

**Phylogeography of lysianassoid amphipods in the Southern Ocean:
investigating the missing link of Eastern Antarctica**

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Background to molecular studies on Southern Ocean lysianassoid amphipods

The Lysianassoidea Dana, 1849 is the largest superfamily belonging to the Gammaridea and comprises more than 1000 currently described species, 172 genera and 18 families worldwide (Horton & De Broyer 2013). Lysianassoids cover a vast range of habitats and are characterized by a wide array of morphological adaptations. Besides algal dwellers and deposit-feeders, many genera comprise species that are benthic-pelagic or demersal scavengers, of which some occupy depths in the abyssal and hadal zones. The superfamily is a typical cold-water group, mainly occupying waters with temperatures below 10°C. Hence, lysianassoids can commonly be found in deep-sea basins and high-latitude shallow waters (e.g. Vader & Romppainen 1986), where they represent one of the most abundant and widespread macrofaunal scavenger groups (Slattery & Oliver 1986). It has been shown that the morphological traits associated with this scavenger mode of feeding has evolved independently several times within the superfamily (Havermans et al. 2010, Corrigan et al. 2013). In the Antarctic region, the food web generates significant quantities of food falls composed of fish, seabirds, seals and cetaceans, which are less seasonally dependent (Dauby et al. 2001). As a consequence, the Antarctic slope is richer in scavenger species compared to elsewhere at the same depth range (De Broyer et al. 2004).

Molecular methods unveiled more cryptic species than expected in the Southern Ocean benthos, in view of the generally assumed circum-Antarctic and eurybathic species distributions (e.g. Held 2003; Held & Wägele 2005, Wilson et al. 2007). Lysianassoid amphipods represent an ideal model group to test hypotheses concerning the Southern Ocean biodiversity since this superfamily comprises a high number of species in the Southern Ocean, of which some are endemic, and many of them known to occupy wide geographic and bathymetric ranges. Hence, these species are of particular interest to test the hypotheses of circumpolarity and eurybathy, and in the cases of widespread lysianassoid deep-sea species, the hypothesis of cosmopolitanism in the deep sea. In addition, amphipods, and peracarids (i.e. brooding crustaceans) in general represent an interesting group for testing these hypotheses on faunal distributions due to their lack of pelagic dispersal stages. This trait renders them particularly subject to allopatric and/or cryptic speciation processes. Even though lysianassoids are brooders, a number of representatives of this superfamily are known to be very mobile. Some species (e.g. *Pseudorchomene plebs*) have the ability to form and migrate in swarms composed of thousands of individuals in the search of pelagic prey or food falls on the seafloor (Dauby et al. 2001; Horton et al. 2013). *Eurythenes gryllus* is known for being able to swim at considerable speed, even against slow currents (Laver et al. 1985; Takeuchi & Watanabe 1998). These dispersal capacities might explain the distributional patterns observed within lysianassoid species such as the assumingly circum-Antarctic (e.g. *Orchomenella* (*O. pinguides*), eurybathic (e.g. *O. (Orchomenopsis) cavimanus*) and even cosmopolitan species (e.g. *Eurythenes gryllus*, *Abyssorchomene chevreuxi*) (De Broyer et al. 2007), in some cases already confirmed by the observation of a genetic homogeneity between populations over a large geographic (e.g. *Pseudorchomene plebs*) and bathymetric scale (*Abyssorchomene* sp. 1) (Havermans et al. 2011).

Conversely, in other closely related species (e.g. *O. (O.) acanthurus*, *O. (O.) franklini*), evidence for cryptic species with seemingly restricted distributional ranges has been observed (Havermans et al. 2011). Finally, by representing a cold-water group that has diversified both in Polar Regions and the deep sea, lysianassoids are an ideal model group for molecular studies aiming to test the past colonization and present connectivity patterns between the Southern Ocean and surrounding deep-sea basins.

