs for each base type. During the sequencing process the fragments of each sample are separate according to their length by introducing a capillary into each sample. A laser is moved along the capillary and the emitted light is detected by the sequencer. The output file of the sequencer is an electropherogram that shows the sequence and the quality of the reading (Fig. 3).

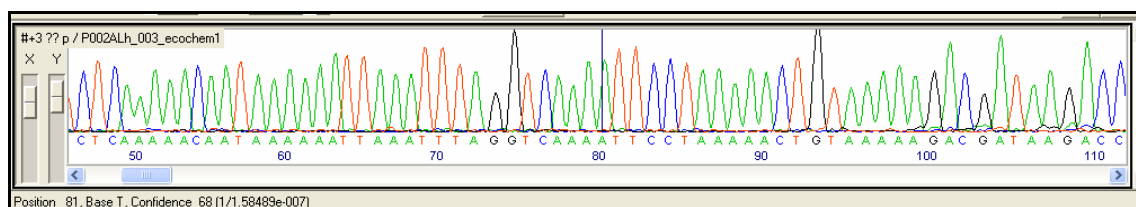


Fig. 3 Electropherogram. Each peak represents a base of the DNA sequence. Here, part of the mitochondrial 16S rDNA of the cumacean species *Leucon antarcticus* Zimmer, 1907.

2.5 Statistical analysis

Faunal communities — Data of macrozoobenthic communities (publication I) and cumacean species assemblages (publication II) off Victoria Land coast were analysed using the PRIMER v. 5.1.2 (Plymouth Routines in Multivariate Ecological Research; Clarke & Gorley 2001) software package developed at Plymouth Marine Laboratory, United Kingdom. A cluster analysis and Multidimensional Scaling (MDS) on the basis of Bray-Curtis Index was used. Since data of the Rauschert dredge are of semi-quantitative nature, relative abundances with arc-sin transformation were used. As a measurement for diversity univariate methods, such as Shannon-Wiener index (H') (Shannon & Weaver 1949) and evenness (J') (Pielou 1966) were applied.

Morphological data — Several morphological characters (carapace height, carapace length, length of carapace and free thoracic segments, total length, and ratio carapace height vs. carapace length) were measured for premature males, premature females, and adult females of the cumacean *Leucon* (*Crymoleucon*) *rossi* n. sp. (publication V). A pair wise comparison of these data between both sexual stages of the premature animals was carried out as well as a comparison of the ratio of carapace height vs. carapace length between premature males and adult females using the Mann-Whitney Rank Sum Test (Mann & Whitney 1947).

2.6 Phylogenetic analysis

Correction of DNA sequence — Sequence files from the sequencer were assembled using the programs Pregap4 and Gap4 of the Staden package (Staden et al. 1989). Following, the consensus sequence was built by aligning the sequences of the forward and the reverse primers. Conflicting sequence data were corrected manually depending on the quality of the signal displayed in the electropherograms.

The Basic Local Alignment Search Tool (BLAST) — Prior to inclusion of genetic data into the phylogenetic analysis, sequences were compared to sequences from the GenBank database of the National Center for Biotechnology Information (www.ncbi.org). With the Basic Local Alignment Search Tool (Altschul et al. 1990) the database was searched for similar published sequences. Hitherto, only three cumacean sequences of the 16S gene have been published previously; thus BLAST searches based on cumacean sequences often lead to other crustacean or even insect sequences as the closest related taxa. These results were obtained due to close relationship between conserved parts of the mitochondrial 16S rDNA of arthropods and the high diversity of

variable sites within the cumacean sequences. Nevertheless, sequences that yielded arthropod relationship were included into phylogenetic analysis as they displayed high agreement with the already known cumacean sequences.

Aligning sequences — In a phylogenetic analysis homologous characters are compared, whether these are morphological or genetic. Homologous areas were determined using the secondary structure of the 16S gene (Fig. 4). Base-pairing regions ('stem regions') are conserved, and thus can be comparatively easily homologized between two sequences. On the other hand a 'stem' consists of two sites on the sequence, which can be identified due to the capability to bind by base pairing. It is important to note that the secondary structure is formed by the rRNA, which allows non-canonical base pairing (e.g. U – G); therefore clear reconstructions might be obscure (Ouvrard et al. 2000). Fortunately, most regions of the sequences could be aligned using the secondary structure model of *Drosophila melanogaster* (GenBank Accession number X53596 (Gutell et al. 1993) (Fig. 4). Non-pairing-regions ('loop regions') were aligned using a hidden Markov model (Churchill 1989; Rabiner 1989) implemented by the program ProAlign version 0.5 (Löytynoja & Milinkovitch 2003). Sites, where alignment was still ambiguous, were excluded from analysis.

Tree construction — The aim of a phylogenetic analysis is to create a tree topology that represents the historical relationship between particular taxa and to estimate the genetic distance (the branch length of a given tree topology). For estimation of the genetic distance, a model of sequence evolution has to be determined. In the present study tree methods were used to reconstruct phylogenetic relationships of cumaceans based on the 16S gene: maximum likelihood, maximum parsimony, and Bayesian analysis (Camin & Sokal 1965; Felsenstein 1973, 1981; Swofford et al. 1996; Nei 1996; Huelsenbeck & Crandall 1997; Mau et al. 1999; Wägele 2001; Huelsenbeck et al. 2001).

First, maximum likelihood methods intend to find a tree for a given data set indicating the most likely phylogeny under a particular model of sequence evolution. Characters (nucleotides) and branch length between taxa are evaluated to calculate a likelihood value for a specific tree and the tree with the highest value is chosen as most favourable. The model of evolution most appropriate for the data set of this study, General Time Reversible Model with invariable sites and gamma distribution (GTR+I+G) (Lanave et al. 1984; Rodriguez et al. 1990) was calculated by the program ModelTest version 3.7 (Posada & Crandall 1998) applying the Akaike information criterion (Akaike 1974; Hasegawa 1990).

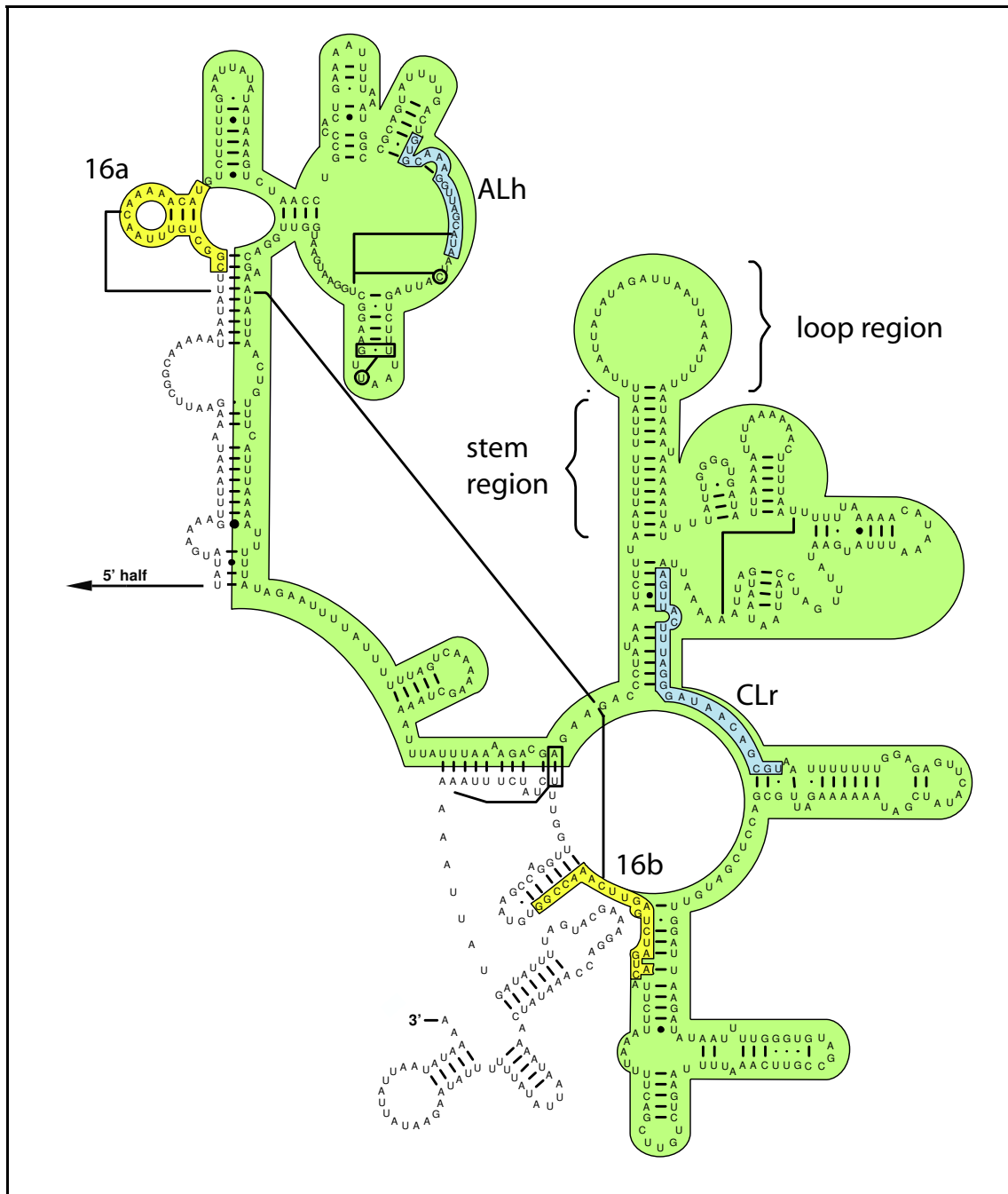


Fig. 4 *Drosophila melanogaster*: mitochondrion. Secondary structure of large subunit (3'-part) (<http://www.rna.icmb.utexas.edu/>). Amplified fragments of 16S rRNA gene (green) is situated between forward (16a/ALh) and reverse (16b/CLr) primers.

The second method used (maximum parsimony) searches for the shortest tree in terms of evolutionary changes. The tree with the least changes (mutations) in the nucleotide sequenced is considered to be most optimal (Yang 1996). Changes are considered to occur in both directions (are not directed). As transitions (substitution from purines to purines A • G, or from pyrimidin to pyrimidin C • T) are more likely to happen than transversions (substitutions between purines and pyrimidines) the ratio of transitions vs. transversions was estimated as 3:1 during the present study.

The third method uses the bayesian theorem, which was introduced by the mathematician Thomas Bayes in the 18th century. The method calculates the probability of a tree based on the dataset. Likelihood values are converted to 'posterior probabilities' from random samples of trees. The statistical method used is based on a 'Markov Chain Monte Carlo' simulation. The result of the analysis is shown in a consensus tree.

Both methods maximum parsimony and maximum likelihood were carried out using the computer program PAUP*, version 4.0b10 (Swofford 2003) using the heuristic search option with the TBR branch-swapping algorithm. Analyses were performed using random-addition of sequences with 10 replicates. Bootstrapping (Felsenstein 1985) applying 500 or 10.000 replicates (corresponding to the computation time of the method) was executed to calculate the trees. The Bayesian analysis was performed with the program MrBayes (Huelsenbeck & Ronquist 2001).

3 SYNOPSIS

3.1 Cumacean phylogeny

Within the supraorder Peracarida cumaceans are proposed to be closely related to Isopoda, Tanaidacea or Spelaeogriphacea (Zimmer 1941; Siewing 1963; Schram 1986; Watling 2000). Assumptions about cumacean phylogeny have been made by Zimmer (1941) and Lomakina (1968). Zimmer (1941) excluded Ceratocumatidae from his study as little was known about the family. The remaining cumacean families are distributed over three family types. The Lampropidae belong to the first and basal type. The second and more advanced group comprises the families Diastylidae and Pseudocumatidae, while the most advanced families are the pleotelson bearing families. For the latter type Zimmer (1941) provides no detailed analysis. Zimmer's observations are mainly based on external morphology, whereas Lomakina (1968) discussed the number and shape of hepatic diverticula resulting in the following succession of families: Lampropidae, Diastylidae, Pseudocumatidae, Ceratocumatidae, Leuconidae, Nannastacidae, and Bodotriidae. Both authors did not recognize the family Gynodiastylidae.

The first extensive computer aided phylogenetic analysis on cumaceans was carried out by Haye et al. (2004). Their study combined morphological with molecular data from the mitochondrial cytochrome oxidase I (COI) gene. Molecular data showed contradicting results concerning monophyly of the Cumacea with Tanaidacea and Isopoda as outgroup taxa. Both datasets agree on more basal cumacean families, which have a telson not fused to the pleon, and a derived 'pleotelson clade'. The Pseudocumatidae are the most basal family followed by Gynodiastylidae and Diastylidae, which resolve paraphyletic. The most derived of the telson bearing family, the Lampropidae, have intermediate support for monophyly only; thus monophyly of the 'pleotelson clade' is not proven. However, morphological data support monophyly of the 'pleotelson clade' including families Bodotriidae, Leuconidae, and Nannastacidae, as derived group of cumaceans. While molecular data lack sufficient signal for detailed results within the clade, morphology suggests that Leuconidae are basal, Nannastacidae intermediate, and Bodotriidae the most derived taxon. With their phylogenetic analysis of COI gene Haye et al. (2004) showed that Lampropidae, contradicting to assumptions of Zimmer (1941) and Lomakina (1968), are more derived of the telson bearing families. They discuss the homoplasy of many of the established morphological characters. Zimmer (1941) mentioned already that all cumacean families show combinations of advanced and primitive traits.

The study of mitochondrial LSU gene (16S rDNA) comparing the families Diastylidae, Bodotriidae, and Leuconidae supports monophyly of Cumacea

Most phylogenetic relationships within cumacean families are obscure. A detailed analysis of the family Bodotriidae was presented by Haye (2007). The family Leuconidae was revised by Watling (1991). Three new subgenera were introduced to the genus *Leucon*, one of which, *Crymoleucon*, was confirmed monophyletic by the analysis of the 16S gene (publication IV). The genus *Leucon* itself resolved paraphyletic. Although results and assumptions are contradicting or vague a synthesis is given in one tree (Fig. 5). The tree does not show results obtained with a parsimony analysis of COI gene data, which lead to the assumption that Pseudocumatidae and Gynodiastylidae are sister taxa within the Diastylidae.

A phylogenetic tree showing the relationships between several families of copepods. The tree is rooted on the left with a dashed line. The families listed on the right are: Pseudocumatidae, Gynodiastylidae, Diastylidae, Lampropidae, Ceratocumatidae, Bodotriidae, Nannastacidae, and Leuconidae. The tree shows that Pseudocumatidae and Gynodiastylidae are sister groups. Diastylidae is sister to a clade containing Lampropidae and Ceratocumatidae. Bodotriidae is sister to a clade containing Nannastacidae and Leuconidae. The clade containing Lampropidae and Ceratocumatidae is highlighted with a grey circle and a question mark, indicating uncertainty in its placement. The clade containing Bodotriidae, Nannastacidae, and Leuconidae is also highlighted with a grey circle and a question mark, indicating uncertainty in its placement.

```

graph LR
    Root(( )) --- Pseudocumatidae
    Root --- Node1(( ))
    Node1 --- Gynodiastylidae
    Node1 --- Node2(( ))
    Node2 --- Diastylidae
    Node2 --- Node3(( ))
    Node3 --- Lampropidae
    Node3 --- Node4(( ))
    Node4 --- Ceratocumatidae
    Node4 --- Node5(( ))
    Node5 --- Bodotriidae
    Node5 --- Node6(( ))
    Node6 --- Node7(( ))
    Node7 --- Nannastacidae
    Node7 --- Leuconidae
  
```

- Cumaceans have a distinct morphology; thus monophyly was not doubted. Recent phylogenetic studies confirm this assumption with respect to Tanaidacea and Isopoda, which are considered to be the closest relatives of the Cumacea.
- The existence of a derived group of Cumacea bearing a fused pleotelson is confirmed, by studies of morphology, the COI gene, and the 16S gene.
- During the last years some progress has been made on cumacean taxonomy. Still, a satisfying phylogenetic analysis of family level or within most families lies ahead.

3.2 Peracarid crustaceans of the Ross Sea

The Antarctic shelf has been subject to intensive studies since the end of the 19th century. Numerous expeditions have provided information on the main characteristics of Antarctic marine benthos some of these are low diversity of higher taxa, high degree of endemism, gigantism, or particular developmental types (e.g. Dell 1972; Picken 1980; White 1984; Dayton 1990; Gutt 1991b; Arntz et al. 1994). Benthic communities of the Antarctic shelf are characterized by assemblages of suspension feeders like sponges, cnidarians, bryozoans, and ascidians or detritus feeders such as holothurians and polychaetes (Voß 1988; Gerdes et al. 1992; Gutt & Starman 1998), the first mainly contribute to the high biomass of benthic Antarctic shelf communities below depths of 10 m (Brey & Gerdes 1997).

A general feature of the benthos of the Antarctic shelf is its high diversity (e.g. Hedgpeth 1969; Dell 1972; White 1984; Picken 1985b; Dayton et al. 1994). The currently documented total number of described species of the Southern Ocean benthos surpasses 4100 (Clarke & Johnston 2003) and is estimated to cover more than 15,000 (Gutt et al. 2004) on the Southern Ocean continental shelf. Peracarid crustaceans are the most intensely studied marine taxa and the most speciose taxon in the Southern Ocean. Still, more than 10 new amphipod species are described every year and no asymptote in species description is reached (De Broyer & Jazdzewski 1996).

Reported diversity in terms of species richness is directly depending on the number of samples taken in a specific area and the Ross Sea is one of the best-sampled regions in the Antarctic (Clarke & Johnston 2003). The number of isopod species described from the Weddell Sea is 68; only 39 species are recorded from the Ross Sea (Brandt 1991). Cumacean species inhabiting the Weddell Sea amount to 29, while the number of species observed from the Ross Sea was 13 until recently (Mühlenhardt-Siegel 1999; publication II). Why is benthic diversity of peracarid crustaceans low in the Ross Sea, whereas in the Weddell Sea, which is also a well-sampled high-Antarctic area, diversity is much higher? Bradford-Grieve & Fenwick (2001) point out that many data are unnoticed or unpublished for the Ross Sea region and other samples have only been sorted at higher level and have not as yet been worked on. They give a review on species richness including unpublished data of zoological collections, but still species numbers are comparatively low (Amphipoda 120, Cumacea 16, Isopoda 48, Mysidacea 13, Tanaidacea 11). Information about macrozoobenthic communities in the Ross Sea is limited to only few restricted shallow water areas as Terra Nova Bay and McMurdo Sound and only little previous work has been accomplished on the deeper benthic environment between 50 m and the shelf break at 800 m (Clark & Rowden 2004; Waterhouse 2001). Moreover, previous sampling was centred on certain benthic groups such as Amphipoda, Mollusca, Polychaeta, and Porifera (e.g. Dayton 1972; Stockton 1984; Gambi et al. 1997; Knox & Cameron 1998;

Cattaneo-Vietti et al. 1999; Cantone et al. 2000). However, an important factor is the selective nature of different types of sampling gear. Formerly, only gear with mesh sizes of 1 cm or more were used in the Ross Sea (Bradford-Grieve & Fenwick 2001), and even during the large-scale survey of the Trans-Antarctic Expedition from 1955 to 1958 mesh sizes of at least 1 cm were used (Bullivant 1967a, b; Dearborn 1967). Many peracarid species are smaller than 1 cm; thus only gear with small mesh size is effective in sampling this group (compare Brenke 2005).

The first attempt to implement sampling with small mesh size along the Victoria-Land coast in the Ross Sea (Choudhury & Brandt 2007; publication I, II) was undertaken during the 19th Italian expedition with RV 'Italica' in 2004. A striking result of the study was the number of newly recorded species for the Ross Sea. For example, the total number of cumacean species known from the Ross Sea increased to 34, which is more than recognized for any other Antarctic region and corresponds to other high Antarctic regions (East Antarctic 32; Weddell Sea 29; publication II). Furthermore, one species and a subspecies were new to science and are described in the present work (publication IV, V). The species *Leucon rossi* (publication V) is common and one of the most abundant species in the Ross Sea. According to its immense occurrence, it is supposed to be an endemic element of the Ross Sea fauna. Still, the Ross Sea has the lowest rate of endemism with respect to the Cumacea when compared to other high-Antarctic regions (publication II).

In the Southern Ocean gears with small mesh size have been used more frequently in recent years (e.g. Brandt et al. 1997; San Vicente et al. 1997; De Broyer & Rauschert 1999; De Broyer et al. 2001, Corbera 2000; Brandt 2004; Arntz et al. 2006). Still the analysis of whole communities sampled with those gears is scarce. From the Ross Sea we know that peracarid crustaceans dominate the community of the smaller macrobenthic fauna from the deeper shelf (100-500 m) and comprise between 28 – 61% of the total abundance. Amphipods contributed up to 56% of peracarid crustaceans, whereas isopods and cumaceans reached dominances of 14 and 11%, respectively (publication I). Proportions of peracarid communities off the South Shetland Islands closely resembled the composition of the Ross Sea during autumn (Amphipoda 66%, Isopoda 18%, Tanaidacea 8%, Cumacea 7%, Mysidacea <1%), whereas major differences in the proportions of the peracarid fauna from the Weddell Sea and off King George Island were observed during summer (Lörz & Brandt 2003, publication II). The Weddell Sea was dominated by isopods (60%) and off King George Island cumaceans (39%) were the dominant group (Linse et al. 2002). It is difficult to evaluate, whether these observations are due to seasonal effects, a different composition of the fauna, or the patchiness of the fauna. Further sampling will provide more reliable information about seasonal differences and similarities between the peracarid community compositions of the different Antarctic areas.

Conclusion

- Peracarid crustaceans are an important element of the fauna of the Ross Sea and diversity (species richness) appears to be at least as high as in other high-Antarctic regions.
- After more than a century of Antarctic research, knowledge about Antarctic benthic communities has increased substantially, but still 'traditional' work in biogeography and taxonomy is needed as it provides important knowledge to achieve a complete picture of Antarctic fauna and its relationship to other marine habitats.

3.3 Origin of Antarctic Peracarida

History and present state of the Antarctic benthic community — A striking feature of the Antarctic benthic fauna is the lack of most decapod crustaceans in particular the lack of anomuran and brachyuran crabs in continental shelf waters (Arntz & Gorny 1991; Gorny 1999; Thatje & Arntz 2004). On the contrary, when climate was temperate in the Austral province at the transition from the Late Cretaceous to the early Cenozoic a rich decapod fauna inhabited the continental shelf (Feldmann & Zinsmeister 1984; Feldmann et al. 1997). The last Antarctic fossil records of benthic decapods date back to the Pliocene (Feldmann & Quilty 1997). The extinction of Antarctic brachyurans and astacids is attributed to the inability to down-regulate (Mg^{2+}) levels in the haemolymph, which causes paralysing conditions at temperatures below 1° C, and the resulting difficulties to maintain an appropriate oxygen supply (Frederich et al. 2001; Thatje et al. 2005a).

Molecular studies suggest that, after the Eocene fish fauna vanished, the notothenioid radiation began in the middle Miocene (Cheng & Chen 1999). This radiation is strongly connected with cold adaptation of notothenioid fish and associated with dropping temperatures (Clarke & Johnston 1996; Clarke et al. 2004). Other taxonomic groups, such as gastropods, isopods, amphipods, and pycnogonids, radiated during the Cenozoic (Brandt 1991, 2000; Brandt et al. 1999; Watling & Thurston 1989; Clarke & Johnston 2003). Besides low temperatures, benthic communities had to face pronounced and short seasonality in primary production beginning in the Eocene about 55 Ma ago when East-Antarctica and Australia started to drift apart (Crame 1999). Altogether, the benthic Antarctic community has undergone fundamental changes driven by Antarctic cooling as a result of the onset of the Antarctic Circumpolar Current (BOX 1; Aronson & Blake 2001). Many taxa lacking cold adaptation got strongly reduced in diversity and/or even went fully extinct from the Southern Ocean due to their incapability to adapt to polar conditions.

Box 1 Geological history and cooling of Antarctica

The initial break-up of Gondwana was driven by a north-eastern drift of India 130 Ma ago and was followed by the separation of Africa about 40 Ma later. The first break-up between Australia and Antarctica occurred about 100 Ma in the past (Lawver et al., 1992; Shackleton & Boersma, 1981). It was supposed that after the separation of Antarctica and Australia by a deep-water current ca. 45 Ma ago, opening of the Drake Passage and the separation of South America and Antarctica happened at about 30 Ma in the past (Lawver et al. 1992). The following development of the Antarctic Circumpolar Current (ACC) took place about 20 Ma ago (Clarke & Crame 1989, 1992). Its development should have been crucial for Antarctic Cooling and the initiation of the last final cooling step in the middle Miocene about 15 Ma ago (Zachos et al. 2000), which since then set the environmental and particularly physiological frame to life in the cold (Clarke 1981; Thatje et al. 2005b).

Recent findings showed that the first sign of Pacific water flowing through the Drake Passage happened about 41 Ma ago during a time of ephemeral glacial advance (Scher & Martin 2004). It is proposed that during that time only small oceanic basins formed with a shallow gateway less than 1000 m and a deep-water connection developed between 34 and 30 Ma (Livermore et al. 2005). However, depending on the method, estimates for the opening of the Drake Passage and the onset of the ACC varies from 6 Ma to 41 Ma ago (Scher and Martin 2004; Lyle et al. 2007; Barkera et al. in press). Thus today, the exact timing of the opening of the Drake passage and the onset of the ACC by tectonics, sedimentary geology, or oceanography, remains obscure. Probably molecular biology is likely to provide a more exact answer to the problem; while Chen et al. (1997) put the radiation of the teleost *Notothenioides* at about 15 Ma, recent estimates date the radiation of amphipods of the Antarctic *Epimeridae* to 15.7 Ma (Lörz & Held 2004).

However, the shift composition and diversity of the Antarctic fauna was only partially caused by physiological constraints. Besides the cooling of the Southern Ocean, it was suggested that the Cenozoic fauna of the continental shelf was eliminated due to the periodic extensions of the Antarctic ice cap on Milankovitch timescales (Clarke & Crame, 1989, 1992, Clarke & Johnson, 1996).

Recent modelling approach (Huybrechts 2002) indicated that although the extent of grounded ice across the continental shelf might have been a diachronous process (=time transgressive); the maximum extent of grounded ice at the Last Glacial Maximum was likely to cover most if not the complete continental shelf surrounding Antarctica. A new hypothesis assumes that the advance of grounded ice sheets during glacial periods of the late Cenozoic might have devastated benthic communities inhabiting the Antarctic shelf and the continental slope (Thatje et al. 2005b). According to that theory, grounded ice masses discharged enormous amounts of rubble leading to mass wasting and turbidity flows on the continental slope, which is well represented in sediment cores. In addition to the large-scale destruction of benthic habitats, reduced food availability due to multi-annual sea ice coverage in glacial periods might have affected the benthic fauna in vast areas of the Southern Ocean (Thatje et al. 2005b). Still today, the effects of food limitation can be seen under the ice shelf of the Ross seas, where abundances of filter and suspension feeders are strongly reduced and

largely depend on particle flux through advection processes (Dayton & Oliver 1977; Thatje et al. 2005b).

Of particular importance was the reduction in skeleton crushing predators (Thatje et al. 2005a), which are a special feature of shallow-water modern benthic communities elsewhere in the sea (Aronson et al. 2007). Today, benthic communities of the Antarctic shelf show similarities to Palaeozoic marine communities and modern deep-sea communities, which largely lack bivalves and are dominated by suspension feeders, like ophiuroids and crinoids, as they face less pressure by durophagous predators as in modern shallow water communities (Aronson & Blake 2001; Aronson et al. 2007). There are no brachyuran crabs, lobsters, sharks, or rays in Antarctica. Additionally, the teleostean fauna consists mainly of non-durophagous species (Clarke 1993; Dayton et al. 1994; Eastman & Clarke 1998; Clarke & Johnston 2003; Thatje et al. 2005b). Today, main predators of Antarctic benthic shallow water communities are starfish (e.g. *Odontaster validus*) and nemertean worms (*Parborlasia corrugatus*) (Aronson & Blake 1991) unable to crush calcified structures. Under the lack of predatory pressure these conditions may have favoured the radiation and diversification of Antarctic benthic invertebrates; the results of this process are particularly stunning in the high diversity seen today in the Antarctic Peracarida (Kussakin 1967; Brandt 1999; De Broyer & Jazdzewski 1996; De Broyer et al. 2003).

Shallow-water – deep-sea relationship in Antarctic Peracarida — Owing to the reduced shelf area during glacial ice extent the geographic and bathymetric ranges of many Antarctic taxa were affected (Zinsmeister & Feldmann 1984; Clarke & Crame 1992). During glacial periods, ice extent across the Continental shelf to the shelf break eradicated or displaced most of the benthic fauna. Benthic species were either displaced to greater depth of the continental slope and/or continental rise, given species were able to tolerate hyperbaric conditions (e.g. Tyler et al. 2000; compare chapter 3.3.1) or presumably went extinct if unable to respond to these conditions (Thatje et al. 2005b).

For many taxa of the Antarctic continental shelf a wide bathymetric distribution was mentioned and evolutionary connections between the Antarctic shelf and the deep sea were demonstrated (e.g. Menzies et al. 1973; Brandt et al. 2007; Zinsmeister & Feldmann 1984; Jacob et al. 2003; Berkman et al. 2004). This relationship is highlighted by life history features that unify both deep-sea and shallow-water Antarctic invertebrates such a gigantism, slow growth, and longevity of many invertebrate species (Aronson et al. 2007; Berkman et al. 2004; Brandt et al. 2007). Brey et al. (1996) stated that many taxa of the Antarctic shelf have greater bathymetric ranges than their counterparts on other continental shelf areas. They suggested submergence and emergence caused by glacial cycles to be of importance in the evolution of the Antarctic benthos.

In contrast to peracarid Isopoda and Amphipoda (Brandt 1991, 1992; Watling & Thurston 1989; Held 2000), the bathymetric distribution of cumacean species from Antarctica has only partially revealed a relationship to the deep sea (Mühlenhardt-Siegel 1999). Only 6–7% of Antarctic cumacean species were found below 1000 m. Virtually nothing is known about Antarctic deep-sea cumaceans and the recorded bathymetric range of many cumacean taxa is extended with every new study (Mühlenhardt-Siegel 1999, Corbera 2000, publication II). Thus, as yet no exact information about the extent of the shallow-water – deep-sea linkage of Antarctic cumaceans exists.

Conclusion

- Although many taxa of Antarctic shelf communities like peracarid Isopoda and Amphipoda display a strong relationship to the deep sea, there is little evidence for a general connection of Antarctic cumaceans with adjacent deep-sea environments.

Faunal linkage with the Subantarctic Magellan Region — The Southern Ocean fauna is characterized by a high degree of endemism (Arntz et al. 1997). The driving force behind this feature is the long time of isolation of Antarctica (Clarke & Crame 1997), which is maintained by the ACC (Clarke 1990), which physically isolated the Southern Ocean from its surrounding seas. Driven by the west winds the ACC is the largest current system in the world's oceans (Fahrbach 1995). It consists of several eastward flowing jets, the most intense of which is the Polar Front (Aronson et al. 2007). The benthic marine faunas of the Antarctic Peninsula and the Magellan Region of South America show close biogeographic relationships despite this separating quality of the ACC (Arntz et al. 2005). It was proposed that the faunal overlap of the two regions resulted from the time before when the two areas were separated by the deep waters of the Drake Passage and development of the Polar Front (Dell 1972). However, observations of Thatje & Fuentes (2003) showed that planktonic larvae of decapods are able to cross the Polar Front by drifting with warm water intrusions or eddies, which permit further development of the larvae for limited periods of time (see also Glorioso et al. 2005). Aronson et al. (2007) suggested, based on satellite imagery of the dynamics of the ACC, that transport via eddies enables biota to cross the ACC in both directions, in and out of Antarctica.

