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BIOGEOGRAPHIC ATLAS
OF THE SOUTHERN OCEAN

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Claude DE BROYER & Philippe KOUBBI (chief editors)

with Huw GRIFFITHS, Ben RAYMOND, Cédric d'UDEKEM d'ACOZ, Anton VAN DE PUTTE, Bruno DANIS, Bruno DAVID, Susie GRANT, Julian GUTT, Christoph HELD, Graham HOSIE, Falk HUETTMANN, Alexandra POST & Yan ROPERT-COUDERT

SCIENTIFIC COMMITTEE ON ANTARCTIC RESEARCH

THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

10.6. Phylogeographic patterns of the Lysianassoidea (Crustacea: Peracarida: Amphipoda)

Charlotte Havermans

Royal Belgian Institute of Natural Sciences, Brussels, Belgium

1. Introduction

The Lysianassoidea Dana, 1849 is the largest superfamily belonging to the Gammaridea and currently comprises more than 1000 described species, 172 genera and 18 families worldwide (Horton & De Broyer 2013). Lysianassoids cover a vast range of habitats and are characterised by a wide array of morphological adaptations. Many genera comprise species that are bentho-pelagic or demersal scavengers of which some occupy abyssal and hadal depths. Other genera comprise soft-bottom deposit-feeders or algal-dwellers (Lowry & Stoddart 1983). Commensal life styles are also well documented in several genera, with species living on other invertebrates (e.g. sponges, ascidians), as well as ectoparasitism on fish (Lowry & Stoddart 1983).

This superfamily is a typical cold-water group, occurring primarily at water temperatures below 10°C (Barnard & Karaman 1991). They are common in both deep-sea basins (e.g. Thurston 1979) and high-latitude shallow waters (e.g. Vader & Romppainen 1986), where they significantly contribute to the benthic species number. In terms of composition, the Antarctic and sub-Antarctic amphipod fauna is mostly dominated by representatives of the Lysianassoidea (158 spp. of 57 different genera; De Broyer *et al.* 2007; Horton & De Broyer 2013). Both in polar oceans and in the world's deep seas, lysianassoids comprise one of the most abundant and widespread macrofaunal scavenger groups (Slattery & Oliver 1986). It has been shown recently that the morphological traits associated with the scavenger mode of feeding evolved several times independently within the Lysianassoidea (Havermans *et al.* 2010, Corrigan *et al.* 2013). Scavenging can be considered as an adaptation to the generally or seasonally low food supply in terms of primary production in the deep sea and polar environments, respectively. The diversification of several scavenging lysianassoid lineages was found to coincide with the Eocene/Oligocene cooling, characterized by an increased productivity and the availability of novel food sources, representing an ecological opportunity for specialized scavengers (Corrigan *et al.* 2013).

Photo 1 *Eurythenes gryllus* (*Polarstern* ANTXXIII-8, st. 683-1). Image © C.d'Udekem (RBINS), Brussels.

The Antarctic food web generates significant quantity of food falls, which are less seasonally dependent, composed of fishes, seabirds, seals and cetaceans (Dauby *et al.* 2001). As a consequence, the Antarctic slope is richer in scavenger species compared to similar depth ranges elsewhere (De Broyer *et al.* 2004). The occurrence in high numbers of lysianassoids at food falls has been widely documented by means of catches with baited traps (e.g. Stockton 1982, De Broyer *et al.* 2004, Jamieson *et al.* 2011, Horton *et al.* 2013) and baited camera studies (e.g. Klages *et al.* 2001, Soltwedel *et al.* 2003, Premke *et al.* 2003), from below the ice shelf in polar regions up to hadal depths in world oceans.

Molecular methods unveiled more cryptic species than expected in the Southern Ocean (SO) benthos, in view of the generally assumed circum-Antarctic species distributions (e.g. Held 2003, Held & Wägele 2005, Wilson *et al.* 2007). In addition, cryptic species have also been observed along depth gradients within species considered to be eurybathic (e.g. Brandao *et al.* 2010, Schüller 2011). In this respect, amphipods, as well as other peracarids, represent an interesting group to test these hypotheses on faunal distributions. Peracarids are brooders and the lack of drifting stages might considerably limit their dispersal, rendering them particularly subject to cryptic speciation processes. However, even though lysianassoids are brooders, a number of representatives of this superfamily are known to be very mobile. For example, species of the genera *Abyssorchomene* De Broyer, 1984 and *Pseudorchomene* Schellenberg, 1926 can form swarms of thousands of individuals, capable of considerable migrations in search of pelagic prey or food falls on the seafloor (Dauby *et al.* 2001, Horton *et al.* 2013). *Eurythenes gryllus* (Lichtenstein, 1822) is known for its impressive swimming speeds, being able to swim against slow currents (Laver *et al.* 1985, Takeuchi & Watanabe 1998). Many species are thought to be circum-Antarctic (*Orchomenella* (*Or-*

chomenella) pinguides) (Walker, 1903) and/or eurybathic (e.g. *Orchomenella (Orchomenopsis) cavimanus*) (Stebbing, 1888), some even cosmopolitan (e.g. *Abyssorchomene chevreuxi* (Chevreux, 1903), *Eurythenes gryllus*), and there is evidence for gene flow between distinct deep-sea basins in the case of *Abyssorchomene* species (France 1994). Finally, by representing a cold-water group that has diversified both in polar regions and the deep sea, lysianassoids are of particular interest for molecular studies aiming to test the connectivity between the Southern Ocean and surrounding deep seas.

2. Molecular results

2.1. Genetic structure within and between species of *Orchomene sensu lato*

DNA barcoding was used to test the hypotheses of circumpolarity and eurybathy within the complex of genera *Orchomene sensu lato* (Havermans *et al.* 2011, Havermans 2012). Orchomenid species' distributions 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 divergences 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% (Kimura 2-parameter distance model, K2P; Kimura 1980) (Havermans 2012).

Within this group of closely related species, distinct genetic structures could be observed. Genetic divergences between clusters observed within *Orchomenella (Orchomenopsis) acanthurus* (Schellenberg, 1931), *O. (O.) cavimanus*, *O. (Orchomenella) franklini* (Walker, 1903) and *O. (O.) pinguides* (Walker, 1903), were congruent with species-level divergences observed between other closely related species of the orchomenid genus complex (K2P: 6.3 – 20.1%; Havermans *et al.* 2011) (Fig. 1). Furthermore, several cases of sympatry were observed: specimens of the same or nearby sampling sites were found in distinct clusters. Both the bimodal distribution of intra- and interspecific divergences and the prevalence of species-level differentiation of sympatric specimens represent criteria for the presence of cryptic or over-
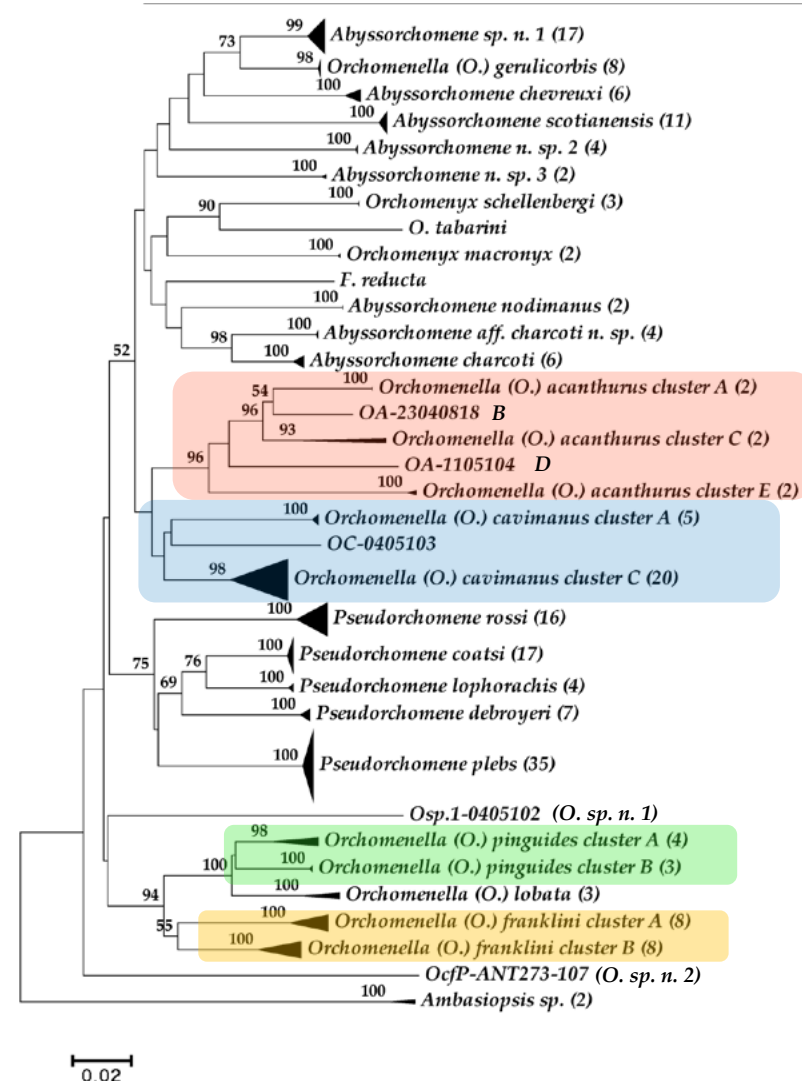

