

Southern hemisphere isopod crustaceans

Stefanie Kaiser

Biocentre Grindel & Zoological Museum (ZIM), University of Hamburg, Martin-Luther-King Platz 3, 20146 Hamburg, e-mail: stefanie.kaiser@uni-hamburg.de

1. General introduction

Isopod crustaceans (also known as woodlice, pill bugs or slaters) are members of the Peracarida - a heterogeneous and highly diverse group, comprising more than a third (~21,000 species) of total described crustaceans (Martin & Davis 2001). Isopoda have been proved a popular and useful taxon to assess large-scale patterns in biodiversity and biogeography (e.g. Hessler & Wilson 1983, Brandt 1992, Svavarsson *et al.* 1993, Wilson 1998) for several reasons. Their dispersal potential is limited to adult movement (such as passive and to a lesser extent active migration). This is because, like all peracarids, isopods brood their offspring in a ventral brooding pouch (marsupium), which is formed by extensions of their thoracic limbs. Thus isopod distributions have the potential to reflect older centres of origin and radiation and so be valuable for biogeographic analyses.

Besides amphipod crustaceans, Isopoda are the most diverse peracarid order occurring across all major realms including terrestrial, freshwater and marine habitats. Many isopod species inhabit groundwater and caves, and some have even been recorded from deserts. In marine habitats isopods are a rich and ubiquitous element and have been described across all oceans and depths (intertidal to hadal; Schotte *et al.* 2009 onwards). Of the 10,000 isopod species described to date, about half occur in the sea (Bruce 2001, Schotte *et al.* 2009 onwards). The remarkable (morphological) diversity of Isopoda (relative to other peracarids) is probably linked to their long evolutionary history. The earliest marine fossil record (a phreatoicidean) dates back to the Carboniferous (~325 mya, Schram 1970); few more ancient isopod taxa may have even occurred in the Devonian (416-359.2, Schram 1974). For the Asellota, a group particularly diverse in the deep sea, it has been suggested that they have evolved between the Carboniferous (359.2 ± 2.5 Mya) and Triassic (250-200 Mya), while the Flabellifera *sensu lato* (e.g. families Serolidae, Cirolanidae) are more derived and probably experienced a major radiation during the late Mesozoic (145.5-65.5 mya, Wilson 1998 and citations therein).

Most isopod species have become well adapted to a benthic lifestyle and only few taxa have secondarily regained the ability to swim (e.g. family Munnospidae; Hessler & Strömberg 1989). The great variety of morphologies and functional traits is, for example, reflected by a wide range of feeding strategies - from detritus- and filter feeders to ecto-parasites and active predators. A highly specialized mating system (particularly in asellotes) has probably been key to explain the ability of

isopods to have colonized and thrived even in ‘extreme’ habitats such as the deep sea and polar regions (cf. Wilson 1991).

In the Southern Ocean, the ecological and evolutionary success of isopod crustaceans has been suggested to be partly due to the Cenozoic extinction of brachyuran decapods, and the subsequent occupation of their niches by isopods and other peracarid orders (e.g. Brandt 1992). Peracarids have some physiological and morphological adaptations to the highly seasonal and cold Antarctic environment, including the possession of a ventral marsupium. Particularly, the inability of Mg^{2+} regulation in combination with general Mg^{2+} sensitivity has been thought to be a reason for the near extinction of benthic decapods in the Antarctic (e.g. Thatje *et al.* 2005). However, recent work by Wittmann *et al.* (2010) revealed similarly high haemolymph magnesium levels in some Antarctic isopods compared to decapods. Thus different eco-physiological and behavioral features must be responsible for the diversification of isopods at high southern latitudes (Wittmann *et al.* 2010).

2. Main body

2.1 Biodiversity of Southern Ocean Isopoda

There has been a long history of systematic, biogeographic and evolutionary research on Southern Ocean isopod crustaceans (e.g. Eights 1833, Vanhöffen 1914, Brandt 1992, Winkler 1994, Held & Wägele 2005, Leese *et al.* 2010). Isopods were amongst the first invertebrate species to be described from the Antarctic and sub-Antarctic regions (*Serolis paradoxa* Fabricius, 1775; *Ceratoserolis trilobitoides* (Eights, 1833)) and to date more than 440 species have been recorded from high southern latitudes (De Broyer *et al.* 2011; Table 1). Yet, relative to the size of the Southern Ocean (i.e. about 9.4% of the world’s seabed, cf. Clarke & Johnston 2003), richness of Antarctic isopods does not seem to be exceptional, that is the number of described species constitutes 10% of the world total (cf. Bruce 2001, Schotte *et al.* 2009; Fig. 1). In comparison, New Zealand’s Exclusive Economic Zone (EEZ), holding 2.7% of the world’s seabed, contains about 4% of global isopod species; from Australia’s EEZ more than 1000 species have been described, that is 20% of total marine Isopoda distributed across 7% of global seabed (cf. Bruce 2001, Fig. 1)). Relative to the Southern Ocean, the Arctic fauna has been often considered to be depauperate; recent inventories of Arctic shelf and deep-sea faunas, however, revealed similar (intermediate) richness levels per unit area (Piepenburg *et al.* 2010, Bluhm *et al.* 2011; Fig.1). Yet, species numbers are probably not a good reflection of “true” species richness, but rather illustrate differences in taxonomic productivity as well as sampling effort between different regions. For example, over the past ten years increased sampling of remote Southern Ocean locations (e.g. deep sea, Amundsen Sea) have more than doubled the number of isopod species known to the Southern Ocean (e.g. Brandt *et al.* 2007a,b, Kaiser *et al.* 2009). Likewise, thorough morphological and molecular analyses have helped to improve accuracy of species

delimitation (e.g. Just & Wilson 2004, Held & Wägele 2005, Leese *et al.* 2010), which, in future, are very likely to significantly change species numbers.

As elsewhere in the world; isopod crustaceans are amongst a few Southern Ocean taxa which are very well represented across depths - from the very shallows to hadal depths. Despite great efforts in describing the Southern Ocean deep-sea fauna over the past ten years (Fig. 2) levels of knowledge are largely biased towards the continental shelf, while data on deep-sea Isopoda are still limited to few samples from few locations across the Atlantic sector of the Southern Ocean (Brandt *et al.* 2007a). Nevertheless, some distinct patterns have emerged; diversity (e.g. using both Shannon H and rarefaction methods) of deep-sea Isopoda has been revealed to be remarkably high, yet with great variability in both abundance and richness on a local to regional scale (Brandt *et al.* 2007a, Kaiser *et al.* 2007). Furthermore richness levels along a depth (shelf to abyss) gradient seem to follow a 'typical' parabolic curve with richness peaking at intermediate (slope) depths (Ellingsen *et al.* 2007).

Across taxonomic scales (species, generic, family and suborder level) some taxa are better represented than others (see Table 1). The suborder Asellota contributes greatly (50%) to overall richness (Map 1); that is 218 and 244 species occurring south of the Polar and Subtropical front respectively (Table 1). Asellotes have usually been found to be well represented across deep-sea environments, where they typically constitute >90% (in terms of richness and abundance) of total Isopoda (Wilson 1998, Brandt *et al.* 2007a). Some (deep-sea) lineages have also successfully colonized cold temperate and polar shelves (e.g. Munnopsidae, Desmosomatidae). Overall, there does not seem to be a latitudinal gradient in asellotan diversity suggesting that these might have been widely distributed prior to modern oceanographic settings (Wilson 1998). However, the deep-sea family Munnopsidae exhibits high species richness in the Southern Ocean (Map 1a)). Although showing great biodiversity on a global scale (400 species described from 40 genera and 9 subfamilies), the variety of munnopsids in the Southern Ocean seems to be exceptional with 21% of world-wide described species and more than 200 waiting further formal description (Malyutina & Brandt 2007).