A comparison of the different Antarctic regions showed that the Magellan region has the greatest affinity to the Antarctic Peninsula. Polychaetes, isopods, and cumaceans follow this pattern (Montiel et al. 2005; Brandt et al. 1997, 1999; Mühlenhardt-Siegel 1999). Recent findings have shown the same ratio in cumacean species of the Ross Sea overlapping with the Magellan region (publication II) as reported from other high Antarctic areas (Mühlenhardt-Siegel 1999; Corbera 2000), but

the ratio of Magellan species is the same as expected from the Weddell Sea or the East Antarctic (publication II). Apparently, the vicinity of the Weddell Sea to the Magellan region does not influence the species numbers, which are shared by both areas.

Studies of Ross Sea cumaceans revealed that all species, which overlap with the Magellan region, show bathymetric distributions that range below the continental shelf in contrast to most species endemic to the Antarctic (publication II). From the Weddell Sea only 50% of the Antarcto-Magellan species are reported from deeper waters (Mühlenhardt-Siegel 1999). Still, there is no evidence that this is related to the proximity of the Weddell Sea to the Magellan region. It is rather likely that this pattern is an artefact created by little sampling effort on cumaceans from the deep sea.

Conclusion

- Several peracarid and polychaete taxa show an increased overlap in species distribution from the Magellan Region with the Antarctic Peninsula. Cumacean biogeography suggests that the influence of Magellan species on high-Antarctic regions does not change with the distance to the Magellan region. The ratio of Magellan species within the cumacean assemblages is similar in all high-Antarctic regions.

3.4 Peracarid diversity

Crustaceans are a dominant and important taxon south of the Polar Front in addition to polychaetes and molluscs (Arntz et al. 1997). Though some crustacean taxa like brachyuran crabs, balaniform cirripeds and stomatopods are scarce or absent in Antarctic zoobenthos (Newman & Ross 1971; Reaka & Manning 1986; Feldmann & Tshudy 1989; Clarke & Crame 1989, 1992). Peracarids from shallow waters (>80 m) off the Victoria-Land coast in the Ross Sea number to more than more than 200 specimens m^{-2} (publication II) and contribute 63% to abundance and 50% to biomass of smaller animals of the macrozoobenthic community (publication I). From King George Island up to about 8000 specimens m^{-2} were reported in depth of less than 30 m (Jażdżewski et al. 1986). Not only do Antarctic peracarids appear in high numbers in the benthic communities, they also are the most specious taxon in the Southern Ocean (Arntz et al. 1997).

What are the mechanisms, which made this group so extraordinarily successful in the Southern Ocean? And how could species richness like that of Antarctic peracarids evolve?

Crame (1999) gave a simple explanation to these questions. He argued that important benthic groups like peracarids already existed when Gondwana fell apart and isolated high latitude continents developed. Yet, a range of different explanations

for high peracarid diversity has been discussed. The diversity of epifauna is fostered by high habitat heterogeneity in cause of the high number of sessile suspension and filter feeders (Dayton 1990), which provide a three-dimensional habitat structure and also might serve as prey or hosts for peracarid crustaceans (De Broyer et al. 2003). Decapod crustaceans are not specialised for feeding on filter feeders that might have affected decapod diversity in the Antarctic in addition to other reasons (compare chapter 3.1.1; Brandt 1999). Brandt (1999) suggested that peracarid crustaceans might occupy the ecological niche of decapod taxa, which vanished during the Cenozoic (Clarke & Crame 1989; De Broyer & Jażdżewski 1996; Brand 1999, 2000). The absence of decapod crustaceans might also have reduced predation and competition for peracarid crustaceans (De Broyer et al. 2003). Furthermore, co-evolution with Antarctic notothenioid teleosts might have influenced peracarid diversification (Wägele 1992; Brandt 2000). Notothenioides prefer prey (Gröhsler 1992; Olaso et al. 2000) without strong body ornamentation, which is a common feature in many amphipods and isopods. Moreover, peracarid crustaceans share peculiar characters, which provide an advantage in benthic Antarctic communities:

- the good swimming ability of isopods, amphipods, and mysids gives an advantage in competition for food in contrast to echinoderm, molluscs and polychaetes (Brandt 1999).
- the possession of very good chemoreceptors (aesthetascs) is important for all feeding types in environments that show strong seasonal conditions like short phytoplankton blooms in the Antarctic. Probably other invertebrate taxa than crustaceans possess less effective sensory organs (Brandt 1999).
- and finally Peracarida are well adapted to an environment, which allows for low growth rates only, due to short seasonal plankton blooms and delaying temperatures. Brood protection is typical for Antarctic species, even in taxonomic groups which typically have different reproduction modes such as bivalves (Brandt 1999).

3.5 Speciation in the context of Antarctic evolution

Early during Antarctic exploration many benthic invertebrates were reported showing widespread distribution on the continental shelf surrounding Antarctica, and therefore circumantarctic distribution was postulated for many invertebrate taxa (e.g. Hedgepeth 1970; White 1984; Clarke 1989; Arntz et al. 1994; Dayton et al. 1994). In recent years, however, cryptic species were discovered in several benthic invertebrate taxa in the Antarctic. These species can not be distinguished clearly from closely related species by morphological criteria. However, molecular studies indicated cryptic

species in several benthic invertebrate taxa (Bernardi & Goswami 1997; Allcock et al. 1997; Held 2003, Held & Wägele 2005; Raupach & Wägele 2006; Linse et al. 2007; Wilson et al. 2007, publication VI). Species, which were supposed of having circumantarctic distribution, broke up into two or more species with differing patterns of distribution. Therefore, discoveries of cryptic species indicated that circumantarctic distribution is not valid for a variety of taxa and that Antarctic biodiversity in terms of species richness might even be much higher than previously believed (e.g. Held & Wägele 2005; Raupach & Wägele 2006; Wilson et al. 2007).

In shallow-water species inhabiting the Antarctic continental shelf, patterns of cryptic speciation are discussed as the result of geographic isolation and mainly glaciation processes over Milankovitch timescale (compare 3.3). As the grounded ice sheet expanded across the continental shelf during glacial periods, shelf habitats would have been fragmented with allopatric populations confined to refugia or even driven down the continental slope (Clarke & Crame 1989, 1992; Thatje et al. 2005b). Geographic isolation is assumed to be the main driving force behind cryptic speciation processes and it might be a coincidence that Antarctic taxa so far found to exhibit cryptic speciation lack pelagic drifting stages (Held 2003; Held & Wägele 2005; Linse et al. 2007; Wilson et al. 2007; publication III).

Only species with pelagic larvae or any kind of drifting stage might have been able to overcome the barriers separating 'islands' on the Antarctic shelf, and thus ensuring substantial and continuous gene flow between isolated populations. From those species a circumantarctic distribution could be expected today. Populations of species without drifting stages, which exhibit brood protection like most of the marsupium-carrying peracarids, were genetically separated. A possible consequence would be the splitting in two species. As these species still inhabit the same biotope no further adaptation would be necessary. Thus, the two species could be morphological very similar i.e. these species were cryptic species.

Most cryptic benthic invertebrate species recorded from the Antarctic exhibit brood protection such as bivalves and isopods (Held 2003; Held & Wägele 2005; Linse et al. 2007). An exception is the crinoid *Promachocrinus kerguelensis*, which presumably has a short planktonic larval stage. Multiple lineages were detected within this species. Reduced gene flow due to a short larval dispersal period, which was found in other comatulid crinoids, might explain the genetic diversity recorded within *Promachocrinus kerguelensis* (Wilson et al. 2007).

Hitherto, the concept of circumantarctic species was based on morphology and challenged in recent years by the discovery of cryptic speciation in species with limited dispersal potential (e.g. Held & Wägele 2005; Linse et al. 2007). First molecular evidence for a circumantarctic distribution with homogeneous populations was demonstrated for two species of Antarctic caridean decapods with a broadcasting mode in reproduction through planktotrophic larvae (publication III).

The observed low genetic diversity within shallow water species *Chorismus antarcticus* indicates post glacial radiation of few populations around Antarctica that either survived in glacial shelters on the Antarctic shelf or in shallow waters of Southern Ocean islands (publication III). The species might have re-colonized the Antarctic continental shelf from these refuges at the onset of deglaciation. *Nematocarcinus lanceopes* displays higher genetic diversity in contrast to *Chorismus antarcticus* (publication III). As a deep-sea species with a bathymetric range to depths of about 4000 m, *Nematocarcinus lanceopes* would have been relatively unaffected by the advance of grounded ice sheets across the Antarctic continental shelf during glacial periods, which may explain its higher genetic diversity.

3.6 Speciation patterns in Antarctic Cumacea

As Cumacea belong to the peracarid crustaceans, which show brood protection and a lifestyle strongly connected to the benthic environment (see chapters 1.2 and 3.3.2) it seems likely that, as shown for other peracarid species (Held 2003, Held & Wägele 2005; Raupach & Wägele 2006), cryptic speciation is also common in the Cumacea. Actually, morphological examinations of cumaceans collected in the Ross Sea during this study showed that several species from the Ross Sea exhibit small differences to previous descriptions of these species from other Antarctic regions (publication IV).

The species *Cumella emergens* Corbera, 2000, represents a distinct example of morphological differences in the context of different geographic populations of cumacean species. Differences in some characters point to a closer relationship of populations from the Ross Sea and the Weddell Sea than populations of the South Shetland Island to the Ross Sea or the Weddell Sea. (Tab. 4, Fig. 6).

Table 4 Morphological differences in populations of *Cumella emergens* Corbera, 2000

Attribute	South Shetland Islands	Weddell Sea	Ross Sea
number of dorsal spines	2-3	5 male/6-7 female	6-7
Distal spine of carpus of 2 nd pereopod	absent	present	present
Carapace	flattened	normal	normal
Pseudorostrum pointing	forward	upward	upward
Ratio between uropodal peduncle and 5 th segment	1	1.2	1.2

On the other hand, there exist differences in general morphology of the carapace, morphology of the pseudorostrum, and further minor variations between populations of the Ross Sea and the Weddell Sea (Fig. 6).

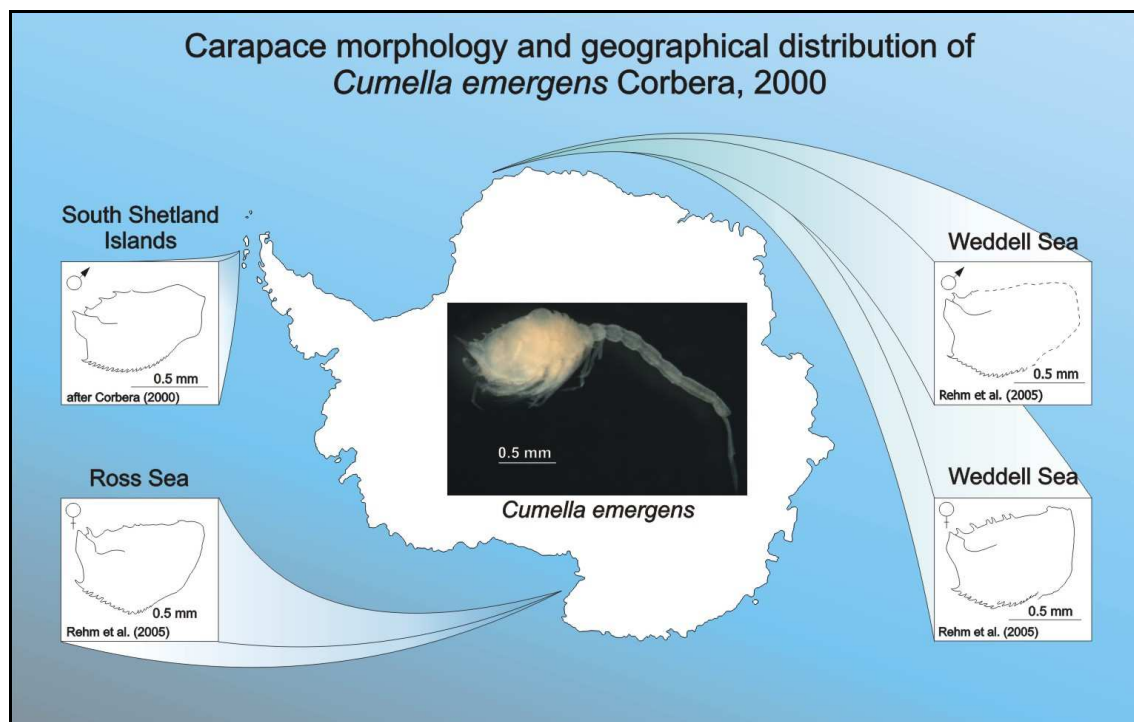


Fig. 6 *Cumella emergens* Corbera, 2000; Carapace morphology and geographical distribution of morphotypes on the Antarctic continental shelf.

Some differences of species appear less distinct than in populations of *Cumella emergens*. Especially proportions of body parts might vary within and overlap between populations. Therefore, it is impossible to judge whether different populations belong to one or more species on the basis of morphology.

Molecular studies of five cumacean species of the genus *Leucon* gave a first indication for restricted gene flow between populations of *Leucon antarcticus* from the Ross Sea and the Weddell Sea. The intraspecific genetic distance of these populations is less than the minimal interspecific distance found for the two closest relatives of the genus *Leucon*, which can be definitely assigned to two different species (publication VI). Accordingly, observed differences in the sequences of the 16S rDNA did not prove cryptic speciation, but can only be explained by genetic separation of populations from the Ross Sea and the Weddell Sea for an extended period of time (publication VI).

However, no indication of restricted gene flow within populations of *Leucon intermedius* of the same regions was observed (publication VI); thus the two distant populations of this brooding species from the Ross Sea and the Weddell Sea belong to only one species.

Both species show a bathymetric distribution, which reaches to depth of more than 2000 m (e.g. Mühlenhardt-Siegel 1999; Mühlenhardt-Siegel pers. comm.; publication II), indicating that limited gene flow in *L. antarcticus* is not caused by isolation of different populations in shallow water refuges. A possible explanation could be submergence after the beginning of genetic separation of two (or more) populations. Moreover, the populations of the present study were collected on the continental shelf. Records from

the continental slope (Ledoyer 1993) might represent a third genetically separated population. Morphological differences to the original description (Zimmer 1907), which represent the morphology of the two populations of the present study, point towards the assumption of a third lineage.

Some cumacean species display periodic nocturnal vertical migrations (e.g. Granger 1969; Anger & Valentin 1976; Steams & Dardeau 1990; Macquart-Moulin 1991; Wang & Dauvin 1994). For Antarctic species such behaviour was so far not observed, but possibly vertical migrations during nighttime might occur in some Antarctic species as well. These migrations are restricted to the night after which cumaceans return to the sediment and do not occur regularly during every night as they are connected to moulting, courtship, and reproduction (Anger & Valentin 1976). For this reason it seems not likely that cumaceans are able to drift over vast distances i.e. from one glacial shelter to the other. As demonstrated for crinoids, cyptic speciation might occur within species with drifting stages of limited duration (Wilson et al. 2007). Continuous and substantial gene flow between populations that allows for homogenous populations over long evolutionary timescale, may require drifting stage that last long periods of time, i.e. up to several months in duration as found in the broadcasting caridean shrimp *Nematocarconis lanceopes* (publication III, Thatje et al. 2005).

Yet, female cumaceans are less mobile than male cumaceans, as they lack pleopods for swimming and were observed less often in less extended periods in the water column than males (Anger & Valentin 1976). Therefore, genetic differences detected within the species *Leucon antarcticus* (publication VI) might only result from the 16S rRNA gene, which is a mitochondrial gene with maternal inheritance. Nuclear genes possibly do not exhibit the same degree of genetic differentiation. Thus, future investigations of cryptic speciation in cumaceans should include the analysis of nuclear genes.

Conclusion

- Molecular studies confirm the theory about the coincidence of speciation patterns in Antarctic benthic species and the reproduction mode.
- Though evidence for cryptic speciation in Cumacea is still lacking, genetic diversity emphasises reduced gene flow within the cumacean species *Leucon antarcticus* for an extended period of time. Concluding from the bathymetric distribution, other effects than shallow-water refuges during glacial cycles might be involved.
- The species *Leucon intermedius* indicates that populations of Antarctic brooding organisms can belong to the same species even if these populations occur over vast distances as between the Ross Sea and the Weddell Sea.

3.7 Future perspectives

Antarctic shallow water communities are unique in terms of species diversity, and archaic community structure, as the benthic fauna adapted to the peculiar conditions of i.e. cold and food limitation over long evolutionary timescale. Antarctic benthos is assumed to be especially vulnerable to climate change; understanding the evolutionary history of the Antarctic benthos is thus key to predicting the response capability of these communities to current climate change scenario (Aronson et al. 2007). In the following I summarize areas of future research, which should be key to significantly enhance our understanding of response capability of the Antarctic fauna to past and present climate change:

- Although many studies have been conducted on benthic Antarctic fauna, there is still a considerable need for further work on this field. The effort put into benthic research of the Antarctic Peninsula, the eastern Weddell Sea, the Ross Sea, and the Scotia arc is reasonable (Clarke & Johnston 2003), but even in those areas knowledge remains restricted to few intensively studied areas. For example in the Ross Sea most of the research has been carried out close to land-based facilities in McMurdo Sound or Terra Nova Bay (Waterhouse 2001). For vast areas of the Antarctic we know hardly anything about the composition, diversity, and structure of benthic communities. A complete species inventory is lacking for most areas. However, knowledge about taxonomy and biogeography of species is important to track shifts in the benthic communities, especially in the light of current climate change.
- We know even less about the benthic fauna of the deep sea surrounding the Antarctic continent. Recent studies revealed that diversity of the Southern Ocean is extraordinary high and emphasized evolutionary relationships between the deep sea and the Antarctic shelf faunas (Brandt et al. 2007). Thus, and in order to understand the origin of Antarctic shelf biodiversity and ecology to its full extend, it is necessary to put more effort into the understanding of the surrounding deep-sea fauna.
- Finally, I like to highlight that modern molecular methods should be used in combination with 'traditional' methods of taxonomy and biogeography, as they offer a powerful tool for the understanding of hidden diversity represented by cryptic species and speciation processes. It is likely that in the near future these methods may lead to a completely different view of the diversity and structure of Antarctic benthic communities as indicated by recent research (Bernardi & Goswami 1997; Allcock et al. 1997; Held 2003, Held & Wägele 2005; Raupach & Wägele 2006; Linse et al. 2007; Wilson et al. 2007, publication VI).

PUBLICATIONS

The publications included in this PhD-thesis are listed below and my contribution to each study is given in detail.

Publication I

Rehm P, Thatje S, Arntz WE, Brandt A, Heilmayer O. 2006. Distribution and composition of macrozoobenthic communities along a Victoria-Land Transect (Ross Sea, Antarctica). *Polar Biology*. 29: 782–790.

I developed the scientific idea with the second author and collected macrozoobenthic samples during the 19th Italian Antarctic Expedition onboard RV “Italica”. I also did the statistical analysis and the taxonomic work. The manuscript was mainly written by me and improved in cooperation with the co-authors.

Publication II

Rehm P, Thatje S, Mühlenhardt-Siegel U, Brandt A. 2007. Composition and distribution of the peracarid crustacean fauna along a latitudinal transect off Victoria Land (Ross Sea, Antarctica) with special emphasis on the Cumacea. *Polar Biology*. 30: 871–881.

I developed the concept of this paper together with the second author, collected the material during the 19th Italian Antarctic Expedition onboard RV “Italica”, and did the statistical analysis. I also did most of the taxonomic work. The third author was partially involved in the taxonomic work. The manuscript was mainly written by me and improved in cooperation with all authors.

Publication III

Raupach MJ, Thatje S, **Rehm P**, Misof B. in press. Molecular evidence for circum-Antarctic distribution in two species of broadcasting benthic Caridea (Crustacea: Decapoda). *Marine Ecology Progress Series*.

I collected a major part of the material during the 19th Italian Antarctic Expedition onboard RV “Italica”. The first author did the molecular work and wrote the manuscript, of which the final version was archived considering the suggestions by all authors.

Publication IV

Rehm P. under review. Description of a new subspecies *Diastylis enigmatica rossensis* (Crustacea: Peracarida: Cumacea) from the Ross Sea, Antarctica. *Helgoland Marine Research*.

Sampling, identification of the material, and scientific drawing was done by me, as well as the interpretation of data and manuscript writing.

Publication V

Rehm P, Heard R. under review. *Leucon* (*Crymoleucon*) *rossi*, a new species (Crustacea: Cumacea: Leuconidae), from the shelf waters of the Ross Sea (Antarctica), with a key to the genus *Leucon* south of 60°S. *Scientia Marina*.

I did the sampling, identification, and statistical analysis. I did most of the scientific drawings. The second author mainly created the key to the species described. The manuscript was written by me and improved in cooperation with the second author.

Publication VI

Rehm P, Leese F, Raupach M, Thatje S, Held C. Phylogenetic relationship within Cumacea (Crustacea, Peracarida) and genetic variability of two Antarctic species of the family Leuconidae. *Antarctic Science*.

The scientific idea was developed by the fourth author and me and was improved with the second and last author. Together with the second author, I did most of the genetic work in the laboratory. Additional laboratory work was carried out by the third author. The manuscript was written mainly by the last author and me and improved in collaboration with all authors.

Further Publications written during working on the PhD thesis

Rehm P, Rachor E. 2007. Benthic macrofauna communities of the submersed Pleistocene Elbe valley in the southern North Sea. *Helgoland Marine Research*. 61: 127–134.

The scientific idea was developed by the second author. I did the sample and statistical analyses. Sampling, improvement of the concept, and writing of the manuscript was done in cooperation with the second author.

Publication I

Polar Biol (2006) 29: 782–790
DOI 10.1007/s00300-006-0115-8

ORIGINAL PAPER

Peter Rehm · Sven Thatje · Wolf E. Arntz
Angelika Brandt · Olaf Heilmayer

Distribution and composition of macrozoobenthic communities along a Victoria-Land Transect (Ross Sea, Antarctica)

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Abstract The Victoria-Land Transect project onboard the Italian research vessel “*Italica*” in February 2004, was a large-scale attempt to obtain benthic samples of smaller macrozoobenthic specimens systematically along a latitudinal and a depth transect along the Victoria-Land coast. Data presented from this survey are based on Rauschert dredge samples, which were taken at four areas at depth ranging from 84 to 515 m. A cluster analysis based on relative numbers of abundance was performed and demonstrated a change in community structure depending on the location along the latitudinal transect. A change in community structure with depth was not recorded. Dominant taxa of the Ross Sea fauna along the Victoria-Land coast were the Arthropoda (65.7%), followed by Annelida (20.7%), Mollusca (9.6%) and Echinodermata (2.5%). Total number of abundance decreased with depth with an exception at Cape Russell, whereas a trend in biomass was not documented. Abundance and biomass proportions of major taxa changed gradually along the latitudinal transect.

Introduction

Numerous studies were performed to describe the benthos of high Antarctic shelf seas (e.g. Dearborn 1967;

Dayton et al. 1970; Dayton and Oliver 1977; Dell 1990; Galerón et al. 1992; Gerdes et al. 1992; Arntz et al. 1994; Starmans et al. 1999), and one of the most striking characteristics, recorded of the benthos of the Antarctic shelf, is its richness in biomass and diversity (e.g. Hedgpeth 1969; Dell 1972; White 1984; Picken 1985; Dayton et al. 1994; Brey and Gerdes 1997). Particularly, the macrozoobenthic community structure of the south-eastern Weddell Sea shelf is rather well known. Thus, three major benthic communities can be found in this area, which are characterized by suspension feeders, such as Porifera and Bryozoa, or mainly Bryozoa, or detritus feeders such as Holothurida and Polychaeta (Voß 1988; Gerdes et al. 1992; Gutt and Starmans 1998).

Most of the research characterizing habitats of the Ross Sea has been done around McMurdo Sound (Waterhouse 2001). Information about macrozoobenthic communities along the Victoria-Land coast (Ross Sea) is limited to only few restricted shallow water areas as Terra Nova Bay. Often previous sampling was centred on certain benthic groups such as Amphipoda, Mollusca, Polychaeta, and Porifera (e.g. Dayton 1972; Stockton 1984; Gambi et al. 1997; Knox and Cameron 1998; Cattaneo-Vietti et al. 1999; Cantone et al. 2000).

A first systematic classification of benthic communities of the southern Ross Sea was described from material obtained during the Trans-Antarctic Expedition from 1955–1958 and material collected by the New Zealand Oceanographic Institute. Bullivant (1967b) described 3 major benthic assemblages, which were linked to the substratum. The Deep Shelf Mixed Assemblage is characterized by Polychaeta, Bryozoa, Gorgonaria, and Echinodermata. Important elements of the Deep Shelf Mud Bottom Assemblage are Polychaeta and Echinodermata, whereas in the Pennell Bank Assemblage Bryozoa, Gorgonaria, Porifera, Tunicata, Cnidaria, and Echinodermata are common (Bullivant 1967b).

During the ROSSMIZE (Ross Sea Marginal Ice Zone Ecology) project carried out from RV “*Italica*” in 1994 and 1995, several macrobenthic samples were taken

P. Rehm (✉) · W. E. Arntz · O. Heilmayer
Marine Animal Ecology, Alfred Wegener Institute for Polar and Marine Research (AWI), Am Alten Hafen 26,
27568 Bremerhaven, Germany
E-mail: prehm@awi-bremerhaven.de

S. Thatje
National Oceanography Centre,
Southampton, School of Ocean and Earth Science,
University of Southampton, European Way,
SO14 3ZH Southampton, UK

A. Brandt
Zoologisches Institut und Museum, Universität Hamburg,
Martin-Luther-King Platz 3, 20146 Hamburg, Germany

using a box-corer. While the sample areas were distributed in shallower waters along the Victoria-Land coast, only three stations in depths of 450, 580, and 810 m were sampled (Gambi and Bussotti 1999).

The cruise with RV “Italica”, which was carried out in cooperation with the New Zealand RV “Tangaroa”, was a large scale attempt to take samples systematically along a latitudinal and depth gradient. As there is little known about the ecosystem of the northern Victoria-Land coast, both the Italian research programme as well as the New Zealand Biodiversity Strategy programme “BioRoss” will essentially enhance our knowledge about biodiversity, structure, and composition of macrozoobenthic communities in the Ross Sea. The results shown in this paper represent some of the first analysed datasets from the study area.

Materials and methods

During the 19th Antarctic expedition of RV “Italica” to the Ross Sea in austral summer 2004, 18 dredge samples were taken along a latitudinal transect between Cape Adare and Terra Nova Bay. Sampling was performed in four areas: Cape Adare, Cape Hallett,

Coulman Island, and Cape Russell (Fig. 1; Table 1). As the sample station at Santa Maria Novella (Terra Nova Bay) is located nearby the Cape Russell area it is treated as part of this area and pooled for further analysis. Samples of area Cape Hallett were obtained from two depths transects inside and outside Cape Hallett Bay. At each area a slightly modified Rauschert dredge (Fig. 2, cf Lörz et al. 1999) with a mesh size of 500 μm and an opening of 0.5 m, was used to take samples from water depth between 84 and 515 m. The dredge was trawled over the ground at a mean velocity of 1 knot. Haul lengths varied from 59 to 575 m (Table 1). As this type of dredge was specially designed to obtain small macrobenthic animals like peracarid crustaceans, an inner net with a mesh size of 1 cm was used to hold back larger objects to prevent the small dredge from being blocked too quickly. The material was sieved on a 500 μm mesh, preserved in 90% pre-cooled ethanol, and kept in -25°C for later DNA extraction.

In the laboratory, samples were sorted into major taxonomic groups using a stereomicroscope. Biomass is given as ash free dry mass (AFDM) calculated from wet mass (WM) using conversion factors presented by Brey (2001).

Fig. 1 Victoria-Land coast (Ross Sea, Antarctica); sample areas: Cape Adare, Cape Hallett, Coulman Island, and Cape Russell, position of sampling marked with dots

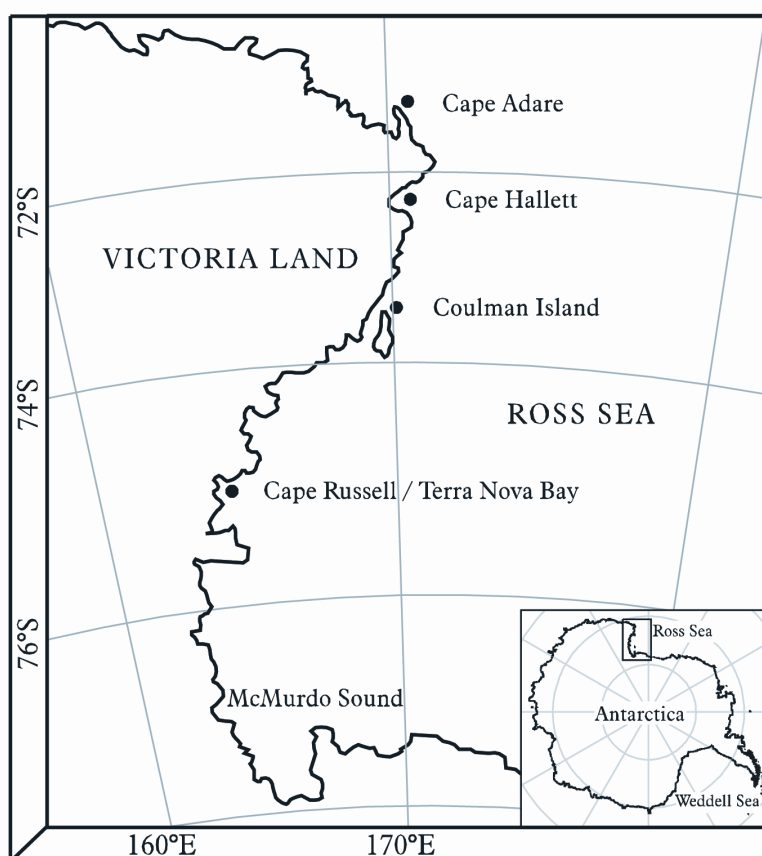
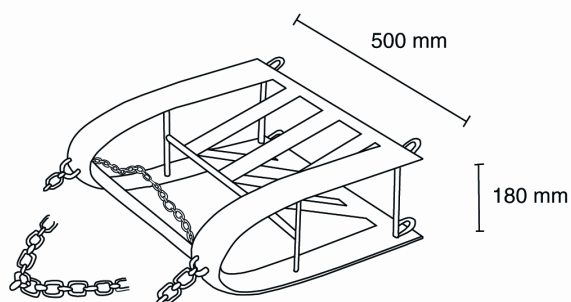


Table 1 Rauschert dredge stations of the Victoria-Land Transect Cruise, Ross Sea

Station north to south	Date	Position		Depth [m]	Haul length [m]	Sediment
		latitude [S]	longitude [E]			
Cape Adare						
A1	15/02/2004	71°15.5′	170°41.9′	515	358	sand with few pebbles and stones
A2	14/02/2004	71°17.3′	170°39.2′	421	298	sand and gravel
A3	14/02/2004	71°18.7′	170°29.2′	305	257	sand
A4	14/02/2004	71°18.4′	170°28.9′	230	376	sand and pebbles
A5	15/02/2004	71°18.7′	170°25.5′	119	59	sand with pebbles and stones
Cape Hallett						
H out 1	09/02/2004	72°15.7″	170°24.8′	458	375	mud and pebbles
H out 2	11/02/2004	72°17.5″	170°29.4′	353	375	sandy mud and stones
H out 4	12/02/2004	72°18.5″	170°26.8′	235	194	sand
H in 2	10/02/2004	72°16.9″	170°12.2′	391	186	coarse sand and small gravel
H in 3	16/02/2004	72°17.0″	170°13.1′	316	194	muddy sand with stones
H in 4	16/02/2004	72°17.1″	170°14.0′	196	169	mud and sand
H in 5	16/02/2004	72°17.2″	170°17.9′	84	113	small gravel
Coulman Island						
C1	18/02/2004	73°24.5′	170°23.2′	474	375	mud and small gravel
C2	18/02/2004	73°22.7′	170°06.9′	410	153	mud and pebbles
Cape Russell						
SMN	20/02/2004	74°43.2′	164°13.1′	366	192	sand with gravel and stones
R2	21/02/2004	74°49.0′	164°18.1′	364	575	fine sand
R3	20/02/2004	74°49.3′	164°11.5′	330	565	rock, sand, mud and pebbles
R4	20/02/2004	74°49.3′	164°11.5′	208	97	rock, mud and large stones

**Fig. 2** Rauschert dredge, changed after Nickel (2003)

A cluster analysis was carried out with the programme Primer (v. 5.1.2) of the Plymouth Marine Laboratory (Clarke and Goreley 2000) using Bray-

Curtis-Index (Bray and Curtis 1957) and group average method. Because of the semi-quantitative nature of data from a dredge, relative numbers of abundance were used to calculate the analysis. As proper transformation for relative data, the function of arc sin was applied.