Figure 1 Neighbour-Joining tree of COI sequences of species of *Orchomene sensu lato* based on the Kimura 2-parameter distance model. Clusters were collapsed and the number of specimens in every cluster is indicated in parentheses. Species complexes are indicated with coloured rectangles. Bootstrap support (number of replicates = 2000) is indicated at each node when higher than 50%.
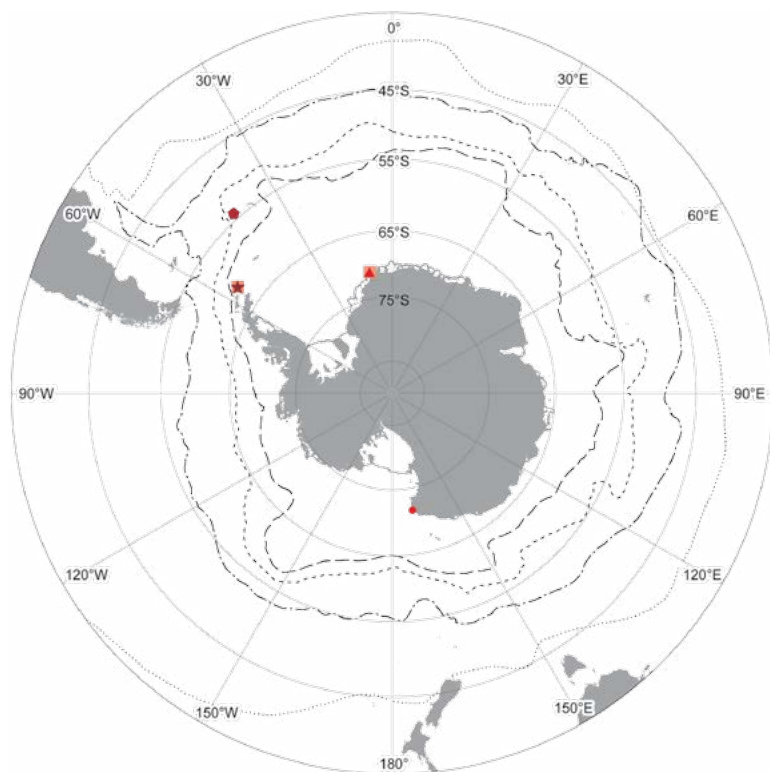
Map 1
- ● *Orchomenella* (*Orchomenopsis*) *acanthurus*
- ▲ *Orchomenella* (*Orchomenopsis*) *acanthurus*
- ■ *Orchomenella* (*Orchomenopsis*) *acanthurus*
- ⬟ *Orchomenella* (*Orchomenopsis*) *acanthurus*
- ★ *Orchomenella* (*Orchomenopsis*) *acanthurus*
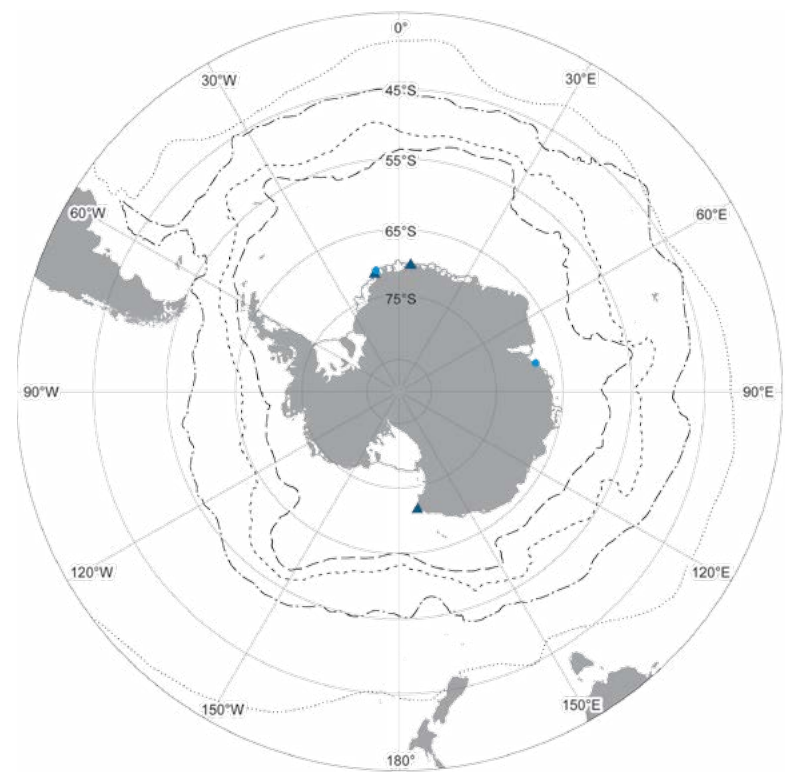
Map 2
- ▲ *Orchomenella* (*Orchomenella*) *pinguides*
- ● *Orchomenella* (*Orchomenella*) *pinguides*
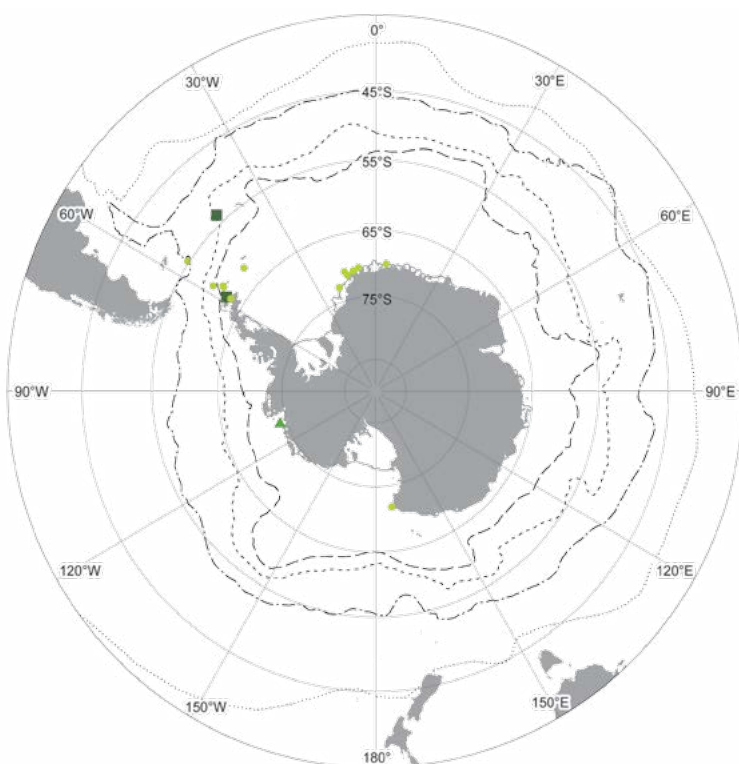
Map 3
- ■ *Orchomenella* (*Orchomenopsis*) *cavimanus*
- ▲ *Orchomenella* (*Orchomenopsis*) *cavimanus*
- ● *Orchomenella* (*Orchomenopsis*) *cavimanus*
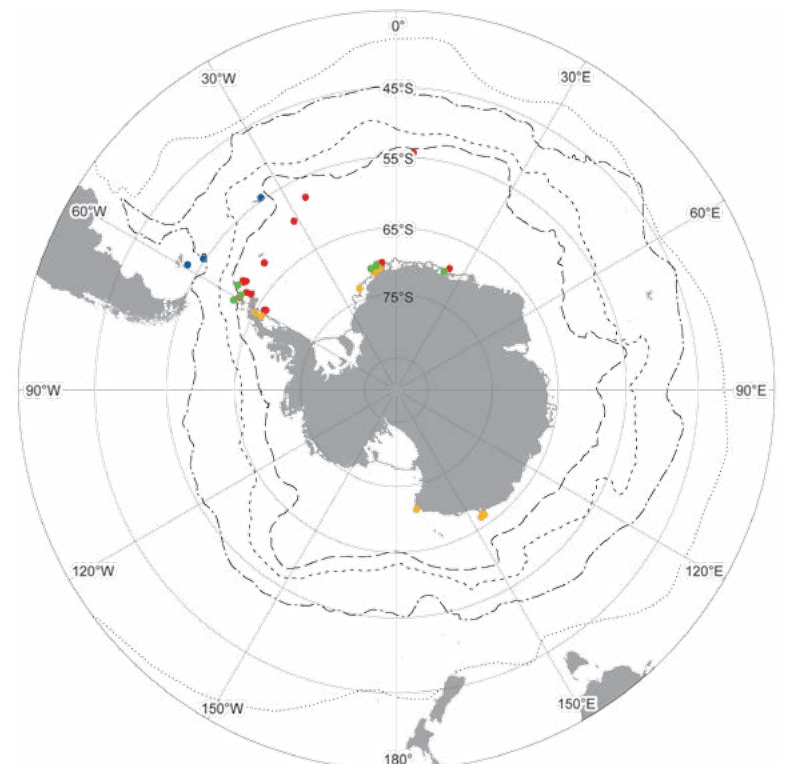
Map 4
- ● *Pseudorchomene plebs*
- ● *Pseudorchomene rossi*
- ● *Pseudorchomene coatsi*
- ● *Pseudorchomene debroyeri*