Initial project introduction

Many lysianassoid species are known to be circum-Antarctic, covering wide bathymetric ranges. My recent molecular studies, focused on phylogeny (using nuclear 28S rRNA & mitochondrial COI gene fragments) and DNA barcoding (using COI), were mainly focused on the Atlantic sector (Scotia and Weddell seas) and, to a lesser extent, on the Ross Sea. Results indicated the presence of cryptic species as well as genetically homogeneous species (Havermans et al. 2011). Nevertheless, the resolution of these DNA barcoding studies has been hampered by the limited spatial coverage and a lack of samples from the eastern part of the Southern Ocean. Scarce genetic studies on benthic taxa from Eastern Antarctica have shown clear patterns of regional differentiation (Arango et al. 2011, Baird et al. 2011), indicating that an increase in genetic diversity of lysianassoid species is expected when additional sampling in Eastern Antarctica is carried out, as well as a significant increase in the number of species new to science. During the CEAMARC (Collaborative East Antarctic Marine Census) cruises, benthic fauna has been sampled in the Dumont d'Urville Sea. Around 150 lysianassoid amphipod specimens have been collected from previously poorly investigated regions and depths. A reference library of sequences derived from specimens of known identity has already been established for lysianassoid species from the Atlantic sector of the Southern Ocean (Havermans et al. 2011) and newly obtained sequences will be incorporated in this database. Phylogeographic analyses will be carried out, comparing these sequences with the sequences of specimens from the Ross, Scotia and Weddell Seas. This will allow us to:

- explore lysianassoid species and genetic diversity in the eastern part of the Southern Ocean
- investigate the phylogeography of target taxa and confirm the true circum-Antarctic genetic structure of some species
- reveal undescribed and cryptic species in the less studied area of the Southern Ocean

Furthermore, additional analyses will be carried out aiming to elucidate the lysianassoid phylogeny by maximizing the species number included.

Methodology

During the visit at the Muséum national d'Histoire naturelle in July 2012, samples from East Antarctic expeditions (CEAMARC, REVOLTA I & II) were sorted out and taxa of interest identified to genus or species level. Around 500 lysianassoid specimens were identified and tissues (pleopod VI) were preserved in ethanol for transport to the home laboratory (RBINS) and subsequent molecular analyses. The lysianassoid species identified in the samples were: *Uristes murrayi*, *Uristes* sp., *Orchomene* sp., *Waldeckia obesa*, *Orchomenella (Orchomenopsis) acanthurus*, *Pseudorchomene* cf. *plebs*, *Orchomenella (O.) pinguides* and *Abyssorchomene nodimanus*. DNA of a selection of these specimens was extracted and amplifications and sequencing of the mitochondrial COI and nuclear 28S rRNA gene fragments was carried out at the home institution (RBINS) during the following months. Furthermore, in spring 2013, additional lysianassoid specimens from newly provided samples from several other

localities in the Southern Ocean have been processed as well, aiming to increase the sampling and taxon coverage of ongoing phylogeographic and phylogenetic studies. These amphipods were sampled in the Haakon VII Sea during the BELARE expedition, in the deep-sea basins of the Atlantic sector of the Southern Ocean with the RV *Polarstern* "SYSTCO II"- expedition (ANT XXVIII/3) and in the Amundsen Sea with RV *James Clark Ross* "BIOPEARL II"- expedition (JR-179). Finally, specimens from the South Atlantic were collected with the RV Meteor DIVA 3 expedition (M79/1). These samples complement the previously established DNA sequence library for large part of the Antarctic species of the genus complex *Orchomene sensu lato* (COI barcodes; see Havermans et al. 2011).

Secondly, the phylogeographic patterns of the cosmopolitan species *Eurythenes gryllus* were investigated by means of three genes (COI, 16S, 28S rDNA) of specimens coming from both poles (several localities in the Southern and Arctic oceans) and other deep-sea basins. Phylogeographic and species delimitation analyses were carried out on our newly established dataset and sequences retrieved from GenBank (France & Kocher 1996a; Escobar-Briones et al. 2010) in order to test the hypothesis of cosmopolitanism in the deep sea. For details I refer to Havermans et al. 2013.

