

First insights into the biodiversity and biogeography of the Southern Ocean deep sea

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Shallow marine benthic communities around Antarctica show high levels of endemism, gigantism, slow growth, longevity and late maturity, as well as adaptive radiations that have generated considerable biodiversity in some taxa¹. The deeper parts of the Southern Ocean exhibit some unique environmental features, including a very deep continental shelf² and a weakly stratified water column, and are the source for much of the deep water in the world ocean. These features suggest that deep-sea faunas around the Antarctic may be related both to adjacent shelf communities and to those in other oceans. Unlike shallow-water Antarctic benthic communities, however, little is known about life in this vast deep-sea region^{2,3}. Here, we report new data from recent sampling expeditions in the deep Weddell Sea and adjacent areas (748–6,348 m water depth) that reveal high levels of new biodiversity; for example, 674 isopods species, of which 585 were new to science. Bathymetric and biogeographic trends varied between taxa. In groups such as the isopods and polychaetes, slope assemblages included species that have invaded from the shelf. In other taxa, the shelf and slope assemblages were more distinct. Abyssal faunas tended to have stronger links to other oceans, particularly the Atlantic, but mainly in taxa with good dispersal capabilities, such as the Foraminifera. The isopods, ostracods and nematodes, which are poor dispersers, include many species currently known only from the Southern Ocean. Our findings challenge suggestions that deep-sea diversity is depressed in the Southern Ocean and provide a basis for exploring the evolutionary significance of the varied biogeographic patterns observed in this remote environment.

Although animal communities inhabiting shallow marine benthic environments around Antarctica, notably parts of McMurdo Sound and the Peninsula region, are well known, there have been few studies of the deep-water faunas in the adjacent Southern Ocean. The ANDEEP (Antarctic benthic deep-sea biodiversity: colonization history and recent community patterns) project was designed to fill this knowledge vacuum⁴. Between 2002 and 2005, we undertook three expeditions in the deep Weddell Sea and adjacent areas aboard the German research vessel *Polarstern*. Biological collections and data on environmental and seafloor characteristics were obtained from diverse settings, including continental slope, rise, abyssal plain,

trench floor, channel levees and adjacent to fracture zones, and from water depths between 774 and 6,348 m (Fig. 1; Supplementary Discussion; Supplementary Tables 1, 2; Supplementary Figs 1, 2). This material has greatly improved our knowledge of the biodiversity of benthic communities in the deep Southern Ocean and enabled us to test ideas about large-scale biogeographic and other macroecological patterns⁵ among deep-water faunas.

The richness of species inhabiting deep-sea sediments was first demonstrated during the 1960s^{6,7}. Since then, scientists have sought to understand the mechanisms that maintain these high levels of benthic diversity at local⁸ and regional⁹ scales. We analysed species assemblages in ANDEEP samples across a range of taxonomic groups, representing the meiofauna, macrofauna and megafauna (Fig. 2) and found substantial levels of unrecorded biodiversity (see Supplementary Material). The Foraminifera were represented by 158 live species, including 72 monothalamous species, most of them undescribed. The nematodes belonged to typical cosmopolitan deep-sea genera (Supplementary Fig. 3), but more than half of the 57

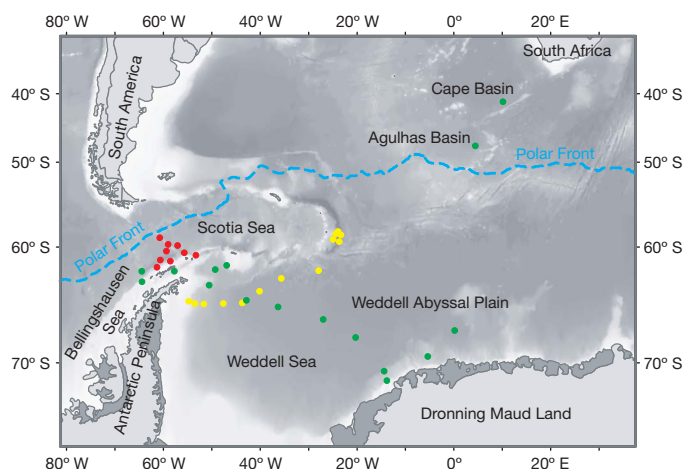


Figure 1 | Station map. Stations from ANDEEP I (2002) red circles, ANDEEP II (2002) yellow circles and ANDEEP III (2005) green circles. The blue line indicates the Polar Front.