Results

A total of 27 taxonomic groups were identified from the area under investigation. The number of taxa varied between 14 and 27 with stations. In terms of abundance and biomass, the macrozoobenthic community of the Ross Sea shelf along the Victoria-Land coast collected with the Rauschert dredge was dominated by Arthropoda, followed by Annelida, Mollusca, and Echinodermata (Fig. 3). The Annelida were dominated by Polychaeta (99.7% of total annelid abundance and

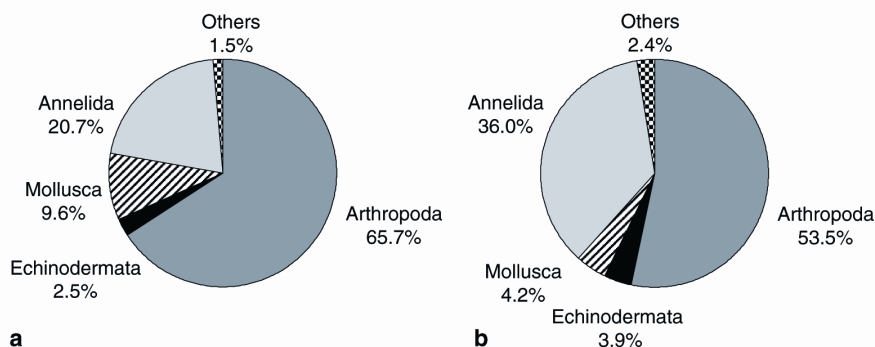
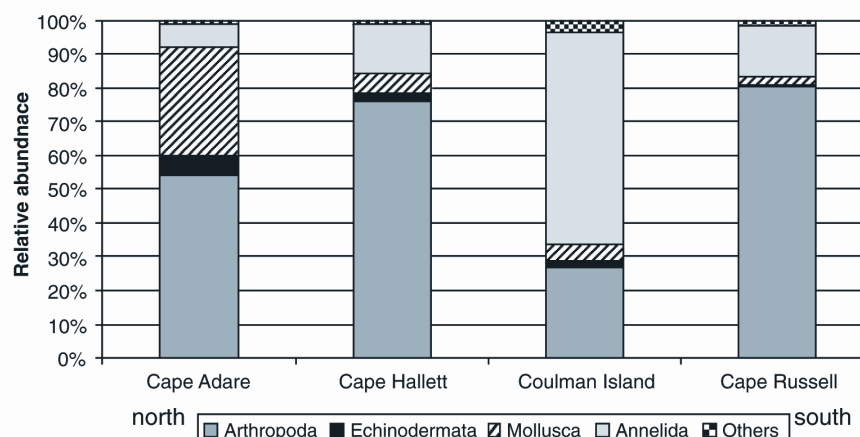
Fig. 3 Relative composition of major taxa from the Antarctic Ross Sea shelf off the Victoria-Land coast; **a** abundance, **b** biomass (AFDM)

Fig. 4 Relative abundance of major macrozoobenthic taxa



100% of total annelid biomass); only few specimens of Hirudinea were found. Most Arthropoda belonged to the Crustacea (95.3% of total abundance and 95.9% of total biomass). Further arthropod taxa, other than Crustacea, belonged to Pycnogonida and Acari.

Sampling areas of Coulman Island and Cape Adare differed in the distribution pattern of major benthic taxa

when compared with the other areas. Most abundant taxon of the Coulman Island area was Annelida (62.8%), whereas the community of Cape Adare is characterized by an increased proportion of Mollusca (32.1%), which is attributed to an increase in Gastropoda (Fig. 4; Table 2) at stations A3 and A4 (Fig. 5). Again, in terms of biomass Annelida (58.9%) showed an

Table 2 Relative abundance (%) of macrozoobenthic taxa from investigated sub-areas of the Antarctic Ross Sea shelf

	Cape Adare	Cape Hallett	Coulman Island	Cape Russell	Ross Sea total
Arthropoda	53.80	76.23	26.56	80.04	65.75
Acari	3.33	0.65	0.00	0.93	0.98
Pycnogonida	1.40	2.75	0.91	1.33	2.13
Amphipoda	31.13	50.19	7.35	27.13	38.64
Cumacea	0.18	2.12	1.51	29.07	4.34
Decapoda	0.00	0.01	0.01	0.05	0.01
Isopoda	12.47	16.77	8.34	14.31	14.61
Mysidacea	0.21	0.02	0.03	0.66	0.11
Tanaidacea	5.02	3.61	8.49	6.49	4.83
Unidentified	0.06	0.11	0.00	0.08	0.08
Echinodermata	6.11	1.99	2.03	0.78	2.50
Asteroidea	0.19	0.09	0.07	0.05	0.10
Crinoidea	0.05	0.03	0.03	0.00	0.03
Echinoidea	0.05	0.03	0.04	0.04	0.04
Holothuroidea	1.32	0.04	0.21	0.13	0.27
Ophiuroidea	4.49	1.80	1.67	0.56	2.06
Mollusca	32.13	6.13	5.12	2.69	9.56
Bivalvia	1.19	0.89	3.31	0.58	1.32
Cephalopoda	0.00	0.00	0.00	< 0.01	< 0.01
Gastropoda	30.43	2.90	0.95	1.29	6.59
Polyplacophora	0.00	0.02	0.00	< 0.01	0.01
Scaphopoda	0.00	0.01	0.55	< 0.01	0.09
Aplacophora	0.52	2.23	0.31	0.80	1.54
Annelida	6.87	14.58	62.80	14.64	20.69
Hirudinea	0.01	0.09	0.03	0.00	0.06
Polychaeta	6.86	14.49	62.77	13.64	20.63
Others	1.09	1.07	3.99	1.85	1.50
Brachiopoda	0.06	0.05	0.20	0.03	0.07
Cnidaria	0.04	0.01	0.00	0.00	0.01
Nemertini	0.72	0.74	1.92	1.08	0.95
Plathelminthes	0.04	0.14	0.00	0.06	0.10
Sipunculida	0.23	0.12	1.27	0.68	0.36
Tunicata	< 0.01	0.01	0.00	0.00	< 0.01
Mean abundance [ind. m ⁻²]	26	74	65	20	26

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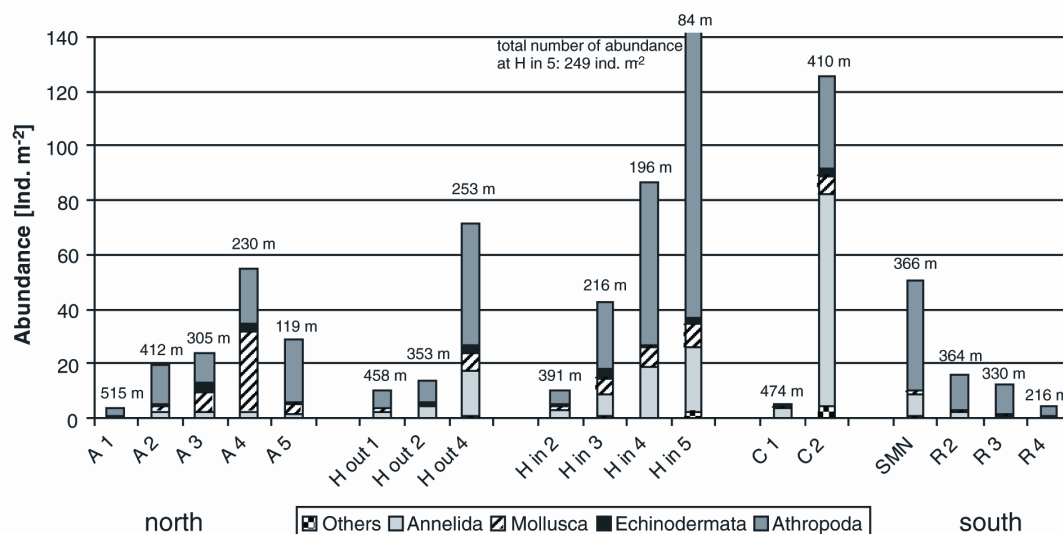


Fig. 5 Abundance of major taxa per Station (areas listed from north to south); A (Cape Adare), H out (Cape Hallett outer transect) H in (Cape Hallett inner transect), C (Coulman Island), SMN (Santa Maria Novella), R (Cape Russell)

exceptionally high portion at Coulman Island, but the biomass of Mollusca (4.6%) was not increased at Cape Adare (Fig. 6; Table 3).

Taking into account an increased proportion of Annelida at Coulman Island, a trend of decreasing portions of abundance with latitude was found for Echinodermata, whereas portions of abundance of the Annelida showed the lowest numbers at the northern area Cape Adare. The portion of Arthropoda abundance increased, but biomass decreased with latitude (Tables 2, 3).

Cape Russell showed the lowest mean abundances (21 ind. m^{-2}), whereas at Cape Hallett mean abundance was highest (75 ind. m^{-2} , Table 4). Mean biomass value was lowest at Cape Russell and varied between 0.018 gm^{-2} (AFDM) (Cape Russell) and 0.033 gm^{-2} (AFDM) (Cape Hallett), (see Table 4).

The samples reflected a tendency of decreasing abundance with increasing depth (Table 5), with the only exception at Cape Russell where abundance increased with depth (Fig. 5). Biomass distribution displayed the same tendency, but both abundance and biomass numbers increased in the deepest samples from 400 to 515 m (Table 5).

The cluster analysis showed a separation of stations into six clusters (Fig. 7). Cluster C (similarity of about 40%) contained the stations off Coulman Island, cluster A₂ (similarity of about 50%) combined stations A3 and A4. Again, stations off Coulman Island and stations A3 and A4 off Cape Adare differed from the other stations. Cluster R (similarity of about 60%) contained the stations of Cape Russell with one exception: station R4 is located in the cluster H of Cape Hallett. The remaining clusters A₁ and H are separated at about 65% similarity

Fig. 6 Relative biomass (AFDM) of major macrozoobenthic taxa

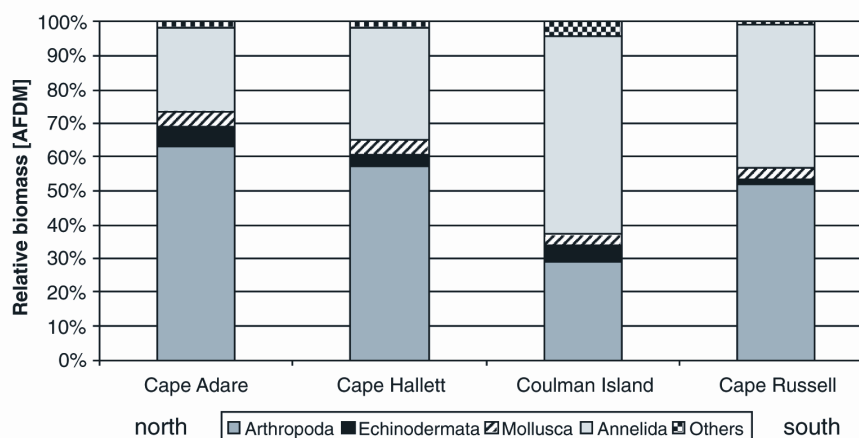


Table 3 Relative biomass (AFDM %) of macrozoobenthic taxa from investigated sub-areas of the Antarctic Ross Sea shelf

	Cape Adare	Cape Hallett	Coulman Island	Cape Russell	Ross Sea total
Arthropoda	63.34	57.08	29.13	51.85	53.76
Acari	0.25	0.03	0.00	< 0.01	0.08
Pycnogonida	1.89	6.23	1.24	1.01	3.75
Amphipoda	56.22	43.88	21.91	24.61	41.16
Cumacea	1.22	1.47	2.30	10.82	2.72
Decapoda	0.00	0.41	0.03	0.66	0.28
Isopoda	3.40	4.72	3.20	14.22	5.38
Mysidacea	0.03	0.00	0.01	0.00	0.01
Tanaidacea	0.32	0.29	0.46	0.50	0.35
Unidentified	< 0.01	0.05	0.00	0.03	0.03
Echinodermata	5.69	3.39	4.79	1.47	3.92
Asteroidea	0.68	0.59	0.29	0.10	0.51
Crinoidea	0.03	0.01	0.22	0.00	0.05
Echinoidea	0.32	0.17	0.07	0.10	0.18
Holothuroidea	0.46	0.70	2.60	1.01	0.97
Ophiuroidea	4.19	1.91	1.60	0.27	2.22
Mollusca	4.59	4.57	3.23	3.51	4.24
Bivalvia	0.37	0.53	1.99	0.54	0.71
Cephalopoda	0.00	0.00	0.00	2.26	0.29
Gastropoda	3.99	3.43	1.02	0.51	2.83
Polyplacophora	0.00	0.02	0.00	0.07	0.02
Scaphopoda	0.00	0.02	0.13	< 0.01	0.03
Aplacophora	0.22	0.57	0.10	0.12	0.36
Annelida	24.88	33.24	58.90	42.15	36.17
Hirudinea	0.00	0.01	0.02	0.00	0.01
Polychaeta	24.88	33.23	58.88	42.15	36.17
Others	1.50	1.73	3.95	1.02	1.92
Brachiopoda	0.33	0.08	0.43	0.13	0.20
Cnidaria	0.06	0.01	0.00	0.00	0.02
Nemertini	0.98	1.18	3.30	0.35	1.34
Plathelminthes	0.05	0.16	0.00	< 0.01	0.09
Sipunculida	0.08	0.15	0.22	0.53	0.19
Tunicata	< 0.00	0.14	0.00	0.00	0.07
Mean biomass [AFDM gm ⁻²]	0.021	0.034	0.032	0.018	0.044

and comprise the stations of Cape Adare and Cape Hallett respectively. Merely station Hin5 is located within Cluster A₁. As a general attribute, with respect to the exceptions mentioned above, stations are grouped according to their sample area.

Most characteristic for cluster C (Coulman Island) is the very high portion of Polychaeta (Table 3) and the lowest portion of Amphipoda and Isopoda. Cluster A₂ as part of the area Cape Adare is characterized by reduced portions of Amphipoda, Tanaidacea, and Polychaeta, whereas Holothuroidea, Ophiuroidea, and especially Gastropoda show increased portions. Differences in between the remaining clusters are less distinct.

Cluster R showed the highest portions of Cumacea and low portions of Polychaeta. Within Cluster A₁ Amphipoda were increased, whereas Isopoda and Cumacea were reduced. On the other hand, Tanaidacea showed a higher portion than in the other clusters.

Discussion

Selectivity of Rauschert dredge

A Rauschert dredge was used for sampling during the cruise with RV “Italica”, which is known for its

Table 4 Benthos data of the investigated sub-areas of the Antarctic Ross Sea shelf

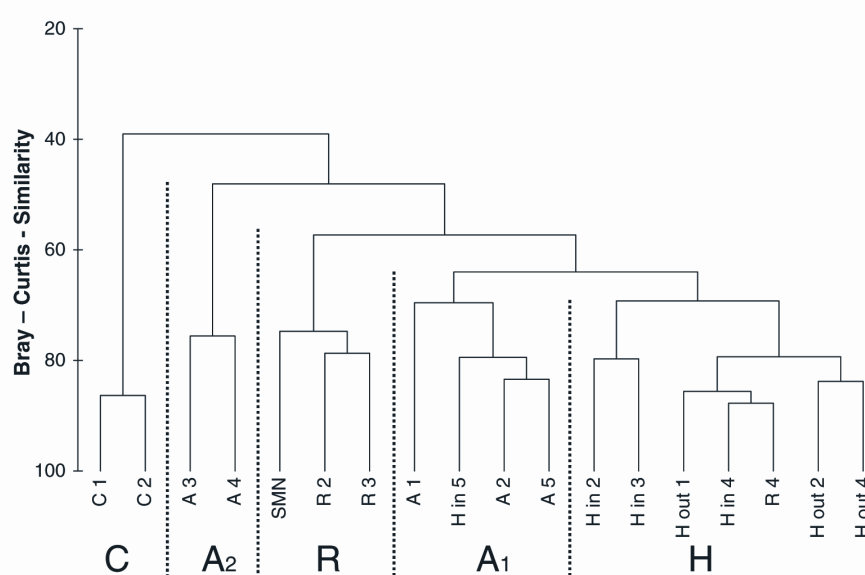
	Cape Adare	Cape Hallett	Coulman Island	Cape Russell
No. of stations	5	7	2	4
Depth range [m]	119–515	84–460	410–474	208–366
Mean abundance [ind. m ⁻²]	26 ± 17	75 ± 91	65 ± 60	21 ± 18
Min-max abundance [ind. m ⁻²]	3–55	10–287	5–125	5–51
Mean biomass [AFDM gm ⁻²]	0.021 ± 0.008	0.033 ± 0.040	0.032 ± 0.038	0.018 ± 0.012
Min-max biomass [AFDM gm ⁻²]	0.010–0.031	0.004–0.108	0.005–0.058	0.011–0.031
Mean biomass [WM gm ⁻²]	0.199 ± 0.232	0.128 ± 0.047	0.178 ± 0.217	0.090 ± 0.057
Min-max biomass [WM gm ⁻²]	0.068–0.177	0.023–0.631	0.024–0.332	0.052–0.156

Table 5 Depth distribution of macrozoobenthic abundance and biomass of the Antarctic Ross Sea shelf

Depth	No. of stations	Mean abundance [ind. m ⁻²]	Min-max abundance [ind. m ⁻²]	Mean biomass [AFDM m ⁻²]	Min-max biomass [AFDM m ⁻²]	Mean biomass [WM m ⁻²]	Min-max biomass [WM m ⁻²]
84–200 m	3	134	29–287	0.043	0.005–0.108	0.124	0.011–0.315
201–300 m	3	44	5–72	0.033	0.026–0.041	0.103	0.082–0.129
301–400 m	7	21	10–51	0.015	0.006–0.031	0.041	0.016–0.078
401–515 m	5	33	3–125	0.026	0.005–0.058	0.075	0.012–0.166

effectiveness of catching smaller macrozoobenthic animals (especially peracarid crustaceans) compared to other sampling gear such as a Agassiz trawl (Lörz et al. 1999). Previous surveys to the Ross Sea were restricted to certain areas of the Victoria-Land coast or used wide-meshed nets for dragged gear only (e.g. Bullivant 1967a; Dayton et al. 1974; Gambi et al. 1997; Cattaneo-Vietti et al. 2000). For that reason only a minor part of the species from the Ross Sea fauna is recorded so far. The use of the Rauschert dredge substantially increased the numbers of recorded cumacean species from the Ross Sea known until now (to 290%) and we expect to find similar situations for other peracarid crustaceans, which are known as a particularly speciose group of the Southern Ocean (DeBroyer and Jazdzewski 1996; Brandt 1999). One disadvantage of the dredge is its semi-quantitative sampling, making comparison with quantitative sampling gear, such as grabs, more difficult (Eleftheriou and Holme 1984; Rumohr 1990). Nevertheless, dragged gear qualifies for collecting samples from a vast surface compared to qualitative sampling gear, which lead to the deployment of dredges and trawls in preliminary studies to give primary insight into distribution and community structures (Arntz et al. 1996; Arnaud et al. 1998). Dragged gears are, in addition, particularly valuable to

assess the species diversity of an area. The Rauschert dredge is equipped with a net to hold back all objects larger than 1 cm, which otherwise would quickly block the net. This selective nature of the dredge explains differences to other studies carried out with other dredges, like Agassiz trawls. For that reason, our samples did contain only very few of Porifera, often these were only fractions; but we know from using other methods such as the SplashCam that Porifera are an important element of the communities in question. Porifera are typical of high Antarctic shelf communities and contribute an important amount, up to 47%, to biomass in the Weddell Sea (Gerdes et al. 1992; Brey and Gerdes 1999). Further taxa, which were not recorded sufficiently, were Ascidiacea, Bryozoa, and Cnidaria these taxa are important in terms of biomass as well (Bullivant 1967b; Dayton et al. 1974, 1994; Voß 1988; Brey and Gerdes 1999), thus a comparison between the two areas has to be treated very carefully, considering different sampling gear. Ascidiacea, Bryozoa, and Porifera were excluded from this quantitative analysis, because of the irregular catches. As a consequence of the method, absolute numbers in biomass were lower than what we can expect for this area by comparison with other studies from the Weddell Sea (0.124–1,640 g wet weight) (Gerdes et al. 1992) and the

Fig. 7 Station dendrogram from the Cluster analysis; Bray-Curtis-Index, group average method

sub-Antarctic Magellan region ($0.01\text{--}22.88\text{ gC m}^{-2}$) (Thatje and Mutschke 1999).

Community structure

The investigation of the macrozoobenthic community along a latitudinal transect was one of the main aims of the Victoria-Land Transect Cruise (Ramorino 2004). We were not able to identify all taxa to species level and thus in this paper we do only present preliminary data for the major 27 groups, which enable us to present an overall assessment of community structure. Species-level identification will be done by specialists for each taxonomic group; a future work that might take years to be completed. Data from this survey showed a gradual change in community composition of major macrozoobenthic taxa along a latitudinal cline. According to the cluster analyses, the structure of the community depended on the sample area.

Special situations were found for the community of Coulman Island and two of the stations (A3, A4) off Cape Adare. In the latter, the community was dominated by Polychaeta (62 %), and Gastropoda (47 %), respectively, instead of Arthropoda. The sediment of Cape Adare showed only slight variation and in contrast to abundance, biomass distribution of the deviating stations corresponded more with the remaining stations of the area. Thrush et al. (2004) recorded iceberg disturbance with a SplashCam for Cape Hallett and Cape Russell, and concluded that the iceberg disturbance regime was an important factor in determining community structure. Therefore the difference of the deviating stations appeared to be caused by iceberg disturbance. Unfortunately only two samples were taken at Coulman Island, thus deviation of community structure of this area might result from a disturbed area as well. However conditions at Coulman Island differed to that of the other areas, since the sediment mainly consisted of mud instead of sandy sediments, what could be an indication for a distinct community at Coulman Island. Furthermore, Bullivant (1967b) described the "Deep Shelf Mud Bottom Assemblage" dominated by polychaetes, which was found close to Coulman Island. In their quantitative analysis of the Ross Sea benthos in 1994 and 1995, Gambi and Bussotti (1999) excluded the very few colonial organisms (sponges, cnidarians, and bryozoans), which were found in the samples. From there a comparison of the two studies should be simplified, still the different gear used has to be taken into account. As the box-corer is predominantly samples infauna, one should expect more infaunal organisms in the samples from 1994 and 1995. During 1994 and 1995 the stations with muddy sediment were dominated by Polychaeta (58–78%), whereas the station with sandy sediment was dominated by Crustacea (mainly Amphipoda) (50%). This reflects similar differences found between the stations with different sediment types of this study.

The contrasting trends found in the change of proportion of arthropod abundance and biomass can be explained with changing proportions of arthropod taxa. The portion of Isopoda and Cumacea increases with latitude, whereas the portion of Amphipoda is low at the southernmost sample area Cape Russell. Amphipoda tend to be larger than Isopoda and Cumacea, and thus the biomass of Amphipoda is higher than that of Isopoda and Cumacea, hence a decreasing proportion of biomass despite an increasing portion of abundance of Arthropoda with latitude.

A tendency towards increasing density with decreasing latitude as it was found further to the south at the west coast of McMurdo Sound (Dayton and Oliver 1977) was not confirmed for the sample areas and therefore might be limited to McMurdo Sound. This result corresponds with the assumption that no distinct latitudinal gradient exists in organism density and biomass from the Magellan region to the high Antarctic (Gerdes and Montiel 1999; Piepenburg et al. 2002). The pattern of decreasing abundance coincided with decreasing depth, as known from several regions, such as the high Antarctic Weddell Sea and the sub-Antarctic Magellan Region (Brey and Gerdes 1998; Thatje and Mutschke 1999; Piepenburg et al. 2002).

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ORIGINAL PAPER

Composition and distribution of the peracarid crustacean fauna along a latitudinal transect off Victoria Land (Ross Sea, Antarctica) with special emphasis on the Cumacea

Peter Rehm · Sven Thatje · Ute Mühlenhardt-Siegel ·
Angelika Brandt

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Abstract The following study was the first to describe composition and structure of the peracarid fauna systematically along a latitudinal transect off Victoria Land (Ross Sea, Antarctica). During the 19th Antarctic expedition of the Italian research vessel “Italica” in February 2004, macrobenthic samples were collected by means of a Rauschert dredge with a mesh size of 500 µm at depths between 85 and 515 m. The composition of peracarid crustaceans, especially Cumacea was investigated. Peracarida contributed 63% to the total abundance of the fauna. The peracarid samples were dominated by amphipods (66%), whereas cumaceans were represented with 7%. Previously, only 13 cumacean species were known, now the number of species recorded from the Ross Sea increased to 34. Thus, the cumacean fauna of the Ross Sea, which was regarded as the poorest in terms of species richness, has to be considered as equivalent to that of other high Antarctic areas. Most important cumacean families concerning abundance and species richness were Leuconidae, Nannastacidae, and Diastylidae. Cumacean diversity

was lowest at the northernmost area (Cape Adare). At the area off Coulman Island, which is characterized by muddy sediment, diversity was highest. Diversity and species number were higher at the deeper stations and abundance increased with latitude. A review of the bathymetric distribution of the Cumacea from the Ross Sea reveals that most species distribute across the Antarctic continental shelf and slope. So far, only few deep-sea records justify the assumption of a shallow-water–deep-sea relationship in some species of Ross Sea Cumacea, which is discussed from an evolutionary point of view.

Keywords Diversity · Cumacea · Benthos · Antarctica · Ross Sea

Introduction

Five of the seven peracarid orders are known to occur in Antarctic waters. Amphipoda are most diverse with 821 species in the Southern Ocean (De Broyer and Jazdzewski 1996), while 365 species of Isopoda are known for this area (Brandt 1999). Cumacea are represented with 66 species (87 including the Magellan area, Mühlenhardt-Siegel 1999), whereas Mysidacea and Tanaidacea are represented with 59 and 36 species, respectively (Brandt et al. 1998; Schmidt and Brandt 2001).

First research on Antarctic cumaceans started with the descriptions of Zimmer (1902, 1907a, b, 1908, 1909, 1913) and Calman (1907, 1917, 1918). Further work followed (e.g., Hale 1937; Gamô 1959, 1987; Lomakina 1968; Ledoyer 1973, 1977; Petrescu (1991); Petrescu and Wittman 2003), and a total of 58 species were mentioned by Ledoyer (1993). Mühlenhardt-Siegel

P. Rehm (✉)
Alfred Wegener Institute for Polar
and Marine Research (AWI), Marine Animal Ecology,
Am Alten Hafen 26, 27568 Bremerhaven, Germany
e-mail: peter.rehm@awi.de

S. Thatje
National Oceanography Centre, Southampton,
School of Ocean and Earth Science,
University of Southampton,
European Way, Southampton, SO14 3ZH, UK

U. Mühlenhardt-Siegel · A. Brandt
Zoologisches Institut und Museum, Universität Hamburg,
Martin-Luther-King Platz 3, 20146 Hamburg, Germany

(1999) summarized 66 cumacean species known from Antarctica. During the last years ten further species, such as *Gynodistylis jazdzewskii* (Błażewicz and Heard 1999) from the Ross Sea, were described.

In “The fauna of the Ross Sea” (Jones 1971) merely ten cumacean species were mentioned; only two additional species were recorded during the last decades (Roccatagliata and Heard 1992; Błażewicz and Heard 1999). The species *Makrokyllindrus baceskei* (Lomakina 1968) was reported from 2,937 m at the Balleny Islands only, but is counted as a Ross Sea species in this study. Thus prior to the present study, the number of cumacean species known from the Ross Sea was 13. Approximately 30 cumacean species are known from other high Antarctic regions (Mühlenhardt-Siegel 1999; Corbera 2000). The great difference in species numbers known from different high Antarctic localities can be attributed to the little work, which has so far been accomplished on the deeper benthic environment of the northern Victoria-Land coast and the eastern Ross Sea (Waterhouse 2001) as well as the gear used for sampling. Conventional gear, such as dredges, trawls, and corers, most likely does not sample the cumacean fauna adequately (Jones and Sanders 1972). During previous expeditions to the Ross Sea, predominantly nets with wide mesh sizes were used for sampling. Cumaceans are small peracarids ranging between 0.1 and 3.5 cm in size (mostly less than 1 cm). Therefore, most of the animals will be washed out of nets with mesh sizes of 1 cm and more.

The present study deals with the distribution of the peracarid orders along a latitudinal and depth transect and the faunistic composition of the cumaceans from the waters of the northern Victoria-Land coast. A Rauschert dredge with a mesh size of 500 μm was used to gain data on abundance, diversity, and bathymetric distribution of the cumacean fauna.

Materials and methods

During the 19th Antarctic expedition with RV “Italia” in February 2004, 18 samples were taken along a latitudinal transect in the four areas of Victoria-Land coast Cape Adare, Cape Hallett, Coulman Island, and Cape Russell (Fig. 1; Table 1). Station Santa Maria Novella (Terra Nova Bay) and the stations off Cape Russell were pooled for further analysis since these stations were sampled in the same region. A depth gradient was sampled at each area: samples of area Cape Hallett were obtained from two depths transects inside and outside Cape Hallett Bay. Owing to severe ice conditions off Coulman Island, only two samples were taken in this area.