Lysianassoidea Maps 1-4 Distribution of the five species-level lineages observed within *Orchomenella* (*Orchomenopsis*) *acanthurus* based on molecular data. Map 2 Distribution of the two species-level lineages observed within *Orchomenella* (*Orchomenella*) *pinguides* based on molecular data. Map 3 Distribution of the three species-level lineages observed within *Orchomenella* (*Orchomenopsis*) *cavimanus* based on molecular data. Map 4 Distribution of *Pseudorchomene plebs*, *P. rossi*, *P. coatsi* and *P. debroyeri* based on molecular data.

looked species (Held 2003). Hence, these four species, consisting of at least two lineages, represent complexes of cryptic or pseudocryptic species, of which the distribution was either more restricted than previously assumed (e.g. for *O.* (*O.*) *acanthurus*) or rather widespread (cluster A of *O.* (*O.*) *franklini*, two clusters of *O.* (*O.*) *pinguides* and cluster C of *O.* (*O.*) *cavimanus*) (Havermans 2012). Within *O.* (*O.*) *acanthurus* (Fig. 1), three well-supported clusters can be observed, as well as two divergent single sequences (pairwise sequence divergences ranging from 5.8 up to 22.6%). These five species-level lineages all seemed to be restricted in distribution to a single Antarctic shelf or shallow-water region (max. depth of 400 m) (Map 1). Conversely, both species-level clades (A and B) of *O.* (*O.*) *pinguides* cover a large geographic distribution (Map 2). Specimens of cluster A were found on opposite sides of the Antarctic continent whilst specimens of cluster B were found in the Eastern Weddell Sea and on the East Antarctic coast. (*O.*) (*O.*) *cavimanus* consisted

of three well-supported species-level lineages, of which two lineages (A and B) seemed to be confined to a particular region whilst cluster C encompassed a wide geographic and bathymetric range (Map 3). Specimens of lineage A were found in shallow waters in the Scotia Sea and near King George Island; lineage B was composed of a single specimen (OC-0405103) from a shallow-water locality in the Amundsen Sea (Fig. 1). On the contrary, cluster C comprised specimens from the Scotia Sea, localities near the South Orkney and South Shetland Islands, the eastern Weddell Sea, the Ross Sea and the Magellan region (Burdwood Bank) (Map 3), covering a large bathymetric range from 130 to more than 3600 m depth. However, no subclusters based on a geographic or bathymetric segregation could be observed within this cluster, characterised by a gradient of intraspecific distances (K2P: 0.0 – 5.6%).

Conversely, in several species of the genera *Abyssorchomene* and *Pseudorchomene* (*A.* sp. 1, *A. chevreuxi*, *P. plebs*, *P. rossi*, *P. coatsi*), a ge-

netic homogeneity was found between specimens from remote sampling sites in the SO (and Atlantic for *Abyssorchomene* species), indicating a widespread or even a truly circum-Antarctic and/or eurybathic distribution (Map 4). In *Pseudorchomene plebs* (Hurley, 1965), a low genetic variation was observed between specimens from the Scotia Sea, the Antarctic Peninsula, the eastern Weddell Sea and the shelf of Bouvet Island, across a depth gradient from 40 up to 2890 m (Havermans *et al.* 2011). The same was true for *P. rossi* (Walker, 1903), between sites in the Weddell and Ross seas, off the George V coast and near the Antarctic Peninsula (Havermans 2012). Specimens of *P. debroyeri* d'Udekem & Havermans, 2012 from shallow-water South Georgia and sub-Antarctic localities (Falkland Islands, Burdwood Bank) were separated by low genetic divergences, across the Polar Front (Map 4). *P. coatsi* (Chilton, 1912) was characterised by a genetic homogeneity between localities in the Scotia, Weddell and King Haakon VII seas (Havermans 2012).

For a number of species, molecular results confirmed the existence of species distributions extending from the SO to surrounding deep-sea basins. Low genetic divergences (K2P: 0.1 to 1.5%) were observed for an undescribed *Abyssorchomene* species (*A.* sp. 1, Map 5) between specimens from the Antarctic Peninsula, Weddell, Ross and Amundsen seas and the Argentine abyssal Basin, at depths ranging from 300 to more than 4500 m (Havermans 2012). This species thus represents a truly circum-Antarctic and eurybathic species, with its distribution extended to the Atlantic abyssal basins. *Abyssorchomene chevreuxi* was confirmed to be a candidate for a cosmopolitan distribution, since only low genetic divergences (K2P: 0.0 to 1.7%) separated specimens from the Weddell Sea, the Antarctic Peninsula region, the Southwest Atlantic and the North Atlantic (Map 5), covering depths from 3070 m to more than 4800 m (Havermans 2012 and unpublished data).

2.2. Phylogeography of *Eurythenes gryllus sensu lato*

Eurythenes gryllus (Lichtenstein, 1822) is one of world's most widely distributed amphipods, occurring in every major ocean over a depth range covering the bathyal, abyssal and hadal zones (De Broyer *et al.* 2007; Brandt *et al.* 2012; and references therein). Previously, the assumption of a cosmopolitan and eurybathic distribution was questioned due to the presence of several genetically and morphologically divergent lineages (Barnard 1961; Bucklin *et al.* 1987; France & Kocher 1996a, b; Escobar-Briones *et al.* 2010). 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 (Havermans *et al.* 2013).