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species recognized in selected genera were new to science. At least 100 ostracod species were distinguished, and >70% of them were new. Among the macrofauna, the isopods were astonishingly diverse with 674 species identified among >13,000 specimens examined, compared with 371 species reported from the entire Antarctic continental shelf¹⁰. Most (86%) of the isopod species were undescribed and are presently known only from the Southern Ocean. More than 200 polychaete species were recognized, 81 of them previously unknown. Our samples yielded 160 species of shelled gastropods and bivalves compared with 279 species on the shelf (<1,000 m)¹¹. Around 40% of species were confined to abyssal depths. Among the megafauna, 76 species of sponges were recognized, 17 of them were undescribed and 37 new for the Southern Ocean (Supplementary Table 3).

Whether shelf faunas have colonized the deep ocean, or vice versa, is a central issue for understanding faunal patterns in the Southern Ocean. Prior to ANDEEP, most of the information on bathymetric distributions around Antarctica concerned shelf and upper-slope faunas¹⁰. A comparison of species distributions on continental shelves and slopes around Europe and Antarctica revealed significantly wider depth ranges off Antarctica for bivalves, gastropods,

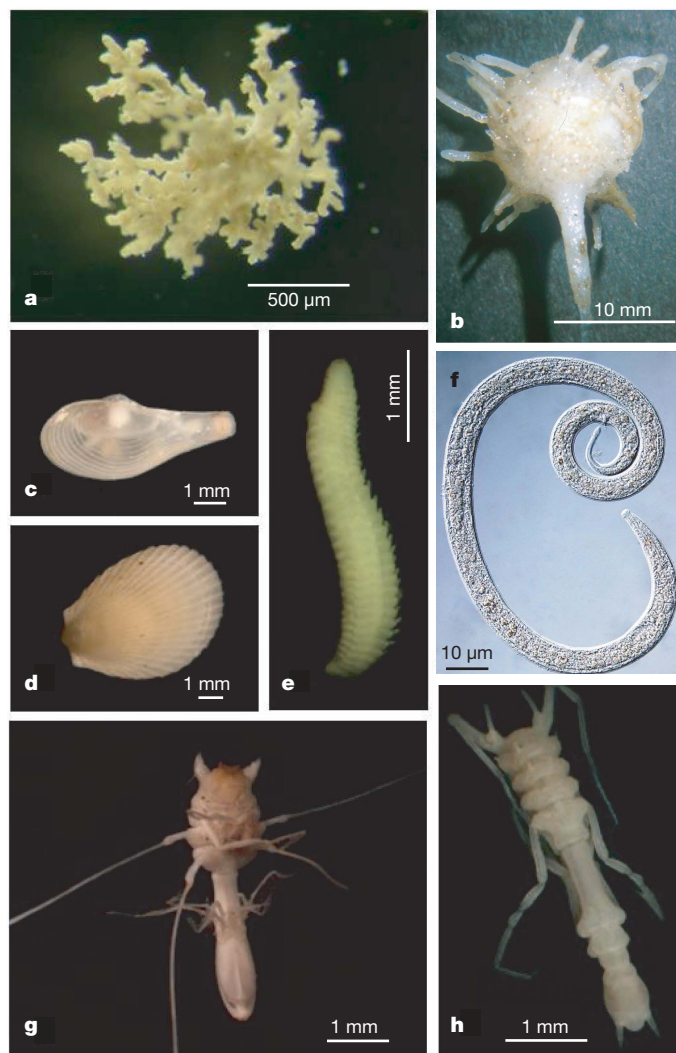


Figure 2 | Selected important ANDEEP taxa. **a**, A new species of komokiacean (*Ipoa* sp. nov.) from the Weddell Sea abyssal plain. **b**, The carnivorous sponge *Chondrocladia* from the Weddell Sea abyssal plain. **c**, Bivalve mollusc *Cuspidaria* sp. from the abyssal Weddell Sea and South African basins. **d**, Bivalve mollusc *Limatula* sp. from the Weddell Sea. **e**, Polychaete *Ophryotrocha* from the Weddell Sea. **f**, Nematode *Molgolaimus* sp. from the Weddell Sea. **g**, Isopod crustacean *Ischnomesus* sp. from the Weddell Sea. **h**, Isopod *Munnopsis* sp. from the western Weddell Sea.