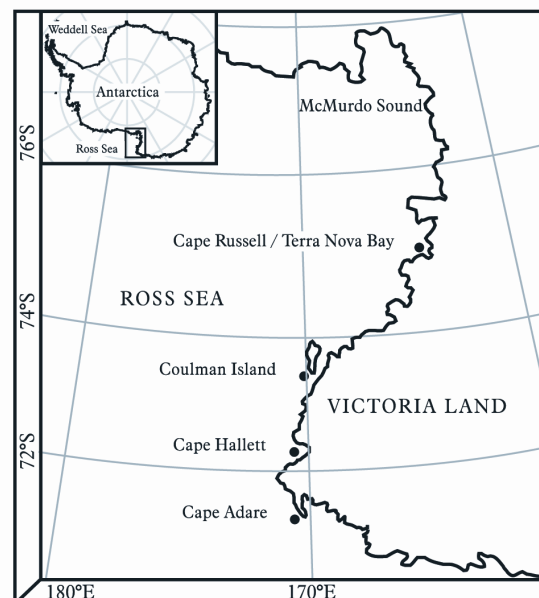


Fig. 1 Victoria-Land coast (Ross Sea, Antarctica); sample areas: Cape Adare, Cape Hallett, Coulman Island, and Cape Russell

A modified Rauschert dredge (Lörz et al. 1999) with a mesh size of 500 μm and an opening of 0.5 m was used to take samples from water depth between 84 and 515 m. A second inner net with a mesh size of 1 cm was used to keep larger objects out of the 500 μm net. The dredge was hauled over the ground at a mean velocity of one knot. Haul lengths varied from 59 to 575 m. For comparison between stations, samples were standardized for 1,000 m^2 hauls. Before the material was preserved in 90% precooled ethanol and kept in -25°C for later DNA extraction, it was sieved on a 500 μm mesh. Afterwards in the laboratory a stereomicroscope was used to sort the samples into major taxonomic groups. Cumacea were identified to species level.

We applied univariate measures of diversity, the Shannon-Wiener index (H') (log base) (Shannon and Weaver 1949), and evenness (J') (Pielou 1966). A Multidimensional Scaling (MDS) analysis was carried out with the software package Primer (v. 5.1.2) of the Plymouth Marine Laboratory using Bray-Curtis Index to analyse the distribution of cumacean species assemblages in the study area. Because of the semi-quantitative nature of data derived from the dredge samples, arc-sin transformed relative abundances were used for analysis.

Due to technical problems during processing, a sample taken at station R4 was only analysed qualitatively. Additional material collected onboard of the New Zealand RV “Tangaroa” was analysed in order to

Table 1 Rauschert dredge stations of the Victoria-Land transect cruise (Ross Sea, Antarctica) taken from onboard RV “Italica”

Station north to south	Date	Position		Depth (m)	Haul length (m)	Sediment
		latitude (S)	longitude (E)			
Cape Adare						
A1	15/02/2004	71°15.5'	170°41.9'	515	358	Sand with few pebbles and stones
A2	14/02/2004	71°17.3'	170°39.2'	421	298	Sand and gravel
A3	14/02/2004	71°18.7'	170°29.2'	305	257	Sand
A4	14/02/2004	71°18.4'	170°28.9'	230	376	Sand and pebbles
A5	15/02/2004	71°18.7'	170°25.5'	119	59	Sand with pebbles and stones
Cape Hallett						
H out 1	09/02/2004	72°15.7'	170°24.8'	458	375	Mud and pebbles
H out 2	11/02/2004	72°17.5'	170°29.4'	353	375	Sandy mud and stones
H out 4	12/02/2004	72°18.5'	170°26.8'	235	194	Sand
H in 2	10/02/2004	72°16.9'	170°12.2'	391	186	Coarse sand and small gravel
H in 3	16/02/2004	72°17.0'	170°13.1'	316	194	Muddy sand with stones
H in 4	16/02/2004	72°17.1'	170°14.0'	196	169	Mud and sand
H in 5	16/02/2004	72°17.2'	170°17.9'	84	113	Small gravel
Coulman Island						
C1	18/02/2004	73°24.5'	170°23.2'	474	375	Mud and small gravel
C2	18/02/2004	73°22.7'	170°06.9'	410	153	Mud and pebbles
Cape Russell						
SMN	20/02/2004	74°43.2'	164°13.1'	366	192	Sand with gravel and stones
R2	21/02/2004	74°49.0'	164°18.1'	364	575	Fine sand
R3	20/02/2004	74°49.3'	164°11.5'	330	565	Rock, sand, mud and pebbles
R4	20/02/2004	74°49.3'	164°11.5'	208	97	Rock, mud and large stones
R4	22/02/2004	74°50.2'	164°05.5'	216	-	Rock, mud

enhance the species inventory list of the Ross Sea cumacean fauna.

Results

Distribution of the peracarid fauna off Victoria Land

During the Victoria-Land cruise 63% of the collected macrobenthic fauna were peracarid crustaceans. In total 45,087 specimens of Peracarida were collected, 5,286 of which belonged to the order of Cumacea.

Amphipoda were the dominant peracarid taxon (66%) followed by Isopoda (18%), Tanaidacea (8%), Cumacea (7%), and Mysidacea (<1%). Abundance values varied remarkably among stations and peracarid groups (Table 2). The highest total abundance of peracarids was found at the shallowest station (H in 5; 84 m) off Cape Adare.

The Cumacea showed a tendency of increasing relative abundance from north to south (Fig. 2): it ranged from 0.5% in the north at Cape Adare to 36% in the south at Cape Russell. In contrast the proportion of Amphipoda was higher in the northern (Cape Adare 63%, Cape Hallett 69%) than in the southern areas (Coulman Island 27%, Cape Russell 36%). The relative abundance of Tanaidacea was three times

higher at Coulman Island (31%) than in the other areas (6–10%). Isopod abundance was highest at Cape Russell, but varied less than in the other peracarid groups (14–26%). Mean abundance of Amphipoda, Isopoda, and Tanaidacea was highest at the shallowest stations, whereas Cumacea and Mysidacea showed maximum abundances at stations from 300 to 400 m (Table 3).

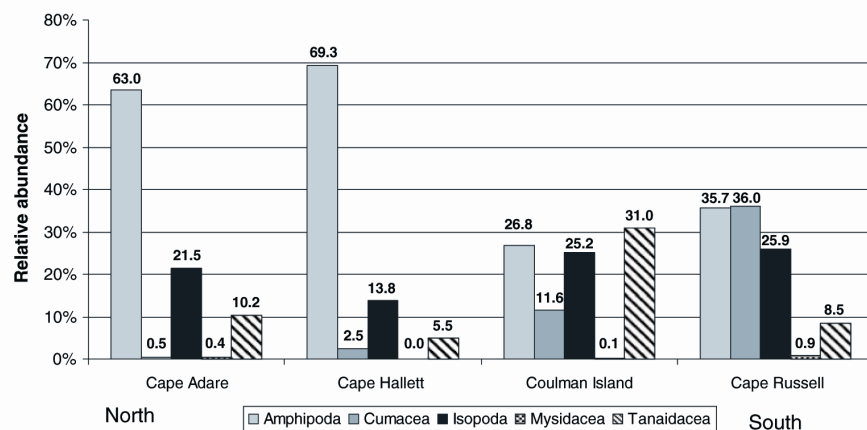
Composition, distribution and diversity of Cumacea off Victoria Land

All five cumacean families known from the Antarctic and 12 genera were represented in the samples. 19 of the 28 cumacean species found in the samples are new records for the Ross Sea. In addition two new records of cumacean species were collected with RV “Tangaroa” (Table 4), thus the number of recorded species totals 34. Leuconidae containing nine species from two genera were the most dominant cumacean family (69%). The genus *Leucon* (6 species) was most abundant (57%). Nannastacidae, comprising nine species of three genera, occurred with 21%. The family Diastylidae (7 species, 4 genera) made up 6% of total cumacean abundance. Only two species of two genera of Bodotriidea and Lampropidae were collected which represented 3% and less than 1%, respectively, of cumacean specimens.

Table 2 Abundance of Peracarida along the Victoria-Land coast

Station north to south	Amphipoda		Cumacea		Isopoda		Mysidacea		Tanaidacea	
	N	N 10 ³ m ⁻²	N	N 10 ³ m ⁻²	N	N 10 ³ m ⁻²	N	N 10 ³ m ⁻²	N	N 10 ³ m ⁻²
Cape Adare										
A1	244	1,363	2	11	23	128	17	95	40	223
A2	1,567	10,517	0	0	173	1,161	14	94	285	1,913
A3	682	5,307	2	16	605	4,708	4	31	57	444
A4	1,209	6,431	37	197	1,034	5,500	3	16	271	1,441
A5	505	17,119	3	101	68	2,305	1	34	75	2,542
Cape Hallett										
H out 1	636	3,392	114	608	301	1,605	0	0	88	469
H out 2	846	4,512	66	352	277	1,477	0	0	45	240
H out 4	2,357	24,299	65	670	1,050	10,825	6	62	154	1,588
H in 2	159	1,710	107	1,151	78	839	4	43	22	237
H in 3	991	10,216	297	3,062	450	4,639	0	0	181	1,866
H in 4	3,185	37,692	219	2,586	1,449	17,148	0	0	486	5,751
H in 5	10,170	180,000	56	991	882	15,611	0	0	490	8,673
Coulman Island										
C1	57	304	10	53	36	192	3	16	27	144
C2	711	9,294	315	4,116	676	8,837	2	26	838	10,954
Cape Russell										
SMN	1,413	14,719	1,252	13,050	1,080	11,250	42	438	448	4,667
R2	1,016	3,534	1,354	4,706	729	2,536	0	0	75	261
R3	694	2,457	1,374	4,864	516	1,827	26	92	78	276
R4	97	2,000	14	288	41	845	1	21	11	227

N = number of specimens collected per station, N 10³ m⁻² = number of specimens per station standardized to 1,000 m²

Fig. 2 Relative numbers of peracarid taxa in the sample areas on the Ross Sea shelf, Antarctica**Table 3** Peracarid abundance per 1,000 m⁻², averaged across four depth zones off Victoria Land, Ross Sea

Depth range (m)	Amphi	Cuma	Isop	Mysid	Tana
84-200	78,270	1,226	11,688	11	5,655
201-300	4,216	243	3,173	19	834
301-400	6,565	3,886	3,897	86	1,142
401-515	8,195	910	3,791	49	2,549

Amphi Amphipoda, Cuma Cumacea, Isop Isopoda, Mysid Mysidacea, Tana Tanaidacea

Most species were found between 200 and 450 m depth. From 100 to about 200 m only six species were found, whereas nine species were confined to depths

below 300 m (Fig. 3). Diversity varied considerably (H' :0–2.5; J' :0.45–0.83) and was highest at station C2 off Coulman Island, which also was the station with the highest number of species (20). Diversity was lowest at stations A1, A3, and A5 off Cape Adare, for only one species was represented at these stations (Table 5). Accordingly, Cape Adare was the area with the lowest mean values of diversity, number of species, and abundance, whereas off Coleman Island mean diversity and mean species number were highest. Cumacean mean abundance increased with latitude (Table 6). Mean diversity and evenness showed a tendency to higher values at deeper stations; mean species number,

Table 4 Cumacean species of the Ross Sea; species collected during the expeditions of RV “Italica” (Ita) and “Tangaroa” (Tan) in 2004, *n* = new record from the Ross Sea

Family/Species	Author	Record	
Lampropidae			
<i>Hemilamprops</i> cf. <i>ultimaspei</i>	Zimmer (1921)	Ita	n
<i>Hemilamprops</i> cf. <i>pellucidus</i>	Zimmer (1908)	Tan	n
<i>Paralamprops</i> <i>rossi</i>	Jones (1971)		
Bodotriidae			
<i>Cyclaspis</i> <i>gigas</i>	Zimmer (1907b)	Ita/Tan	
<i>Vaunthompsonia</i> <i>inermis</i>	Zimmer (1909)	Ita	n
Leuconidae			
<i>Eudorella</i> <i>fallax</i>	Zimmer (1909)	Tan	n
<i>Eudorella</i> <i>gracilior</i>	Zimmer (1909)	Ita	
<i>Eudorella</i> cf. <i>sordida</i>	Zimmer (1907a)	Ita	n
<i>Eudorella</i> <i>splendida/similis</i>	Zimmer (1902)		
<i>Eudorella</i> sp. A		Ita	
<i>Leucon</i> <i>antarcticus</i>	Zimmer (1907a)	Ita	
<i>Leucon</i> <i>assimilis</i>	Sars (1887)	Ita	n
<i>Leucon</i> <i>intermedius</i>	Mühlenhardt-Siegel (1996)	Ita	n
<i>Leucon</i> <i>parasiphonatus</i>	Mühlenhardt-Siegel (1994)	Ita	n
<i>Leucon</i> cf. <i>sagitta</i>	Zimmer (1907a)	Ita	n
<i>Leucon</i> sp. A	spec. nov.	Ita	n
Nannastacidae			
<i>Campylaspis</i> <i>antarctica</i>	Calman (1907)	Ita	
<i>Campylaspis</i> <i>frigida</i>	Hansen (1908)	Ita	n
<i>Campylaspis</i> <i>ledoyeri</i>	Petrescu and Wittman (2003)	Ita	n
<i>Campylaspis</i> <i>maculata</i>	Zimmer (1907b)	Ita	n
<i>Campylaspis</i> <i>quadridentata</i>	Ledoyer (1993)	Ita	n
<i>Campylaspis</i> <i>quadriplicata</i>	Lomakina (1968)	Ita	n
<i>Cumella</i> <i>australis</i>	Calman (1907)	Ita	
<i>Cumella</i> cf. <i>emergens</i>	Corbera 2000	Ita	n
<i>Procampylaspis</i> <i>meridiana</i>	Jones (1971)		
<i>Procampylaspis</i> <i>compressa</i>	Zimmer (1907b)	Ita	n
Diastylidae			
<i>Diastylis</i> <i>corniculata</i>	Hale (1937)	Ita	n
<i>Diastylis</i> <i>enigmatica</i>	Ledoyer (1993)	Ita/Tan	n
<i>Diastylis</i> <i>helleri</i>	Zimmer (1907a)	Ita/Tan	
<i>Diastylis</i> juv. cf. <i>mawsoni</i>	Calman (1918)	Ita	n
<i>Diastylopsis</i> <i>goeki</i>	Roccatagliata and Heard (1992)	Ita	
<i>Leptostylis</i> <i>antipus</i>	Zimmer (1907a)	Ita	n
<i>Makrokyllindrus</i> <i>baceskei</i>	Lomakina (1968)		
<i>Makrokyllindrus</i> <i>inscriptus</i>	Jones (1971)	Ita	
<i>Gynodiastylis</i> <i>jazdzewskii</i>	Błażewicz and Heard (1999)		

abundance, and diversity were highest at stations between 301 and 400 m (Table 7).

After the MDS analysis stations were roughly arranged corresponding to their geographical order (Fig. 4). The only exception was station A1 (Cape Adare), which was clearly different to the remaining stations. Species, which only occurred in one area, were found. Thus the species *Eudorella* sp. A and *Makrokyllindrus* *inscriptus* were only recorded from Cape Hallett. *Leucon* *parasiphonatus* and *Diastylopsis* *goeki* solely

occurred off Coulman Island. Species confined to Cape Russell were *Campylaspis* *frigida* and *Diastylis* *enigmatica*. No species occurred exclusively at Cape Adare.

Discussion

Almost nothing has been known about sub-tidal ecosystems off the northern Victoria-Land coast, and most recent studies of shallow benthic communities in the Ross Sea focused rather on ecological interactions than on classifications (Waterhouse 2001). A first attempt to describe the community structure of smaller macrozoobenthic species along the northern Victoria-Land coast was made onboard of the 19th expedition of RV “Italica” (Rehm et al. 2006).

Gears with small mesh sizes, such as the Rauschert dredge or epibenthic sledges, are very effective for sampling smaller peracarid crustaceans. As the Rauschert dredge (see Rehm et al. 2006) was used for the first time in the Ross Sea, it gave us a first insight into the peracarid community of the northern Victoria-Land coast and helped to considerably improve our knowledge of cumaceans from the Ross Sea.

Comparison of the peracarid fauna

The peracarid community sampled during the 19th Italian expedition with research vessel “Italica” was dominated by amphipods. Isopods represented the second dominant group, followed by Tanaidacea, Cumacea, and Mysidacea. Only few quantitative studies of peracarids sampled with gears with small mesh size were so far carried out in Antarctic waters. Samples taken off the South Shetland Islands at depth between 200 and 400 m and taken with an epibenthic sledge in autumn 2000 showed comparable results in the mean proportions of peracarid orders: 62% Amphipoda, 16% Isopoda, 13% Tanaidacea, 11% Cumacea, and less than 1% Mysidacea (Lörz and Brandt 2003). Nevertheless, samples taken during summer in the southern Weddell Sea and off King George Island in depths ranging from 200 to 400 m showed different values (Linse et al. 2002); Isopoda 60%, Amphipoda 26%, Mysidacea 10%, Cumacea 4%, and Tanaidacea 1% in the Weddell Sea; Cumacea 39%, Amphipoda 31%, Mysidacea 17%, Isopoda 13%, and Tanaidacea 1% off King George Island. Differences in the gear are one explanation for the variations in the results of the different studies. The epibenthos sledge samples from over 20 cm to more than 120 cm above the seafloor (Brandt and Barthel 1995; Brenke 2005), but the Rauschert dredge is bound to the first about 18 cm above the ground. Thus, the increased number of

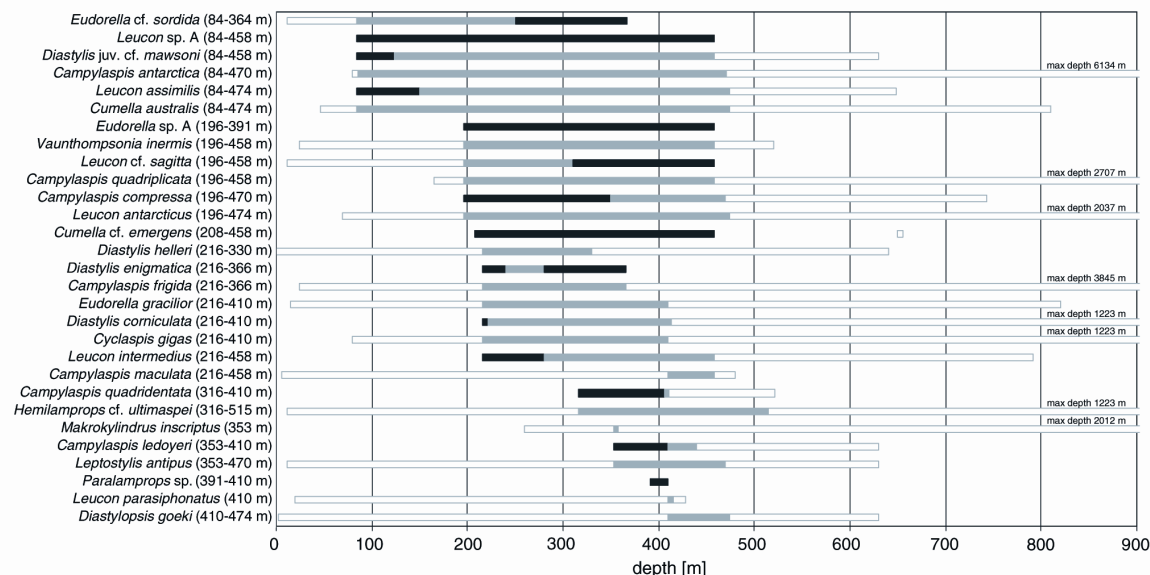


Fig. 3 Bathymetric distribution of the Cumacea collected during the Victoria-Land transect cruise to the Ross Sea, Antarctica (black shade); general depth range (white shade), data based on

Jones (1971, 1984) Ledoyer (1993), Mühlenhardt-Siegel (1999), Corbera (2000), Petrescu and Wittman (2003), Corbera and Ramos (2005); overlapping depth range (grey shade)

Mysidacea in the epibenthic sledge samples might be attributed to their suprabenthic life style. However, only few mysids were sampled with the epibenthic sledge in autumn 2000. Variations of the contribution of peracarid orders to the peracarid fauna were high during all studies and the number of samples from shallower water than 500 m depth taken in the Weddell Sea and the South Shetland Islands was limited. Therefore, it is difficult to judge whether differences might result from the patchiness of the fauna obtained, a different compositions of the fauna, or seasonal effects. Further sampling with and comparison of multiple gears will provide more reliable information about seasonal differences and similarities between the different Antarctic areas.

Composition and distribution of the cumacean fauna

In the Weddell Sea as around the South Shetland Islands (Corbera 2000; Lörz and Brandt 2003) most speciose family was the Nannastacidae. In the Ross Sea, the most abundant family was the Leuconidae, whereas the Diastylidae (Lörz and Brandt 2003) or Bodotriidae (Corbera 2000) dominated the cumaceans off the South Shetland Islands. Mean species number off the South Shetland Islands was half of the Ross Sea, whereas total species number varied between 50 (Lörz and Brandt 2003) and 100% (Corbera 2000).

Cumacean diversity index was higher at deeper stations and maximal in a depth of 410 m at station C2,

which was one of the stations with muddy sediment. At the South Shetland Islands, cumacean diversity was extremely variable. Nevertheless, a tendency towards higher values at deeper stations was recorded as well; this trend extended to depths below 500 m on the continental slope (Corbera 2000). Density and species number of the Cumaceans of the Beagle Channel was found to increase with depth and reduced grain size of the sediment (Brandt et al. 1999).

During this study one group of species was found ranging from 100 to 500 m, a second group of species was found in between 200 and 500 m, and a third group ranges from 300 to 500 m. From the Weddell Sea, three bathymetric groups of cumaceans were reported between 200 and 500–600 m, below 500 m, and finally between 200 and 2,000 m (Ledoyer 1993). Corbera (2000) described a situation with three groups between 45 and 300 m, 300 and 650 m, 45 and 650 m. Concluding from the three studies, there appear to be two important changes in cumacean depth distribution around 300 and 500–600 m depth.

The most striking result of this work is the large number of newly recorded cumacean species from the Ross Sea. One reason to explain this remarkable increase in known species can be ascribed to the little previous work from the area under investigation, which has now been accomplished on the deeper benthic environment, between 50 m and the shelf break at 800 m (Clark and Rowden 2004; Waterhouse 2001). The new species

Table 5 Species station list of the Cumacea collected during the Victoria-Land transect cruise; data standardized to 1,000 m² hauls; total abundance of families are given in bold numbers; + species present, no quantitative data available

Station	A1	A3	A4	A5	H out 1	H out 2	H out 4	H in 2	H in 3	H in 4	H in 5	C1	C2	SMN	R2	R3	R4	R4
Depth (m)	515	305	230	119	458	353	470	391	316	196	84	474	410	366	364	330	208	216
Species number	1	1	3	1	12	12	4	13	16	12	6	4	20	14	13	13	5	14
Abundance	11	16	197	101	608	351	670	1,152	3,060	2,587	992	53	4,114	13,082	4,705	4,864	289	-
Diversity (H')	0	0	0.49	0	1.82	1.81	1.13	1.94	2.00	1.56	1.22	1.15	2.50	1.76	1.68	1.92	1.26	-
Evenness (J')	-	-	0.45	-	0.73	0.73	0.82	0.76	0.72	0.63	0.68	0.83	0.83	0.66	0.65	0.75	0.78	-
Lampiroidea	11				27	5		11	10				26					
<i>Hemilamprops cf. ulimaspei</i>	11				27	5		11	10									
<i>Paralamprops</i> sp.																		
Bodotriidae					5	5		43	51	24			496	229	3	67	165	+
<i>Cyclaspis gigas</i>						5			10				65		3	7		+
<i>Vaanthompsonia inermis</i>					5			43	41	24			431	229		60	165	+
Nannastacidae		16	181	101	203	197	567	173	475	945	177	16	1,802	1,981	173	843	62	+
<i>Campylaspis antarctica</i>					5	5	196		31	24	159		13	63	42	67		+
<i>Campylaspis frigida</i>			11											73	45	57		
<i>Campylaspis tedoyerii</i>						5							91					
<i>Campylaspis maculata</i>					11								78					+
<i>Campylaspis quadridentata</i>									41				378					
<i>Campylaspis quadriplicata</i>					5	11		11	51	12			118					
<i>Procampylaspis compressa</i>					32	32	31	11	59				26	10				
<i>Cumella australis</i>	16	170		101	139	144	340	119	330	850	18	16	993	1,647	83	719	21	+
<i>Cumella cf. emergens</i>					48			32	21				105	188	3	41		
Leuconidae		16			341	102		765	1,979	1,594	602	32	1,477	10,466	4,286	3,749	62	+
<i>Eudorella gracilior</i>									103	118	35		92	1,272	1,300	1,030		+
<i>Eudorella cf. sordida</i>						16		97	103					80				
<i>Eudorella</i> sp. A										35								
<i>Leucon antarcticus</i>					48			474	866	260		27	353	4,253	1,926	1,303		+
<i>Leucon assimilis</i>					27			22		12	18	5	353	803	94	85	21	+
<i>Leucon intermedius</i>					16	11		32	10				235	10	97	85		+
<i>Leucon parasiphonatus</i>													13					
<i>Leucon cf. sagitta</i>					5				72	106				198	497	333		+
<i>Leucon</i> sp. A			16		245	75		140	825	1,063	549		431	3,930	292	913	41	+
Diastylidae					32	42	103	161	546	24	213	5	313	406	243	205	+	+
<i>Diastylis corniculata</i>													52	10				+
<i>Diastylis enigmatica</i>														396	243	198		+
<i>Diastylis helleri</i>																		+
<i>Diastylis juv. cf. mawsoni</i>					32			31	371	24	213							+
<i>Diastylopsis goeki</i>												5	78					
<i>Leptostylis antipus</i>						37	103	129					183					
<i>Makrokylindrus inscriptus</i>						5												

Table 6 Average measurements of cumacean diversity by latitude (Victoria-Land transect, Ross Sea)

Sample area north to south	S mean/total	N	H'	J'
Cape Adare	2/4	81	0.45	0.12
Cape Hallett	11/24	1,346	0.72	1.64
Coulman Island	12/20	2,084	0.83	1.82
Cape Russell	11/17	5,727	0.71	1.65

S species number, N abundance per 1,000 m², H' diversity, J' evenness

Table 7 Average measurements of cumacean diversity by depth (Victoria-Land transect, Ross Sea)

Depth range (m)	S mean/total	N	H'	J'
84–200	6/12	1,227	0.92	0.65
201–300	4/15	243	0.87	0.61
301–400	12/26	3,885	1.59	0.71
401–515	8/23	1,091	1.32	0.80

S species number, N abundance per 1,000 m², H' diversity, J' evenness

Leucon sp. A shows that the area is truly undersampled, as the species was one of the most common species with up to 2,000 specimen per square meter in the present study. Only *Leucon antarcticus* occurred more frequently. *Leucon* sp. A was found along the whole Victoria-Land coast and it was missing only at the deepest samples below 460 m. In addition, this species is very easy to distinguish from other species of the genus *Leucon*. Nevertheless, there has been no data published about this species before. What might be even more important for the many species newly recorded from the Ross Sea was the use of a Rauschert dredge, as this gear

is specially designed to catch animals of small size. In the case of the Cumacea, the number of species, which were reported for the Ross Sea before, increased from 13 to 32 species. Moreover, two further species, *Hemilamprops* cf. *pellucidus* and *Eudorella fallax* were found on the parallel cruise with RV “Tangaroa”. Thus, 34 species are recorded in total for the Ross Sea. We expect that investigations of the other peracarid orders will lead to similar results.

A summary of the Antarctic cumacean species and their distribution in the Antarctic and Subantarctic regions was given by Mühlenhardt-Siegel (1999). The highest numbers of cumacean species were recorded from the East Antarctic (32), the Magellan region (31), and the Weddell Sea (29). In the Scotia region numbers varied between 15 and 20 species, whereas, in the Ross Sea only 11 species were recorded. Here we documented that the Ross Sea harbours more cumacean species than the other high Antarctic regions, although it was formerly regarded as the poorest Antarctic area concerning cumacean species richness. This finding highlights the need for more explorative sampling in the Ross Sea area and in deeper waters off the continental slope off Antarctica.

Most species from the Ross Sea show a wide range of geographic distribution (Table 8). Fifteen species occur in Antarctic regions, seven species are restricted to high Antarctic regions. Antarcto-Magellan species divide into a Subantarctic/Antarctic (6) and a Subantarctic/high Antarctic (2) group. The species of the latter group are probably also Subantarctic/Antarctic. After all, seven species making up 21% of the species from the Ross Sea occur in the Magellan area as well as in the Ross Sea. The species

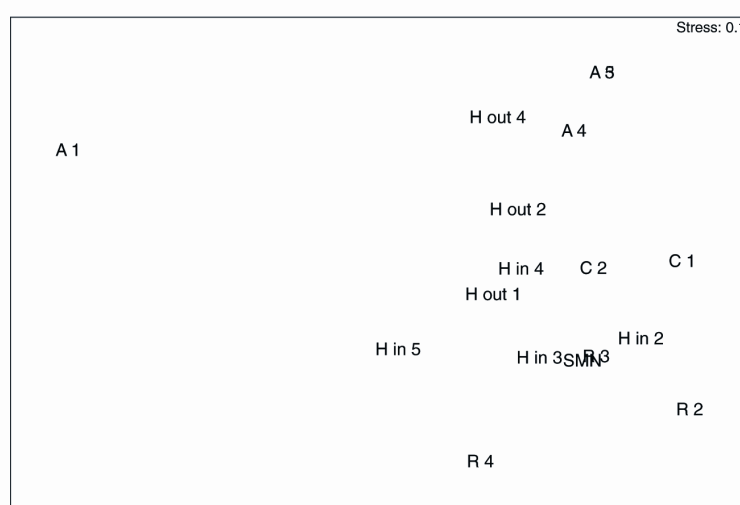
Fig. 4 MDS-plot of Ross Sea Cumacea; A Cape Adare, H Cape Hallett, C Coulman Island, R Cape Russell, SMN Santa Maria Novella

Table 8 Biogeography of cumacean species from the Ross Sea; data based on Hansen (1908), Mühlenhardt-Siegel (1999), Petrescu and Wittman (2003), Corbera and Ramos (2005), the presentstudy and unpublished data from the BENTART-06¹ cruise (J. Corbera, pers. comm.) and the ANT XXI-2² cruise with RV “Polarstern”

Species	Subantarctic		Antarctic						
	Magel	Kerg	S Geo	S Ork	S Shetl	Ant P	Wedd	BS	E Ant
Subantarctic and Antarctic									
<i>Campylaspis maculata</i>	+		+	+	+	+	+		+
<i>Campylaspis antarctica</i>	+				+		+	+ ¹	+
<i>Eudorella splendida/similis</i>		+	+		+				
<i>Hemilamprops ultimaspei</i>	+				+		+		
<i>Leucon assimilis</i>	+	+			+	+	+		+
<i>Leucon sagitta</i>	+	+	+	+	+	+			+
Antarctic									
<i>Cumella australis</i>			+	+	+	+	+	+	+
<i>Cumella cf. emergens</i>					+		+ ²	+ ¹	
<i>Cyclaspis gigas</i>			+		+	+	+	+	+
<i>Diastylis corniculata</i>				+	+		+		+
<i>Diastylopsis goeki</i>				+	+	+	+		+
<i>Diastylis helleri</i>				+	+	+	+		+
<i>Eudorella fallax</i>			+	+	+	+	+		+
<i>Eudorella gracilior</i>			+	+	+	+	+		+
<i>Eudorella cf. sordida</i>			+						
<i>Hemilamprops cf. pellucidus</i>					+	+	+		+
<i>Leptostylis antipus</i>			+	+	+	+	+		
<i>Leucon antarcticus</i>				+		+	+		+
<i>Leucon intermedius</i>					+	+	+ ²		+
<i>Leucon parasiphonatus</i>					+		+		
<i>Vaunthompsonia inermis</i>			+	+	+	+	+	+	+
high Antarctic									
<i>Campylaspis ledoyeri</i>							+		
<i>Campylaspis quadridentata</i>							+		+
<i>Diastylis enigmatica</i>							+		
<i>Diastylis juv. cf. mawsoni</i>							+	+	+
<i>Makrokyllindrus inscriptus</i>							+		
<i>Paralamprops rossi</i>							+		+
<i>Procampylaspis compressa</i>							+	+	
Subantarctic and high Antarctic									
<i>Campylaspis frigida</i>	+	+						+	
<i>Campylaspis quadriplicata</i>	+						+	+	
Ross Sea									
<i>Leucon</i> sp. A									
<i>Procampylaspis meridiana</i>									
<i>Makrokyllindrus baceskei</i>									
<i>Gynodiastylis jazdzewskii</i>									

Ant P Antarctic Peninsula, BS Bellingshausen Sea E Ant East Antarctic, Kerg Kerguelen, Magel Magellan Area, S Geo South Georgia, S Ork South Orkneys, S Shetl South Shetlands, Wedd Weddell Sea

of both areas total to 66. An overlap of 11% is the same rate as reported for the Magellan area and Antarctica (Mühlenhardt-Siegel 1999). Four species (11%) are endemic to the Ross Sea, the rate of endemism is less than in the Weddell Sea (28%) and in the East Antarctic (13%) (Corbera 2000). In conclusion, not only species number but also biogeographical connection to the Magellan area of the cumaceans of the Ross Sea resembles that of other high Antarctic regions. Still, the rate of endemism is the lowest of high Antarctic areas and similar to the East Antarctic only.