Nine genetic lineages within *Eurythenes gryllus* were revealed based on the most extensive dataset of 16S sequences, of which five were corroborated by the three-gene dataset (COI, 16S, 28S) (Havermans *et al.* 2013). Bimodal distributions of intra- and interspecific divergences were observed for all three genes and for COI a clear barcoding gap could be distinguished. Tree-construction methods on the three-gene dataset revealed five clades within *E. gryllus* (Map 6): Eg1, comprising specimens from bathyal depths (<3000 m) in various sites in the Arctic and Southern oceans, Eg2, comprising specimens from Antarctic abyssal (>3000 m) sites, Eg3, grouping specimens from the Antarctic and Atlantic at abyssal depths, Eg4 and Eg5, both comprising specimens from the abyssal Brazil Basin but separated by high genetic divergences. For the 16S dataset, based on sequences from Havermans *et al.* (2013) and sequences from previous studies (France & Kocher 1996b; Escobar-Briones *et al.* 2010), the same clades were recovered, complemented by four additional well-supported clades (Eg6-9). Eg3 now also comprised specimens from abyssal sites in the North Atlantic and the Pacific Ocean. In addition to the clades Eg4 and Eg5, another abyssal cluster (Eg6) was revealed comprising a specimen from the Brazil Basin and one from the Gulf of Mexico. Clade Eg8 grouped specimens from bathyal depths in the Iceland Basin and the Bahamas, whilst Eg9 comprised specimens at abyssal depths (3193 m) on the slope of a seamount in the Pacific. Finally, Eg7 represents a single sequence from a specimen from the same seamount but sampled at a different depth (3982 m).

A morphological analysis on the available specimens revealed small but consistent phenotypical differences between Eg1, Eg2, Eg3, Eg4+5 and Eg6 and for the specimen(s) of each clade, a unique combination of character states could be identified. Overall, five putative morphospecies were recognized within *E. gryllus* based on the material examined but no differences were detected between the clades Eg4 and Eg5, although characterised by relatively high genetic divergences. Specimens from the bipolar clade (Eg1), collected in proximity of the type locality (Greenland Sea), were the most similar to the holotype of *E. gryllus* (illustrated by Stoddart & Lowry 2004).

Results of the statistical parsimony network analysis (Fig. 2) recovered eight of these lineages as unconnected networks but Eg4 and Eg5 were grouped in one single network. Since these two sympatric clades were well-supported with a clear barcoding gap between intra- and interclade divergences for COI, but not for 16S and 28S, this might represent a case of recent or ongoing speciation. The bathyal network Eg1 (Map 6) comprised specimens from both Arctic (Svalbard, Canada Basin, Eastern Fram Strait) and SO regions (King George Island, Antarctic Peninsula, South Sandwich Islands, Weddell Sea) sampled from 839 to 2743 m depth. Additional specimens from the Kerguelen Islands (1947 m depth) were also found to cluster in Eg1 (Havermans, unpublished data). This bipolar clade grouped specimens of *E. gryllus* separated by distances up to 16,750 km but characterised by low genetic divergences (COI K2P: 0.8–2.0%) and sharing a single 16S haplotype.

More genetic lineages were encountered in abyssal than in bathyal regions: two species-level clades could be distinguished above 3000 m and at

least six species-level clades below 3000 m (Fig. 2). The two bathyal species-level clades identified here are both characterised by a very wide geographic range: one is bipolar and the other is found to occur both in the Bahamas and in the Iceland Basin. Conversely, all abyssal lineages but Eg3 and Eg6, seemed to be restricted to a single ocean basin. Finally, networks showed no overlap between bathyal and abyssal depths: two networks grouped specimens exclusively from above 3000 m depth each and six networks comprised only specimens from below 3000 m (Fig.2). This break around 3000 m also appeared in the phylogenetic trees.
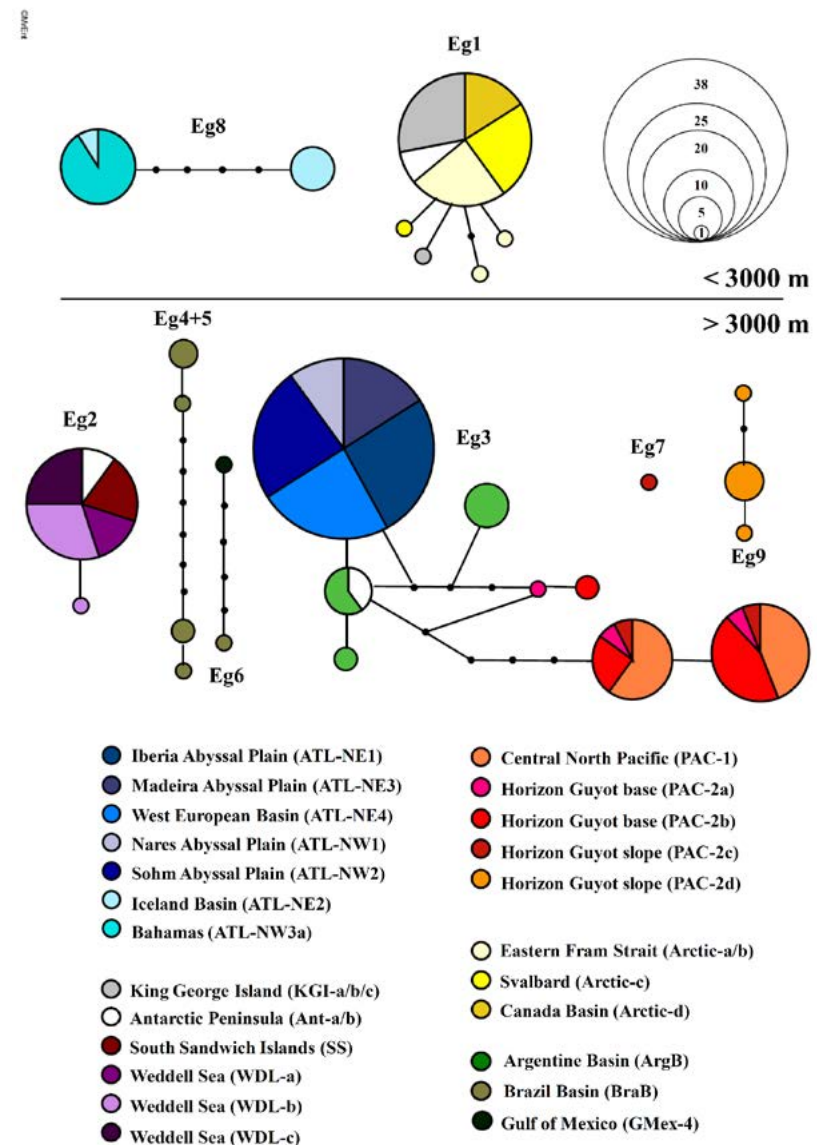
Figure 2 Statistical parsimony haplotype networks based on the 16S rDNA sequences of *Eurythenes gryllus* (from Havermans *et al.* 2013). The dataset includes sequences from this study, that of France and Kocher (1996b) and Escobar-Briones *et al.* (2010). The area of each circle is proportional to the frequency of the haplotype in our sampling (a scale is presented). Each line represents a single substitution, nodes represent hypothetical haplotypes and colors refer to the sampling localities. Haplotype networks (95% probability threshold) are numbered (Eg1-9) according to the different clusters identified in Bayesian trees (see Havermans *et al.* 2013).

2.3. (Pseudo)cryptic speciation in other lysianassoid species

Similar patterns of genetic structure as in *Orchomene sensu lato* have been observed in other (non-orchomenid) lysianassoid taxa. For the circum-Antarctic species *Waldeckia obesa* (Chevreux,1905), two well-supported clusters were revealed with overlapping distributional ranges, separated by genetic distances (K2P: min. 15%) in the range of interspecific divergences known for lysianassoid taxa (Fig. 3) (Havermans 2012). One species-level lineage (B) was truly circum-Antarctic, occurring in the Lazarev, King Haakon VII, Amundsen and Dumont d'Urville seas, whilst the other (A) seemed to be restricted to the Atlantic sector of the SO (Map 7). Previously, small morphological differences have been reported between specimens from different regions (Chapelle pers. comm.). Hence, an in-depth morphological study is needed to confirm whether these lineages represent pseudocryptic species. Furthermore, the closely related epifaunal lysianassid species *Parawaldeckia kidderi* (Smith, 1876) represents a single species across the sub-Antarctic and a single mitochondrial haplotype was shared by Kerguelen, Macquarie, Marion and Possession Islands (Nikula *et al.* 2010).

Based on a limited sampling, two geographical lineages could be distinguished within *Uristes murrayi* (Walker, 1903) (Fig. 3): cluster A grouped specimens from the eastern Weddell and the King Haakon VII seas, while cluster B grouped specimens from the Ross Sea (Havermans 2012). By means of a multigene molecular study based on a more extensive sampling, Feldkamp (2010) observed the presence of three distinct species-level lineages within *U. murrayi*. Using morphometrics and scanning electron microscopy, consistent phenotypical differences were detected between specimens of these clades (Seefeldt 2012).