amphipods and decapods but not for polychaetes, asteroid and ophiuroids¹². The generally higher degree of eurybathy among Antarctic invertebrates was attributed to glacial–interglacial cycles of shelf ice advance and retreat, which periodically eliminated shelf faunas, pushing species into deeper water or causing their extinction. These cycles probably also led to regular pulses of migration in and out of Antarctica¹. Experimental studies of the pressure and temperature tolerances of the pelagic larvae of the shallow-water Antarctic echinoid *Sterechinus neumayeri* suggested that embryonic stages potentially could penetrate into deep water¹³. The unusually deep shelf around Antarctica could also facilitate faunal exchanges between shelf and deep-sea habitats².

ANDEEP data strongly suggest that a combination of emergence and submergence on Antarctic margins has led to an intermingling of species originating in shallow- and deep-water habitats (Fig. 3). The

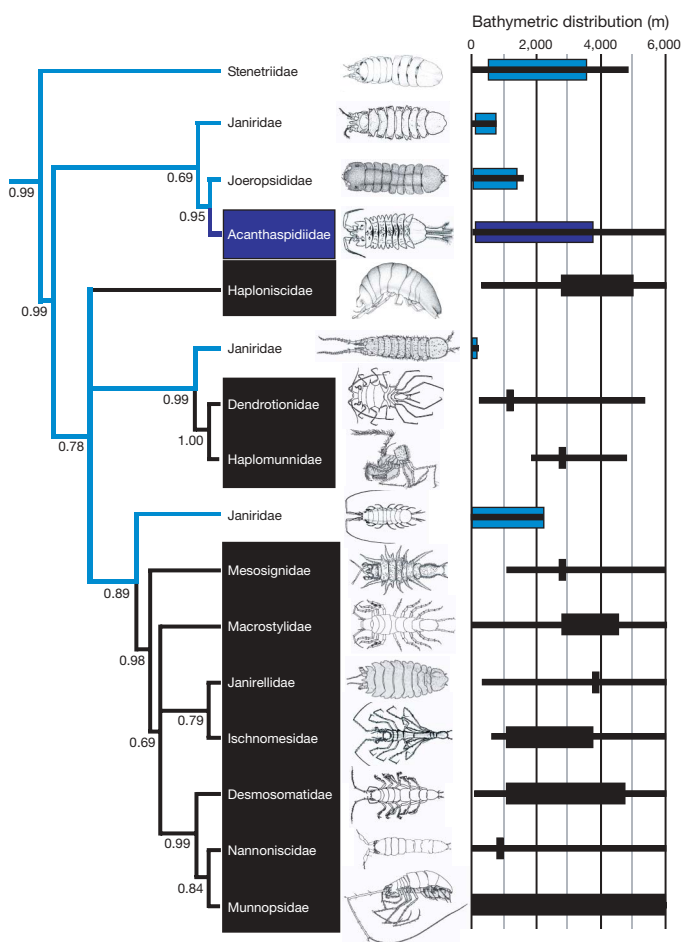


Figure 3 | Isopod phylogenetic relationships and multiple colonizations of the deep sea. Bayesian consensus tree based on the complete 18S rRNA gene (excluding hypervariable regions; numbers on nodes represent statistical support) of 53 species of marine Asellota, and bathymetric distribution of the analysed species (broad lines). Family distribution (thin black lines) is based on ANDEEP data and the world list of isopods (www.nmnh.si.edu/iz/isopod/). Eye-bearing, shallow-water taxa are marked light blue; blind, deep-sea taxa are marked black. The family Acanthaspidiidae includes both shallow-water and deep-sea species (dark blue colour). The scattered distribution of the shallow-water forms within the tree, caused by the polyphyletic nature of the 'Janiridae', indicates a multiple colonization of the deep sea. In at least four cases, asellote families (including the Acanthaspidiidae) have invaded the deep sea. The Munnopidae are most speciose and include seven dominant deep-sea subfamilies. The bathymetric distribution of the analysed species provides evidence of polar submergence within the Stenetriidae, Joeropsididae and some janirid species, whereas polar emergence can be observed within the Acanthaspidiidae (genus *Acanthaspidia*), Dendrotonidae, Ischnomesidae, Desmosomatidae, Nannoniscidae and Munnopsidae.