In contrast to Munnopsidae, paramunnid isopods are shallow water asellotes containing few deep-sea representatives (Map 1b)). Given that 78% of paramunnid species occur in the southern hemisphere, this region has been suggested to represent an important speciation centre for this group (Wilson 1980). In total 27 paramunnid species have been described from the Southern Ocean. Greatest taxonomic effort was made at the start of the last century and in this time more than 80% of currently known species were described (cf. Schotte *et al.* 2009 onwards). Recent taxonomic revisions of this family by Just & Wilson (2004) have helped to re-evaluate taxonomic concepts and led to a re-assessment of biodiversity and biogeographic patterns. For example, Just & Wilson (2004) showed that some paramunnid species, which had been considered to have a circum-Antarctic distribution, seem to represent a species complex with each species having a restricted geographic and bathymetric distribution. Based on molecular techniques, similar patterns have been found in some other Antarctic taxa (summarized in Janosik & Halanych 2010).

A most conspicuous component of the Antarctic isopod fauna (in terms of e.g. body size, morphology and diversity) are probably members of the suborder Valvifera. *Glyptonotus antarcticus* Eights, 1952, for instance, the only chaetiliid isopod described from Antarctic waters (but see Held & Wägele 2005), represents the largest isopod species in the Southern Ocean, reaching a size of up to 9 cm. Arcturid-like isopods (e.g. Arcturidae, Antarcturidae and Austrarcturellidae) show a characteristic specialization of their anterior thoracic legs, which are used to filter particles out of the water. Most valviferans have their distributional centre in the (temperate) southern hemisphere. Antarcturidae, however, are very well represented in the Southern Ocean with more than 50% of total described species occurring in Antarctic waters (Schotte *et al.* 2009 onwards). Some groups (e.g. in the families Arcturidae, Chaetiliidae and Ideoteidae) have extended their ranges into the deep sea or north (boreal or Arctic waters; Brandt & Poore 2003).

Amongst sphaeromatidean isopods, Serolidae are very well represented in the Antarctic and sub-Antarctic (i.e. 32% of total serolids; Map 2), while, for example, the Sphaeromatidae (= marine pill bugs) are remarkably poor (0.4% of global species). Likewise cirolanid isopods (suborder Cymothoida, Map 3) seem to be impoverished in south polar waters (Bruce & Brandt 2006); only five species in two genera have been described to date (Bruce & Brandt 2006) – a mere 1% of global cirolanid richness. Reasons for great disparity in richness between (and within) different taxa are two-fold and may be partly related to both sampling and taxonomic effort (see also discussion above). For example there has been a sustained taxonomic effort to describe large serolid or valviferan Isopoda over the past 180 years, while some small-sized groups (e.g. Paramunnidae, Macrostylidae, Nannoniscidae) received comparably little attention. In the deep-sea family Nannoniscidae, for example, only six species in two genera have been described from the Antarctic to date, yet large deep-sea collections yielded a great numbers of undescribed species (with most currently known nannoniscid genera being present in the Southern Ocean; Brandt *et al.* 2007a). Given the large body size of cirolanid and sphaeromatid isopods, though, low species numbers in the Southern Ocean probably reflect true underrepresentation.

2.2 Bathymetric and geographic distribution

The Southern Ocean ‘famously’ contains a high proportion of species with wide spatial distributions (e.g. Clarke & Johnston 2003). This has been linked to both current environmental conditions as well as historical factors. For example, glacial cycles and similarity of conditions across depths may be important drivers of wide bathymetric ranges (termed eurybathy, Brey *et al.* 1996), while strong prevailing currents (e.g. via Antarctic Circumpolar Current (ACC)) may have promoted broad geographic distributions. Developmental mode has also been suggested to be an important determinant of species’ dispersal ability and thus range size. Yet, despite their reproduction mode (brooding), several Antarctic isopod species seem to be widely distributed. Amongst asellotes, the species *Notopais quadrispinosa* (Beddard, 1886) (family Munnopsidae; Map 1a)), *Nannoniscus bidens*

Vanhöffen, 1914 (Nannoniscidae) and *Munna antarctica* (Pfeffer, 1887) (Munnidae) have been recorded from several locations around Antarctica, though only one species (*Munneurycope antarctica* Schultz, 1977) has a near-circumpolar distribution (longitudinal range >300°, Kaiser 2011). Four asellote species have latitudinal ranges greater than 100°, which include the munnopsids *Ilyarachna antarctica* Vanhöffen, 1914 and *Betamorpha fusiformis* (Barnard, 1920). Ten species span more than 50° latitude, of which nine are munnopsids. However, about half of total asellote species have a very restricted range size (within a 5° by 5° latitude-longitude square) with many species only known from their type locality (Kaiser 2011). Narrow species ranges do not necessarily reflect rarity of species, but sampling bias. For example, most asellote records come from the Atlantic sector of the Southern Ocean, and only few from East-Antarctic locations (see Map1)

Wide spatial distribution in some isopod crustaceans implies, for example, presence of some distinct dispersal mechanisms. Species within the genus *Munna* have the potential to colonize even remote locations (e.g. Hawaii and Easter Island, Wilson 1980), and are amongst the few isopod species inhabiting the highly disturbed Antarctic intertidal and shallows (*Munna antarctica*, see Smale *et al.* 2007), which may be an indication of great physiological tolerance to environmental variability (cf. Wilson 1980). Many munnopsid isopods are amongst the widest ranging species, which may reflect their good swimming abilities along with general ecological flexibility (Malyutina & Brandt 2007). The extent of geographic and bathymetric distribution in limnoriid isopods is strongly shaped by substrate availability. Limnoriidae (also called gribbles) are a group of wood-, algal- and seagrass boring Isopoda and as such, have great dispersal potential. *Limnoria stephenseni* Menzies, 1957, for example, is distributed across sub-Antarctic islands (Nikula *et al.* 2010). Attached to drifting seagrass, kelp or wooden ship's hulls, some limnoriid species have been widely transported across ocean basins (Map 4). Algal- and seagrass boring limnoriids have only been recorded from very shallow waters (< 30 m), while wood-boring species can be found down to 1500 m depths (Cookson 1991).

Depths (and correlates) have been revealed to be amongst the most effective barrier structuring benthic communities (cf. Held & Wägele 2005). Nevertheless, a high proportion of isopod taxa occurs across wide depth ranges and thus would seem to be eurybathic. Eurybathy is here defined as shallow-water (eye-bearing) taxa occurring below the shelf break and vice versa (cf. Raupach *et al.* 2004). Most Southern Ocean isopod families can be found from shelf to abyssal depths, while some are restricted to the shelf (e.g. Limnoriidae, Santiidae, Protognathiidae and Sphaeromatidae; Brandt *et al.* 2009, see Fig. 3). Haploniscidae, Ischnomesidae and Macrostylidae, on the other hand, have rarely been recorded from the Antarctic shelf, supporting suggestions that they are specialised deep-sea families (cf. Svarvarsson *et al.* 1993). Wide depth distributions are also a feature of isopods at species level. The species with the widest bathymetric range in the Southern Ocean, *Ilyarachna antarctica*, spans more than 7000 m in depth, whereas *Notopais quadrispinosa* has been recorded across more than 4000 m (Fig. 4). *Disparella maiuscula* Kaiser & Brix, 2005 also has a wide bathymetric distribution, yet this species is currently only known from bathyal and abyssal depths (Fig. 4). In contrast, species within the Santiidae and Paramunnidae, have almost exclusively

been recorded from the shelf. In fact, Santiidae have only been found on the shelf with each species having a very limited depth distribution (Fig. 4). Likewise, Paramunnidae mostly contain shallow-water species with many occurring in the top 100 m (e.g. Just & Wilson 2004; Figure 3, 4), while few species have extended their bathymetric ranges into the deep sea (e.g. species within *Abyssianira*, *Bathygonium* and *Holodentata*).