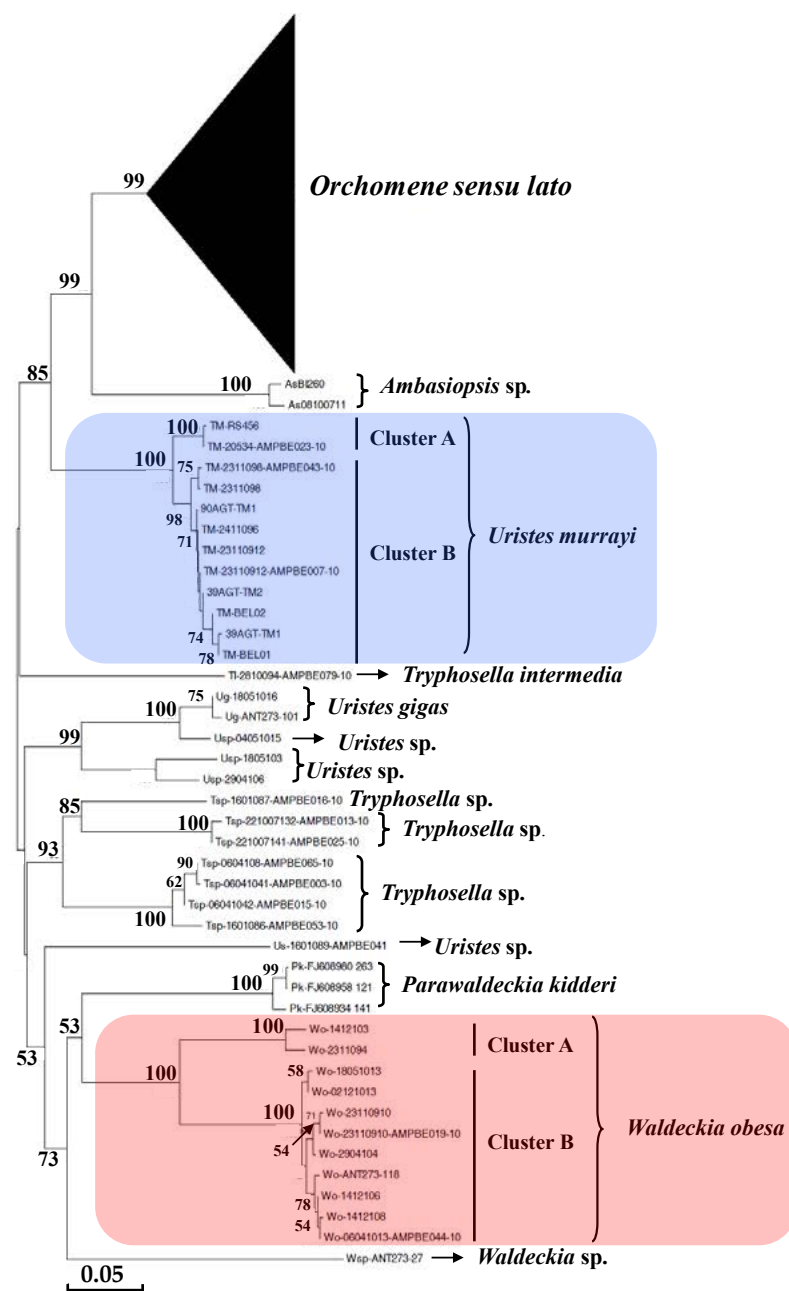**Figure 3** Neighbour-Joining tree of COI sequences of lysianassoid species based on K2P distances. (number of replicates = 2000) is indicated at each node when higher than 50%. Species where a high intraspecific variation was detected are indicated with coloured rectangles and the clusters are indicated next to the tree.

3. Geographic and bathymetric distributions

3.1. Circum-Antarctic, bipolar and cosmopolitan species

Molecular studies have shown evidence for circumpolarity in the species *Abyssorchomene* sp. 1, *Pseudorchomene rossi* and one species-level clade of *Waldeckia obesa* (Havermans 2012). *Parawaldeckia kidderi* exhibited a wide-scale circum-Antarctic distribution throughout a number of sampled sub-Antarctic islands (Nikula *et al.* 2010). Even though several species complexes were revealed as anticipated for Antarctic benthos, there was a limited number of cases where the distinct lineages showed a more restricted distribution than originally thought (e.g. all lineages of *Orchomenella* (*Orchomenopsis*) *acanthurus*, lineage A of *Waldeckia obesa*). Several complexes comprised lineages which were characterised by a widespread or even circumpolar distribution (cluster C of *O.* (*O.*) *cavimanus*, cluster B of *W. obesa*). *Abyssorchomene chevreuxi* represents a single species throughout sampling sites in the SO, the South and North Atlantic, indicating this species as a candidate for a truly cosmopolitan species. The bathyal species-level clades within *Eurythenes gryllus* (Eg1, Eg8) are characterised by distributions encompassing several ocean basins, as well as the abyssal lineage Eg3, comprising specimens of the Atlantic, Pacific and Southern oceans. The bathyal clade Eg1 represents the first case of a bipolar distribution in a macro-benthic deep-sea organism confirmed by genetic data (Havermans *et al.* 2013). Finally, the distribution of both the species-level clade C of *O.* (*O.*) *cavimanus* and *P. debroyeri* encompasses sub-Antarctic and Antarctic regions across the Antarctic Polar Front, suggesting that this physical boundary has not been an absolute barrier through time (Havermans 2012).

3.2. Eurybathy versus vertical segregation

Several SO orchomenid species were confirmed to be truly eurybathic, of which a number cover both bathyal (<3000 m, according to Smith *et al.* 2008) and abyssal (>3000 m) zones (*Abyssorchomene* sp. 1, *A. scotianensis*, species-level lineage C of *Orchomenella* (*Orchomenopsis*) *cavimanus*). Although encompassing a wide bathymetric range, *Abyssorchomene chevreuxi* was confirmed to be restricted to exclusively abyssal depths (3070 – 4800 m).

Some species were shown to cover a much wider depth range than initially thought (e.g. *Orchomenella* (*O.*) *franklini*, up to more than 1100 m while literature records were limited to sites of 250 m depth).

Conversely, in the deep-sea species *Eurythenes gryllus*, which was originally thought to cover bathyal, abyssal and even hadal zones, a genetic break has been observed around 3000 m (Havermans *et al.* 2013). Although no species-level lineages covered both bathyal and abyssal zones, most of them covered vast bathymetric gradients of 1000 to 2000 m (e.g. Eg3: 3070 - 5770 m). Hence, this genetic break within *E. gryllus* around 3000 m, ubiquitously present in each sampled ocean region, might represent evidence for an ecotone between the bathyal and abyssal zone (i.e. a narrow transition of a distinct species composition between two habitats; Jamieson *et al.* 2011). A similar barrier for gene flow around this depth was observed for a deep-sea bivalve species (Zardus *et al.* 2006). Vertical partitioning of closely related species has also been observed in other deep-sea benthic (Blankenship *et al.* 2006, Duffy *et al.* 2012) and pelagic crustaceans (Laakmann *et al.* 2012). In deep-sea lysianassoids, several examples of differing depth ranges for congeneric species exist, e.g. for *Paralicella* (Duffy *et al.* 2012). This is thought to result from competition for resources (Blankenship & Levin 2007, Laakmann *et al.* 2012) or to be linked with the occurrence of favorable habitats at particular depths. Suitable habitats could be determined by the physiological limits of a species in relation to the synergistic effects of high pressure and low temperature (Brown & Thatje 2012). For example, the maximum pressure tolerated at a certain temperature by the bathyal lysianassoid *Stephonyx biscayensis* (Chevreux, 1908), is consistent with its bathymetric and geographic distribution (Brown & Thatje 2011).