Finally, COI and 28S rDNA was sequenced for several so far unexamined lysianassoid species from the Southern Ocean and elsewhere (Arctic, Atlantic). This was done in order to elucidate their phylogenetic relationships and historical colonization patterns, by extending the taxonomic resolution to the entire lysianassoid superfamily, as a complement to the phylogenetic study of Havermans et al. 2010 that was focusing mainly on a single lysianassoid genus complex (*Orchomene sensu lato*). To do so, sequences were obtained from individuals belonging the following genera: *Tryphosa*, *Hirondellea*, *Aristias*, *Hippomedon*, *Tryphosella*, *Parschisturella*, *Euonyx*, *Tmetonyx*, *Eurythenes*, *Paralicella*, *Cyphocaris*, *Kerguelenia*, *Socarnes*, *Anonyx*, *Onisimus*, *Scopelocheirus*, *Paracallisoma*, *Shackletonia* and *Waldeckia*. These various lysianassoids were sampled mainly in the Southern Ocean with RV *Polarstern* expeditions but some species were sampled in the Arctic with the RV *Jan Mayen*, in the North Atlantic with the RV *Meteor* and RV *Poseidon* "IceAge I & II" expeditions (M85/3 & POS456) and in the South Atlantic with the RV Meteor DIVA 3 expedition (M79/1).

Results

DNA barcoding results on lysianassoid species

Genus *Orchomene sensu lato*

DNA barcoding was used to test the well-accepted paradigms of circumpolarity and eurybathy for Southern Ocean benthos. Species distributions of orchomenids were evaluated by comparing intra- versus interspecific distances of COI sequences and linking these to geographic and bathymetric data. For all lysianassoid species investigated, intra- and interspecific COI distances followed a bimodal distribution with a mean intraspecific variation of 1.7% and a mean interspecific divergence of 14.8% separated by a barcoding gap of 1.5% using the Kimura-2-parameter (K2P; Kimura 1980) distance model (Havermans 2012). In a previous DNA barcoding study (Havermans et al. 2011), distinct genetic patterns were found amongst the orchomenid species. Several species were characterized by a low genetic divergence between specimens from remote sampling localities, indicating a widespread and/or eurybathic distribution (e.g. *Pseudorchomene plebs*, *Abyssorchomene* sp. 1, *P. coatsi*), whilst for some species, (pseudo)cryptic lineages were observed within the species, either characterized by restricted, non-overlapping distributions (e.g. *Orchomenella (Orchomenopsis) acanthurus*) or by widespread, overlapping distributions (e.g. *O. (O.) cavimanus*, *O. (O.) franklini*). Circum-Antarctic distributional ranges could not be confirmed due to the lack of samples from sites all around the continent, mainly the Amundsen Sea and East Antarctic region. The additional specimens of

orchomenid species sequenced for this study increased the geographic coverage, including now the Haakon VII Sea, the Amundsen Sea, the Eastern Antarctic and the Southwest Atlantic Ocean. In the case of species complexes, the additional sampling increased the number of species-level lineages observed e.g. within *O. (O.) acanthurus*, within *O. (O.) cavimanus* and *O. (O.) pinguides*. Other orchomenid species were confirmed to be widespread (*Abyssorchomene rossi*) and truly circum-Antarctic (e.g. *Abyssorchomene* sp. 1). Several species, for which bathymetric and geographic distributions were assessed by DNA barcoding were shown to be more widespread than recorded in literature. Results are summarized in Havermans (in press).