The evaluation of species range size in Southern Ocean isopods (as in any other group) is strongly influenced by the patchy distribution of samples around Antarctica; particularly the paucity of deep-sea data confines the investigation of species ranges. Furthermore taxonomic misidentifications and presence of cryptic or previously overlooked species across depths and region (cf. Held & Wägele 2005; Raupach *et al.* 2007) may obscure spatial patterns. For example, the widespread deep-sea species *Betamorpha fusiformis* has been revealed to be a species flock of geographically separated haplotypes (Raupach *et al.* 2007). Equally, *Ilyarachna antarctica* most likely represents a species complex of morphologically similar, but genetically distinct species (M. Malyutina pers. comm.). However, recent molecular-genetic analyses provided evidence for long-distance dispersal in the serolid species *Septemserolis septemcarinata* (Miers, 1875) (Leese *et al.* 2010). This species has been found across isolated locations (e.g. South Georgia, Kerguelen, Bouvet, Crozet and Falkland Is.), which are separated by hundreds to thousands of kilometers of deep seafloor. In this case, Leese and co-workers (2010) proposed rafting via the ACC as a potential mechanism to maintain gene flow between sub-populations over vast geographic distances. The distribution of *S. septemcarinata* highlights the potential of small isolated islands, which are connected by the ACC, to serve as reservoirs for past, present and future colonization events of the Antarctic continental shelf (cf. Leese *et al.* 2010).

2.3 Patterns of endemism and origin of Southern Ocean isopods

In the Southern Ocean, biodiversity and biogeographic patterns have been shaped by complex interactions of factors at varying scales. Long-term oceanographic and thermal isolation by the ACC coupled with recurrent glaciations probably drove vicariant speciation and have been key to the evolution of a highly endemic Antarctic fauna (Clarke & Johnston 2003). In isopods, a high proportion (87%) of shelf and deep-sea isopods are (putatively) endemic to the Southern Ocean indicating *in situ* radiation across depths (Brandt 1992, Brandt *et al.* 2007a). Yet, given paucity of data from bathyal and abyssal depths in the Southern Ocean, deep-sea endemism might be significantly overrated (Brandt *et al.* 2007a). Generic and family endemism is very low in Antarctic isopods, as has been described for many benthic taxa (e.g. Arntz *et al.* 1997). For example, the distribution of the genera *Coulmannia*, *Holodentata* and *Lionectes* is restricted to the Southern Ocean and only one family (Protognathiidae) has exclusively been found in Antarctic waters. The low number of isopod genera and families endemic to the Southern Ocean suggests that this region may have not been isolated for isopods long enough to generate many genera and families.

It is now well established that Antarctic isopod fauna is the result of several submergent, emergent and geographic migrations (Brandt 1992). In the Southern Ocean, shelf and deep-sea areas are unusually closely linked due to comparable conditions in some environmental parameters, which have aided exchange between shelf and deep-sea faunas. The formation of Antarctic bottom water on the shelf could have been important for the colonization of the Southern Ocean deep sea and other ocean basins further north across evolutionary times. In contrast, submergent migration may have been driven by the advance of ice sheets during last glacial maxima, which may have eradicated much (to possible all) of the shelf fauna. High levels of eurybathy imply that sub-populations of some species may have endured past glaciations on the slope or deeper (see Brey *et al.* 1996). However, limited depth distributions of many shelf isopod species could serve as evidence for survival through glaciations in ice-free refuges on the continental shelf.

Kussakin (1973) noticed the close relationship between the isopod fauna of cold-temperate and polar shelves and the deep sea. He concluded that the deep-sea isopod fauna is quite young (~10-14 mya) and has derived from shelf ancestors (i.e. *polar submergence*). In contrast, Hessler & Wilson (1983) have hypothesized that some isopod lineages have thrived in the Southern Ocean deep sea and have colonized the Antarctic shelf from there (i.e. *polar emergence*). Phylogenetic analyses have provided evidence for both scenarios (Brandt 1992, Raupach *et al.* 2004). Brandt (1992) found that at least some lineages have radiated on the Antarctic continental shelf; Antarctic Serolidae are probably descendents of a fauna inhabiting former Gondwanian coasts (i.e. Antarctica, Australia and South America). Held (2000) suggested that a Southern Ocean lineage has evolved from South American ancestors and radiated on the Antarctic shelf subsequent to the opening of the Drake's passage. From there several serolid taxa have probably colonized the Southern Ocean deep sea independently - such as *Ceratoserolis meridionalis* (Vanhöffen, 1914) (Held 2000; Fig. 3, Map2a)). A similar distribution pattern has been described for the valviferan family Antarcturidae; primitive antarcturid species with well-developed eyes occur on the Antarctic continental shelf, while derived species, with reduced functional eyes, can be found in the deep sea (Brandt 2005). The disjunct distribution found in the primitive families Pseudidotheidae (recorded from New Zealand, Australia, the Antarctic and South America), Xenarcturidae (Patagonia) and Holidoteidae (South Africa, Antarctic) most likely reflects a distribution of a previous Gondwanian relict fauna (Brandt 1992).

In Southern Ocean Acanthaspidiidae, all eye-bearing species belong to the genus *lanthopsis*, which can be predominantly found on the shelf, while blind species within the genus *Acanthaspidia* usually inhabit greater depths (>500 m, Fig. 4). Thus, Just (2001) concluded that deep-sea Acanthaspidiidae (i.e. species within *Acanthaspidia*) evolved from eye-bearing ancestors (*lanthopsis*) inhabiting Southern hemisphere shelf and slope habitats. However, recent investigations by Raupach *et al.* (2009) did not support the monophyly of *Acanthaspidia* and *lanthopsis* respectively suggesting multiple independent submergent migrations within Acanthaspidiidae.

In contrast, a deep-sea origin has been postulated for the asellote families Munnopsidae, Desmosomatidae, Nannoniscidae, Mesosignidae and Macrostylidae. The so-called munnopsoid radiation has probably evolved *in situ* and even survived major catastrophic events in the deep sea

(such as Permian anoxia; 250 Mya; Raupach *et al.* 2009). Some deep-sea lineages have successfully emerged onto continental shelves predominantly in cold-temperate and polar waters (e.g. Munnopsidae, Desmosomatidae; Raupach *et al.* 2004, 2009).

3. Acknowledgements

The author would like to thank Dr. David K.A. Barnes (BAS) for comments on an earlier version of the manuscript. Drs Huw Griffiths (BAS), Karin Meißner (DZMB Hamburg) and Dario Fiorentino (ZIM) are thanked for their help to produce the maps. Funding was provided by the University of Hamburg ('Innovationsfond').