In several cases the determination of the species was difficult, as some of the original descriptions show only parts of the animal or the drawings are vague. We believe that good re-descriptions are necessary to simplify future work on Antarctic cumaceans. Another problem was that some of the species showed slight but consistent differences to specimens from original descriptions. It is rather likely these species show geographic variations, but there is also a chance that we found sibling species. Genetic analysis of the Antarctic isopod species *Ceratoserolis trilobitoides* demonstrated that sibling species, which were described as variations

before (Wägele 1986), were even found in the same location (Held 2003). Possibly this is true for other Antarctic peracarid crustaceans as well. The Ross Sea is the southernmost ocean on earth and in contrast to most other Antarctic regions it is characterized by a very wide continental shelf. Furthermore, the Ross Sea polynya encloses the most productive phytoplankton primary production found in Antarctica (Smith et al. 1996), which might particularly foster benthic diversity.

Morphological variability in the Antarctic Cumacea and cryptic speciation, as already proven in Antarctic peracarid isopods (Held 2003; Held and Wägele 2005), are an indication of recurrent isolation processes of populations on an evolutionary timescale. Considering that most species of the Ross Sea Cumacea have a limited depth distribution that only covers the Antarctic continental shelf and slope, the deep-sea might not have served as refuge for many species during glacial ice advance in Antarctica (Thatje et al. 2005). This again poses the question of isolated shallow water refuges for benthic fauna in glacial periods and under severest environmental conditions (for discussion see Thatje et al. 2005). Such geographically isolated shelters, in addition, might have driven speciation process in the Peracarida, which have flourished in Antarctica. Molecular studies are needed to unravel this important and controversial question in the evolution of the Antarctic fauna.

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Publication III

Molecular evidence for circum-Antarctic distribution in two species of broadcasting benthic Caridea (Crustacea: Decapoda)

Michael J. Raupach^{1,*}, Sven Thatje², Peter Rehm³ and Bernhard Misof¹

¹Forschungsmuseum Alexander König, Molekularbiologisches Labor, Adenauerallee 160, D-53113 Bonn, Germany.

²National Oceanography Centre, Southampton, School of Ocean and Earth Science, University of Southampton, European Way, Southampton, SO14 3ZH, United Kingdom.

³Alfred Wegener Institute for Polar and Marine Research, Marine Animal Ecology, Am Alten Hafen 26, D-27568 Bremerhaven, Germany.

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ABSTRACT: We analysed the mitochondrial cytochrome oxidase I (COI) gene sequences from specimens of the shallow-water shrimp *Chorismus antarcticus* and the deep-sea shrimp *Nematocarcinus lanceopes* from populations around Antarctica. In both species, molecular variance analyses of the mitochondrial COI gene revealed low population structures giving evidence of homogeneous populations inhabiting the Southern Ocean. This first record of homogeneous populations in two species of marine broadcasters reinforces the concept of circum-Antarctic species, which was challenged by the increased recovery of cryptic species in Antarctic seafloor invertebrates with limited mode of dispersal. Lower complexity in haplotype diversity in the shallow-water species *Chorismus antarcticus* when compared with the deep-water species *Nematocarcinus lanceopes* points at post-glacial radiation of few populations of *Chorismus antarcticus* around Antarctica that either survived in glacial shelters on the Antarctic continental shelf or in shallow waters off Southern Ocean islands. The data support the importance of larval drifting stages for the success of a widespread shallow-water species thriving in Antarctica over long evolutionary periods of time.

KEYWORDS: Southern Ocean, ecosystem evolution, population structure, broadcaster

INTRODUCTION

Effects of climate change on the evolution of marine communities and diversity over long evolutionary timescale of millions of years are relatively well understood within the climatologically and physically isolated waters of the Southern Ocean (Clarke & Johnston 2003; Thatje *et al.* 2005a, b). Today, high levels of endemism and circum-Antarctic species distribution commonly characterize Antarctic marine diversity (Clarke & Johnston 2003). This diversity pattern is principally a result of Antarctic cooling, with the last major cooling step occurring about 15 Ma ago, and the effects of climate oscillation in glacial–interglacial cycles on Milankovitch timescales (see Thatje *et al.* 2005b).

The concept of circum-Antarctic species

distribution as suggested for many seafloor-inhabiting invertebrates found in Antarctica, is traditionally based on the identification of morphospecies. With the discovery of cryptic species using molecular methods, describing a hidden genetic diversity indistinguishable by traditional morphology, the concept of circum-Antarctic distributed species has been challenged and Antarctic diversity is likely to increase significantly. So far, cryptic speciation was unravelled in many different Antarctic taxa (e.g. Darling *et al.* 2000; Raupach & Wägele 2006; Linse *et al.* 2007). Geographic isolation in ice-free shelters on the continental shelf of Antarctic during glacial periods is discussed as one possible factor explaining cryptic speciation in shallow-water species (Held 2005; Thatje *et al.* 2005b).

Here, we present for the first time a comparison of the genetic structure of an Antarctic shallow-water and a deep-sea crustacean species, which both possess a broadcasting mode in

*E-mail: michael.raupach@rub.de

Table 1. Studied populations and summary of statistical parameters (n : number of individuals analyzed, h : haplotypic diversity; π : nucleotide diversity) for the CO1 shrimp data.

Species	Sampled area	Depth range [m]	n	Number of haplotypes	h	π
<i>Chorismus antarcticus</i>	Austasen	166 – 405	42	8	0.6260 \pm 0.0550	0.001843 \pm 0.001318
	South Shetland Islands	183 – 277	3	2	0.6667 \pm 0.3143	0.002928 \pm 0.002761
	Kapp Norvegia	191 – 228	16	5	0.6500 \pm 0.1083	0.002086 \pm 0.001504
	Cape Russell	330	22	6	0.7100 \pm 0.0705	0.002428 \pm 0.001655
	Coulman Island	410	42	8	0.6028 \pm 0.0637	0.001840 \pm 0.001316
	Cape Hallett	196	44	8	0.6385 \pm 0.0447	0.001959 \pm 0.001377
	Total		169	23	0.6407 \pm 0.0256	0.001999 \pm 0.001373
<i>Nematocarcinus lanceopes</i>	Austasen	1488 – 1525	6	5	0.9333 \pm 0.1217	0.005098 \pm 0.003487
	South Sandwich Islands	630 – 834	8	6	0.8929 \pm 0.1113	0.005777 \pm 0.003684
	Kapp Norvegia	754 – 1055	91	28	0.8979 \pm 0.0175	0.005270 \pm 0.002992
	Powell Basin	1181 – 1584	10	6	0.8667 \pm 0.0850	0.006176 \pm 0.003787
	Bransfield Street	2108 – 2124	21	13	0.9190 \pm 0.0418	0.006232 \pm 0.003594
	Western Weddell Sea	1114 – 1115	1	1	1.0 \pm 0	0 \pm 0
	Spiess Sea Mount	568 – 575	5	4	0.9000 \pm 0.1610	0.006471 \pm 0.004484
	Ross Sea	1300 - 1350	2	2	1.0 \pm 0.5	0.007353 \pm 0.008055
	Total		144	45	0.9017 \pm 0.0144	0.005482 \pm 0.003082

reproduction by producing pelagic larvae. Results are discussed in relation to the glaciological history of Antarctica and the evolutionary history of its marine fauna.

MATERIAL AND METHODS

All analysed shrimp specimens of *Chorismus antarcticus* and *Nematocarcinus lanceopes* were collected during expeditions in the Southern Ocean in the years 2002 to 2006. Shrimps were caught using various gears (see Arntz & Brey 2003, 2005;

Fütterer *et al.* 2003; Fahrbach 2006; Rehm *et al.* 2006). Studied specimens and sample localities are listed in a sample data sheet as electronic supplement.

Genomic DNA was extracted from pleon muscle of 169 specimens of *Chorismus antarcticus* and 144 specimens of *Nematocarcinus lanceopes*, using the QIAmp® Tissue Kit (Qiagen GmbH) and following the extraction protocol. The polymerase chain reaction was used to amplify a part of the mitochondrial cytochrome oxidase subunit I (CO1) gene. Amplifications were performed in 25 μ l reactions containing 2.5 μ l 10x PCR buffer, 2.5 μ l

dNTPs (2 mmol/μl), 0.3 μl of each primer (LCO1490, HCO2198, both 50 pmol/μl; Folmer *et al.* 1994), 1–2 μl of DNA template, 5 μl Q-Solution®, 0.2 μl Qiagen Taq (5 U/μl), filled up to 25 μl with sterile H₂O, on a Progene Thermocycler (Techne Ltd.). The temperature profile of the PCR consisted of an initial denaturation of 94°C (5 min), followed by 38 cycles of 94°C (45 s), 44°C (45 s) and 72°C (75 s). Purified PCR products were cycle sequenced and sequenced at a contract sequencing facility (Macrogen, Seoul, South Korea), using the same primer set used for PCR. All sequences were deposited in GenBank: EF407603 – EF407647 for CO1 haplotypes of *Nematocarcinus lanceopes*, EF407580 – EF407602 for *Chorismus antarcticus* haplotypes.

Sequences were aligned and edited by eye, generating two alignments of 683 bp (*Chorismus antarcticus*) and 680 bp (*Nematocarcinus lanceopes*). Phylogenetic relationships among haplotypes were inferred using statistical parsimony implemented in TCS 1.13 (Clement *et al.* 2000). ARLEQUIN 3.01 (Schneider *et al.* 2000) was used to calculate haplotype (*h*) and nucleotide diversity (π), and to estimate levels of population structure within species by analyses of molecular variance (AMOVA) (Excoffier *et al.* 1992).

RESULTS

Figure 1 shows statistical parsimony networks of the CO1 haplotypes of both analysed decapod species. Uncorrected pairwise genetic distances (p-distances) among observed haplotypes (*n* = 23) of *Chorismus antarcticus* ranged from 0 to 0.009, while 45 haplotypes with p-distances ranging from 0 to 0.015 were recovered within the deep-sea species *Nematocarcinus lanceopes*, revealing a more complex haplotype network in comparison to *Chorismus antarcticus*. These results coincide with other examples of high genetic variability which have been observed within other deep-sea decapods (e.g. Shank *et al.* 1999; Weinberg *et al.* 2003).

The analyses of molecular variance revealed only low population structures within both species whether stations were grouped by geographic region or depth (not shown), giving evidence of homogeneous populations and a circum-Antarctic distribution of both species (table 1). Total haplotype diversity *h* and nucleotide diversity π were greater for the analysed *Nematocarcinus lanceopes* specimens (*h* = 0.902, π = 0.0031) than for *Chorismus antarcticus* (*h* = 0.641, π = 0.0020) (see table 1). Haplotype diversity in both species did not dramatically change with increased sample size during our analyses, giving evidence for a stable pattern of haplotypes within both species.

DISCUSSION

Both analysed species, the shallow-water decapod *Chorismus antarcticus* and the deep-sea shrimp *Nematocarcinus lanceopes*, reinforce the concept of circum-Antarctic species distribution based on molecular analyses. The concept was so far based only on morphological work, and challenged in recent years by the discovery of cryptic speciation in species with limited potential for dispersal (e.g. Held & Wägele 2005; Linse *et al.* 2007).

The haplotype diversity pattern in both species is of striking consequence for our understanding of Antarctic evolution: given that molecular substitution rates between a shallow-water Antarctic and a primarily deep-sea organism are comparable (Held 2001), the observed low haplotype diversity in *Chorismus antarcticus* points at post-glacial radiation of few populations around Antarctica that either survived in glacial shelters on the Antarctic continental shelf or around shallow waters of Southern Ocean islands. *Nematocarcinus lanceopes* basically presents a deep-sea distribution in the Southern Ocean to about 4,000m water depth (Thatje *et al.* 2005c), and only emerges on the Antarctic Continental Slope to about 600m water depth. Based on this distribution pattern, the species should have been rather unaffected by the advance of grounded ice sheets across the Antarctic Continental Shelf during glacial periods, and thus developed/maintained a more complex population structure (figure 1).

The record of *Chorismus antarcticus* depicts the importance of the reproductive mode, and in particular drifting stages of any kind, in shallow-water Antarctic invertebrates to cope with climate oscillation. However, in this context it should be considered that Antarctic benthic invertebrates rarely have pelagic modes in development when compared with overall diversity found there (Thatje *et al.* 2005b). The example of genetic homogeneity at species level presented here does undoubtedly mark the importance of drifting stages for the success of a widespread shallow-water species thriving in Antarctica over long evolutionary timescale.

Modelling data (Huybrechts 2002) suggest the advance of grounded ice masses to the continental shelf edge around Antarctica at the Last Glacial Maximum (LGM), which would have left no glacial refuges to benthos restricted to shallow waters. However, it is not impossible that geographically isolated shelters for benthic organisms existed on the continental shelf during the LGM, due to a diachronous ice advance and retreat pattern; a concept that is discussed controversially (Huybrechts 2002; Thatje *et al.* 2005b). Our data show that the survival of refuge populations in glacial shelters and radiation

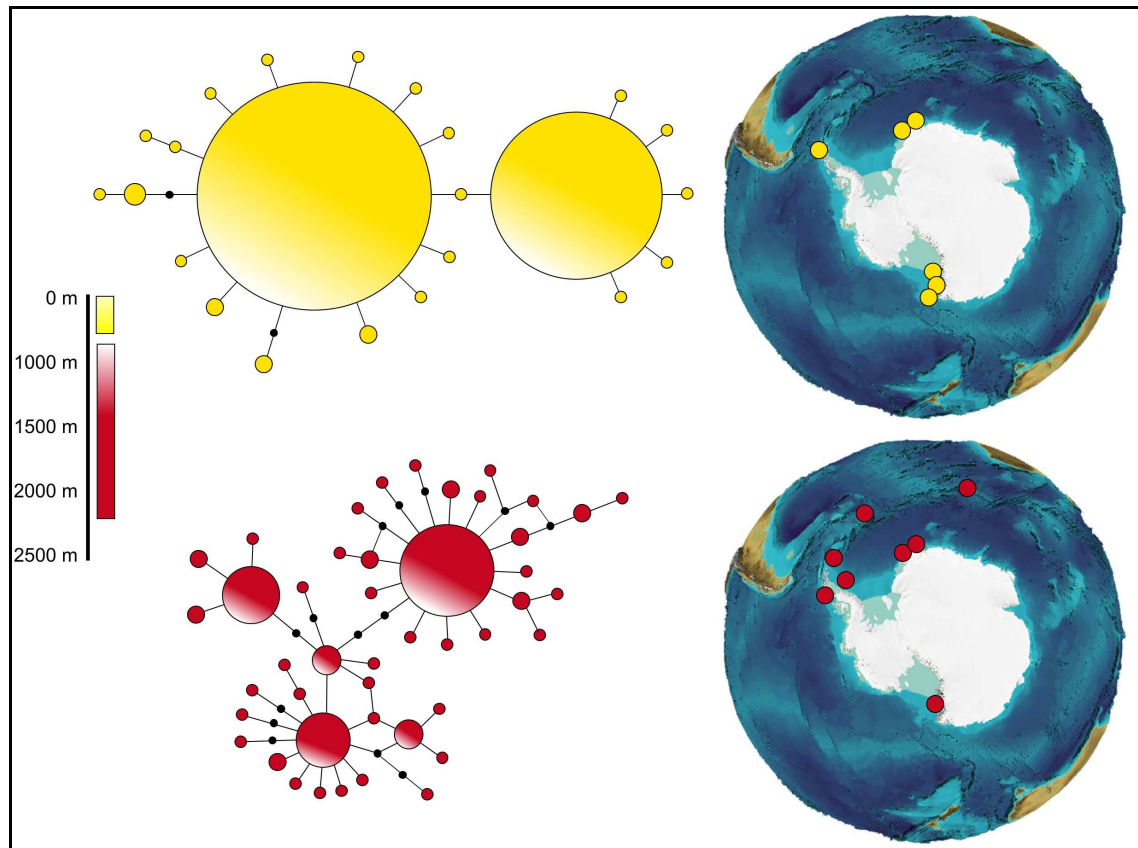


Fig. 1. Statistical parsimony network of CO1 haplotypes of the Antarctic decapods *Chorismus antarcticus* (shallow-water species, yellow) and *Nematocarcinus lanceopes* (deep-sea species, red) with sample locations and bathymetric distribution of the analysed populations. Size of the nodes is proportional to haplotype frequency in both species. Black nodes indicate missing haplotypes, lines between nodes correspond to one mutational step.

following ice retreat is a likely scenario for Antarctic broadcasters. It does however, not exclude the possibility that populations of *Chorismus antarcticus* survived the LGM in shallow waters of sub-Antarctic islands, and re-colonized the Antarctic continental shelf at the onset of deglaciation. Because of the diachronous ice extent pattern in glacial periods, ice-free shelters on the continental slope did not serve permanent refuge sites for benthic organisms and it is likely that species had to migrate from one shelter to another in order to escape obliteration. In any case, a pelagic drifting stage must have been a key condition for widespread shallow-water species to respond to these conditions. Where such capability was lacking, geographic isolation in glacial refuges might have caused cryptic speciation, which was recently suggested to be a common pattern in many Antarctic shallow-water species (Held & Wägele 2005). Molecular data should increasingly be taken into account for the calibration and validation of ice advance and retreat patterns in glacial Antarctica and the evolution of the Antarctic biota (Thatje *et al.* 2005b).

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Publication IV

Description of a new subspecies *Diastylis enigmatica rossensis* (Crustacea: Peracarida: Cumacea) from the Ross Sea, Antarctica

Peter Rehm

Helgoland Marine Research (under review)

Abstract *Diastylis enigmatica rossensis* n. ssp. is described and illustrated on the basis of new specimens from the Antarctic shelf in the Ross Sea. The material was collected off the Victoria Land coast during the 19th Antarctic expedition of the Italian research vessel *Italica* in 2004. *Diastylis enigmatica* Ledoyer, 1993 was first obtained during the EPOS 3 campaign at Halley Bay in the Weddell Sea. A redescription based on further material from the Weddell Sea was published by Petrescu and Wittmann in 2003, which shows several differences to the newly collected material from the Ross Sea. The most obvious differences from *Diastylis enigmatica rossensis* n. ssp. to *Diastylis enigmatica enigmatica* Petrescu and Wittmann, 2003 is the presence of 4 spines on the merus of the second paraeopod, an increased number of setae on the uropodal endopod, and an additional transverse denticulate ridge on the pseudorostrum in the latter subspecies.

Key words Antarctica, Crustacea, Cumacea, Diastylidae, Ross Sea, Victoria Land

Introduction

Diastylis enigmatica Ledoyer, 1993 was first described from material collected during the EPOS 3 campaign (Arntz et al., 1990) at Halley Bay in the Weddell Sea. The original description is based on a juvenile male with incomplete uropods, which was found between 270 and 280 m water depth. In 1989/90, five further specimens were found at a depth between 240 to 260m during the Expedition Antarktis-VIII/5 with RV *Polarstern*. Based on this material Petrescu and Wittmann (2003) redescribed a subadult female of *Diastylis enigmatica*. Additional specimens from the Antarctic shelf in the Ross Sea (216–366 m) were obtained off the

Victoria Land coast during the 19th Antarctic expedition of the Italian research vessel *Italica* in 2004 (Rehm et al., 2007). A first examination of the material from the *Italica* cruise already showed slight differences in some of the cumacean species to the original descriptions. With the present study the description of a marsupial female of the new subspecies *Diastylis enigmatica rossensis* and a detailed analysis of sexual and developmental differences in the subspecies of *Diastylis enigmatica* is provided.

Materials and methods

Material for this study was collected during the 19th Antarctic expedition of RV “*Italica*” to the Ross Sea. In total 173 specimens were sampled at 4 stations and examined with a Leica MZ125 and an Olympus SZX12 dissecting microscope with camera (Olympus Colour View I). Dissected appendages were mounted on slides in glycerine and studied with a Zeiss AxioSkop 1 with attached camera (Olympus DP70). Drawings were created from digital photographs using a digital drawing tablet (Wacom Intuos3 9x12) as described by Coleman (2003, 2006). Material has been deposited in the collection of the Zoological Museum Hamburg (ZMH). For further data on the sampling stations and on species diversity and distribution found at these stations refer to Rehm et al. (2007).

Body length is measured from the tip of the pseudorostrum to the tip of the telson. Length of articles are measured according to Mühlenhardt-Siegel (2005) and given as relative length of peduncle (RLP) articles 1 to 3 of antenna 1 compared to total peduncle length. The ratio basis to rest (B/R) is given for maxillipeds and paraeopods, which is the proportion of the basis to the combined length from ischium to dactylus, not including terminal setae. RLA refers to the relative length of each article from ischium to dactylus, excluding terminal setae.

The following types of setae were distinguished: simple setae are slender and completely lack outgrowths on the setal shaft; setulate setae have irregularly distributed setules

Alfred Wegener Institute for Polar and Marine Research (AWI)
Am Alten Hafen 26, 27568 Bremerhaven, Germany.
E-mail: peter.rehm@awi.de

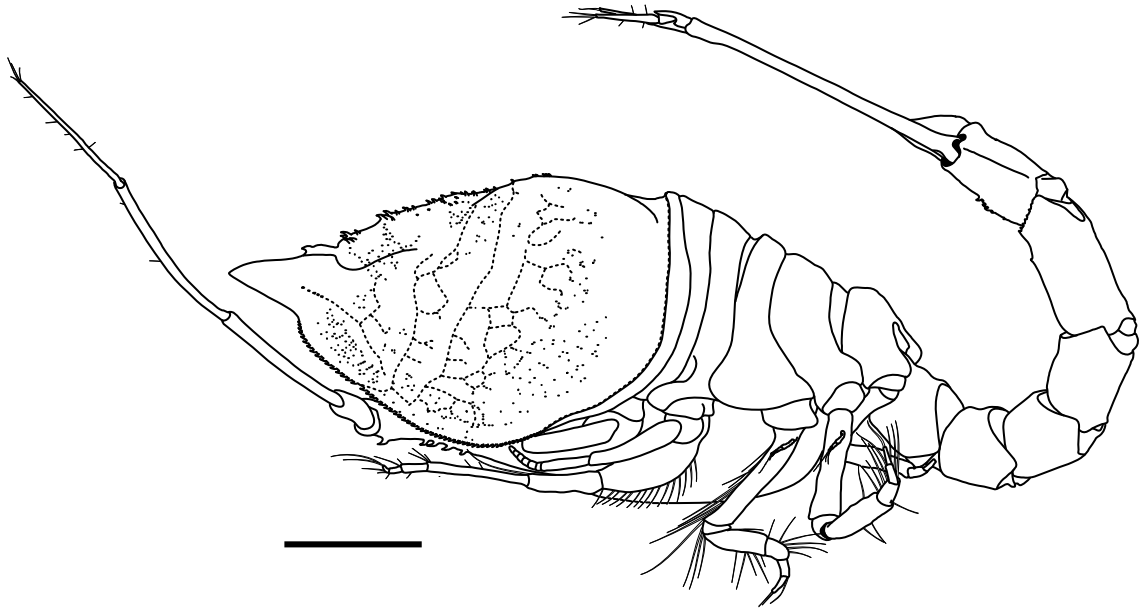


FIG. 1 *Diastylis enigmatica rossensis* n. ssp. Adult female. Scale = 1 mm.

along the shaft; plumose setae have many setules arranged in two strict opposite rows, giving the setae a feather-like appearance; serrate setae have one or two rows of denticles in their distal half; setulate-serrate setae have long setules on proximal half and one or two rows of denticles on distal half; spiniform setae are spine like; broom setae are tiny and have a pedestal and extremely thin setules distally; and annulate setae are simple and have a distinct internal spiral structure in their distal half.

Results

Order **Cumacea Kröyer, 1846**
 Family **Diastylidae Bate, 1856**
 Genus ***Diastylis* Say, 1818**

***Diastylis enigmatica rossensis* n. ssp.** (Fig. 1–5)

Material was deposited in the Zoological Museum Hamburg.

Holotype: Incubating female (partially dissected); station R2 74°49.0'S/164°18.1'E, fine sand, 364 m, 21 February 2004.

Paratypes: Subadult female (ZMH 41273), same station data as holotype; both specimen were dissected. Two juvenile females, a juvenile male, and a subadult male (ZMH 41274), station R3 74°49.3'S/164°11.5'E, rocky sand substratum with mud and pebbles, 330 m, 20 February 2004. Juvenile male (ZMH 41275), station SMN 74°43.2'S/164°13.1'E, 366 m, sand with gravel and stones, 20 February 2004.

Description

Adult female. Body length 8.9 mm.

Carapace (Fig. 1), 1.6 times longer as high, with four denticulate transversal ridges; some small simple setae, slightly more concentrated on frontal lobe and on anterior and ventral margin; minor denticulate ridges, with slight variations on both sides of carapace. Eyelobe with two spines; 6 spines on frontal lobe as described in Petrescu and Wittmann (2003), further dorsal spines of varying size along three fourths of carapace length. Pseudorostrum moderately produced, about 1/6 of total carapace length (including pseudorostrum); slightly turning downward. Antennal notch shallow. Lateral lower margin serrated. Integument of segments with honeycomb-like structure; margins with fine serrations. Sternites of last three thoracic segments with median spine decreasing in length. Last pleon segment ventrally with two rows of 5 denticles forming a 'v' opening to the posterior end. Carapace and free thorax segments approximately 1.2 times longer as abdomen.

Antenna 1 (RLP 54/23/23) (Fig. 2e). First article of peduncle bearing three spines on distal margin; one slightly separated from others; a setulate seta at distal margin and a broom seta next to it; some minute and hair-like setae; row of hair-like setae along little more than distal third of article, turning back along integumental fold, and ending with a curved simple seta. Second article with few hair-like setae, proximal end with many hair-like setae; four small simple setae; three minute simple setae and a broom seta close to distal margin. Third article with seta close to distal margin only, two small simple and three broom setae.

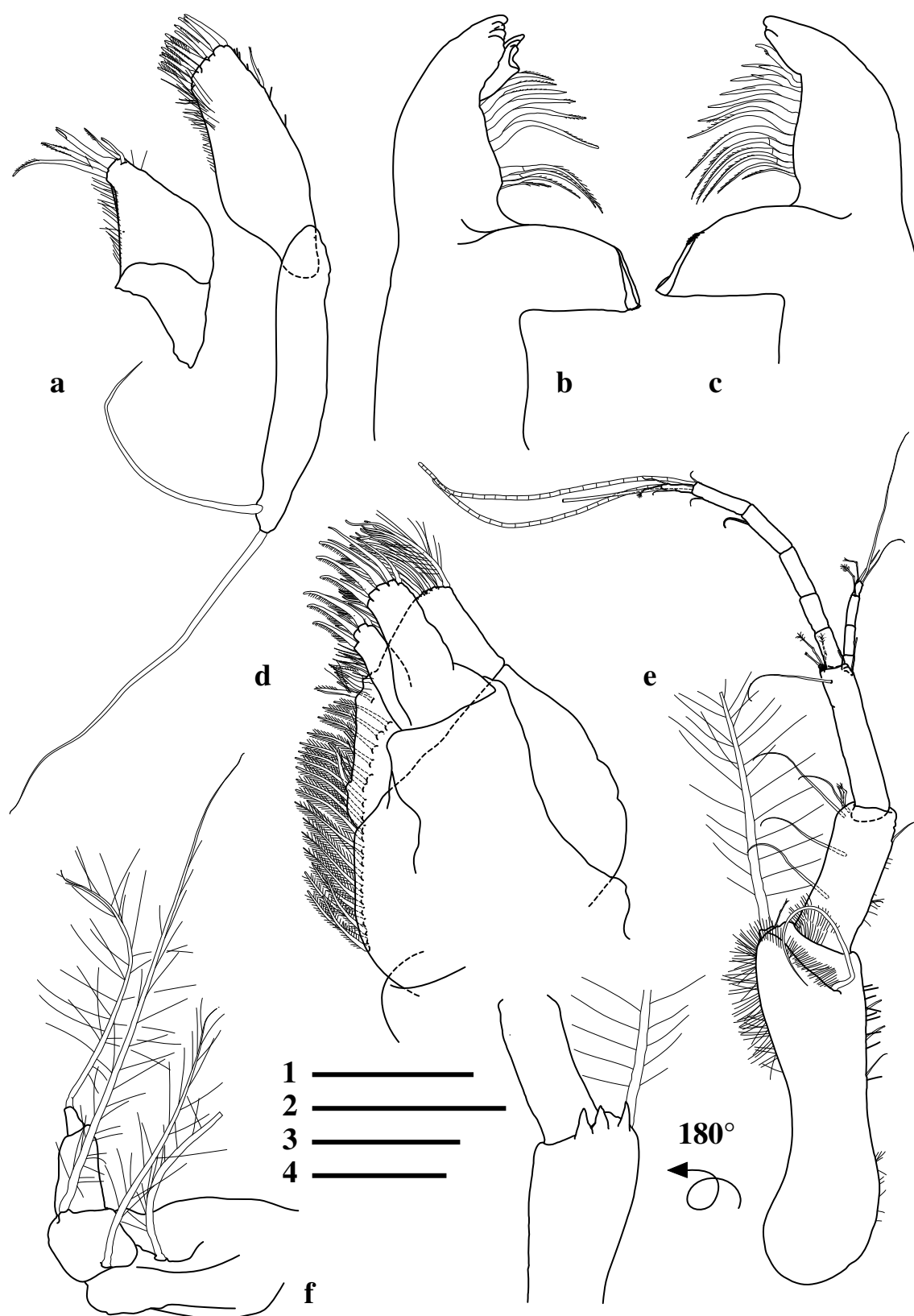


FIG. 2 *Diastylis enigmatica rossensis* n. ssp. Adult female. a, maxilla 1; b, left mandible; c, right mandible; d, maxilla 2; e, antenna 1; f, antenna 2. Scales = 0.2 mm; 1 = a; 2 = d; 3 = e, f; 4 = b, c.