Other lysianassoid species

Similar patterns in genetic structure as in *Orchomene sensu lato* have been observed in other (non-orchomenid) lysianassoid taxa. The genetic diversity within other lysianassoid taxa (*Waldeckia obesa* and *Uristes murrayi*, *U. gigas*) was also investigated in order to assess their distributions and detect additional cases of cryptic speciation. For *Waldeckia obesa*, cryptic species were revealed with overlapping distributional ranges, with specimens from each of the two lineage separated by distances in the range of interspecific divergence (min. 15 % -K2P). One lineage was shown to be truly circum-Antarctic, whilst the other seemed restricted to the Atlantic sector of the Southern Ocean. For *U. murrayi*, interclade divergences were less high (3.0 – 4.3 %) but still at the upper range of intraspecific distances observed for other lysianassoid species. Specimens from cluster A were sampled in the Ross Sea whilst specimens from cluster B in the eastern Weddell Sea. Hence, the observed clusters might correspond to geographically remote populations characterized by a limited gene flow. Only a small number of non-orchomenid lysianassoid taxa were investigated and intraspecific sampling was often limited. The two well-sampled taxa both showed evidence of distinct genetic lineages and thus, a higher number of species complexes will probably be uncovered with additional molecular studies. Results are summarized in Havermans (in press).

Phylogeographic patterns of *Eurythenes gryllus sensu lato*

Eurythenes gryllus is one of world's most widely distributed amphipods, occurring in every ocean and covering a depth range including the bathyal, abyssal and hadal zones (De Broyer et al. 2007; Brandt et al. 2012 and references herein). Previously, it has been shown that this assumingly cosmopolitan and eurybathic deep-sea species was actually characterized by several genetically (Bucklin et al. 1987; France & Kocher 1996a, b; Escobar-Briones et al. 2010) and morphologically (Barnard 1961, Thurston et al. 2002) divergent lineages. In this study, this was further tested on a global scale by means of phylogeographic and species-delimitation analyses on mitochondrial (COI, 16S rDNA) and nuclear (28S rDNA) sequence data. Nine species-level lineages within *E. gryllus* were revealed based on the most extensive dataset (16S rDNA: GenBank and newly collected sequences for this study). Bimodal distributions of intra- and interspecific divergences were observed for all three genes and for COI a clear barcoding gap could be distinguished. A clear distinction could be observed between bathyal and abyssal depths with a genetic break occurring around 3,000 m. Two bathyal and two abyssal species-level lineages showed a widespread distribution, while five other abyssal species-level clades seemed to be restricted to a single oceanic basin each. The observed higher species diversity in the abyss compared to the bathyal zone stands in contrast to the depth-differentiation hypothesis (reviewed in Rex & Etter 2010), stating that genetic differentiation decreases with depth. These results show that, despite the more uniform environment of the abyss and its presumed lack of isolating barriers, abyssal populations might be more likely to show population differentiation than previously assumed. Results are more extensively discussed in Havermans et al. (2013), where hydrostatic pressure, hydrography,

topography of the seafloor and food supply are discussed as factors influencing species' origins and distributions. Finally, the molecular and morphological studies demonstrated that the bipolar bathyal clade within *E. gryllus sensu lato* corresponds to the 'true' *E. gryllus*. This represents the first molecular evidence for a bipolar distribution in a macrobenthic deep-sea organism. Five of the nine species detected, for which specimens are available, are currently being (re)described (d'Udekem d'Acoz & Havermans in prep.).

Phylogeny of polar components of the Lysianassoidea

In a previous molecular phylogenetic study on Antarctic orchomenid species (Havermans et al. 2010), the systematics of this group was shown to be problematic, showing that several genera and subgenera of the genus complex *Orchomene sensu lato* were non-monophyletic. However, in order to proceed to a further revision of the genus- and family-level systematics, and to investigate the origin of the Antarctic representatives of these genera, a more complete taxon sampling was needed. Hence, in this study, strictly Antarctic species, widespread Atlantic species as well as species from the Northern Hemisphere were included in phylogenetic analyses, using 28S rDNA and COI sequences. In order to further investigate the phylogeny at the level of the superfamily, species from different lysianassoid genera were also included in this study. The phylogenetic analyses comprised successfully sequenced species from the genera *Pseudorchomene*, *Abyssorchomene*, *Tryphosa*, *Falklandia*, *Orchomenyx*, *Orchomenella* (subgenera *Orchomenella* and *Orchomenopsis*), *Ambasiopsis*, *Uristes*, *Waldeckia*, *Pseudowaldeckia*, *Hirondellea*, *Aristias*, *Hippomedon*, *Tryphosella*, *Parschisturella*, *Euonyx*, *Tmetonyx*, *Eurythenes*, *Paralicella*, *Cyphocaris*, *Kerguelenia*, *Socarnes*, *Anonyx*, *Onisimus*, *Scopelocheirus*, *Paracallisoma* and *Shackletonia*. Hence, these analyses covered 8 families out of the 18 currently described lysianassoid families, i.e. the Uristidae, the Lysianassidae, the Scopelocheiridae, the Aristiidae, the Acidostomatidae, the Cyphocaridae, the Eurytheneidae and the Hirondelleidae. Results are currently being analyzed.