foraminiferan *Epistominella vitrea* provides a good example of submergence. Populations from 18 to 28 m in McMurdo Sound and from 1,080 m on the opposite side of the continent in the Weddell Sea are genetically identical¹⁴. This species, which typically resides on the shelf, has a much greater depth range in the Southern Ocean than it does on other continental margins, suggesting a migration from the shelf into deep water. *Epistominella exigua*, the deep-water counterpart of *E. vitrea*, which is reported from depths of 5,000 m in the central Weddell Sea¹⁵ and 314 m on the shelf¹⁶, may have migrated in the opposite direction. Among nematodes, typical deep-sea members of the genus *Acantholaimus* have emerged onto the Southern Ocean shelf¹⁷. Deep-sea emergence of isopods was postulated by several authors¹⁸, but others have regarded submergence of shelf species into the deep sea as more likely¹⁹. Probably, both exchange pathways have been followed by different isopod families over evolutionary time-scales; for example, submergence by the Acanthaspidiidae, Antarcturidae, Munnidae, Serolidae, Stenetriidae, Paramunnidae and emergence by the Desmosomatidae, Ischnomesidae, Munnopsidae. ANDEEP samples reveal that isopod species typical of the shelf penetrate to 1,500–2,000 m depth. Some of the deep-water antarcturid species have eyes, suggesting that they evolved from shelf species. The abyssal ANDEEP isopods, however, are completely different from those on the shelf, consisting almost entirely (97%) of asellotes. Molecular genetic analyses demonstrate that the remarkable radiation of deep Southern Ocean asellotes encompasses at least four different lineages that have colonized the deep-sea independently (Fig. 3). This group also includes some species that emerge to depths of a few 100s of metres on the shelf²⁰. In other crustacean taxa, the occurrence of the thaerocytherid ostracod *Australicythere cf. polylyca* at 1,030 m depth in the eastern Weddell Sea may indicate submergence from the Antarctic shelf, whereas three macrocypridid species that occur from shelf to abyssal depths provide an example of emergence in this deep-sea family. Among polychaetes, a eurybathic shelf assemblage extends beyond 2,000 m, at which depth it is replaced by a lower-slope/abyssal-plain assemblage. Although the depth ranges themselves are not unusual for polychaetes, the downslope species turnover is different from temperate regions. Among molluscs, there is evidence for the emergence of species evolved from the deep-sea bivalve *Limopsis tenella* onto shelf. However, abyssal Southern Ocean buccinoid gastropods share no genera with sublittoral and bathyal faunas.

Although the Polar Front (Fig. 1) limits the distribution of many pelagic species, this surface ocean feature is no barrier to the benthos². Indeed, the northward movement of deep water formed in the Weddell Sea makes close faunal connections between the Southern Ocean and other ocean basins more likely^{2,21}. ANDEEP samples yielded many cosmopolitan foraminiferal morphospecies¹⁵. Molecular genetic studies of three such species support the conspecificity of geographically distant populations²². The majority of internal transcribed spacer rDNA sequences from *Epistominella exigua*, *Cibicidoides wuellerstorfi* and *Oridorsalis umbonatus*, obtained in the Weddell Sea and Arctic Ocean (water depths 572–4,975 m), were almost identical, despite this being one of the most rapidly evolving region of the nuclear genome (Supplementary Table 4). These results provide the first molecular evidence for bipolar and possibly global distributions among deep-sea benthic organisms of meiofaunal size. In the case of *E. exigua*, the species for which we have most information, a study of population genetics suggests substantial levels of gene flow from Antarctic (2,600–4,600 m) to Arctic populations but extremely low levels in the opposite direction. In contrast, foraminiferal species living on the shelf exhibit a much stronger divergence between Arctic and Antarctic populations (Fig. 4; Supplementary Table 5). Among metazoans, more than half of all polychaete species found during the ANDEEP expeditions also occur from north of the Polar Front and about 20% occur north of the equator (Supplementary Fig. 5). The first comprehensive analysis of hexactinellid phylogeny on the basis of molecular data revealed close phylogenetic links between the Arctic and the Antarctic taxa, for example,

species of the genus *Caulophacus*. Together with palaeontological data, this pattern indicates an ancient colonization of the Southern Ocean deep sea by glass sponges, possibly dating from the Early Cenozoic after this group disappeared from the shelf habitats and migrated into the deep sea at the end of their Cretaceous radiation.