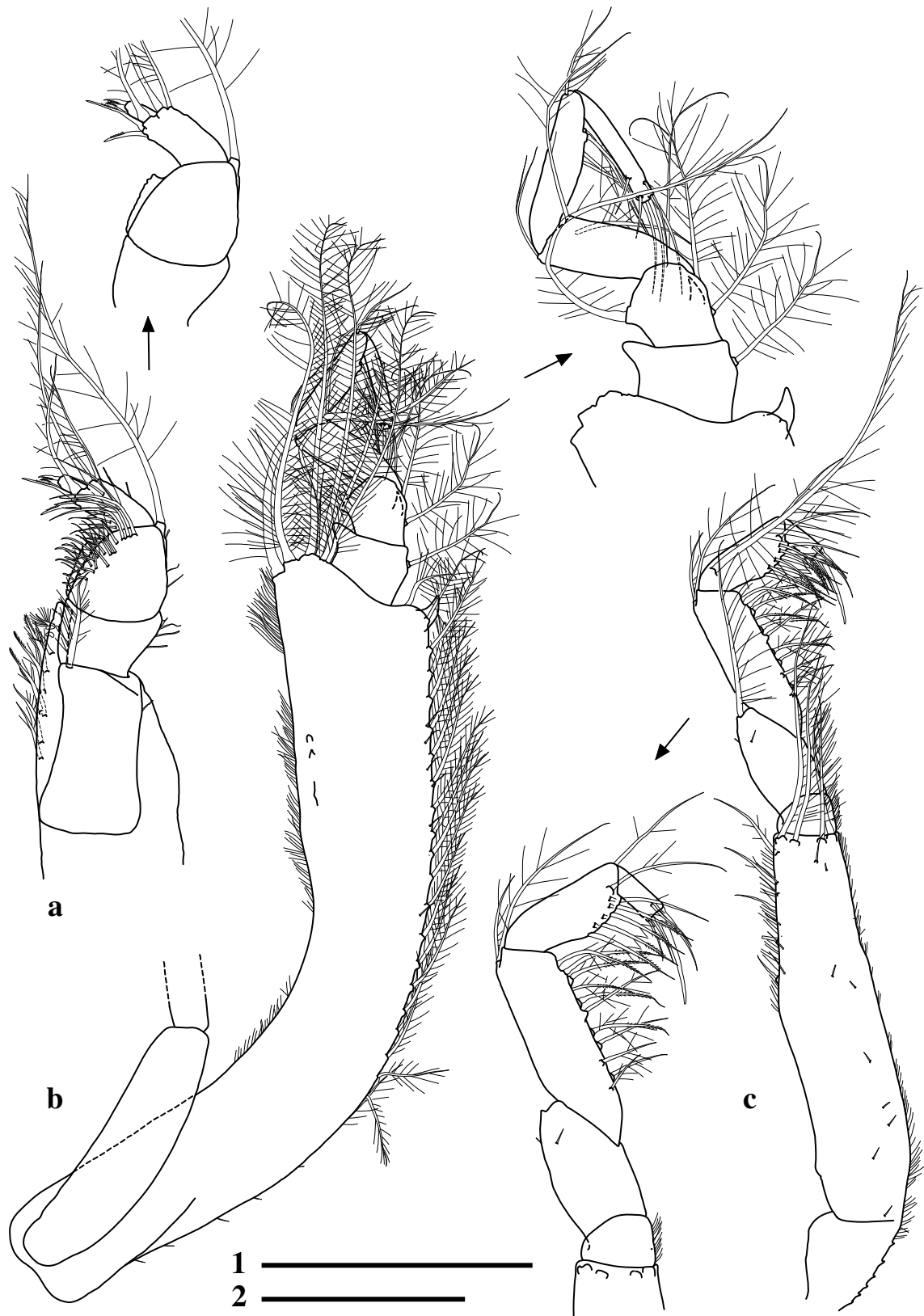


FIG. 3 *Diastylis enigmatica rossensis* n. ssp. Adult female. a, maxilliped 1; b, maxilliped 3; c, maxilliped 2. Scales = 0.5 mm; 1 = a, c; 2 = b.

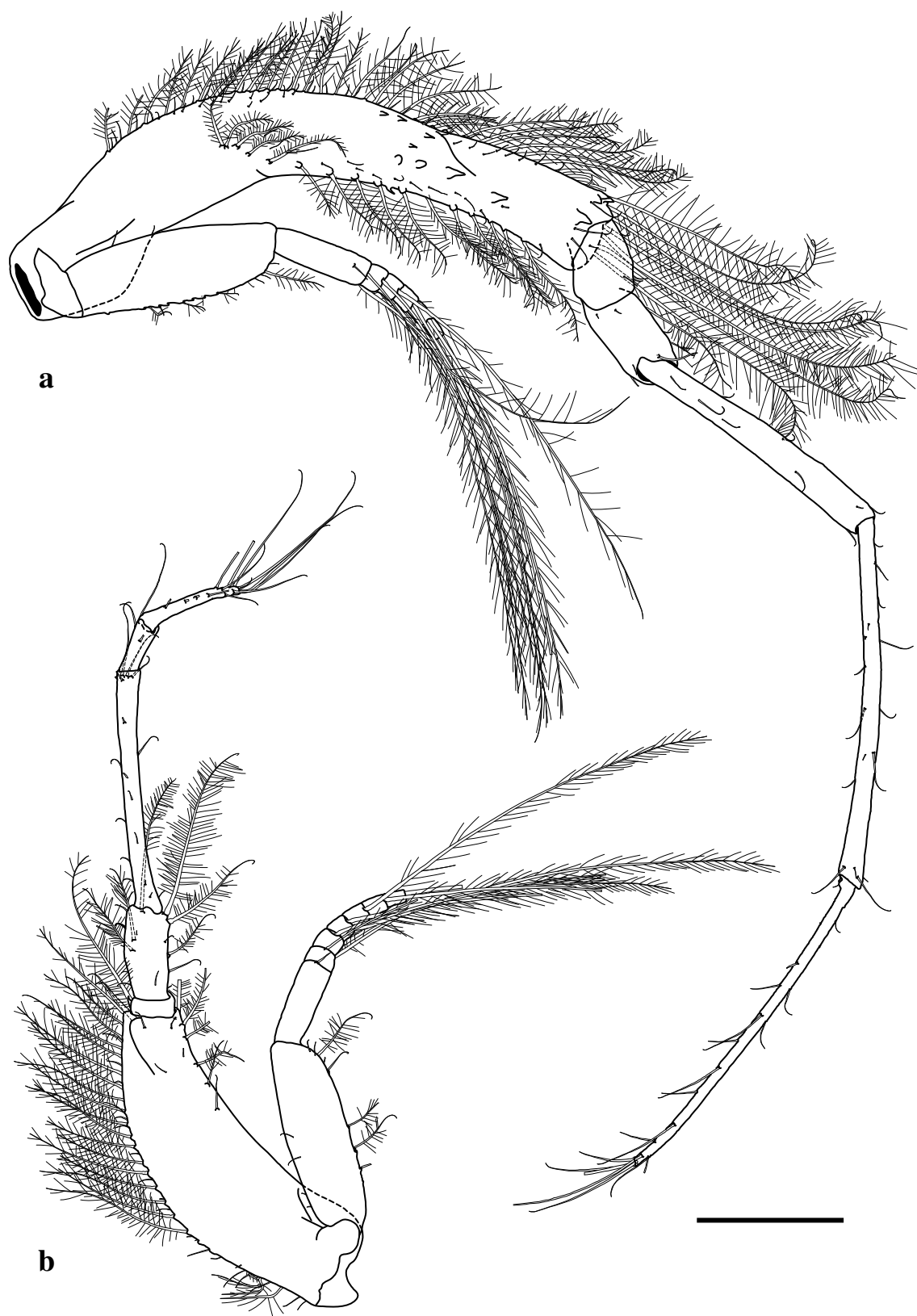


FIG. 4 *Diastylis enigmatica rossensis* n. ssp. Adult female. a, paraeopod 1; b, paraeopod 2. Scale = 0.5 mm.

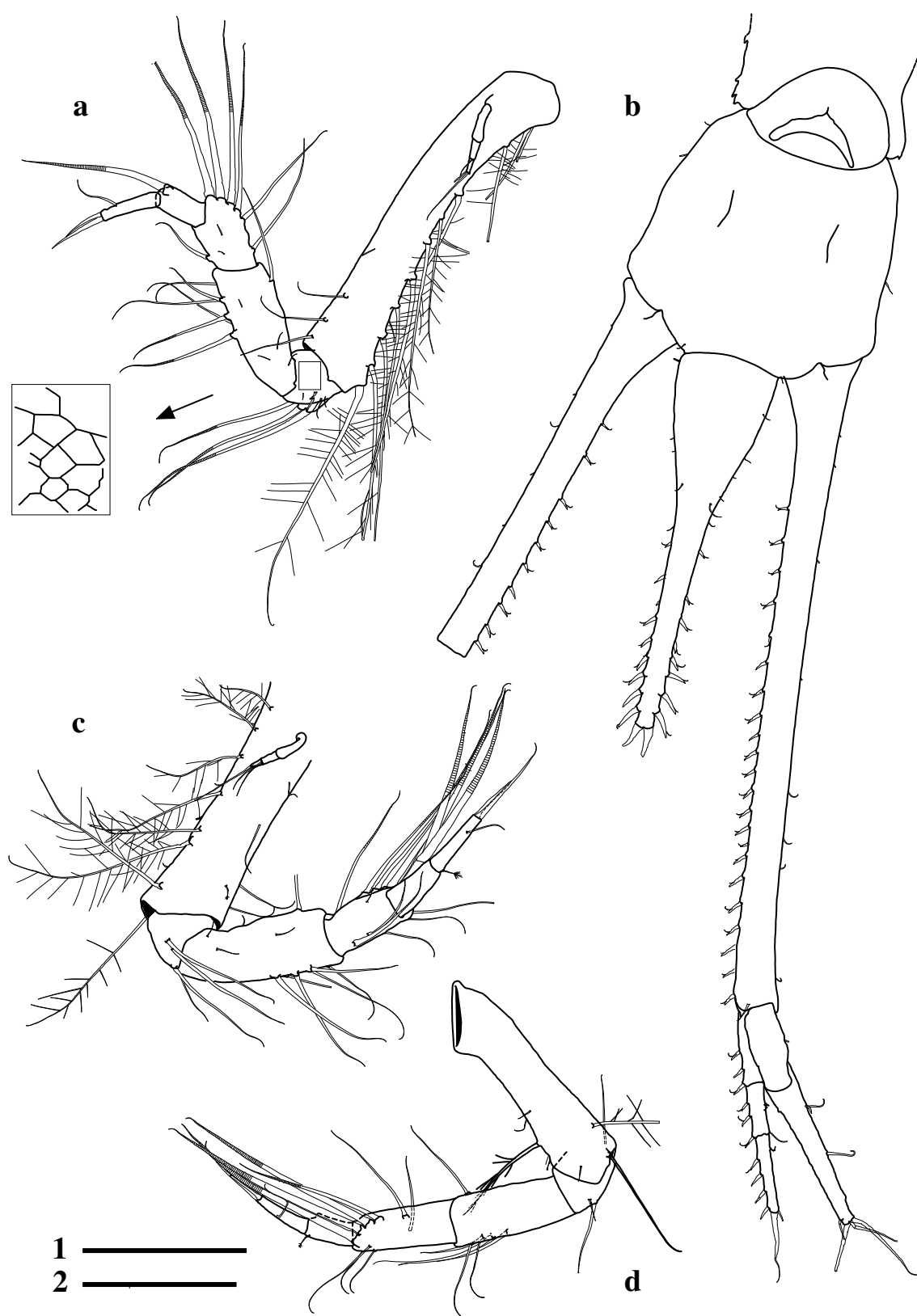


FIG. 5 *Diastylis enigmatica rossensis* n. ssp. Adult female. a, paraeopod 3; b, uropod; c, paraeopod 4; d, paraeopod 5. Scale = 0.5 mm; 1 = a, c, d; 2 = b.

Accessory flagellum with four articles, articles 1 and 4 approximately half as long as articles 2 and 3; first article with a seta (was broken in the specimen), third article with a broom seta, fourth article with a broom seta and three simple setae (1 long, 2 short). Main flagellum with 6 articles; articles 1 and 2 shorter than article 3, article 3 slightly shorter than article 4 and 5, article 6 shortest article; article 4 with a minute simple seta, article 5 distally two minute simple setae and two aesthetascs, article 6 with two minute simple setae, a simple seta (was broken in the specimen), and a broom seta.

Antenna 2 (Fig. 2f). Four articles decreasing in length to tip of antenna, article 3 longer than article 2; first article with a setulate seta; second with two setulate setae, fourth article bearing terminal a setulate seta.

Mandibles (Fig. 2b, 2c). Typical of genus; left mandible lacinia mobilis and 12 or 13 (one or two setae broken off) setae of various shapes (simple and serrate); right mandible with 13 setae of various shape (serrate and bifurcate), most distal seta trifurcate.

Maxilla 1 (Fig. 2a). Outer endite having 14 spiniform simple or serrate setae; single subdistal seta on outer margin; several hair-like setae subdistal and on distal half of margins, only few at inner margin. Inner endite with three serrate setae, a bifurcate seta, and a simple seta of varying size. Palp terminating in two long setae.

Maxilla 2 (Fig. 2d). A row of plumose setae parallel to inner edge of protopod slightly turning outward subdistally; inner edge with some hair-like setae and a serrate seta in distal third; inner distal edge with a setulate-serrate seta; distal margin with setae of various types and shapes (simple, serrate) and a longer setulate seta at outer edge. Outer lobe of endite with three inner serrate setae, three outer simple setae; inner lobe with three inner serrate setae and an outer simple seta.

Maxilliped 1 (B/R 0.6; RLA – /27/32/30/11) (Fig. 3a). Basis with many small hair-like setae (not drawn in the figure), a setulate seta at distal margin; endite with four setulate setae and four setulate-serrate setae at inner margin, two retinacula present. Ischium absent. Merus with three simple setae along distal half of outer margin; a minute seta and a protuberance on outer distal margin; Carpus inner margin with simple setae and a dense group of simple, trifurcate-setulate, and setulate setae close to distal two thirds of inner margin; inner margin with a lamelliform structure; three curved setulate seta on distal margin; three simple setae at outer margin and a large setulate seta at outer distal edge. Propodus, simple and setulate

setae mainly close to outer margin; distal edge with three setulate setae, inner distal edge with 2 serrate setae. Dactylus with two terminal spiniform and serrated setae.

Maxilliped 2 (B/R 1.0; RLA 9/24/34/23/10) (Fig. 3c). Basis, several minute simple setae mainly at proximal part; eight small or minute simple and two small setulate setae along distal outer edge; hair-like setae at outer margin of distal third and along three quarters of inner margin; distal edge with five setulate setae and (one of small size) close to distal margin. Ischium, inner margin with hair-like setae. Merus, outer edge of distal margin with a setulate seta; inner margin with a setulate seta. Carpus, along inner margin 11 setae (setulate and setulate-serrate), two setulate setae close to outer distal edge. Propodus having a large setulate seta proximally; 8 setulate-serrate setae in distal half of inner margin; distal margin with 3 setulate setae. Dactylus, terminal and subterminal four simple setae and a spiniform simple seta.

Maxilliped 3 (B/R 1.4; RLA 14/12/24/28/22) (Fig. 3b). Basis curved, minute simple setae scattered over article more frequent in distal half; outer margin with hair-like setation, proximal third without setation; along inner margin 20 setulate setae; inner distal edge with a curved setulate seta; distal edge with six large setulate setae and a setulate seta of normal size; close to outer margin after distal third two minute spines; a strong spine at inner distal edge, (four spines in a row along inner margin in premature females). Ischium, a setulate seta subdistally at inner margin, outer margin bearing a process subdistally. Merus, two setulate setae at inner margin; a large and curved plumose setae at outer margin pointing inward; close to inner margin a spine. Carpus, two setulate setae, one subdistally and one at outer distal edge; a bifurcated seta at inner distal edge. Propodus, four setulate setae at outer margin, one setulate seta at inner distal edge. Dactylus, six simple setae, two subterminal and four terminal setae.

Paraeopod 1 (B/R 0.5; RLA 7/10/22/32/31) (Fig. 4a). Basis, hair-like setae along margins; four small simple setae at distal margin; a row of 16 setulate setae along upper margin starting subdistally, last six setae turning to midline of article, and ending before proximal third; 45 setulate setae along lower and distal margin; a loose row of small and minute simple setae along both rows of setulate setae, but slightly shifted to midline of article; a row of four spines along midline; a second row of small spines starting after distal first fourth close to lower margin; more small spines less developed (some scale-like) may follow proximal; a spine between 7th and 8th setulate seta of upper margin (probably not in every specimen, as spine was not observed in premature females); a group of three spines at lower distal edge, separated from se a larger spine in middle of distal margin. Ischium, few minute simple setae. Merus, few minute simple spines; two small simple spines and two small

setulate spines distally. Carpus, some small simple setae at proximal part; four small simple setae distally. Propodus, few small simple setae along article; subdistally two simple and a small simple seta. Dactylus eight simple setae of varying size along the article; terminal and subterminal six simple setae.

Paraeopod 2 (B/R 0.7; RLA 4/18/48/10/19) (Fig. 4b). Basis, few minute setae; 25 setulate setae along lower margin; small simple setae along lower margin; four setulate setae at distal fourth of upper margin; a small simple seta on an elevation close to upper distal margin, a spiniform simple seta with a thin and curved tip and a setulate seta at distal end of elevation (drawn with dotted lines, as it was broken off, but was observed in subadult specimens of both sexes), a second seta of that morphology at lower distal margin; a setulate seta at upper distal margin; close to upper distal margin a broom seta. Ischium, small without setation. Merus, some small and minute simple setae, upper margin with a simple and a setulate seta; lower margin with a setulate seta; distal edge with four setulate seta. Carpus, some simple seta of varying size along article, distally five simple setae of varying size. Propodus, distal lower margin with a simple seta and a small simple seta; a broken subdistal seta; distally a broom seta and second broken seta. Dactylus, four seta along article (broken), five simple subdistal setae, and four terminal large simple setae.

Paraeopod 3 (B/R 1.0; RLA 15/36/21/12/15) (Fig. 5a). Basis, 11 setulate setae along lower margin; close to upper margin in distal half three simple setae and a broken seta; integument of distal and proximal margin with a honeycomb-like structure (not drawn, compare Fig. 5a). Ischium, with a honeycomb-like structure (partially drawn only; Fig. 5a); five small simple setae close to lower margin; three large annulated setae at lower margin. Merus, three simple setae and three annulated setae at lower margin; an annulated seta at upper margin. Carpus, an annulated seta at lower margin and two annulated setae at upper margin; upper distal margin with four long and strong annulated setae. Propodus upper distal margin with a strong annulated seta. Dactylus, a simple seta and two spiniform terminal setae. Exopod, poorly developed with three articles; second articulation with three simple setae; terminating with a plumose seta.

Paraeopod 4 (B/R ?; RLA 14/39/17/14/16) (Fig. 5c). Basis (not completely preserved); few minute simple setae; seven setulate setae at upper margin,

increasing in size to distal margin; a setulate seta at upper distal margin; three simple, and a broom seta at lower margin; distal margin with a honeycomb-like structure (compare Fig. 5a). Ischium with a honeycomb-like structure (compare Fig. 5a), two annulate setae; at upper distal edge an annulate seta and a small simple seta. Merus, minute simple seta at lower margin; an annulated seta distally at lower margin; three annulated setae and two simple setae at distal half of upper margin. Carpus, three simple setae at distal half of upper margin; five long and strong annulated setae along distal half of lower margin and distal margin; lower margin with a proximal annulate seta. Propodus, strong annulated seta at lower margin and broom seta distally. Dactylus, two terminal setae, one simple and one spiniform. Exopod, poorly developed with two articulations; terminating with three simple setae.

Paraeopod 5 (B/R 0.5; RLA 16/31/26/12/15) (Fig. 5d). Basis, few minute setae; upper and lower margin with a setulate seta each; two simple seta at upper distal margin; upper distal edge and distal margin with a broom seta; further broom seta in the upper middle of article; honeycomb-like structure at distal and proximal margin (compare Fig. 5a). Ischium, with a honeycomb-like structure (compare Fig. 5a); lower distal margin with a small simple and a simple seta. Merus, few minute setae; distally a simple seta at upper margin; two simple setae and three annulated seta in distal half of lower margin; distal margin with a simple seta. Carpus, two annulated setae; three simple setae at lower distal margin; a row of four long and strong annulated setae close to upper distal margin. Propodus, lower distal margin with a broom seta; upper distal margin with a strong annulated seta. Dactylus, with a simple seta and a strong terminal seta. Exopod, absent.

Uropod (Fig. 5b). All spiniform setae with a filament. Peduncle, three times longer than endopod. Inner margin of peduncle with 22 short spiniform setae; a simple seta at distal margin. Exopod, 1.2 times longer than endopod; outer margin with two small simple setae and two minute simple setae; subterminal a small simple seta and three terminal simple setae. Endopod triarticulate; inner margin of first article with three short spiniform setae; inner margin of second article with four short spiniform setae; outer margin of second article with two broom setae and a simple seta distally; inner margin of third article with four short spiniform setae; outer margin of third article with a broom seta; terminal with a small simple seta and a strong seta with a terminal filament. Telson 0.6 times length of peduncle; some small and minute simple setae on broader proximal part of telson; eight short spiniform setae on both sides of distal part, enlarging to distal end; two distal spiniform setae.

Subadult males. Second antenna incompletely developed and lacking articulation and setae, reaching posteriorly to abdomen. Median row of spines of paraeopod 1 comprising about 15 spines;

Table 1 Differences observed in the different specimens of *Diastylis enigmatica* between the Weddell Sea and the Ross Sea and between different developmental stages

	female Ross Sea	sa female Ross Sea	sa male Ross Sea	sa female Weddell Sea ³	juv female ¹ Ross Sea	juv female ² Ross Sea	juv male ¹ Ross Sea	juv male ² Ross Sea	juv male Weddell Sea ⁴
R UP to last Pleon segment	3.1	2.8	2.8	2.2	2.7	2.3	2.9	2.9	?
R UP to exopod	2.7	?	2.1	2.3	1.9	1.8	2.1	1.8	?
R postanal to preanal part of telson	1.9	1.4	2.0	~1.2	1.3	1.2	1.4	1.4	2 ⁵
R distal to proximal part of P1	1.3	1.2	1.2	1.0	1.3	1.2	1.1	1.1	1.2
Transverse dent ridges on pr lobes	4	4	4	5	4	4 ⁶	4	4	3
Satation of endopod of Uropod	3/3/4	3/3/4	3/4/4	5/4/3	3/3/3	2/2/2	3/3/3	2/2/3	?
Number of spines ⁷ on basis of Mp3	4	4	5	5	3	2	5	3	3
Number of spines on merus of P2	0	0	0	4	0	0	0	0	0
Gap between spines of basis of A1	+	+	-	-	+	+	+	+	?
Number of spines on Ped of A1	3	3	7	3	3	2	3	?	?
Number of articles of MF/AF of A1	6/4	6/4	6/4	3/3	5/3	4/3	4/3	3/3	?

A1: Antenna 1, AF: accessory flagellum, MF: main flagellum, Mp: Maxilliped, dent: denticulate, juv: juvenile, P: paraeopod, Ped: peduncle, pr: pseudorostral, R: ratio, UP: uropodal peduncle; ¹older stage than in Ledoyer (1993), ²same stage as in Ledoyer (1993), ³Petrescu and Wittmann (2003), ⁴Ledoyer (1993), ⁵the text of the original description differs to the drawing, in which the postanal part is as long (or even longer) as the preanal part; ⁶one only weakly developed; ⁷the maximum number observed is given, but may be less as the spines seem to be broken off or not developed (numbers may vary in the same specimen).

lower margin with six spines more developed than in female. Basis of maxilliped three with five spines along inner distal margin, instead of four as in the female. Exopods developing on maxilliped 3 and on paraeopods 1–4. Pleopod buds present on abdominal segments 1 and 2, with 3 or 4 minute setae distally.

Discussion

In all specimens of the present study the ratio of telson length vs. uropodal peduncle was 0.6, as described by Petrescu and Wittmann (2003). In the description of Ledoyer (1993) the exopod of the third paraeopod has two segments, whereas in Petrescu and Wittmann the exopod is three-segmented. During the present study it was possible to explain this variation by sexual dimorphism, as juvenile males were collected, which have two-segmented exopods, whereas the exopods of juvenile females are three-segmented. Concluding from the number of segments and the large size of the exopod, the specimen of Ledoyer must have been a juvenile male. In Petrescu and Wittmann the length of the postanal part of the telson from Ledoyer's description is mentioned as being smaller than the preanal part. This ratio is probably obtained from the drawing, but in the text Ledoyer described the telson as being three times longer than the preanal part.

Presently, two subspecies of *Diastylis enigmatica* are distinguished according to differences found from the description of Petrescu and Wittmann (2003) to the material of the Ross Sea (Table 1). Due to obscure or contradicting morphological characters of the first description of *Diastylis enigmatica* (Ledoyer 1993) it is impossible to assign it to one of the subspecies. This problem can be addressed in the future, when further material from the type locality (Weddell Sea), including adult males and females, is available. Nevertheless, the

geographical distribution supports the assumption that both descriptions from the Weddell Sea refer to the same subspecies *Diastylis enigmatica enigmatica*. The second subspecies, *Diastylis enigmatica rossensis*, was found only in the Ross Sea.

The study of the Ross Sea cumacean fauna revealed minor morphological differences in some of the cumacean species to the original descriptions (Rehm et al. 2007). For the species *Diastylis enigmatica* these differences are interpreted as differences between subspecies, but future genetic analysis might show that genetic diversity is higher than would be expected to be intraspecific. Genetic variability of the mitochondrial 16S ribosomal RNA gene gave first evidence for cryptic speciation in the Antarctic isopods *Glyptonotus antarcticus* Eights, (1852) and *Ceratoserolis trilobitoides*, Eights, (1833) (Held and Wägele 2005, Held 2003). *Ceratoserolis trilobitoides* was regarded as a single species with high morphological plasticity (Wägele 1986), but genetic and morphological data support a scenario of cryptic speciation with more than one species (Held and Wägele 2005).

Peracarid crustaceans display brood protection, which results in a reduced dispersal potential and might lead to reduced gene flow. As isopods and cumaceans belong to the peracarid crustaceans they possibly exhibit similar speciation patterns. In that case it would be very likely that the two subspecies of *Diastylis enigmatica* are separate species.

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PUBLICATION V

***Leucon (Crymoleucon) rossi*, a new species (Crustacea: Cumacea: Leuconidae), from the shelf waters of the Ross Sea (Antarctica), with a key to the genus *Leucon* south of 60°S**

PETER REHM¹ and RICHARD W. HEARD²

¹Alfred Wegener Institute for Polar and Marine Research (AWI), Marine Animal Ecology, Am Alten Hafen 26, 27568 Bremerhaven, Germany. E-mail: peter.rehm@awi.de

²Department of Coastal Sciences, University of Southern Mississippi, P.O. Box 7000, Ocean Springs, MS 39566-7000, USA.

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SUMMARY: A new leuconid cumacean, *Leucon (Crymoleucon) rossi* n. sp., is described from depths of 84 to 458 m in the Ross Sea off the Victoria Land coast. *Leucon rossi* n. sp. is distinguished from other members of the genus by a combination of characters including 1) a blunt, horizontally directed pseudorostrum lacking distinctly protruding siphon; 2) strongly developed antennal notch; 3) entire dorsomedian margin of carapace appearing serrate, armed with 14-19 anteriorly curved spines in female (up to 21 in subadult males); 4) a small, but distinct, spine behind the frontal lobe; and 5), the uropodal peduncle slightly shorter than the exopod. After *Leucon antarcticus* Zimmer, 1907, *L. rossi* was the second most frequently occurring cumacean in the samples collected off Victoria Land. Statistical analyses showed significant differences in the proportion of carapace length and height of adult and immature females to immature males; no adult males were available for study.

Key words: Crustacea, Cumacea, Leuconidae, *Leucon rossi*, new species, Antarctica, Ross Sea.

RESUMEN: Se describe un nuevo cumáceo, *Leucon (Crymoleucon) rossi* n. sp., hallado entre los 84 y 458 m de profundidad en el Mar de Ross, frente a la costa de la Tierra de Victoria. *Leucon rossi* n. sp. se distingue de los otros miembros del género por poseer la siguiente combinación de caracteres: 1) un pseudorostrum truncado, horizontal, sin un sifón proyectándose más allá de este; 2) una escotadura antenal bien desarrollada; 3) el margen dorsal del caparazón aserrado en toda su extensión, con 14-19 dientes dirigidos hacia adelante en la hembra (hasta 21 en el macho subadulto); 4) una pequeña espina por detrás del lóbulo frontal; y 5) el pedúnculo del urópodo es ligeramente más corto que el exopodito. Luego de *Leucon antarcticus* Zimmer, 1907, *L. rossi* fue el cumáceo más abundante en las muestras recolectadas frente a la costa de Tierra de Victoria. La proporción alto/largo del caparazón de las hembras inmaduras y adultas difiere estadísticamente de aquella de los machos adultos. No se contó con machos adultos para su estudio.

Palabras clave: Crustacea, Cumacea, Leuconidae, *Leucon rossi*, nueva especie, Antártida, Mar de Ross.

INTRODUCTION

Leucon antarcticus, Zimmer 1907 is the only species of the genus *Leucon* Krøyer, 1846 currently reported from the Ross Sea (Jones, 1971). During the Victoria Land Transect Project onboard the Italian research vessel *Italica* in 2004, five additional species of the genus were obtained: *Leucon assimilis* Sars, 1887; *Leucon intermedius* Mühlenhardt-Siegel, 1996; *Leucon parasiphonatus* Mühlenhardt-Siegel, 1994; *Leucon* cf. *sagitta* Zimmer, 1907; and a new species, *Leucon* sp. A (Rehm et al., 2007), the description of which is the subject of this report.

MATERIAL AND METHODS

The material of *Leucon rossi* was collected during the 19th expedition of RV *Italica* to the Ross Sea. From February 9 to 22, 2004, 13 of 19 samples containing specimens of the species

were collected off the coast of Victoria Land with a modified Rauschert dredge (compare Rehm et al., 2006). For detailed data on the stations and further information on the species diversity and distribution see Rehm et al. (2007; there *Leucon* sp. A refers to *L. rossi*).

Drawings were created from digital photographs using a digital drawing tablet as described by Coleman (2003, 2006). Measurements of body dimensions were statistically compared using the Mann-Whitney Rank Sum Test. Body length is measured from the tip of the pseudorostrum to the tip of the pleotelson. Carapace length is measured from the tip of the pseudorostrum to the posterior margin of the carapace, whereas carapace height is measured from the ventralmost to the dorsalmost margins. Length of articles are measured according to Mühlenhardt-Siegel (2005) and given as relative length of peduncle articles 1 to 3 of antenna 1 compared to total peduncle length (RLP). The ratio basis to rest (B/R) is given for maxillipeds and pereopods, which is the

proportion of the basis to the combined length from ischium to dactylus, not including terminal seta. RLA refers to the relative length of each article from ischium to dactylus, excluding terminal seta.

Type material has been deposited in the Zoological Museum Hamburg (ZMH) and in Senckenberg Museum, Frankfurt (SMF). Additional paratypes have been deposited in the Museum of the University of Southern Mississippi Gulf Coast Research Laboratory (GCRL).