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Outcome of the project

Publications that benefited from the Antarctic Science bursary:

Havermans C (2012). DNA barcoding, phylogeography and phylogeny of the Lysianassoidea (Crustacea: Amphipoda) from the Southern Ocean and the World's deep seas. PhD thesis, Université Catholique de Louvain, 423 pp.

Havermans C, Sonet G, d'Udekem d'Acoz C, Nagy ZT, Martin P, Brix S, Riehl T, Agrawal S, Held C (2013). Genetic and morphological divergences in the cosmopolitan deep-sea amphipod *Eurythenes gryllus* reveal a diverse abyss and a bipolar species. PLoS ONE 8(9): e74218

Havermans C (in press). Phylogeographic patterns of the Lysianassoidea (Crustacea: Peracarida: Amphipoda). In: De Broyer C, Koubbi P, Griffiths HJ et al. (eds). Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, UK, Cambridge.

d'Udekem d'Acoz C, **Havermans C (in prep).** Contribution to the systematics of the genus *Eurythenes* S.I. Smith in Scudder, 1882: an integrative study (Crustacea: Amphipoda: Lysianassoidea).

Havermans C et al. (in prep). Phylogeny of polar representatives of a cold-water amphipod superfamily (Crustacea: Lysianassoidea). To be submitted to Antarctic Science.

Presentations at conferences and workshops with reference to the Antarctic Science bursary:

Havermans C (2012). Biodiversity of the Antarctic deep sea: Phylogeny, phylogeography and DNA barcoding of the Lysianassoidea (Crustacea: Amphipoda). Colloquium at the Biological Station of Helgoland, Alfred Wegener Institute for Polar and Marine Research, Helgoland, Germany.

Havermans C (2012). Evidence for a diverse abyss: unveiling hidden species within the eurybathic and widespread deep-sea amphipod *Eurythenes gryllus* (Crustacea: Lysianassoidea). Paper presented at the IceAGE (Icelandic marine Animals: Genetics and Ecology) Workshop, Wilhelmshaven, Germany.

Havermans C, d'Udekem d'Acoz C (2012). Molecular and morphological evidence for the existence of several species with restricted range within the cosmopolitan eurybathic deep-sea lysianassoid amphipod *Eurythenes gryllus sensu lato*. Paper presented at the 10th Colloquium on Crustacea: The Crustacean Society Summer Meeting, Athens, Greece.

Havermans C, Sonet G, Nagy ZT, Riehl T, Brix S, Martin P, Held C, d'Udekem d'Acoz C (2012). Molecular and morphological evidence for several species within the cosmopolitan eurybathic deep-sea lysianassoid amphipod *Eurythenes gryllus sensu lato*. Poster presented at the 19th Benelux Congress of Zoology, Brussels, Belgium.

Havermans C (2012). Phylogeny, phylogeography and DNA barcoding of the Antarctic Lysianassoidea (Crustacea: Amphipoda). Oral communication presented at the APECS (Association of Polar Early Career Scientists) Benelux meeting, Gent, Belgium.

Havermans C (2013). Phylogeography of lysianassoid amphipods: Evidence for circumpolarity, eurybathy, bipolarity and (pseudo)cryptic speciation. Oral communication at the SCAR (Scientific Committee on Antarctic Research) Biology Symposium, Barcelona, Spain.