4. References:

- Arntz, W.E., Gutt, J. & Klages, M., 1997. Antarctic marine biodiversity: an overview. In: B. Battaglia, J. Valencia & D.W.H. Walton (eds.). *Antarctic communities. Species, structure and survival*, Cambridge University Press, Cambridge, UK. pp. 3–14.
- Barnes, D.K.A., Kaiser, S., Griffiths, H.J., Linse, K., 2009. Marine, intertidal, fresh-water and terrestrial biodiversity of an isolated polar archipelago. *Journal of Biogeography*, doi:10.1111/j.1365-2699.2008.02030.x.
- Bluhm, B.A., Ambrose Jr, W.G., Bergmann, M., Clough, L.M., Gebruk, A.V., Hasemann, C., Iken, K., Klages, M., MacDonald, I.R., Renaud, P.E., Schewe, I., Soltwedel, T., Włodarska-Kowalczyk, M., 2011. Diversity of the arctic deep-sea benthos. *Marine Biodiversity*, **41**, 87–107
- Brandt, A., 1992. Origin of Antarctic Isopoda (Crustacea, Malacostraca). *Marine Biology*, **113**, 415–423.
- Brandt, A., 2005. Evolution of Antarctic biodiversity in the context of the past: the importance of the Southern Ocean deep sea. *Antarctic Science*, **17**(4), 509–521.
- Brandt, A. & Poore, G.C.B., 2003. Higher classification of the flabelliferan and related Isopoda based on a reappraisal of relationships. *Invertebrate Systematics*, **17**, 893–923.
- Brandt, A., Brix, S., Brökeland, W., Choudhury, M., Kaiser, S., Malyutina, M., 2007a. Deep-sea isopod biodiversity, distribution and endemism in the Atlantic sector of the Southern Ocean – results from the ANDEEP I - III expeditions. *Deep Sea Research II*, **54**, 1760–1775.
- Brandt, A., Gooday, A.J., Brandão, S.N., Brix, S., Brökeland, W., Cedhagen, T., Choudhury, M., Cornelius, N., Danis, B., De Mesel, I., Diaz, R.J., Gillan, D.C., Hilbig, B., Howe, J., Janussen, D., Kaiser, S., Linse, K., Malyutina, M., Pawlowski, J., Raupach, M. & Vanreusel, A., 2007b. First insights into the biodiversity and biogeography of the Southern Ocean deep sea. *Nature*, **447** (7142), 307–311.
- Brandt, A., Linse, K., Schüller, M., 2009. Bathymetric distribution patterns of Southern Ocean macrofaunal taxa: Bivalvia, Gastropoda, Isopoda and Polychaeta. *Deep Sea Research II*, **56**, 2013–2025.
- Brey, T., Dahm, C., Gorny, M., Klages, M., Stiller, M. & Arntz, W.E., 1996. Do Antarctic benthic invertebrates show an extended level of eurybathy? *Antarctic Science*, **8**, 3–6.
- Bruce, N.L., 2001. Marine isopod crustaceans in New Zealand. *NIWA Water & Atmosphere*, **9**(3), 12–13.
- Bruce, N.L. & Brandt, A., 2006. A new species of *Cirolana* Leach, 1818 (Crustacea, Isopoda, Cirolanidae) from the western Ross Sea, Antarctica, the first record of the genus from polar waters. *Zoosystema*, **28** (2), 315–324.
- Bruce, N.L., 2007. Provisional list of the marine and freshwater isopods (Crustacea) of New Caledonia. In: Payri, C.E., Richer de Forges, B. (Eds.): *Compendium of marine species of New Caledonia*. Doc. Sci. Tech., **117**, seconde édition, IRD Nouméa, pp.275–279.

- Brusca, R.C., 1987. Biogeographical relationships of Galapagos marine isopod crustaceans. *Bulletin of Marine Sciences*, **41(2)**, 268–281.
- Clarke, A. & Johnston, N.M., 2003. Antarctic marine benthic diversity. *Oceanography and Marine Biology an Annual Review*, **41**, 47–114.
- Cookson, L.J., 1991. Australasian species of Limnoriidae (Crustacea: Isopoda). *Memoirs of the Museum Victoria*, **52(2)**, 137–262.
- De Broyer, C., Danis, B., 2011. *SCAR-MarBIN: The Antarctic Marine Biodiversity Information Network.. World Wide Web electronic publication*. Available online at <http://www.scarmarbin.be/>. Accessed 15 June 2011
- De Broyer, C. & Danis, B. with 64 SCAR-MarBIN Taxonomic Editors, 2011. How many species in the Southern Ocean? Towards a dynamic inventory of the Antarctic marine species. *Deep-Sea Research II*, **58 (1-2)**, 5–17.
- Eights, J., 1833. Description of a new crustaceous animal found on the shores of the South Shetland Islands, with remarks on their natural history. *Transactions of the Albany Institute* 2 (1): 53–69.
- Eldredge, L.G. & Miller, S.E., 1995. How many species are there in Hawaii? *Bishop Museum Occasional Papers*, **41**, 1–18.
- Ellingsen, K., Brandt, A., Hilbig, B., Linse, K., 2007. The diversity and spatial distribution of polychaetes, isopods and bivalves in the Atlantic sector of the deep Southern Ocean. *Polar Biology*, **30**, 1265–1273.
- Griffiths, C.L., Robinson, T.B., Lange, L., Mead, A., 2010. Marine Biodiversity in South Africa: An Evaluation of Current States of Knowledge. *PLoS ONE*, **5(8)**, doi:10.1371/journal.pone.0012008.
- Held, C., 2000. Phylogeny and Biogeography of Serolid Isopods (Crustacea, Isopoda, Serolidae) and the Use of Ribosomal Expansion Segments in Molecular Systematics. *Molecular Phylogenetics and Evolution*, **15(2)**, 165–178.
- Held, C. & Wägele, J.W., 2005. Cryptic speciation in the giant Antarctic isopod *Glyptonotus antarcticus* (Isopoda: Valvifera: Chaetiliidae). *Scientia Marina*, **69** (Suppl. 2), 175–181.
- Hessler, R.R. & Strömberg, J.-O., 1989. Behaviour of janiroidean isopods (Asellota), with special reference to deep-sea genera. *Sarsia*, **74**, 145–159.
- Hessler, R.R. & Wilson, G.D.F., 1983. The origin and biogeography of malacostracan crustaceans in the deep sea. In: R.W. Sims, J.H. Price & P.E.S. Whalley (eds.). *Evolution, Time and Space: The Emergence of the Biosphere*. Systematic Association **23**, pp. 227–254.
- Janosik, A.M. & Halanych, K.M., 2010. Unrecognized Antarctic Biodiversity: A Case Study of the Genus *Odontaster* (Odontasteridae; Asteroidea). *Integrative and Comparative Biology*, 1–12.
- Just, J., 2001. New species of *Mexicope*, stat. nov. and *Ianthopsis* from Australia and a rediagnosis of the Acanthaspidiidae (Isopoda: Asellota). *Invertebrate Taxonomy*, **15**, 909–925.
- Just, J. & Wilson, G.D.F., 2004. Revision of the *Paramunna* complex (Isopoda: Asellota: Paramunnidae). *Invertebrate Systematics*, **18**, 377–466.
- Kaiser, S., Barnes, D.K.A., Brandt, A., 2007. Slope and deep-sea abundance across scales: Southern Ocean isopods show how complex the deep sea can be. *Deep-Sea Research II*, **54**, 1776–1789.