4. Dispersal capacities and historical events

The feeding ecology of a species could have a major influence on its dispersal capacities, which in turn, can explain the genetic patterns observed across a species' distributional range. Feeding ecology strongly differs between SO lysianassoid species, and even within closely related species, varying from commensals of sponges or ascidians (*Orchomenyx* De Broyer, 1984) to more common feeding types such as opportunistic scavenging and/or deposit feeding (*Orchomenella* (*O.*) *franklini*, *O.* (*O.*) *pinguides*, *Abyssorchomene chevreuxi*) to exclusive scavenging (e.g. *Pseudorchomene coatsi*, *P. plebs*) or even predation (*P. rossi*) (Chevreux 1903, Dauby *et al.* 2001, Nyssen *et al.* 2002, Baird & Stark 2013). For commensal species, active swimming might be limited when spending partial or entire life cycles inside the host, severely reducing their dispersal potential. Even though olfactive stimulations trigger a quick swimming reaction in both opportunistic and obligate scavengers, opportunistic ones display a passive sit-and-wait strategy with swimming reactions limited to the vicinity of the bottom while exclusive scavengers and predators are known for an active swimming behaviour, often in swarms, in the search of chemical cues in the water column. It has even been suggested that marine scavengers make use of currents for finding food falls, in order to reduce the energetic costs between subsequent meals (Ruxton & Houston 2004). Drift with currents is known to play a role in amphipod dispersal (e.g. Havermans *et al.* 2007) and the combination of active swimming and passive transport by currents can significantly increase the extent of dispersal between remote populations. This might explain the genetic homogeneity observed within obligate scavenger species (*W. obesa*, *P. plebs*, *P. rossi*, *P. coatsi*) between sites all around the Antarctic continent. Passive transportation with the thermohaline circulation, i.e. the Antarctic Bottom Water (AABW), originating in the Weddell Sea and covering much of the world ocean floor (Mantyla & Reid 1983) could facilitate the connectivity within and between deep-water populations of species such as Eg1 and Eg3 of *Eurythenes gryllus*, *A. chevreuxi* and *A.* sp. 1. For less active swimmers, passive dispersal by rafting can also be responsible for gene flow among remote populations (Highsmith 1985, Barnes 2002, Leese *et al.* 2010, Fraser *et al.* 2011). Rafting on drifting kelp holdfasts with the Antarctic Circumpolar Current (ACC) has likely been responsible for the circum-Antarctic establishment of the sub-Antarctic kelp-dweller *Parawaldeckia kidderi* (Nikula *et al.* 2010) (see Fig. 4). To our knowledge, only two studies aiming to test gene flow within lysianassoid species have been conducted, which confirmed that, even within a group of closely related species, actual dispersal capacities can differ. For unidentified *Abyssorchomene* species, France (1994) has shown evidence for gene flow between distinct deep-sea basins, supporting their high dispersal capacities. In a population genetic study on *O.* (*O.*) *franklini* focused on the East Antarctic shelf, gene flow was shown to be limited to nearby populations situated at distances in the order of hundreds of metres (Baird *et al.* 2012).