Other evidence, however, points to some strong contrasts between deep Southern Ocean faunas and those from other oceans. The isopods in ANDEEP samples are particularly distinctive with many species presently unknown outside the Southern Ocean. Among the Munnopsidae, the most successful deep-sea family, as well as in other important Southern Ocean taxa (for example, Desmosomatidae, Haploniscidae and Ischnomesidae), >95% of the ANDEEP species are undescribed. Although we know that some species complexes have radiated in the deep Southern Ocean (for example, the Haploniscidae), it is unclear whether they have evolved here and subsequently spread into other ocean basins. The few Southern Ocean deep-sea isopod species that have been described show closest zoogeographical links to Atlantic faunas. Many ANDEEP ostracod species recognized on the basis of their soft-part anatomy are presently unknown outside the Southern Ocean. Furthermore, the markers 16S rDNA, cytochrome oxidase I mtDNA and internal transcribed spacer rDNA indicate large genetic distances between intraspecific populations collected in the western and eastern Weddell Sea. The ostracod family Macrocyprididae was common in ANDEEP material, but usually rare in deep-sea samples from other oceans. The majority (~75%) of mollusc species are currently unknown outside the Southern Ocean, and wide-ranging Atlantic deep-sea species, such as the gastropod *Benthonella tenella*, were not collected. Certain polychaete families (Spionidae, Paraonidae, and Cirratulidae), which are common and species-rich at temperate latitudes, were rare and represented by few species¹¹. Many Southern Ocean nematode species are unrecorded and apparently confined to particular parts of the Weddell Sea, although some have wider distributions.

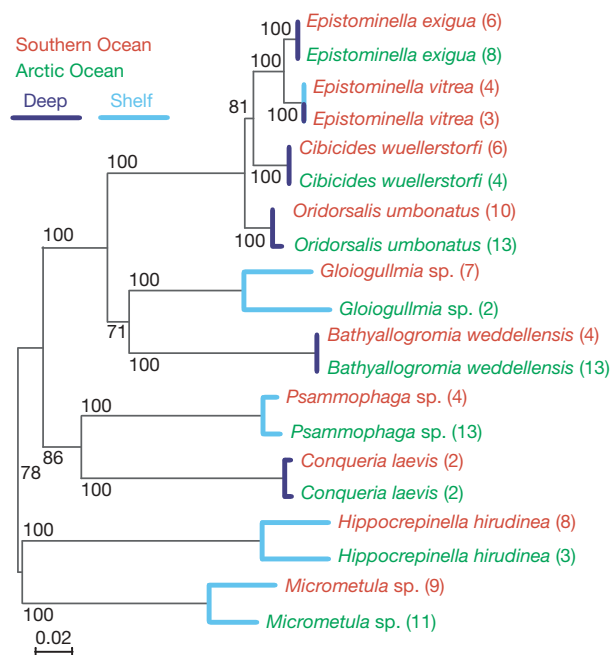


Figure 4 | Phylogenetic relationships of deep-sea foraminifera. Phylogenetic relations between Southern Ocean and Arctic Ocean populations of selected shelf and deep-sea foraminiferal species on the basis of small subunit rDNA sequences. All the shelf species examined are highly divergent, whereas most of the deep-sea species have almost identical sequences. The genetically homogenous species *Epistominella vitrea*, which occurs at shallow and deep sites in the Southern Ocean, is also illustrated. The number of obtained sequences is indicated after species names. Detailed data on sampling sites and sequence divergence are given in Supplementary Material (Supplementary Table 4).

These biogeographic patterns may be linked to larval ecology. The isopods, ostracods and nematodes have poor dispersal capabilities (isopods, for example, are brooders¹⁰) and hence reduced gene flow, making restricted species distributions more plausible, albeit difficult to prove. The recent discovery of cryptic isopod species in the Southern Ocean and Angola Basin support this assumption²³. On the other hand, groups in which species are widely distributed, for example, Foraminifera, have easily transported propagules or larval stages²⁴.