- Kaiser, S. & Barnes, D.K.A., 2008. Southern Ocean deep-sea biodiversity; sampling strategies and predicting responses to climate change? *Climate Research*, **37**, 165–179.
- Kaiser, S., Barnes, D.K.A., Sands, C.J., Brandt, A., 2009. Biodiversity of an unknown Antarctic Sea: assessing isopod richness and abundance in the first benthic survey of the Amundsen continental shelf. *Marine Biodiversity*, **39**(1), 27–43.
- Kaiser, S., 2011. Isopoda (Crustacea, Malacostraca) of the Southern Ocean and adjacent seas. *World Wide Web electronic publication*.
- Kensley, B., 2001. Biogeography of the marine Isopoda of the Indian Ocean, with a check-list of species and records. *Crustacean Issues*, **13**, 205–264.
- Kussakin, O.G., 1973. Peculiarities of the geographical and vertical distribution of marine isopods and the problem of deep-sea fauna origin. *Marine Biology*, **23**, 19–34.
- Leese, F., Agrawal, S., Held, C., 2010. Long-distance island hopping without dispersal stages: transportation across major zoogeographic barriers in a Southern Ocean isopod. *Naturwissenschaften* DOI 10.1007/s00114-010-0674-y
- Malyutina, M. & Brandt, A., 2007. Diversity and zoogeography of Antarctic deep-sea Munnopsidae (Crustacea, Isopoda, Asellota). *Deep-Sea Research II*, **54**, 1790–1805.
- Martin J.W. & Davis G.E, 2001. An updated classification of the recent Crustacea. *Science Series (Los Angeles)*, **39**. Natural History Museum of Los Angeles County: Los Angeles. VII, 123 pp.
- Merrin, K.L., 2004. Review of the deep-water asellote genus *Notopais* Hodgson, 1910 (Crustacea: Isopoda: Munnopsididae) with description of three new species from the south-western Pacific. *Zootaxa*, **513**, 1–27.
- Nikula, R., Fraser, C.I., Spencer, H.G., Waters, J.M., 2010. Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. *Marine Ecology Progress Series*, **405**, 221–230.
- Piepenburg, D., Archambault, P., Ambrose Jr., W.G., Blanchard, A.L., Bluhm, B.A., Carroll, M.L., Conlan, K.E., Cusson, M., Feder, H.M., Grebmeier, J.M., Jewett, S.C., Lévesque, M., Petryashev, V.V., Sejr, M.K., Sirenko, B.I., Włodarska-Kowalczyk, M., 2010. Towards a pan-Arctic inventory of the species diversity of the macro- and megabenthic fauna of the Arctic shelf seas. *Marine Biodiversity*, DOI 10.1007/s12526-010-0059-7.
- Raupach, M.J., Held, C., Wägele, J.-W., 2004. Multiple colonization of the deep-sea by the Asellota (Crustacea: Peracarida: Isopoda). *Deep Sea Research II*, **51**, 1787–1795.
- Raupach, M.J., Malyutina, M., Brandt, A. & Wägele, J.-W., 2007. Molecular data reveal a highly diverse species flock within the munnopsoid deep-sea isopod *Betamorphus fusiformis* (Barnard, 1920) (Crustacea: Isopoda: Asellota) in the Southern Ocean. *Deep-Sea Research II*, **54**, 1820–1830.
- Raupach, M.J., Mayer, C., Malyutina, M., Wägele, J.W., 2009. Multiple origins of deep-sea Asellota (Crustacea: Isopoda) from shallow waters revealed by molecular data. *Proceedings of the Royal Society B*, **276**, 799–808.

- Schotte, M., Kensley, B.F., Shilling, S., 2009. *World list of Marine, Freshwater and Terrestrial Crustacea Isopoda*. National Museum of Natural History Smithsonian Institution: Washington D.C., USA. <http://www.nmnh.si.edu/iz/isopod/>. Accessed June 2011
- Schram, F.R., 1970. Isopod from the Pennsylvanian of Illinois. *Science* (Washington, D.C.), **169**, 854-855.
- Schram, F.R., 1974. Paleozoic Peracarida of North America. *Fieldiana Geology*, **33**, 95–124.
- Sieg, V. & Wägele, J.W. (Eds), 1990. *Fauna der Antarktis*. Hamburg; Verlag Paul Parey: 114-120.
- Smale, D.A., Barnes, D.K.A., & Fraser, K.P.P., 2007. The influence of ice scour on benthic communities at three contrasting sites at Adelaide Island, Antarctica. *Austral Ecology*, **32**, 878–888
- Svavarsson, J., Strömberg, J.-O., Brattegard, T., 1993. The deep-sea asellote (Isopoda, Crustacea) fauna of the Northern Seas: species composition, distributional patterns and origin. *Journal of Biogeography*, **20**, 537–555
- Thatje, S., Hillenbrand, C.D., Larter, R., 2005. On the origin of Antarctic marine benthic community structure. *Trends in Ecology and Evolution*, **20**, 534–540.
- Vanhöffen, E., 1914. Die Isopoden der Deutschen Südpolar Expedition 1901-1903. *Deutsche Südpolar Expedition 15, Zoologie*, **7(4)**, 447–598.
- Winkler, H., 1994. Charakterisierung der Isopodenfauna (Crustacea, Malacostraca) des Scotia Bogens aus biogeographischer Sicht: Ein multivariater Ansatz. *Berichte zur Polarforschung*, **139**, 1–196.
- Wilson, G.D., 1980. New insights into the colonization of the deep sea: Systematics and zoogeography of the Munnidae and the Pleurogoniidae comb. nov. (Isopoda; Janiroidea). *Journal of Natural History*, **14**, 215–236.
- Wilson, G.D.F., 1991. Functional morphology and evolution of isopod genitalia. In: Bauer, R. et al. (Ed.). *Crustacean Sexual Biology*. pp. 228–245.
- Wilson, G.D.F., 1998. Historical influences on deep-sea isopod diversity in the Atlantic Ocean. *Deep-Sea Research II*, **45(1–3)**, 279–301.
- Wittmann, A.C., Held, C., Pörtner, H.O., Franz J. Sartoris, F.J., 2010. Ion regulatory capacity and the biogeography of Crustacea at high southern latitudes. *Polar Biology*, **33**, 919–928.

Maps

Map 1: Asellota

In Asellota, more than 2000 species are currently described, which include both freshwater and marine taxa (Schotte *et al.* 2009 onwards). Asellota have a global distribution, yet are particularly successful in the deep sea. The map illustrates the distribution of southern hemisphere Asellota (occurring south of 30°S, from Kaiser 2011). In total, 219 asellote species occur in the Southern Ocean, about 244 south of Subtropical front. The families Munnopsidae and Paramunnidae represent some of the richest asellote families in the Southern Ocean, containing 85 and 27 species respectively.

a) *Notopais quadrispinosa* (Beddard, 1887), size ca. 6 mm; belongs to the deep-sea family Munnopsidae and has a circum-Antarctic distribution (drawing modified after Merrin, 2004).

b) *Harrietonana subtriangulata* (Richardson, 1908), size: ca. 1.3 mm; a paramunnid species common in the Antarctic shallows (modified after Just & Wilson, 2004).

Map 2: Serolidae (suborder Sphaeromatidea)

The Sphaeromatidea show greatest richness on southern temperate shelves. At family level, this group is slightly underrepresented in the Southern Ocean, in that only three (out of nine) families have been recorded from Antarctic waters to date (i.e. Sphaeromatidae, Plakarthriidae and Serolidae). Whilst Sphaeromatidae and Plakarthriidae only contain few Antarctic species, Serolidae are amongst the richest isopod group at high southern latitudes comprising more than 45 described species (De Broyer & Danis 2011).

a) *Ceratoserolis meridionalis* (Vanhöffen, 1914), size: ca. 80 mm (modified from Sieg & Wägele, 1990).

Map 3: Cirolanidae (suborder Cymothoida)

Cirolanidae belong to the suborder Cymothoida, a highly diverse isopod group containing more than 2700 described species in about 60 genera (Schotte *et al.* 2009). A high proportion of cirolanid species have been described from tropical shallow waters (>200 m), while they are poorly represented in the Southern Ocean.

a) *Cirolana mclaughlinae* Bruce & Brandt 2006 (size ca. 14 mm) is the only species in this genus occurring in Antarctic waters (drawing modified from Bruce & Brandt 2006).