RESULTS

Family LEUCONIDAE Sars, 1878

Genus *Leucon* Krøyer, 1846

Subgenus *Crymoleucon* Watling, 1991

***Leucon (Crymoleucon) rossi* sp. n.**

(Figs. 1-4)

Synonym. *Leucon* sp. (A Rehm et al. 2007)

Material examined. Holotype. Incubating female (ZMH K-41271). *Type locality.* Station SMN: 74°43.2' S/164°13.1' E, sand substratum with gravel and stones, 366 m, 20 February 2004. *Paratypes.* 4 incubating female, 1 premature female, 5 premature males (ZMH K-41272) same collection data as holotype; 2 incubating females (SMF 31783) same collection data as holotype; 3 premature females, 2 premature males (SMF 31784) Station R3: 74°49.3' S/164°11.5' E, rocky sand substratum with mud and pebbles, 330 m, 20 February 2004.

Etymology. The new species is named after the Antarctic explorer Sir James Clarke Ross (1800-1862), who discovered Victoria Land, the Ross Sea, and Ross Island

Diagnosis. Pseudorostrum blunt, protruding horizontally. Carapace with 14-19 anteriorly curved spines along entire dorsomedian margin; single small, distinct, spine behind the frontal lobe. Antennal notch large and well developed. Peduncle of uropod slightly shorter than exopod.

Description. Adult female.

Carapace (Fig. 1B), without setae, ridges or tubercles, but with single spine directly behind frontal lobe; surface granulated. Dorsomedian line entirely serrated, bearing 14 to 19 denticles, first and last two often very small or weakly indicated. Pseudorostrum moderately produced, about 1/6 of total carapace length (including pseudorostrum), directing forward; anterior margin with 5 to 7 serrations, ventral margin with few (up to nine) minute serrations, with 8-13 setae on anterior and ventral margin. Siphonal tube not discernable. Eye lobe rudimentary, eyes missing. Antennal notch distinct. Ventral margin of carapace strongly serrated starting with forward pointed spine at antero-ventral edge. First and second free thoracic segments overlapped by the antero-lateral margin of the

following segments. Pleon approximately as long as cephalothorax, with a pair of pleopods on first and second segments; pleonite 6 shorter than uropod peduncle. For dimensions of body see Table 1.

Antenna 1 (RLP 25/32/43) (Fig. 1A). Peduncle geniculate between basal and second article. First article with group of three sensory setae close to distal margin, next to these sensory seta, and plumose seta on distal third of article; proximal half of article with several hair-like setae. Second article with simple seta and sensory seta close to distal margin, group of three sensory on tubercle close to distal margin. Third article with seta near distal end and two composed setae at distal margin. Accessory flagellum uniarticulate slightly longer than article 1 of main flagellum; with 3 strong bifurcate terminal setae and a sensory seta. Main flagellum with 3 articles; article 2 bearing seta and single aesthetasc; terminal article (article 3) about one fourth length of articles 2 and 1, with an aesthetasc, 2 simple seta, and two long terminal setae

Antenna 2 (Fig. 1D). Diminutive; peduncle slightly shorter than wide, with two plumose setae. Flagellum 2 articulate; article 1 slightly shorter than wide, about one third of size of article 2, with one simple seta; article 2 cylindrical, nearly equal in size of peduncle; terminal 3 sensory setae.

Mandibles (Fig. 1F-H). Left mandible, lacinia mobilis and a simple seta between molar and incisor process. Right mandible with single stout seta bearing denticles on inner margin distally and two simple setae between incisor and molar processes.

Maxilla 1 (Fig. 1E). Outer endite having 10 stout spiniform setae, single subdistal curved seta inserted on outer margin. Inner endite with two minute simple setae, two plumose setae of intermediate length, and two long plumose setae, innermost ending trifurcate; inner edge with hair-like setae. Palp ending in single seta.

Maxilla 2 (Fig. 1C). Distal margin of protopod with row of plumose setae and long simple setae at outer distal edge. Outer lobe of endite with 4 stout setae, outer most plumose; inner lobe of endite with 4 stout setae. Inner margin with hair-like setae.

Maxilliped 1 (B/R 0.5; RLA -/25/33/26/17) (Fig. 2A). Endite of basis with plumose setae at inner margin and distal end; 2 retinacula present. Ischium not present. Strongly developed plumose seta between basis and merus (probably inserting at basis) directed proximally turning 180° at about half length of endite of basis, slightly exceeding endite. Merus with two plumose seta on inner edge of distal margin. Numerous simple setae at and close to inner margin of carpus and propodus. Carpus with large plumose seta on distal outer margin.

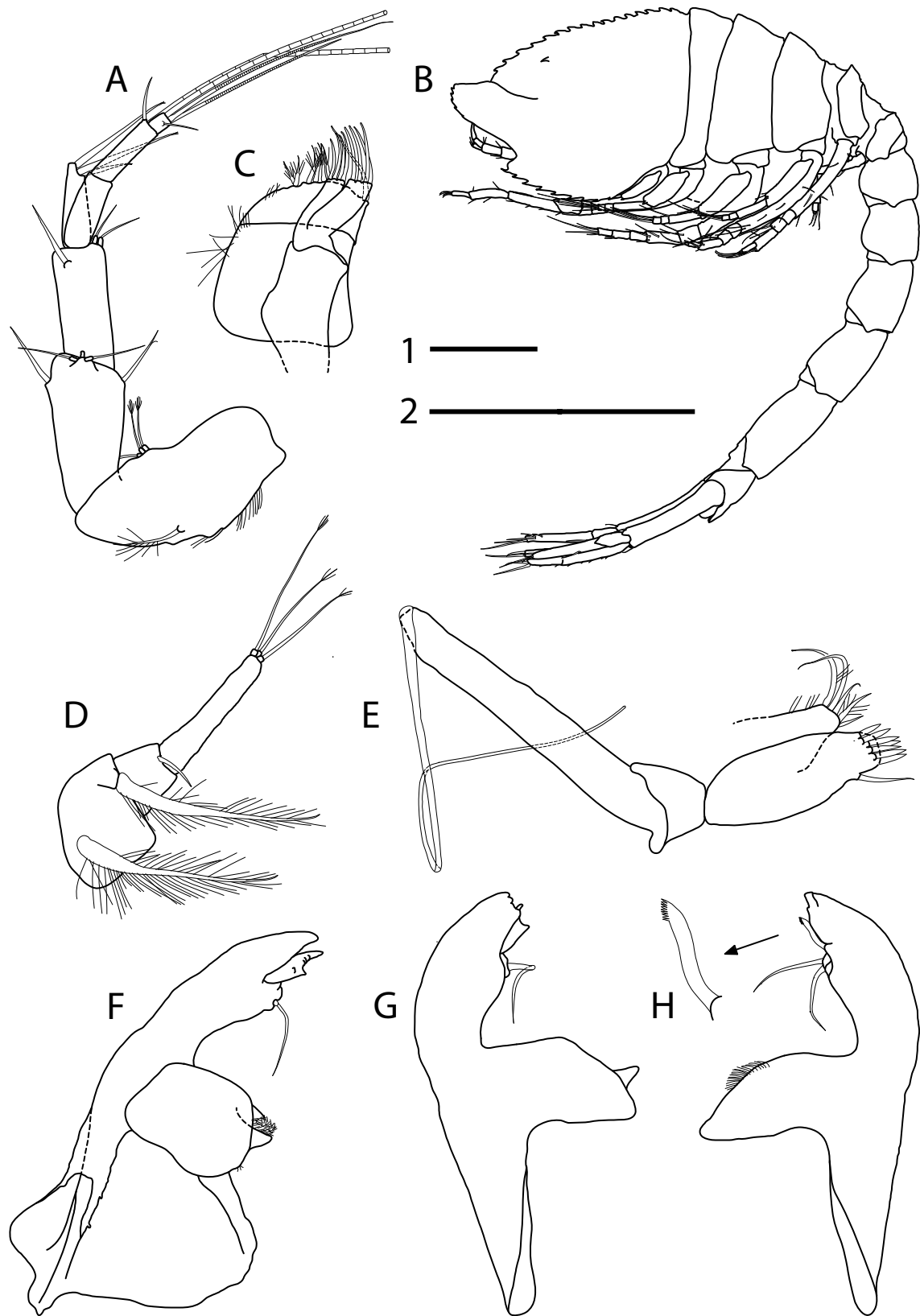


FIG. 1. – *Leucon* (*Crymoleucon*) *rossi* n. sp. Ovigerous female. A, antenna 1; B, habitus; C, maxilla 2; D, antenna 2; E, maxilla 1; F, left mandible, inner aspect; G, left mandible; H, right mandible. Scale 1 = 0.2 mm (A, C-H); Scale 2 = 0.5 mm (B).

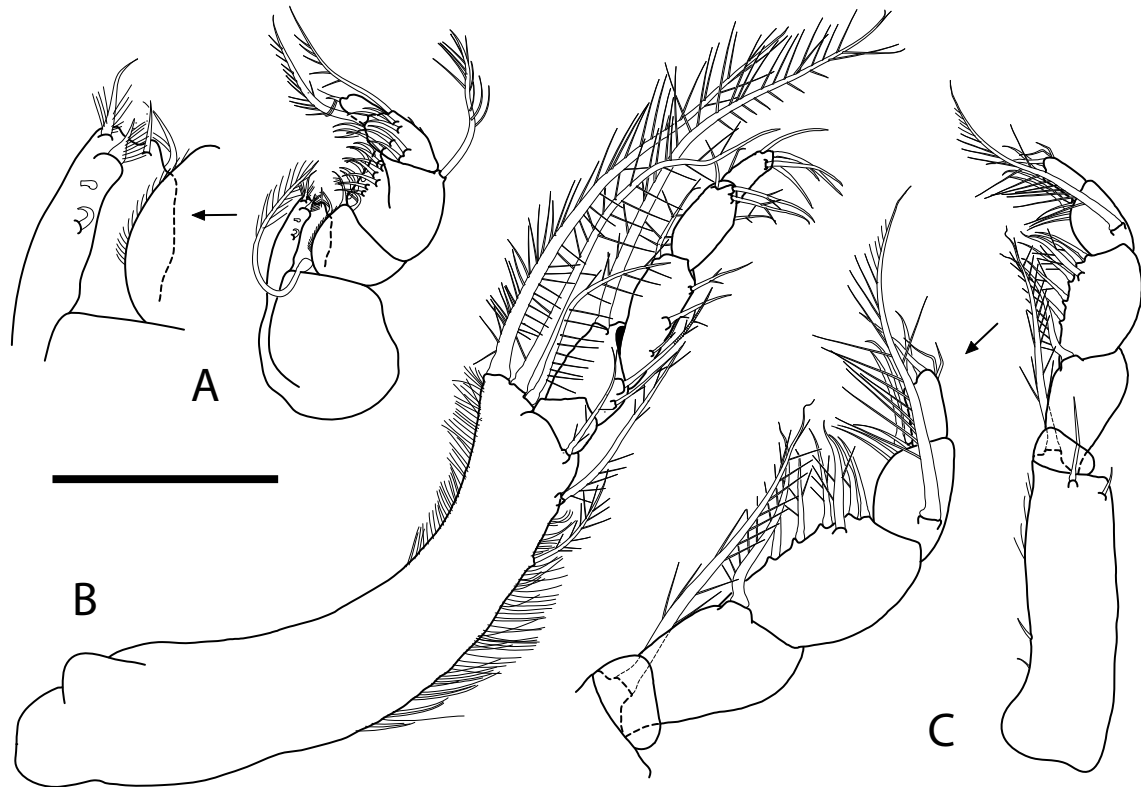


FIG. 2. – *Leucon* (*Crymoleucon*) *rossi* n. sp. Ovigerous female. A, maxilliped 1 (palp not shown); B maxilliped 3 (exopod not shown); C, maxilliped 2. Scale = 0.2 mm.

Propodus with 2 large plumose setae, one at distal end and one on outer margin. Dactylus with single plumose seta distally.

Maxilliped 2 (B/R 0.7; RLA 9/28/30/21/12) (Fig. 2C). Basis, two small simple setae at inner margin and several small hair-like setae at inner margin of distal third, close to distal margin simple seta and small simple seta, inner edge of distal margin with strong plumose seta. Merus, inner edge of distal margin with strong plumose seta. Carpus, along inner margin five setae, all but distal most seta plumose, two plumose setae close to inner margin. Propodus having well-developed plumose seta proximally, distal margin with several simple and plumose setae. Dactylus, terminal two plumose setae, few simple setae, and hair-like setae.

Maxilliped 3 (B/R 1.5; RLA 7/24/30/25/13) (Fig. 2B). Basis curved, distal half of inner margin and distal third of outer margin with hair-like setae, 4 plumose setae at distal margin, 2 well-developed and extending beyond dactylus, 2 plumose setae at distal fourth of inner margin; ischium present; merus with 2 plumose setae close to inner margin, one annulated and one strong, long, and plumose seta distally at outer margin; carpus with 3 plumose setae at inner margin and 1 plumose seta distally at outer margin; propodus distally 3 plumose setae and simple seta; dactylus small setae on outer proximal margin, two seta subterminal, three

terminal setae; exopod with spine on distal margin of basal article.

Pereopod 1 (B/R 0.9; RLA 11/19/30/24/17) (Fig. 3A). Basis with 4 small sensory setae at proximal half of lower margin, distal half with 2 plumose setae, close to distal margin one plumose seta, one long plumose seta, and sensory seta; ischium with tooth at distal lower margin; merus, plumose, long and plumose seta at upper margin, simple seta at lower margin; carpus, 2 plumose and 2 long and plumose setae at upper margin, 3 simple setae at lower margin, 2 long plumose setae at distal margin; propodus, 9 simple setae of very small to moderate size; dactylus, small seta and strong seta at distal third, terminal 4 strong and small seta; exopod with spine at distal margin of basal article.

Pereopod 2 (B/R 0.4; RLA 5/20/29/14/32) (Fig. 3C). Basis, 2 small simple setae at margin of proximal third, simple seta close to distal margin, 4 plumose setae at distal half of lower margin; ischium, a plumose seta at edge of lower distal margin; merus, 2 plumose, 2 sensory, and simple seta close to distal margin. Carpus, 2 simple and sensory seta at margins; a plumose, 2 simple, and sensory seta at distal margin; propodus, no setae; dactylus with 3 simple seta, terminal 2 simple, 2 annulated, and a elongated annulated seta; exopod with spine at distal margin of basal article.

Pereopod 3 (B/R 1.7; RLA 17/19/37/20/7)

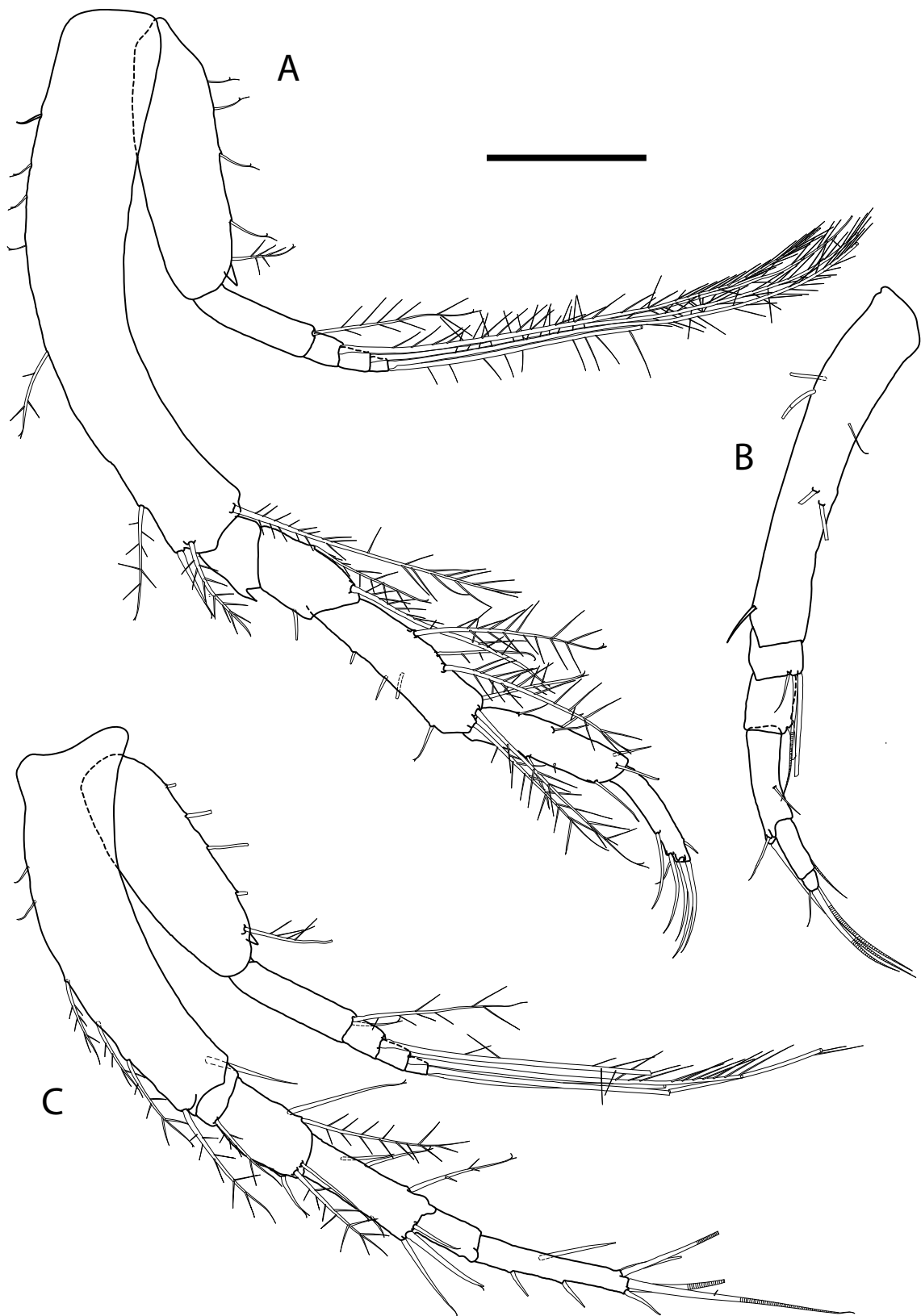


Fig. 3. – *Leucon* (*Crymoleucon*) *rossi* n. sp. Ovigerous female. A, pereopod 1; B, pereopod 4; C, pereopod 2. Scale = 0.2 mm.

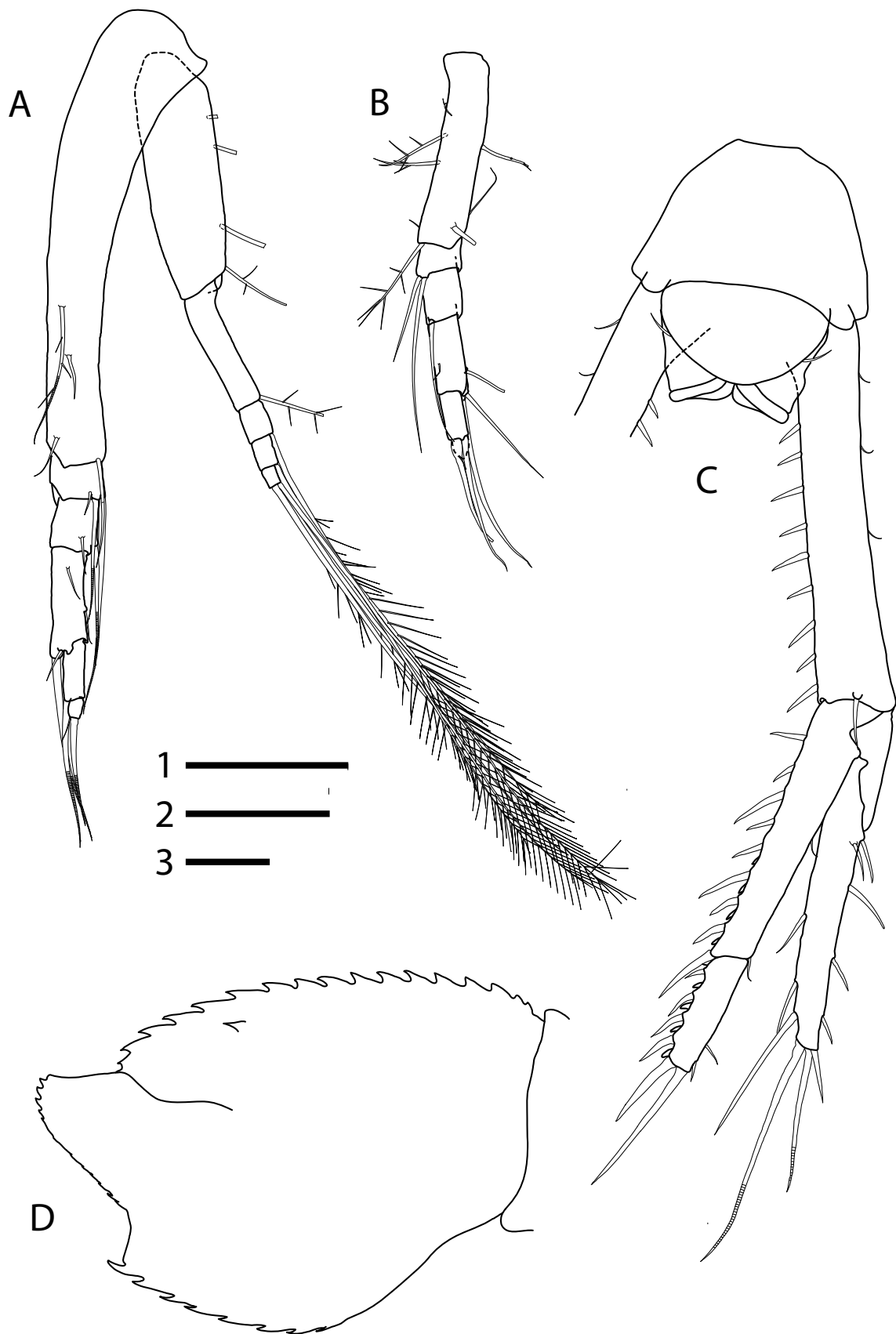


FIG. 4. – *Leucon* (*Crymoleucon*) *rossi* n. sp. Ovigerous female. A, pereopod 3; B, pereopod 5; C, pleotelson and right uropods. *Leucon* (*Crymoleucon*) *rossi* n. sp. subadult male. D, carapace. Scale 1 = 0.2 mm (A,B); Scale 2 = 0.2 mm (C); Scale 3 = 0.2 mm (D).

(Fig. 4A). Basis, 2 simple and plumose annulated seta at distal third, simple seta at edge of distal margin; ischium, small simple seta close to distal margin, 2 strong annulated setae at edge of distal margin, one reaching tip of dactylus; merus, simple seta close to distal margin and strong annulated seta at edge of distal margin; carpus, small simple seta in proximal and distal part each, small simple seta, strong and annulated seta and blunt tooth-like structure at distal margin; propodus cylindrical with strong annulated seta at distal margin; dactylus, terminal small seta and strong annulated seta; exopod with spine at distal margin of basal article.

Pereiopod 4 (B/R 1.3; RLA 18/19/37/19/7) (Fig. 3B). Basis, with 5-7 plumose setae, 2 sensory setae, and simple seta in proximal half of article, simple seta at lower edge of distal margin; ischium, small simple seta close to distal margin, 2 longer setae at edge of upper distal margin (one annulated); merus, strong seta close to edge of upper distal margin; carpus, small simple seta at middle of article, at edge of lower distal margin small simple seta and strong, elongated, and annulated seta; propodus, annulated seta distal at upper margin, strong annulated seta at distal margin; dactylus, small simple seta and strong annulated terminal seta; exopod with spine at distal margin of basal article.

Pereiopod 5 (B/R 0.9; RLA 17/23/34/16/10) (Fig. 4B). Basis, small sensory seta, 2 simple seta (one minute), 4 plumose setae and plumose setae at distal margin; ischium with two annulated seta at edge of distal margin; merus, annulated seta close to distal margin; carpus, 2 simple setae (one minute), 2 annulated setae at edge of distal margin (one strong and elongated); propodus, strong (annulated) seta at distal margin; dactylus small seta and annulated seta distally; exopod in premature males only.

Uropod (Fig. 4C). Length of peduncle and endopod equal; inner margin of peduncle with about 8-9 stout spiniform setae, outer margin with few (3-4) hair-like setae, simple seta at distal margin. Exopod 0.9 times length of endopod. Endopod two segmented, inner margin of basal article of endopod with 9 stout spiniform setae, between distal 6-7 minute stout spines each, outer distal edge with simple seta. Inner margin of distal article with 4 stout spiniform setae and 4 stout minute spines alternating; 2 terminal setae; outer margin of distal article with two small simple setae. Inner margin of exopod with 2 simple setae and longer seta, outer margin with 5 setae, terminal two long annulated setae and shorter seta.

Subadult males. Second antenna incompletely developed and lacking articulation and setae, reaching posteriorly to free thoracic segments. Carapace (Fig. 4D) with dorsomedian margin

bearing more denticles than in females (up to 21); denticles of ventral margin of pseudorostrum in premature males more distinct. Exopods developing on pereopods 1-4 and on maxilliped 3; the spine at the distal margin of the basal article in females is followed by one or two additional spines in the subadult males. Pleopod buds present on abdominal segments 1 and 2, with 3 or 4 minute setae distally.

Remarks. *Leucon* (*Crymoleucon*) *rossi* n. sp. resembles *L. (Crymoleucon) antarctica* Calman Zimmer, 1907 by the general shape of the carapace, which is slightly stouter in *L. rossi*. Both species have an uninterrupted row of dorsomedian denticles from the eyelobe to the posterior margin. They may be distinguished by the lateral spines on the carapace. Only a single spine is situated dorsal directly behind the frontal lobe in *L. rossi*, whereas *L. antarctica* is armed with a spine on the border of the frontal lobe, closely to this spine is a second on the rostral lobe. A third spine is located below the serrate ridge in a similar position as in *L. rossi*. In addition 2 or more spines are placed in the gastric region. The pseudorostrum of *L. rossi* is blunt and directing straight forward, while in *L. antarctica* it is pointed and slightly turned upward. The uropod peduncle is slightly shorter than the exopod and equal to the endopod in *L. rossi* and differs to the peduncle of *L. antarctica*, which is shorter than both rami.

The first antenna of *Leucon rossi* is geniculate between articles 1 and 2, following the key presented by Watling (1991) the species should either belong to the genus *Bytholeucon* or *Pseudoleucon*. However in *Leucon rossi* two pleopods occur in premature males (*Bytholeucon* only 0 or 1), the uropod endopod is somewhat longer than the exopod (*Pseudoleucon* much smaller), and the pseudorostrum is extending straight forward (*Pseudoleucon* upturned). The remaining characters indicate, that the species belongs to the genus *Leucon*, subgenus *Crymoleucon* since the accessory flagellum of antenna 1 is longer than the first article of the main flagellum. The character states "antenna 1 not or weakly geniculate" and "antenna 1 geniculate between peduncle article 1 and 2" are unfavourable features to divide the genera *Nippoleucon* and *Leucon* from *Bytholeucon* and *Pseudoleucon*. The key itself contains contradicting information, because in the pictures provided, which were taken from the original descriptions, the angles between peduncles one and two of the first antenna of the species *Bytholeucon hiscens* and *Leucon (Atyloleucon) medius* are about 90° (Bishop, 1981, 1982). The first antenna of *Pseudoleucon japonicus* is geniculate as indicated in the text of the original description. However, in the drawing it is straight, only an articulation is indicated between

the peduncles 1 and 2 (Gamô, 1964). This demonstrates that this character state of the first antenna can be variable within a species, therefore it should be treated carefully.

Bionomy. The species was found along a latitudinal transect off the Victoria Land coast, in depths ranging from 84 to 458 m. Depth distribution was limited by the samples taken. Specimens were found in high numbers (in total 1090 specimens from 2 to as many as 378 were found in 12 samples from 13 stations) and in all areas sampled. Adult specimen were restricted to females and occurred in low number only (3%). Premature (12%) and juvenile (24%) females were found more frequently than males of the same stages (8% and 14% respectively), while

mancas (39%) dominated the samples. The species is a typical component of the cumacean fauna of the Victoria Land cost Ross Sea and it appears to be endemic to the Ross Sea.

The statistical comparison between premature males and premature females showed significant differences ($p < 0.001$) in all variables measured (Table 1), but carapace height ($p = 0.681$). The index of carapace height vs. carapace length was also compared with the incubating females; premature males and incubating females show significant differences ($p < 0.001$), whereas differences in premature and incubating females were not significant ($p < 0.072$).

TABLE 1. – Body dimensions of *Leucon* (*Crymoleucon*) *rossi*, n. sp.; C = carapace, inc = incubating, pm = premature, SD = standard deviation

	stage/sex	n	range (mm)	mean (mm)	SD
Carapace height	inc female	29	0,66-0,91	0,81	0,06
	pm female	95	0,58-0,98	0,80	0,07
	pm males	75	0,68-0,90	0,79	0,09
Carapace length	inc female	29	0,97-1,22	1,11	0,06
	pm female	95	0,87-1,30	1,11	0,08
	pm male	75	1,05-1,30	1,18	0,06
Carapace and free thorax segments length	inc female	28	1,85-2,32	2,06	0,11
	pm female	94	1,53-2,25	1,92	0,14
	pm males	74	1,76-2,25	2,04	0,09
Total length	inc females	28	3,69-4,54	4,01	0,24
	pm females	91	3,01-4,49	3,76	0,28
	pm males	71	2,01-4,28	3,94	0,27
C height / C length	inc females	29	0,62-0,84	0,73	0,06
	pm females	95	0,62-0,82	0,72	0,04
	pm males	75	0,56-0,79	0,67	0,04

Artificial key to the females of the genus *Leucon* from Antarctic waters south 60°S

- 1 Siphon greatly attenuated, as long as carapace..... 2
- Siphon not greatly attenuated, much shorter than length of carapace 3
- 2 Carapace with 2 dorsomedian spines near mid-anterior margin of frontal lobe and with 7 spines on lateral surface *Leucon weddelli* Ledoyer, 1993
- Carapace lacking dorsomedian and lateral spine.....
..... *Leucon parasiphonatus* Mühlenhardt-Siegel, 1994
- 3 Dorsomedian teeth (“serrations”) confined to the anterior 2/3 of carapace..... 4
- Dorsomedian teeth extending from anterior margin of frontal lobe to or immediately adjacent to posterior margin of carapace 7

- 4 Carapace with 4-8 dorsomedial teeth the last 1-3 after a gap..... *Leucon intermedius* Mühlenhardt-Siegel, 1994
 - Carapace with 9-12 acute dorsomedial teeth in uninterrupted row 5
- 5 Carapace with distinct slanting dorsolateral ridge..... 6
 - Carapace without dorsolateral, slanting ridge *Leucon breidensis* Gamô, 1987
- 6 Uropod peduncle longer than last abdominal segment; ischium of paraeopod 2 present.....
 *Leucon costatus* Corbera, 2000
 - Uropod peduncle little shorter than last abdominal segment; ischium of paraeopod 2 fused to basis
 *Leucon sagitta* Zimmer, 1907
- 7 Carapace lacking small spine or spines on lateral face of frontal lobe; second article of uropodal
 endopod with distal article acutely tipped (without apical or terminal seta) with long subdistal seta
 on outer margin *Leucon plarsterni* Ledoyer, 1993
 - Carapace with at least one spine on lateral face of frontal lobe; uropodal endopod with distal
 article with apical seta, not acutely tipped, long subdistal seta absent 8
- 8 Carapace with row of dorsomedial teeth interrupted posteriorly; lateral margin of frontal lobe with
 3 spines..... *Leucon assimilis* Sars, 1887
 - Carapace with row of dorsomedial teeth **not** interrupted posteriorly, lateral margin of frontal lobe
 with no more than 1 spine present..... 9
- 9 Carapace with dorsomedial teeth becoming smaller posteriorly; 1 small spine present near mid-
 ventral margin of frontal lobe (*sensu* Ledoyer 1993) or having an additional 4 or 5 spines on
 antero- and mid-lateral region (*sensu* Zimmer 1907). Pereopod 1 with exopod lacking ventrodistal
 spine on first article *Leucon antarcticus* Zimmer, 1907
 - Carapace with dorsomedial teeth well-developed posteriorly; 1 dorsolateral spine present just
 posterior to end of ventrolateral suture of frontal lobe. Pereopod 1 with exopod having distinct
 ventrodistal spine or tooth on first article *Leucon rossi*, n. sp.