Our data can be used to test the suggested existence of global latitudinal diversity trends in the deep sea^{3,5,25,26}. A decrease in isopod biodiversity with increasing latitude in the Southern Hemisphere has been claimed on the basis of data from up to 40° S (ref. 26), although species richness data point to considerable regional variation for isopods on continental slopes^{3,25–27}. ANDEEP data, however, indicate high levels of diversity among certain animal groups in the deep Southern Ocean. Values of $E(S_{100})$ (expected number of species per 100 individuals) for isopods from the Weddell and Scotia Seas (22–25 species) are comparable to those from many temperate and tropical slopes in the Southern Hemisphere²⁵. Reported $E(S_{100})$ and $E(S_{200})$ values for bivalves, gastropods and isopods from the southeastern Weddell Sea (500–2,000 m) fall within the upper range of those from the tropics²⁷. Isopod diversity is even higher ($E(S_{100}) = 55$ species at 3,100 m) than on the southern Australian shelf (40 species)¹⁰ and the Argentine basin^{28,29}. Our results further indicate that these high levels of biodiversity extend to abyssal depths; for example, $E(S_{100})$ for isopods is >30 at almost 5,000 m (Supplementary Fig. 4). Possibly, this is a regional phenomenon and diversity is lower in other parts of the deep Southern Ocean. Nevertheless, the extraordinary richness of species in ANDEEP samples when compared with literature data from tropical and temperate sites in the South Atlantic challenges the idea that deep-sea diversity is depressed towards the Antarctic continent. Moreover, the Atlantic is the youngest ocean. A longer period of faunal evolution and diversification in the Pacific and Indian Oceans may have led to greater species richness than in the Atlantic sector of the Southern Ocean. Continuing studies at the morphological and molecular levels of bathyal and abyssal Antarctic faunas may provide further insights into the evolutionary processes that have helped to shape these important communities.

METHODS

A sediment profile imaging system (SPI) was used to obtain photographs and video footage of the seafloor and sediment profiles. Two Barnett-type, hydraulically damped multicorers equipped with 57-mm and 100-mm diameter tubes (25.5 and 78.6 cm² surface area respectively), and two box corers (2,500 cm² surface area) subdivided into 100 cm² 'vegetatic' subcores recovered sediment samples with well-defined surface areas. Multicorers were used principally for the meiofauna (32–300 µm size range) and characterization of sediment parameters; box corers were used to sample the macrofauna (>300 µm). Two towed gears, an epibenthic sledge for macrofauna and an Agassiz trawl for megafauna, obtained material from a much larger but less well-defined area of seafloor and provided most of the taxonomic material in these two size classes. The sledge comprised a lower epibenthic net (500 µm mesh size) and an upper suprabenthic net (300 µm mesh size), each 1 m wide. It was pulled across the seabed for 10 min at a mean velocity of 1 knot. Total distances covered varied from 711 to 6,464 m. The 3-m-wide Agassiz trawl had a cod-end mesh size of 500 µm, except at stations 74, 78 and 81, at which a 10-mm mesh was used. It was fished in a similar way to the epibenthic sledge. Sledge catches were usually fairly clean, whereas the trawl often recovered large quantities of mud which required sieving. Specimens for morphological study were sorted either on board or in a shore laboratory. Metazoans for DNA extraction were picked from samples that had been transferred immediately after collection into pre-cooled 96% ethanol and kept for at least 48 h at –20 °C. Foraminifera for molecular study were picked from unfixed samples in an ice-chilled dish and either frozen in liquid nitrogen or the DNA individually isolated using guanidine lysis buffer.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Danis and D.C.G. worked on archaeobacteria. Foraminiferal data are from N.C., T.C., A.J.G. and J.P.; J.P. was responsible for the molecular work on the Foraminifera. I.D.M. and A.V. delivered the data for Nematoda. A.B., S.B., W.B., M.C., S.K. and M.M. were responsible for the isopod analysis, M.R. was mainly responsible for the molecular isopod data. S.N.B. was responsible for the Ostracoda, B.E. for the Polychaetes, K.L. for the Mollusca and D.J. for the Porifera analysis.

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