However, dispersal capacities may not be the only influence on the genetic structure observed within a species, historical events should also be taken into account. (Pseudo)cryptic speciation events can be explained by the repeated glacial and interglacial cycles causing an alternation of periods of population contraction in isolated glacial refugia and periods of population expansion when available habitats increased (e.g. Rogers 2007). The use of different refugia (shelf vs. deep sea) during glacial maxima could provide another explanation for the observed genetic structures in lysianassoids. For species restricted to shallow waters, a migration to deeper waters could have been hampered, for example due to physiological constraints. Hence, these species could only have survived in shelf refugia, and the isolation of populations in these shelters might have favoured allopatric speciation events (Thatje *et al.* 2005). Conversely, eurybathic species could have migrated to deeper waters and established on the less affected slope, or in the deep sea. In these envi-
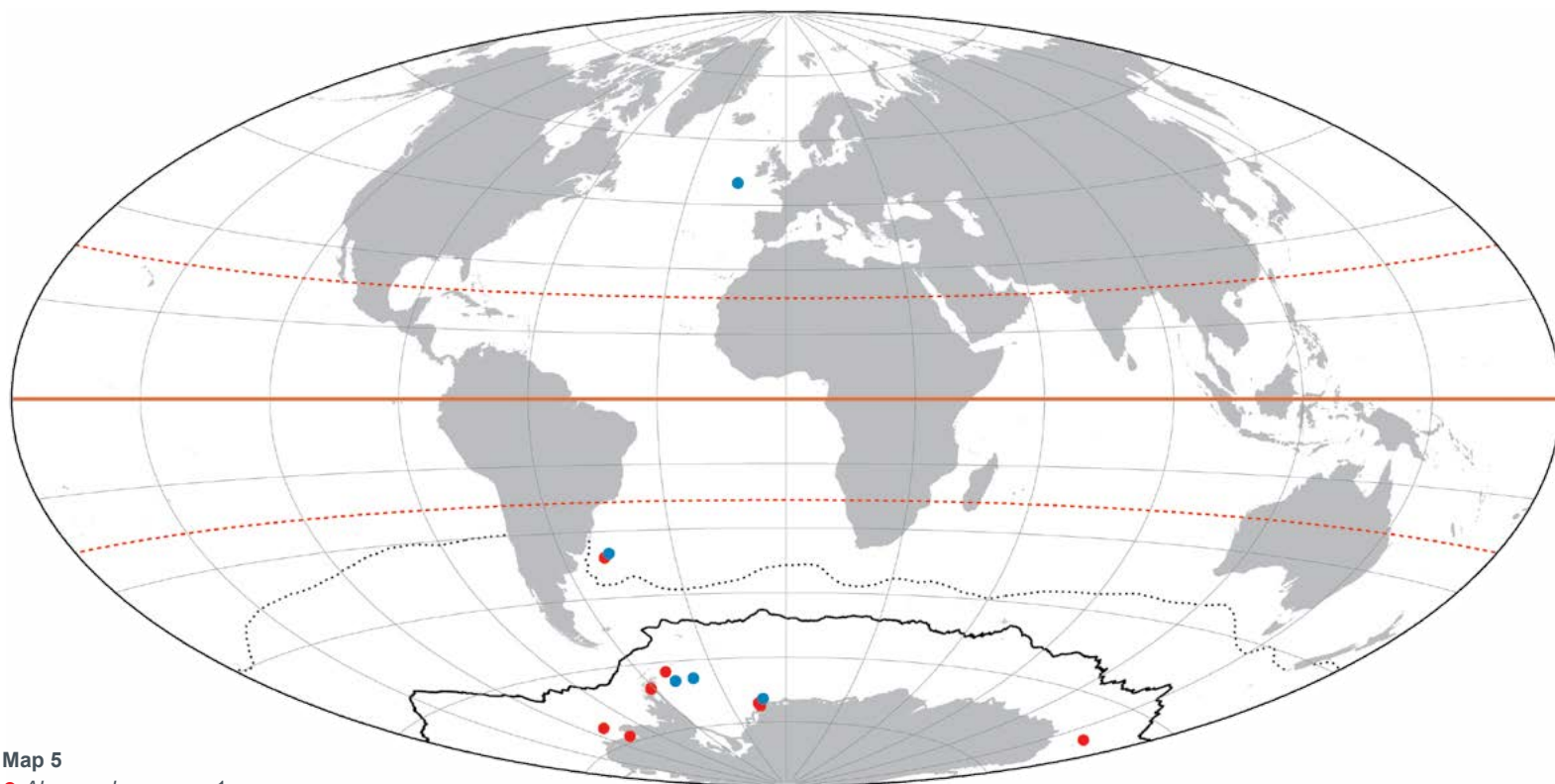
Map 5
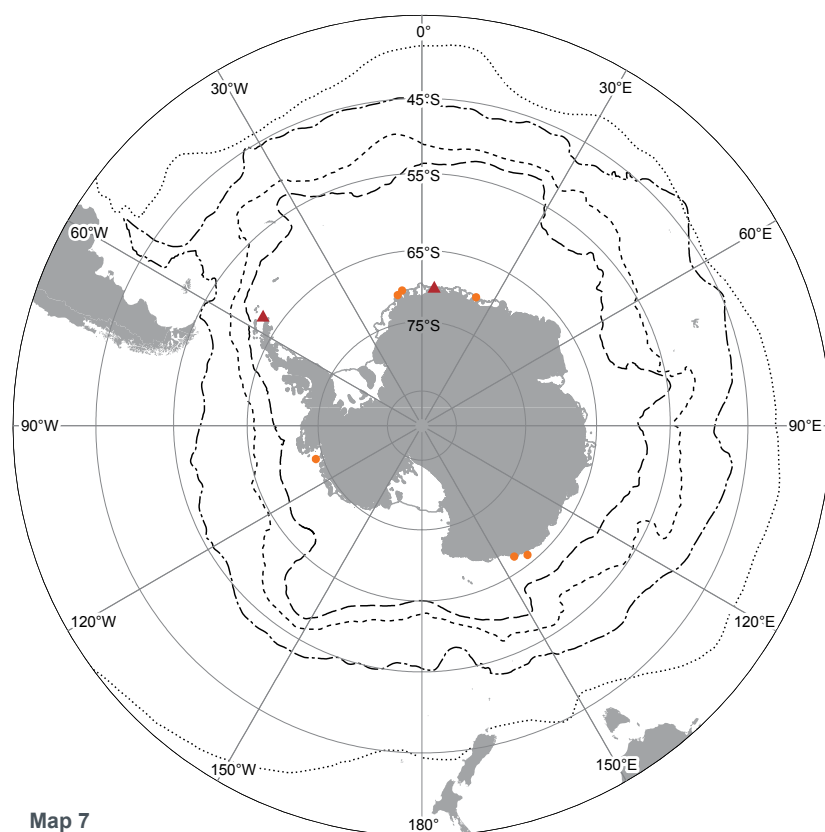- 🔴 *Abyssorchomene* sp1.
- 🔵 *Abyssorchomene chevreuxi*
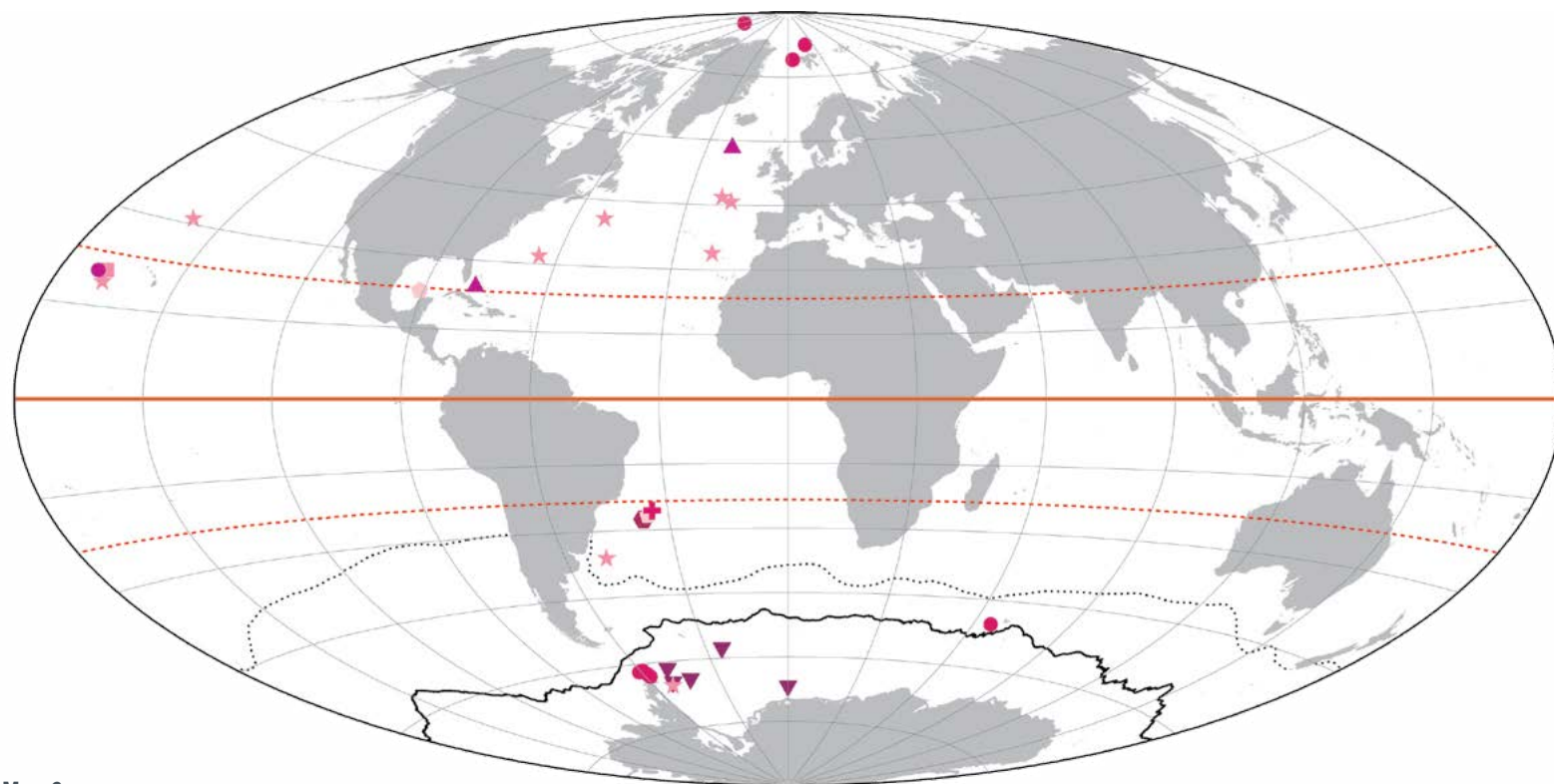
Map 6
- ● *Eurythenes* sp. (Eg1)
- ▲ *Eurythenes* sp. (Eg2)
- ■ *Eurythenes* sp. (Eg3)
- ★ *Eurythenes* sp. (Eg4)
- ⬟ *Eurythenes* sp. (Eg5)
- ✚ *Eurythenes* sp. (Eg6)
- ★ *Eurythenes* sp. (Eg7)
- ▼ *Eurythenes* sp. (Eg8)
- ● *Eurythenes* sp. (Eg9)

Lysianassoidea Maps 5, 6 Map 5 Distribution of two *Abyssorchomene* species, *A.* sp. 1 and *A. chevreuxi*, based on molecular data. Map 6 Distribution of the nine species-level lineages observed within *Eurythenes gryllus* based on molecular data.

ronments, population size would not have been severely reduced as in shelf refugia, owing to the extent of the available habitat (Allcock & Strugnell 2012). The colonisation of deeper waters may have reduced the probability for allopatric speciation events to occur and might also have favoured these species to occupy the released habitat more quickly after glacial cycles (Thatje *et al.* 2005). This could have been the case for eurybathic species such as *O. (O.) cavimanus*, *A.* sp. 1, *P. plebs*. Recolonisation of populations from shelf refugia will have been comparatively slow, however, widespread dispersal may have been achieved over time, through postglacial colonisation events: this has been hypothesised for *O. (O.) franklini* (Baird *et al.* 2012) and *P. kidderi* (Nikula *et al.* 2010). The interaction between dispersal capacities and historical events on the genetic structure of Antarctic lysianassoid species is summarised in Figure 4. Future population genetic studies based on fast-evolving nuclear markers will permit to test these hypotheses.