Map 4: Limnoriidae (suborder Limnoriidea)

Limnoriidae (suborder Limnoriidea) are a group of wood- and algal boring isopods, which have their distributional centre in the tropical shallows (Brandt & Poore 2003).

a) *Limnoria antarctica* Pfeffer, 1887 (size ca. 5 mm) represents the only species in this family occurring south of the Polar Front (drawing modified from Sieg & Wägele, 1990).

Table and Figure legends

Table 1 Species, generic and family level richness of isopod suborders occurring south of the subtropical front (~43°S). In parentheses: proportion of total number of isopod species/genera/families (from Brandt & Poore 2003, Schotte *et al.* 2009 onwards, De Broyer & Danis 2011, Kaiser 2011). Numbers represent described taxa only.

Figure 1 Relationship between total species richness and area size [km₂] in isopod crustaceans from different locations around the world: Galapagos archipelago (from Brusca 1987), South Orkney islands (Barnes *et al.* 2009), South Georgia (Winkler 1994), Hawaiian archipelago (Eldredge & Miller 1995), New Caledonia's Exclusive Economic Zone (EEZ, from Bruce 2007), South Africa's EEZ (Griffiths *et al.* 2010), New Zealand's and Australia's EEZ (Bruce 2001, 2007), the Arctic Ocean (Piepenburg *et al.* 2010, Bluhm *et al.* 2011), the Southern (De Broyer *et al.* 2011) and Indian Ocean (Kensley 2001). Both shelf and deep-sea data of described species only were included; Arctic data represent pooled values for the shelf and deep sea from Piepenburg *et al.* (2010) and Bluhm *et al.* (2011).

Figure 2 The rate of species descriptions in Antarctic shelf vs. deep-sea Isopoda over the past 180 years, modified from Kaiser & Barnes (2008); deep sea is here defined as areas below the shelf break (> 1000 m).

Figure 3 Bathymetric range size of selected Antarctic and sub-Antarctic isopod families: 1) Santiidae; 2) Limnoriidae; 3) Chaetiliidae; 4) Cirolanidae; 5) Munnidae; 6) Serolidae; 7) Desmosomatidae; 8) Mesosignidae; 9) Macrostylidae; 10) Nannoniscidae; 11) Paramunnidae; 12) Haploniscidae; 13) Ischnomesidae; 14) Acanthaspidiidae; 15) Munnopsidae; grey: shelf lineages; black: deep-sea lineages.

Figure 4 Bathymetric range size of selected Southern Ocean isopod species: 1) *Limnoria antarctica* Pfeffer, 1887 (Limnoriidae); 2) *Harrietonana subtriangulata* (Richardson, 1908) (Paramunnidae); 3) *Santia charcoti* (Richardson, 1906) (Santiidae); 4) *Ianthopsis multispinosa* Vanhöffen, 1914 (Acanthaspidiidae); 5) *Coulmannia australis* Hodgson, 1910 (Paramunnidae); 6) *Munna antarctica* (Pfeffer, 1887) (Munnidae); 7) *Coperonus pulcher* Brandt, 1992 (Munnopsidae); 8) *Desmosoma brevipes* Nordenstam, 1933 (Desmosomatidae); 9) *Austrosignum glaciale* Hodgson, 1910 (Paramunnidae); 10) *Austroniscus ovalis* Vanhöffen, 1914 (Nannoniscidae); 11) *Nannoniscus bidens* Vanhöffen, 1914 (Nannoniscidae); 12) *Acanthaspidia longiramosa* Vasina & Kussakin, 1982 (Acanthaspidiidae); 13) *Ceratoserolis meridionalis* Vanhöffen, 1914 (Serolidae); 14) *Lionectes humicephalotus* Wilson, 1989 (Munnopsidae); 15) *Mesosignum antarcticum* Schultz, 1979 (Mesosignidae); 16) *Antennuloniscus latoperculus* Brökeland, 2006 (Haploniscidae); 17) *Contrarimesus curtispinis* (Brandt, 1992) (Ischnomesidae); 18) *Notopais quadrispinosa* (Beddard, 1886) (Munnopsidae); 19) *Disparella maiuscula* Kaiser &

Brix, 2005 (Desmosomatidae); 20) *Ilyarachna antarctica* Vanhöffen, 1914 (Munnopsidae); grey: shelf lineages; black: deep-sea lineages.

Table 1

Suborder	n species	n genera	n families	Distributional focus
Asellota	244 [11%] ¹	121 [45%] ¹	19 [64%]	Deep sea, cosmopolitan
Cymothoida	51 [2%] ¹	33 [7.5%] ¹	16 [67%]	Tropical to temperate, shallow water
Limnoriidea	3 [5%]	2 [40%]	2 [67%]	Mostly tropical shallow water with few southern temperate and polar exceptions
Sphaeromatidea	59 [7%] ¹	20 [15%] ¹	3 [33%]	Southern temperate and polar, shelf; some lineages have extended their ranges to the northern seas
Valvifera	88 [15%]	20 [24%]	11 [100%]	Southern temperate and polar, shelf; some lineages have extended their ranges to the northern seas
Total	445 [10%] ¹	196 [21%] ¹	51 [75%]	

¹includes freshwater taxa (data from Schotte *et al.* 2009)