Havermans C (2014). Genetic connectivity of Southern Ocean amphipods: circumpolarity, eurybathy, bipolarity and (pseudo)cryptic speciation. To be presented at the SCAR Open Science Conference, Auckland, New Zealand (August).

References cited in this report

- Arango, C.P., Soler-Membrives, A., Miller, K.J., 2011. Genetic differentiation in the circum-Antarctic seaspider *Nymphon australe* (Pycnogonida; Nymphonidae). *Deep-Sea Research Part II: Topical studies in Oceanography*, **58**, 212-219.
- Baird, H. P., Miller, K.J., Stark, J.S., 2011. Evidence of hidden biodiversity, ongoing speciation and diverse patterns of genetic structure in giant Antarctic amphipods. *Molecular Ecology*, **20**, 3439-3454.
- Barnard, J.L., 1961. Gammaridean Amphipoda from depths of 400 to 6000 meters. *Galathea Report*, **5**, 23-128.
- Brandt, A., Błazewicz-Paszkowycz, M., Bamber, R.N., Mühlenhardt-Siegel, U., Malyutina, M.V., Kaiser, S., De Broyer, C., Havermans, C., 2012. Are there widespread peracarid species in the deep sea (Crustacea: Malacostraca)? *Polish Polar Research*, **33**, 139-162.
- Bucklin, A., Wilson, R.R.Jr., Smith, K.L.Jr., 1987. Genetic differentiation of seamount and basin populations of the deep-sea amphipod *Eurythenes gryllus*. *Deep Sea Research Part A: Oceanographic Research Papers*, **34**, 1795-1810.
- Corrigan, L.J., Horton, T., Fotherby, H., White, T.A., Hoelzel, A.R. (2013). Adaptive evolution of deep-sea amphipods from the superfamily Lysianassoidea in the North Atlantic. *Evolutionary Biology*, doi:10.1007/s11692-013-9255-2.
- Dauby, P., Scailteur, Y., De Broyer, C., 2001. Trophic diversity within the eastern Weddell Sea amphipod community. *Hydrobiologia*, **443**, 69-86.
- De Broyer, C., Nyssen, F., Dauby, P., 2004. The crustacean scavenger guild in Antarctic shelf, bathyal and abyssal communities. *Deep-Sea Research Part II: Topical studies in Oceanography*, **51**, 1733-1752.
- De Broyer, C., Lowry, J.K., Jazdzewski, K., Robert, H. 2007. Catalogue of the Gammaridean and Corophiidean Amphipoda (Crustacea) of the Southern Ocean with distribution and ecological data. In: De Broyer, C. (ed.), Census of Antarctic Marine Life: Synopsis of the Amphipoda of the Southern Ocean. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie*, **77(suppl. 1)**, 1-325.
- Escobar-Briones, E., Nájera-Hillman, E., Alvarez, F., 2010. Unique 16S rDNA sequences of *Eurythenes gryllus* (Crustacea: Amphipoda: Lysianassidae) from the Gulf of Mexico abyssal plain. *Revista Mexicana de Biodiversidad*, **81**, 177-185.
- France, S.C., Kocher, T.D., 1996a. DNA sequencing of formalin-fixed crustaceans from archival research collections. *Molecular Marine Biology and Biotechnology*, **5**, 304-313.
- France, S.C., Kocher, T.D., 1996b. Geographic and bathymetric patterns of mitochondrial 16S rDNA sequence divergence among deep-sea amphipods, *Eurythenes gryllus*. *Marine Biology*, **126**, 633-643.
- Havermans C., Nagy Z.T., Sonet G., De Broyer C., Martin P., 2010. Incongruence between molecular phylogeny and morphological classification in amphipod crustaceans: A case study of Antarctic lysianassoids. *Molecular Phylogenetics and Evolution*, **55**, 202-209.
- Havermans, C., Nagy, Z.T., Sonet, G., De Broyer, C., Martin, P., 2011. DNA barcoding reveals new insights into the diversity of Antarctic species of *Orchomene sensu lato* (Crustacea: Amphipoda: Lysianassoidea). *Deep-Sea Research Part II: Topical studies in Oceanography*, **58**, 230-241.