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PUBLICATION VI

Phylogenetic relationship within Cumacea (Crustacea, Peracarida) and genetic variability of two Antarctic species of the family Leuconidae

Peter Rehm^{1*}, Florian Leese¹, Michael J. Raupach², Sven Thatje³,
Christoph Held¹

¹Marine Animal Ecology, Alfred Wegener Institute for Polar and Marine Research (AWI), Am Alten Hafen 26, 27568 Bremerhaven, Germany

²Molekularlabor, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany

³National Oceanography Centre, School of Ocean and Earth Science, University of Southampton, European Way, SO14 Southampton 3ZH, UK

*prehm@awi-bremerhaven.de

Abstract: Phylogenetic hypotheses presented for the peracarid order Cumacea are scarce and have not provided solution to the full extent. Formerly, hypotheses on cumacean phylogeny have been proposed on morphological characters and on amino acid sequences of the cytochrome oxidase I gene. In the present study the mitochondrial LSU (16S) was used to erect a phylogenetic hypothesis for three cumacean families, Diastylidae, Bodotriidae, and Leuconidae along with intra-family relationships of the latter. The Cumacea resolved monophyletic with tanaids and isopods as outgroup taxa. The Diastylidae were placed monophyletically at the basis of the tree topology. Bodotriidae were paraphyletic and monophyly of the Leuconidae was only weakly supported. The genus *Leucon* showed paraphyly whereas the subgenus *Crymoleucon* was monophyletic. Two leuconid species *Leucon antarcticus* Zimmer, 1907 and *L. intermedius* Mühlenhardt-Siegel, 1996 were tested for cryptic speciation. 16 specimens of *L. antarcticus* and eight specimens of *L. intermedius* from the Weddell Sea and the Ross Sea showed different patterns in genetic variability. Intraspecific p-distances variation of *L. intermedius* sequences ranged from 0 to 0.033, while sequences of the species *L. antarcticus* showed bimodal distribution (0 to 0.014; 0.038 to 0.052). The bimodal distribution of sequence similarity correlated with geographical and depth distributions between Ross and Weddell Sea, where specimens were sampled at depth from 316 to 358 m and 900 m, respectively. Although a clear evaluation of cryptic speciation in these species is yet not possible and requires work on more specimens from more geographic regions, still differences shown in the sequences of 16S rDNA can only be explained by genetic separation of populations from the Weddell Sea and the Ross Sea for extended period of time.

Key words: Cumacea; Peracarida; Mitochondrial DNA; 16S rDNA; Cryptic speciation; Molecular phylogeny

Introduction

Cumaceans are a group of peracarid crustaceans predominantly inhabiting marine soft bottom habitats. They can occur in high numbers (e.g. Rachor et al. 1982; San Vicente et al. 1997, Linse et al. 2002, Rehm et al. 2007) and are an essential component of the benthic fauna, thus being an important food source for demersal fish and other macrofauna (e.g. Kühl 1964, Arntz 1971, Arntz & Finger 1981, Cartes 1993). The first report of an Antarctic cumacean was published by Sars in 1873. Additional descriptions of five Antarctic cumaceans followed during the next decade (Sars 1887). Today, about 100 cumacean species from all

known families (Bodotriidae, Ceratocumatidae, Diastylidae, Gynodiastylidae, Lampropidae, Leuconidae, Nannastacidae, and Pseudocumatidae) are described for the Antarctic and Subantarctic (Błazewicz & Heard 1999, Mühlenhardt-Siegel 1999; Corbera 2000). However, knowledge about Antarctic cumaceans is still incomplete and restricted to species inventory, diversity, and biogeography. Suggestions for possible evolution of cumacean families have been proposed by Zimmer (1941) and Lomakina (1968). Both regard the Lampropidae and Diastylidae as basal taxa, but their assumptions differ in the more derived families. Nevertheless, both authors are of the opinion that the pleotelson bearing families are most derived. Testing phylogenetic hypothesis has been difficult for cumaceans as characters used for the taxonomy of

this peracarid order are inconsistent within and often extend beyond families. Haye et al. (2004) discuss the monophyly of the pleotelson bearing Bodotriidae, Leuconidae, and Nannastacidae as indicated by the phylogenetical analysis of the cytochrome oxidase I gene and morphological characters. With respect to the 'pleotelson clade' their findings are in accordance with Zimmer and Lomakina, but monophyly was confirmed only for the families Gynodiastylidae and Lampropidae by molecular data. The present study is aimed to investigate the phylogenetic relationship of three cumacean families and within the family Leuconidae using a fragment of the mitochondrial LSU gene (16S rDNA).

Furthermore, genetic variation in Antarctic species of the genus *Leucon* is studied to reveal possible patterns of cryptic speciation, which have been demonstrated for Antarctic isopod (Held 2003, Held & Wägele 2005, Raupach & Wägele 2006), mollusc (Allcock et al. 1997, Linse et al. 2007), and crinoid species (Wilson et al. 2007). Recent discoveries of cryptic speciation indicated that Antarctic diversity is much higher than expected and that circumantarctic distribution, which was postulated for many taxa, is not valid for a variety of these. In shallow-water species inhabiting the Antarctic continental shelf, patterns of cryptic speciation were assumed to be caused by geographic isolation and mainly glaciation processes over Milankovitch timescale, which might have led to isolated shelters on the Antarctic shelf (Thatje et al. 2005). Only species with pelagic larvae or drifting stages might have been able to overcome the barriers separating 'islands' on the Antarctic shelf, and thus ensuring gene flow between isolated populations. First support for circumantarctic distribution was discovered for two caridean decapods, which highlights the importance of the reproduction mode and drifting stages for the success of a widespread shallow-water species on the Antarctic continental shelf (Raupach et al. in press). As cumaceans belong to the brooding crustacean supraorder Peracarida the hypotheses presented above is tested for evidence in this crustacean taxon.

Materials and Methods

Source of material and choice of outgroup sequences

Antarctic Cumacea were collected during 19th Italian Antarctic expedition with RV 'Italica' along the Victoria Land coast in the Ross Sea (Rehm et al. 2007). Further material was

obtained from the BENDEX (ANT XXI-2) expedition and ANDEEP cruises I and II to the Scotia-Arc region, Antarctic Peninsula and the Weddell Sea carried out with RV 'Polarstern' in the years 2002 and 2004 (Fütterer et al. 2003, Arntz & Brey 2005). The species *Diastylis rathkei* was sampled in the Kiel Fjord in the Baltic Sea (Table 1). The material was sorted by hand from trawled gear (Rauschert dredge and epibenthos sledge) using a dissecting microscope. Samples were preserved in pre-chilled 80 % (0°, -80°, resp.) ethanol. Samples were obtained from depths between 15 and 3685 m. The samples were stored at -30° C for at least 4 month and were kept at 5° C until further processing. During the cruise with RV 'Italica' samples were stored at -80° C during the first four days. Further sequences of the mitochondrial 16S ribosomal RNA gene were downloaded from GenBank (Table 2). According to morphological data, Cumacea are placed in close relationship to Tanaidacea and Isopoda (Schram 1986, Watling 2000). Therefore, tanaid and isopod sequences were chosen as outgroup sequences.

Molecular Work

DNA was extracted from individual legs, the pleon without telson and uropods, or from total smaller specimens. The following alterations were applied to the protocol of the QIAamp DNA Mini Kit, which was used for DNA extraction: the spin column loaded with elution buffer was incubated for 5 min at 70°C before elution of the DNA from it and the volume of the elution buffer was decreased from 200 to 50 µl in order to increase the concentration of DNA.

PCRs were carried out in 50-µl volumes with 0.15 µl HotMaster Taq polymerase 5 U/µl, 2.5 µl 10x PCR buffer, 0.5 µl dNTPs 2 mmol/µl, 0.25 µl BSA, 0.125 µl of each primer both 100 pmol/µl, and 3 µl of DNA template filled up to 25 µl with sterile H₂O. All amplification reactions were performed on an Eppendorf Master Cycler.

Primer choice and creation

For DNA amplification the broadly applicable primers 16Sar 5'-CGCCTGTTTATCAAAAACAT-3' and 16Sbr 5'-CCGGTCTGAACTCAGATCACGT-3' (Palumbi et al. 1991) were used. Despite the general application of these primers on arthropod taxa amplification of cumacean DNA was weak. Therefore, cumacean specific primers were designed based on the sequences obtained in our pilot study and from GenBank. The programme 'Fast PCR' (Kalender 2003) was used to construct primers. Primers ALh (5'-GTACTAAGGTAGCATA-3') and CLr (5'-ACGCTGTTAYCCCTAAAGTAATT-3') were assembled for the cumacean family

Table I. Sequence data for phylogenetic analysis. Lat = latitude; Long = longitude.

Taxon	Location	Lat	Long
<i>Atlantocuma</i> sp.	western Weddell Sea	60°39.2 S	53°56.9 W
<i>Cyclaspis</i> sp.	western Weddell Sea	65°20.4 S	54°14.1 W
<i>Diastylis rathkei</i>	Kiel Fjord, Germany	-	-
<i>Diastylopsis</i> sp.	western Weddell Sea	60°39.2 S	53°56.9 W
<i>Leucon antarcticus</i> Zimmer, 1907	Cape Russell, Ross Sea	74°49.0 S	164°18.1 E
<i>L. assimilis</i> Sars, 1887	Cape Russell, Ross Sea	74°49.0 S	164°18.1 E
<i>L. intermedius</i> Mühlenhardt-Siegel, 1996	Cape Russell, Ross Sea	74°49.0 S	164°18.1 E
<i>L. rossi</i> Rehm and Heard, (under review)	Cape Russell, Ross Sea	74°49.0 S	164°18.1 E
<i>Leucon</i> sp.	Antarctic Peninsula	59°39.9 S	57°53.9 E

Leuconidae in highly conserved regions of the 16S gene and used during this study. The amplification protocol was 2 min at 94°C for initial denaturing, 38 cycles of 20 s at 94°C, 10 s at 46°C, and 1 min at 65°C, followed by 8 min for final extension.

DNA Sequencing

PCR products were purified with the QIAquick PCR-purification kit of Qiagen, Hilden, Germany. To achieve higher concentrations of purified DNA only 30 µl elution buffer were used. DNA purity and amount of DNA were controlled on an ethidium bromide-stained 1.5% agarose gel. In the present study cycle sequencing was performed according to the manufacturer's instructions of the BigDye Terminator v3.1 kit of Applied Biosystems (ABI) using the ABI 3130 sequencer (96°C 1 min initial denaturing, 30 cycles of 10 s 96°C, 50 s 50°C, 4 min 60°C). In general 1-3 µl of purified DNA was used for cycle sequencing with an Eppendorf Master Cycler (4 µl were used for samples with low DNA concentration). Excessive dye was removed with the DyeEx 2.0 spin kit (Qiagen) and 10 µl samples were denatured for 3 min at 95°C with 10 µl ABI HighDiye formamide (Applied Biosystems). Samples were kept on ice prior to sequencing.

Sequence Alignment and Phylogenetic Analysis

Raw pherograms from the sequencer were assembled using the programmes Pregap4 and Gap4 of the Staden package (Staden et al. 1989). For a first alignment of the contig sequences the 'ClustalW Multiple alignment' option (Thompson et al. 1994) of the program BioEdit (Hall 1999) was used. The alignments were further improved manually by identifying secondary structure elements of the homologous molecules in *Drosophila melanogaster* (mitochondrial ribosomal LSU, Accession No. X53506; Gutell et al. 1993). Loop regions were locally re-aligned using a

hidden Markov model (Churchill 1989, Rabiner 1989) implemented in the program 'ProAlign' version 0.5 (Löytynoja & Milinkovitch 2003). Default parameters were used for alignment sampling with 1.000 replicates, if not stated otherwise: character frequencies were estimated (A=0.366; C=0.149; G=0.171; T=0.3131). The analysis included sites, which could only be aligned in the ingroup or within the family Leuconidae. Corresponding sites of the outgroup or cumaceans other than Leuconidae, respectively, were substituted with gaps. Sites that were still ambiguously aligned at this stage were excluded from analysis. The nexus files are available from the authors.

Table II. Cumacean sequences obtained from GenBank.

Taxon	GenBank Accession No.
Cumacea taxa	
<i>Cumopsis fagei</i> Bacescu, 1956	AJ388111
<i>Diastylis sculpta</i> Sars, 1871	U811512
<i>Eudorella pusilla</i> Sars, 1871	U81513
Outgroup taxa	
<i>Apeudes latreillei</i> ^T	AJ38810
<i>Asellus aquaticus</i> ^I Linnaeus 1758	DQ305106
<i>Colubotelson thompsoni</i> ^I Nicholls, 1944	AF260869
<i>Creniopus buntiae</i> ^I Wilson & Ho, 1996	AF260870
<i>Haploniscus</i> sp. ^I	AY693421
<i>Paramphisopus palustris</i> ^I (Glauert, 1924)	AF259533
<i>Proasellus remyi remyi</i> ^I (Monod, 1932 ¹)	DQ305111

^T Tanaidacea; ^I Isopoda; ¹ subspecies remyi described by (Karaman, 1953)

Phylogenetic analyses were performed using parsimony (Camin & Sokal 1965), maximum likelihood (Felsenstein 1973, 1981; Huelsenbeck & Crandall, 1997) and Bayesian (Mau et al. 1999, Huelsenbeck et al. 2001) approaches. Bayesian analyses were performed with MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001) on preset parameters, whereas maximum likelihood and maximum parsimony analyses were performed with the programme PAUP* 4.0b10 (Swofford 2000). We used the General Time Reversible Model with invariable sites and gamma distribution (GTR+I+G) (Lanave 1984, Rodriguez et al. 1990), the parameters of which were estimated using the

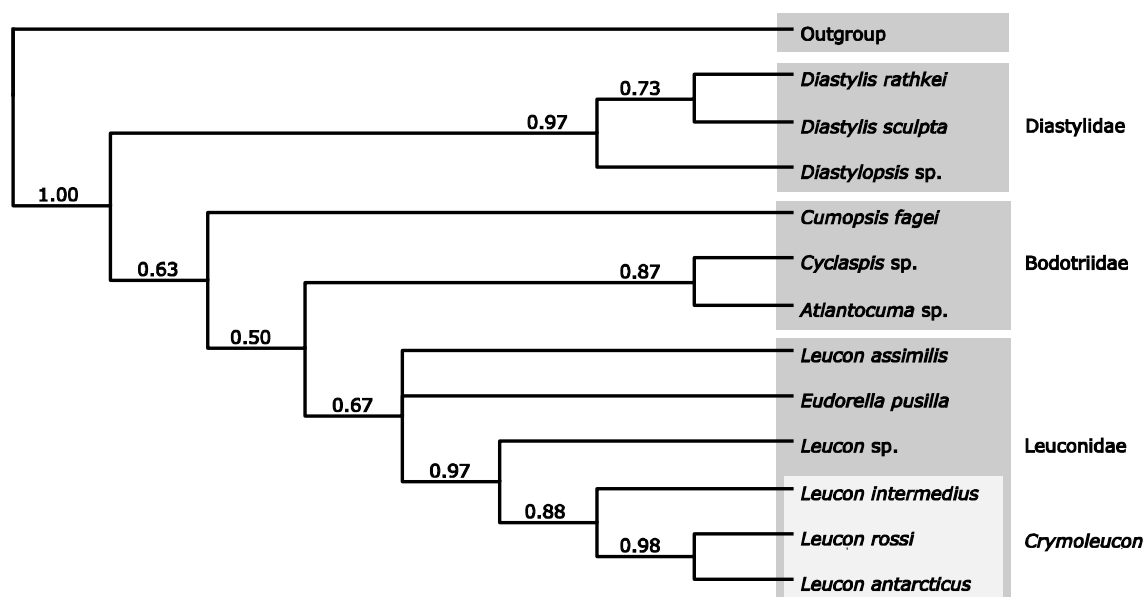


Fig. 1. Bayesian analysis consensus tree based on 16S rDNA. The GTR+I+ Γ model was used according to the Akaike information criterion test. Numbers represent the portions of sampled trees, in which the corresponding node was found (Outgroup taxa see Table 1).

program ModelTest version 3.7 (Posada & Crandall 1998) implementing the Akaike information criterion (Akaike 1974). The ratio of invariable sites was 0.1935; Gamma distribution shape parameter was 0.7813; and base frequencies were A=0.3629, C=0.1332, G=0.1742, and T=0.3297. Rates for the six substitution types estimated from the dataset were AC=3.2491, AG=13.2695, AT=5.3873, CG=2.2114, CT=21.8755, and GT=1.0000).

The settings for maximum likelihood and maximum parsimony were a heuristic search with random sequence addition (10 replicates); tree bisection reconnection (TBR). The robustness of the tree topologies was assessed with bootstrapping with 500 and 10,000 replicates for likelihood and parsimony, respectively.

Results

The fragment amplified with primers ALh/CLr varied between 255 and 256bp, while primers 16Sa/16Sb amplified fragments from 470 to 472bp. The alignment is based on sequences obtained with primers 16Sa/16Sb, sequences of *Leucon antarcticus* and *Leucon rossi* were solely obtained using primers ALh/CLr. Total length of the alignment was 437bp. After the exclusion of ambiguously aligned positions 376 remained, of which 130 were constant and 63 were parsimony-uninformative.

Maximum parsimony resulted in a tree with most taxa included in only one polytomy. Transition/transversion ratios from

0–10 were tested all yielding similar trees with differences only in the bootstrapping support. The cumacean family Diastylidae was the only well supported monophylum (bootstrap support 83%).

The Bayesian analysis (Fig. 1) indicated that the Cumacea are monophyletic supported by a Bayesian score (BS) of 1. Furthermore, the Diastylidae are well supported (0.97 BS) as the basal taxon within the Cumacea, followed by the weakly supported paraphyletic Bodotriidae. The Leuconidae is the most derived and monophyletic family, but with a BS of 0.67 only. At this node the tree is trichotomous with *Leucon assimilis*, *Eudorella pusilla*, and the remaining Leuconidae. The latter have good support (0.97 BS). The subgenus *Crymoleucon* is monophyletic and also well supported (0.88 BS). Species pairs, which exhibit high BS are *Leucon antarcticus* and *L. rossi*, *Cyclaspis* sp. and *Atlantocuma* sp., and with intermediate support, *Distylis sculpta* and *D. rathkei*.

The sequence belonging to species of the genus *Leucon* are split into three groups (Fig. 2) when compared with pairwise p-distances. The first group comprises within species comparison with p-distances from 0 to 0.05, whereas the second group gives the minimum distance (0.20–0.21) of interspecific variation of the two closely related species *Leucon antarcticus* and *L. rossi*. Interspecific distances of the remaining species are confined to the third group (p-distance 0.30–0.36). Intraspecific variation in the 16S rDNA of the two species *L. antarcticus* and *L. intermedius* follow different patterns. Interspecific p-distances of *L. intermedius* (Fig. 3A) range from 0 to 0.033, while sequence similarity of *L. antarcticus* (Fig. 3B) show higher variation (0–0.052) and a bimodal distribution with no intermediate sequence and

correlating to geographical distance and depth distribution. Pairs of sequences with p-values from 0 to 0.014 were obtained from specimens collected either in the Ross Sea (depth ranging from 316 to 358 m) or in the Weddell Sea (900 m), whereas p distances from 0.038 to 0.052 were observed between these groups.

Discussion

Sampling Methods

Extraction and sequencing of cumacean material collected during the BENDEX expedition was less successful than treating the material from the campaign with RV 'Italica'. In contrast to sample processing during the BENDEX expedition, where samples were fixed with 0°C cold ethanol, samples were fixed at -80°C onboard of RV 'Italica'. Deep temperatures at the beginning of the fixation might be the reason for better results during molecular work; therefore we suggest cooling newly collected material at -80°C or lower during the first weeks of fixation.

Phylogenetic analysis of 16S rDNA

Because the Akaike information criterion recommended a complex model (GTR+I+G) and that maximum likelihood and Bayesian methods lead to more resolved tree topologies, it is obvious that maximum parsimony is not suitable for the dataset. As maximum parsimony describes observed changes of characters the method does not consider the complex evolutionary assumptions, which are contained in the GTR model. According to the rescaled consistency index (0.0980) calculated with the program PAUP*, certain homoplasy is indicated for the data set. Consequently, the result of maximum parsimony is regarded as less informative and will not be discussed further.

Tree topologies observed from Bayesian and likelihood analyses both show that cumaceans including the families Diastylidae, Bodotriidae, and Leuconidae are monophyletic with regard to the outgroup and the Diastylidae as a monophyletic and basic taxon. In the phylogenetic analysis of molecular data from the cytochrome oxidase I (COI) by Haye et al. (2004) Bayesian and maximum likelihood methods, in contrast to maximum parsimony, could not confirm monophyly for the Cumacea. They assume that this is due to the low taxon number of Pseudocumatidae represented in their study, which do not group with the remaining

cumaceans. COI data suggest that the Diastylidae may be paraphyletic. As the number of diastylid taxa was less than half in the present study we can not rule out that 16S data might prove paraphyly for a greater number of Diastylidae as well. Nevertheless, Haye et al. (2004) point out that constraining the Diastylidae to be monophyletic results in a tree not significantly longer to the Bayesian tree.

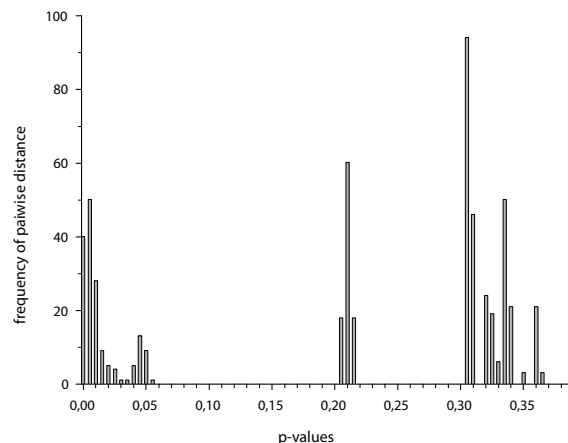


Fig. 2. Frequency spectrum of pairwise genetic distances (p-distance) of 16S rRNA gene among specimens of the cumacean genus *Leucon* Krøyer, 1846. Distances on the right side of the graph display interspecific variation, distances on the left display intraspecific variation. Distances in the middle display variation between *L. antarcticus* Zimmer, 1907 and *L. rossi* Rehm & Heard, (under review).

Bodotriidae resolved paraphyletic containing the Leuconidae during the present study and therefore resembles the result of the COI data where Bodotriidae were paraphyletic with the other pleutelson bearing families, Leuconidae and Nannastacidae, nested within. Still, the support for a 'pleutelson clade' has very low support in both studies. On the other hand this clade is confirmed by morphological data with the three families monophyletic each and the Nannastacidae as a possible intermediate taxon between the more basal Leuconidae and derived Bodotriidae. (Haye et al. 2004).

The genus *Atlantocuma* was originally placed in the family Bodotriidae (Băcescu & Muradian 1974). Jones (1984) mentioned the nannastacid-like character of the species, but preferred to leave it as aberrant form within the Bodotriidae, while Haye (2002) used the taxon as outgroup in the phylogenetic analysis of the Bodotriidae as it grouped as sister taxon to the nannastacid genera *Cumellopsis* and *Scherocumella*. The recent morphological analysis of Bodotriidae (Haye 2007) does not include *Atlantocuma* in the Bodotriidae. In the present study *Atlantocuma* is sister taxon to *Cyclaspis*; thus close relationship of *Atlantocuma* to the Bodotriidae is highlighted. Nevertheless, the placement of *Atlantocuma* can not be solved finally

since no sequences of 16S rDNA for the family Nannastacidae were available.

Monophyly of the Leuconidae is only weakly supported by the data presented here, but within the family a monophyletic group comprises the monophyletic subgenus *Crymoleucon* and an undescribed species of the subgenus *Leucon* (pers. comm. Mühlenhardt-Siegel). The tree topology suggests good evidence that the subgenus *Leucon* is paraphyletic as *L. assimilis* also belongs to the subgenus *Leucon*. The species *L. antarcticus* and *L. rossi* which represent a monophyletic group are also morphological closely related. Besides decreasing size of the dorsomedial teeth to the posterior end of the carapace the species can be distinguished by the shape of the pseudorostrum, which is blunt in *L. rossi* and tipped and slightly upturned in *L. antarcticus*, as well as by a spine present on the first article of the exopod of the first pereopod (Rehm & Heard under review).

Phylogenetic information provided during this study is reliable partially within the Leuconidae, in delimiting Cumacea from the outgroup, and in the monophyly of the Diastylidae with respect to the other ingroup taxa. It is discussed that the Diastylidae are the most derived family (in Băcescu & Petrescu 1999), while Lomakina (1968) and Zimmer (1941) placed this family following the Lampropidae to the basis of the Cumacea. The results of this study and of the phylogenetic analysis of morphological characters and the cytochrome oxidase I gene presented by Haye et al. (2003) both indicate a more basal position of the Diastylidae. Therefore, the assumption of Zimmer and Lomakina considering the position of the Diastylidae has to be regarded as confirmed. For a well-founded analysis of cumacean families more taxa of all families have to be analysed. Since cumaceans represent a relative old group a more conserved gene than the mitochondrial 16S gene might provide more detailed information about phylogeny of higher cumacean taxa. The slower evolving 18S gene is a possible candidate for further investigations; in addition more genes should be included to enhance the resolution cumacean phylogeny (Hillis et al. 1996).

Variation in 16S rDNA of Antarctic Leuconidae

Cryptic speciation can be detected by a set of criteria stated by Held (2003). One criterion is the bimodal distribution of pairwise distances with no intermediate values (Fig.

3B). The sequences of *Leucon antarcticus* show a bimodal distribution pattern and thus might indicate cryptic speciation. The sequences divide into two groups, one was obtained from the Weddell Sea at a depth of 900 m the other, from the Ross Sea, was sampled at about 350 m water depth. From the Weddell Sea only two sequences were available for genetic analysis; therefore it is possible that intermediate sequences exist. Even if the results represent true haplotype distribution intermediate sequences could exist in geographically intermediate populations of *L. antarctica*. Nevertheless, 14 sequences of the 'Ross Sea haplotype', sampled at two stations with a distance of 340 km, vary only in one position in the alignment, whereas nine positions are different to the "Weddell Sea haplotype".

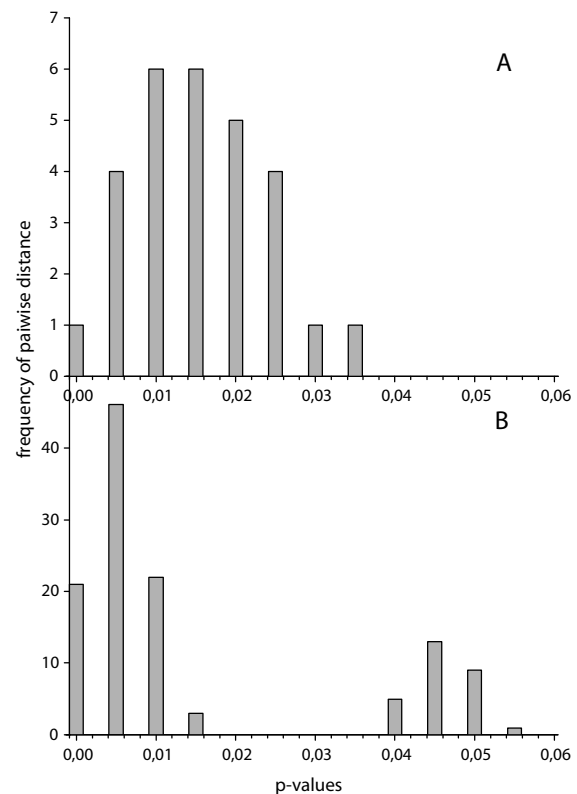


Fig. 3. Frequency spectrum of pairwise genetic distances (p-distance) of 16S rDNA gene among specimens of the cumacean subgenus *Crymoleucon* Watling, 1991. A: *L. intermedius* Mühlenhardt-Siegel, 1996. B: *L. antarcticus* Zimmer, 1907. On the right side of graph: distances between specimens of the Weddell Sea and the Ross Sea. On the left side of graph: distances between specimens from within the Weddell Sea or the Ross Sea, respectively.

The second criterion to distinguish cryptic species is the differentiation level of the gene, which should be in the range of clearly separated but closely related species. The differentiation between *L. antarcticus* and *L. rossi*, which are closely related species (see phylogenetic analysis) is less than between *L. antarcticus* and other leuconid species, but still five times higher than within the two

observed haplotypes of *L. antarcticus*. The study of 16S rDNA of brachyuran crabs from Jamaica has shown that cryptic speciation may take place at lower levels than revealed for *L. antarcticus* (Schubart & Koller 2005). On the other hand p-values observed for the differentiation of cryptic Antarctic isopod species (Held 2003, Held & Wägele 2005) is at the upper range or even higher than in *L. antarcticus*. A further indication for cryptic speciation might be the different distance pattern observed in *L. intermedius* with the upper limit of p-values at 0.033 and intermediate values. The third criterion mentioned by Held is not applicable, as it demands constantly high level of differentiation in sympatry.

Morphological record of *L. antarctica* is ambiguous. The species was first described by Zimmer (1907) from the East Antarctic (compare also Zimmer 1913) and by Calman (*L. australis*) from the Ross Sea in the same year. Ledoyer described the species for a third time from the Weddell Sea. Zimmer presented a more detailed description, whereas the descriptions of Calman and Ledoyer are vague in several aspects. Zimmer mentioned five lateral spines on the carapace, while no spine is mentioned in Calman's description. For *L. antarctica* (sensu Ledoyer 1993) also no spine is mentioned but in the drawing one spine is depicted. All descriptions cover only a part of the appendages. Moreover, due to low quality of the drawings and insufficient descriptions given in the text it is not possible to judge about the possible geographical differences reflected in morphology. Specimens from the Weddell Sea used for the present study bear a similar spine pattern on the carapace as specimen from the Ross Sea. Both populations show same variation, which does not allow a differentiation according to the lateral spines of the carapace.

Concluding, morphological descriptions of *L. antarctica* are indistinct, the number of samples of the 16S rDNA gene and the geographical distribution of sample sites are not sufficient to allow a final evaluation of genetic variability and cryptic speciation. Still, differences exist in the sequences of 16S rDNA which can only be explained by genetic separation of populations from the Weddell Sea and the Ross Sea for extended period of time. Further studies with more sequences and extended geographical range of samples will provide a more detailed image of the genetic diversity of this species and finally bring the stage of speciation to light.

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