Figure 1

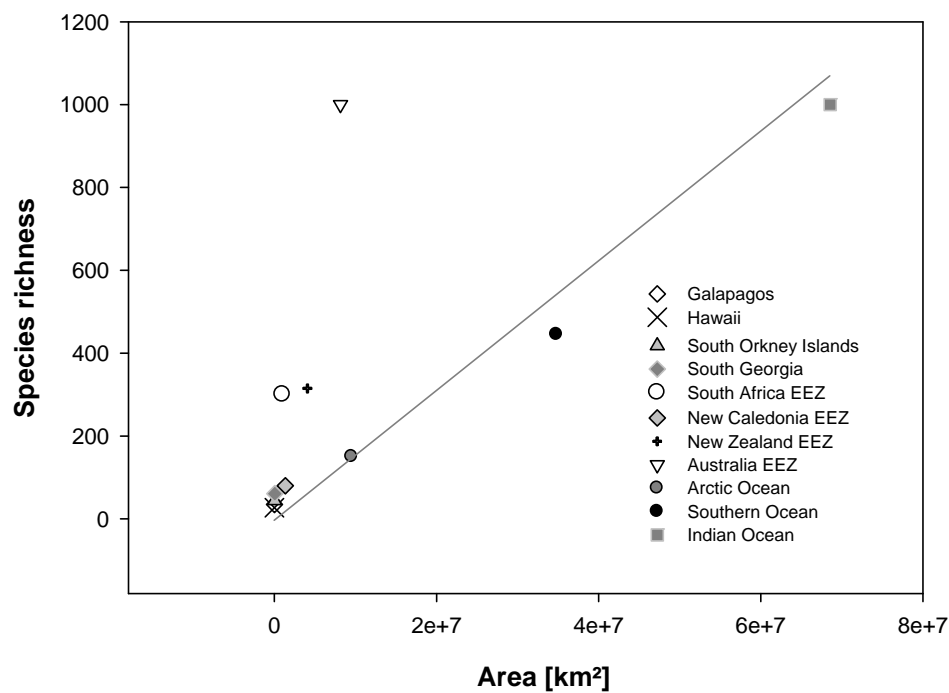


Figure 2

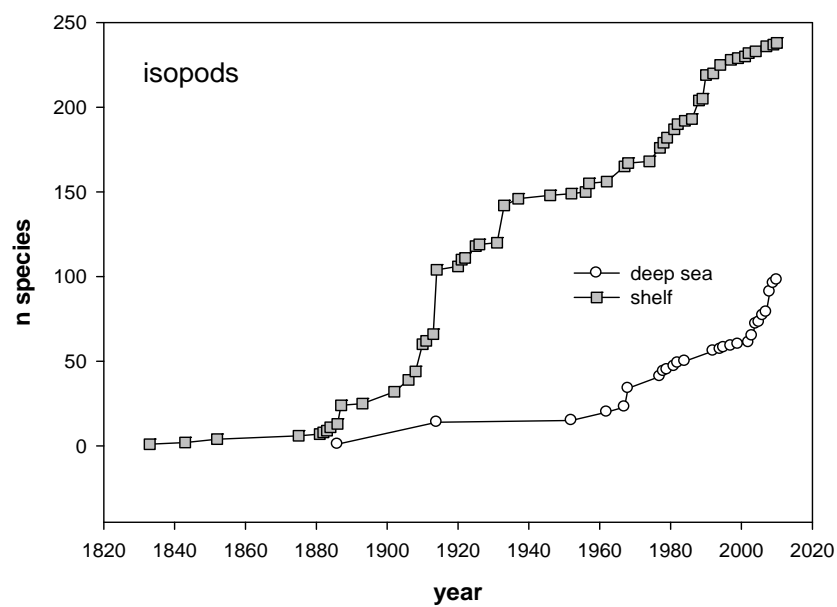


Figure 3

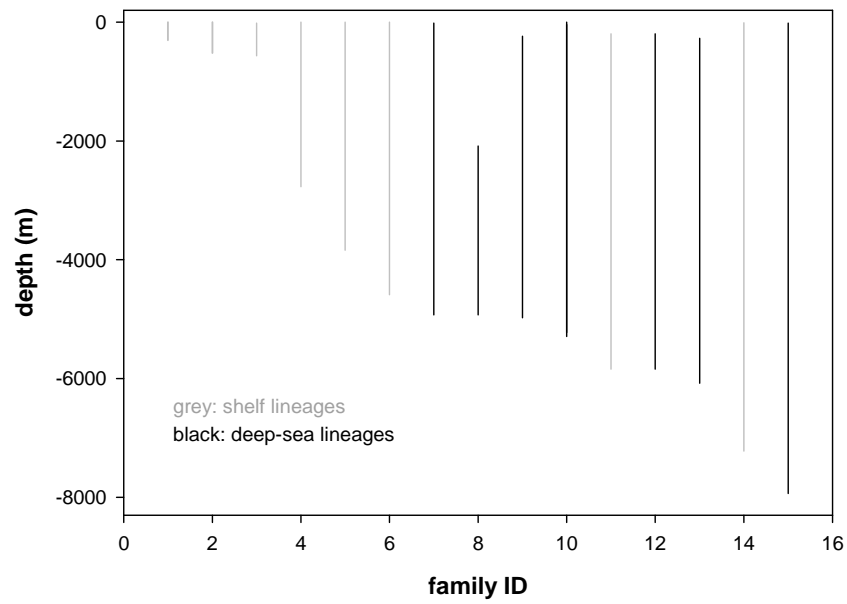
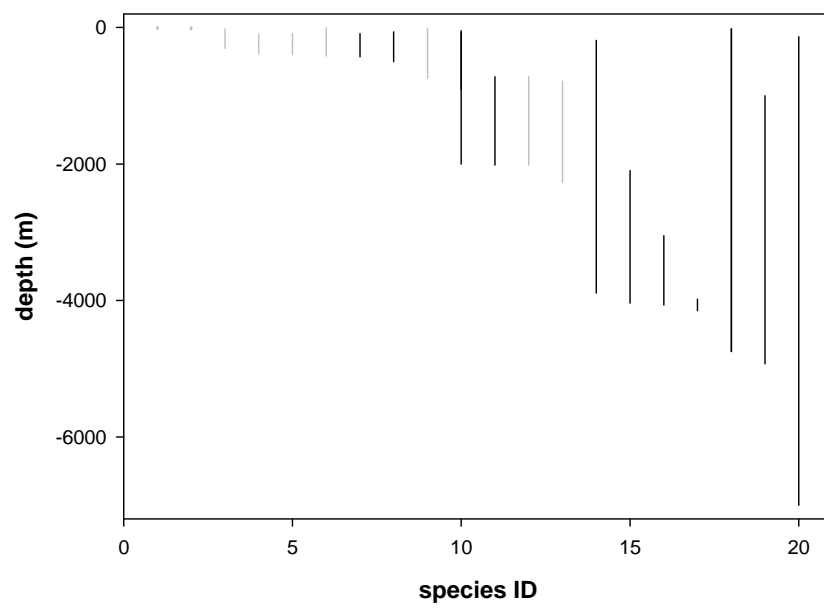
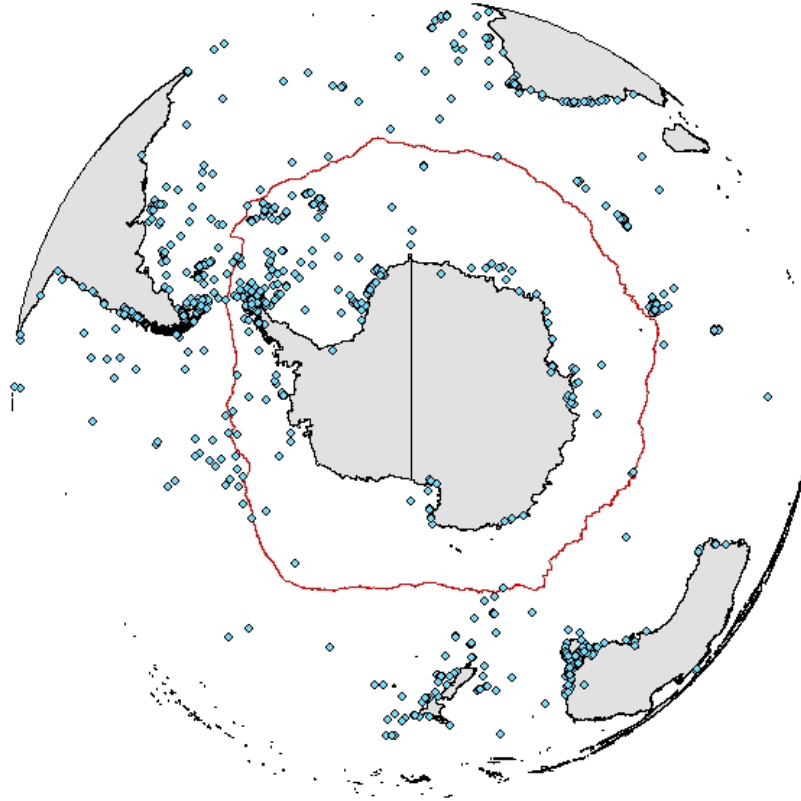