Map 7
● *Waldeckia obesa*
▲ *Waldeckia obesa*

Lysianassoidea Map 7 Distribution of the two species-level lineages observed within *Waldeckia obesa* based on molecular data.
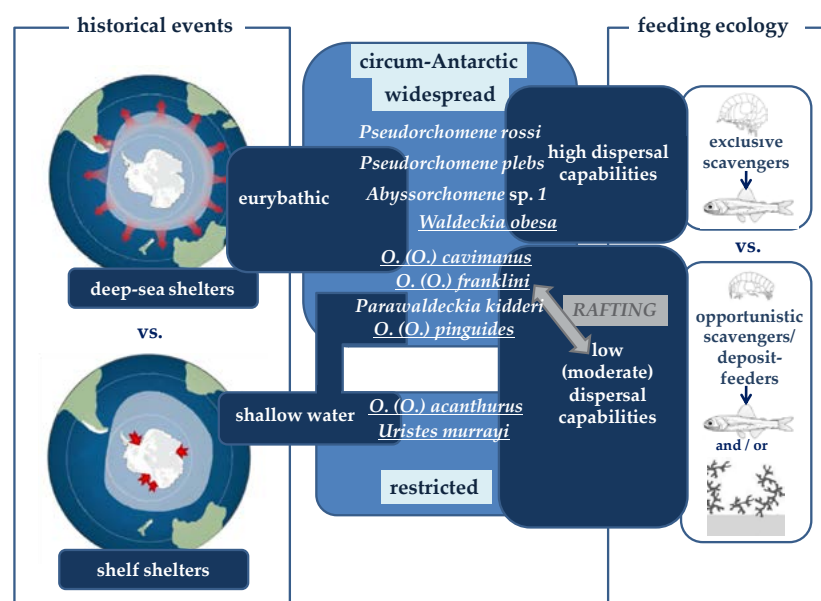

Fig.ure 4 Schematic representation of the hypothetical links between feeding ecology – dispersal capacities and bathymetric distribution – historical events, and their respective influences on lysianassoid species' distributions (widespread or circum-Antarctic versus restricted). Species of which the names are underlined were found to represent of species complexes. Rafting is suggested as a dispersal mechanism for species with relatively lower dispersal capacities. Figures modified with permission from Fraser *et al.* 2012

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope

Biogeographic information is of fundamental importance for discovering marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future distributions, monitoring biodiversity, or supporting conservation and sustainable management strategies.

The recent extensive exploration and assessment of biodiversity by the Census of Antarctic Marine Life (CAML), and the intense compilation and validation efforts of Southern Ocean biogeographic data by the SCAR Marine Biodiversity Information Network (SCAR-MarBIN / OBIS) provided a unique opportunity to assess and synthesise the current knowledge on Southern Ocean biogeography.

The scope of the Biogeographic Atlas of the Southern Ocean is to present a concise synopsis of the present state of knowledge of the distributional patterns of the major benthic and pelagic taxa and of the key communities, in the light of biotic and abiotic factors operating within an evolutionary framework. Each chapter has been written by the most pertinent experts in their field, relying on vastly improved occurrence datasets from recent decades, as well as on new insights provided by molecular and phylogeographic approaches, and new methods of analysis, visualisation, modelling and prediction of biogeographic distributions.

A dynamic online version of the Biogeographic Atlas will be hosted on www.biodiversity.aq.

The Census of Antarctic Marine Life (CAML)

CAML (www.caml.aq) was a 5-year project that aimed at assessing the nature, distribution and abundance of all living organisms of the Southern Ocean. In this time of environmental change, CAML provided a comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. CAML was initiated in 2005 as the regional Antarctic project of the worldwide programme Census of Marine Life (2000-2010) and was the most important biology project of the International Polar Year 2007-2009.

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS, www.iobis.org), under the aegis of SCAR (Scientific Committee on Antarctic Research, www.scar.org). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with biodiversity.aq provided free access to more than 2.9 million Antarctic georeferenced biodiversity data, which allowed more than 60 million downloads.

The Editorial Team

Claude DE BROYER is a marine biologist at the Royal Belgian Institute of Natural Sciences in Brussels. His research interests cover structural and ecofunctional biodiversity and biogeography of crustaceans, and polar and deep sea benthic ecology. Active promoter of CAML and ANDEEP, he is the initiator of the SCAR Marine Biodiversity Information Network (SCAR-MarBIN). He took part to 19 polar expeditions.

Huw GRIFFITHS is a marine Biogeographer at the British Antarctic Survey. He created and manages SOMBASE, the Southern Ocean Mollusc Database. His interests include large-scale biogeographic and ecological patterns in space and time. His focus has been on molluscs, bryozoans, sponges and pycnogonids as model groups to investigate trends at high southern latitudes.

Cédric d'UDEKEM d'ACOZ is a research scientist at the Royal Belgian Institute of Natural Sciences, Brussels. His main research interests are systematics of amphipod crustaceans, especially of polar species and taxonomy of decapod crustaceans. He took part to 2 scientific expeditions to Antarctica on board of the *Polarstern* and to several sampling campaigns in Norway and Svalbard.

Bruno DANIS is an Associate Professor at the Université Libre de Bruxelles, where his research focuses on polar biodiversity. Former coordinator of the scarmarbin. be and antabif.be projects, he is a leading member of several international committees, such as OBIS or the SCAR Expert Group on Antarctic Biodiversity Informatics. He has published papers in various fields, including ecotoxicology, physiology, biodiversity informatics, polar biodiversity or information science.

Susie GRANT is a marine biogeographer at the British Antarctic Survey. Her work is focused on the design and implementation of marine protected areas, particularly through the use of biogeographic information in systematic conservation planning.

Christoph HELD is a Senior Research Scientist at the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven. He is a specialist in molecular systematics and phylogeography of Antarctic crustaceans, especially isopods.

Falk HUETTMANN is a 'digital naturalist' he works on three poles (Arctic, Antarctic and Hindu-Kush Himalaya) and elsewhere (marine, terrestrial and atmosphere). He is based with the university of Alaska-Fairbank (UAF) and focuses primarily on effective conservation questions engaging predictions and open access data.

Philippe KOUBBI is professor at the University Pierre et Marie Curie (Paris, France) and a specialist in Antarctic fish ecology and biogeography. He is the Principal Investigator of projects supported by IPEV, the French Polar Institute. As a French representative to the CCAMLR Scientific Committee, his main input is on the proposal of Marine Protected Areas. His other field of research is on the ecoregionalisation of the high seas.

Ben RAYMOND is a computational ecologist and exploratory data analyst, working across a variety of Southern Ocean, Antarctic, and wider research projects. His areas of interest include ecosystem modelling, regionalisation and marine protected area selection, risk assessment, animal tracking, seabird ecology, complex systems, and remote sensed data analyses.
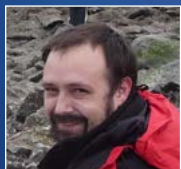
Anton VAN DE PUTTE works at the Royal Belgian Institute for Natural Sciences (Brussels, Belgium). He is an expert in the ecology and evolution of Antarctic fish and is currently the Science Officer for the Antarctic Biodiveristy Portal www. biodiversity.aq. This portal provides free and open access to Antarctic Marine and terrestrial biodiversity of the Antarctic and the Southern Ocean.

Bruno DAVID is CNRS director of research at the laboratory BIOGÉOSCIENCES, University of Burgundy. His works focus on evolution of living forms, with and more specifically on sea urchins. He authored a book and edited an extensive database on Antarctic echinoids. He is currently President of the scientific council of the Muséum National d'Histoire Naturelle (Paris), and Deputy Director at the CNRS Institute for Ecology and Environment.

Julian GUTT is a marine ecologist at the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, and professor at the Oldenburg University, Germany. He participated in 13 scientific expeditions to the Antarctic and was twice chief scientist on board Polarstern. He is member of the SCAR committees ACCE and AnT-ERA (as chief officer). Main focii of his work are: biodiversity, ecosystem functioning and services, response of marine systems to climate change, non-invasive technologies, and outreach.

Graham HOSIE is Principal Research Scientist in zooplankton ecology at the Australian Antarctic Division. He founded the SCAR Southern Ocean Continuous Plankton Recorder Survey and is the Chief Officer of the SCAR Life Sciences Standing Scientific Group. His research interests include the ecology and biogeography of plankton species and communities, notably their response to environmental changes. He has participated in 17 marine science voyages to Antarctica.

Alexandra POST is a marine geoscientist, with expertise in benthic habitat mapping, sedimentology and geomorphic characterisation of the seafloor. She has worked at Geoscience Australia since 2002, with a primary focus on understanding seafloor processes and habitats on the East Antarctic margin. Most recently she has led work to understand the biophysical environment beneath the Amery Ice Shelf, and to characterise the habitats on the George V Shelf and slope following the successful CAML voyages in that region.

Yan ROPERT COUDERT spent 10 years at the Japanese National Institute of Polar Research, where he graduated as a Doctor in Polar Sciences in 2001. Since 2007, he is a permanent researcher at the CNRS in France and the director of a polar research programme (since 2011) that examines the ecological response of Adélie penguins to environmental changes. He is also the secretary of the Expert Group on Birds and Marine Mammals and of the Life Science Group of the Scientific Committee on Antarctic Research.