- Havermans, C., 2012. DNA barcoding, phylogeography and phylogeny of the Lysianassoidea (Crustacea: Amphipoda) from the Southern Ocean and the World's deep seas. PhD thesis, Université Catholique de Louvain, 423 pp.
- Havermans, C., Sonet, G., d'Udekem d'Acoz, C., Nagy, Z.T., Martin, P., Brix, S., Riehl, T., Agrawal, S., Held, C., 2013. Genetic and morphological divergences in the cosmopolitan deep-sea amphipod *Eurythenes gryllus* reveal a diverse abyss and a bipolar species. *PLoS ONE*, **8(9)**, e74218.
- Havermans C., (in press). Phylogeographic patterns of the Lysianassoidea (Crustacea: Peracarida: Amphipoda). In: De Broyer C, Koubbi P, Griffiths HJ et al. (eds). Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, UK, Cambridge.
- Held, C., 2003. Molecular evidence for cryptic speciation within the widespread Antarctic crustacean *Ceratoserolis trilobitoides* (Crustacea, Isopoda). In: Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M., Wolff, W.J. (eds.) *Proceedings of the SCAR Biology Symposium Amsterdam, Antarctic Biology in a global context*. Backhuys Publishers, Leiden, The Netherlands, 87–95.
- Held, C., Wägele, J.W., 2005. Cryptic speciation in the giant Antarctic isopod *Glyptonotus antarcticus* (Isopoda: Valvifera: Chaetiliidae). *Scientia Marina* 69: 175-181.
- Horton, T., De Broyer, C., 2013. Lysianassoidea. In: Horton, T., Lowry, J. & De Broyer, C. (eds.) World Amphipoda database at <http://www.marinespecies.org/amphipoda/aphia.php?p=taxdetails&id=176788> on 2013-12-18
- Horton T., Thurston M., Duffy, G. (2013) Community Composition of Scavenging Amphipods at Bathyal Depths on the Mid-Atlantic Ridge. *Deep-Sea Research Part II: Topical studies in Oceanography*, **98**, 352–359. <http://dx.doi.org/10.1016/j.dsr2.2013.01.032>
- Kimura, M., 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, **16**, 111–120.
- Laver, M.B., Olsson, M.S., Edelman, J.L., Smith, K.L., 1985. Swimming rates of scavenging deep-sea amphipods recorded with a free vehicle video camera. *Deep-Sea Research*, **32**, 1135–1142.
- Rex, M.A., Etter, R.J. (2010). Deep-sea biodiversity: pattern and scale. Cambridge, MA, Harvard University Press, pp. 199-240.
- Slattery, P.N., Oliver, J.S., 1986. Scavenging and other feeding habits of Lysianassid amphipods (*Orchomene* spp.) from McMurdo Sound, Antarctica. *Polar Biology*, **6**, 171–177.
- Takeuchi, I., Watanabe, K., 1998. Respiration rate and swimming speed of the necrophagous amphipod *Eurythenes gryllus* from Antarctic deep waters. *Marine Ecology Progress Series*, **163**, 285–288.
- d'Udekem d'Acoz, C., Havermans, C. (in prep). Contribution to the systematics of the genus *Eurythenes* S.I. Smith in Scudder, 1882: an integrative study (Crustacea: Amphipoda: Lysianassoidea).
- Vader, W., Romppainen, K., 1986. Notes on Norwegian marine Amphipoda. 10. Scavengers and fish associates. *Fauna Norvegica*, Series A, Volume 6, pp. 3–8.
- Wilson, N.G., Hunter, R.L., Lockhart, S.J., Halanych, K.M., 2007. Multiple lineages and absence of panmixia in the “circumpolar” crinoid *Promachocrinus kerguelensis* from the Atlantic sector of Antarctica. *Marine Biology*, **152**, 895–904.