Figure 4

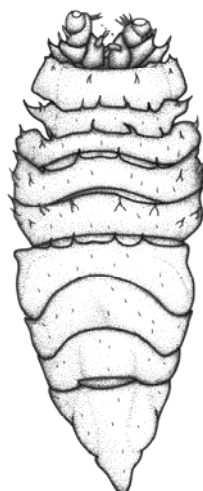


Map 1 Asellota

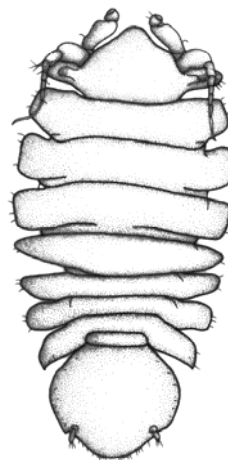
- a) *Notopais quadrispinosa* (Beddard, 1886) (Munnopsidae)
- b) *Harrietonana subtriangulata* (Richardson, 1908) (Paramunnidae)



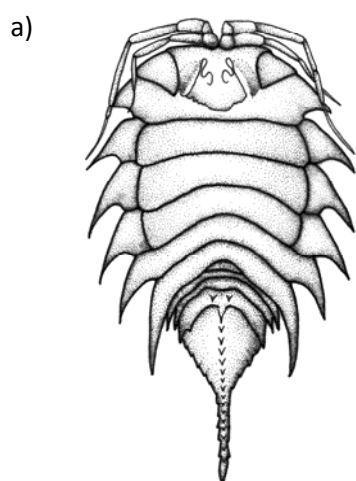
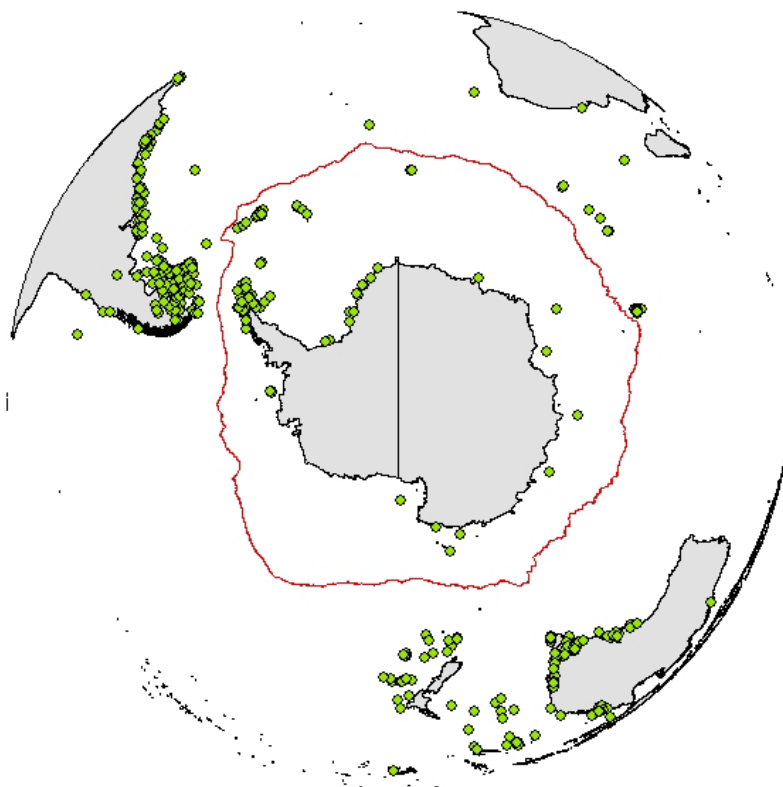
a)



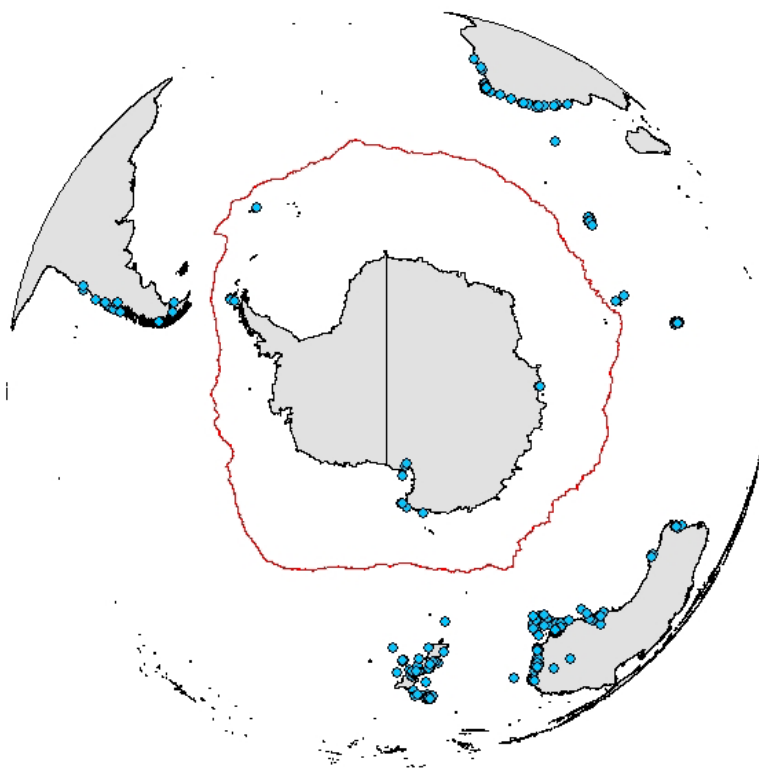
b)



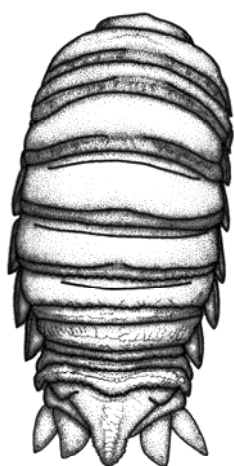
Map 2 Serolidae; a) *Ceratoserolis meridionalis* Vanhöffen, 1914



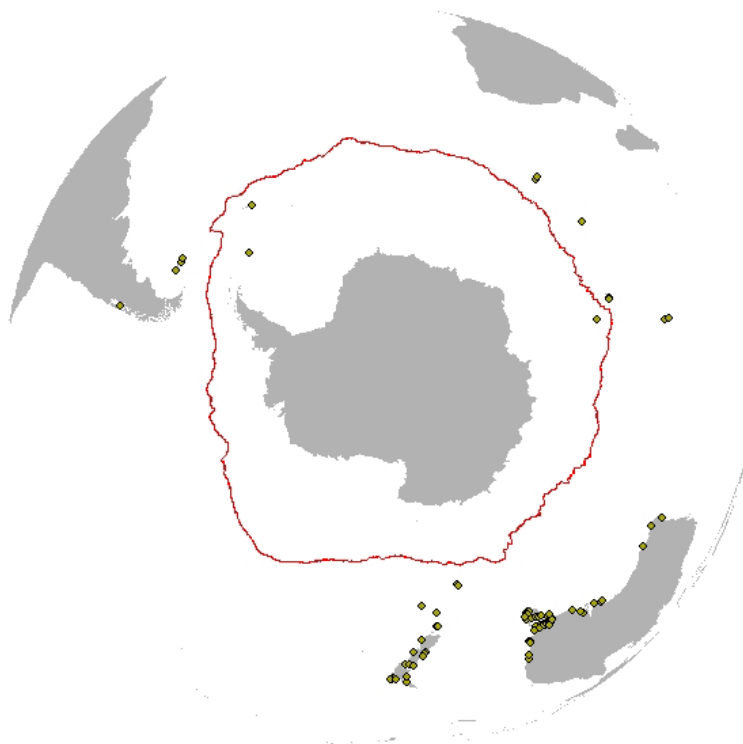
Map 3 Cirolanidae, a) *Cirolana mclaughlinae* Bruce & Brandt, 2006



a)



Map 4 Limnoriidae; a) *Limnoria antarctica*



a)

