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CHAPTER 5.10. GASTROPODA.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.10. Gastropoda

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1. Introduction

Gastropoda is a very diverse class of molluscs (seashells) that occurs in terrestrial, marine and freshwater environments. Most gastropods have an external shell (snails) while some groups are shell-less (slugs). They include well-known groups like periwinkles, whelks, cowries and sea-butterflies. In the fossil record, gastropods were found for the first time in Late Cambrian deposits (~499–488 Ma) but were less common in Paleozoic deposits then bivalves and often also poorly preserved. During the Mesozoic (248–65 Ma) the ancestors of the recent gastropod clades evolved and underwent a radiation that is still going on today. Convergent evolution appeared frequently in the diversification of the gastropods and this is reflected in the significant disagreement between solely morphology based and molecular-morphological phylogenies. The total number of living species is estimated around 80,000 (Bouchet *et al*. 2005).

The first gastropod fossils in Antarctica are reported from Upper Cambrian deposits in Northern Victoria Land (Stilwell & Long 2011). The past biogeographic affinities of Antarctic fossil molluscan faunas, including gastropods, have been studied quite in detail (Beu 2009 and references therein). During the Cretaceous, the Antarctic gastropod fauna was very different from the one known today and, by following the K-T boundary (65 Ma), the gastropod composition and richness changed significantly. The Early Palaeocene fauna of Seymour Island (northern Antarctic Peninsula) comprises 36 species of bivalves belonging to 17 families (Beu 2009), of which 11 families are still extant, although none of the identified genera. During the Early Eocene (50 Ma) patterns of fossil richness in the La Meseta Formation from Seymour Island show a strong Eocene radiation of the gastropods. More than 92 species and 56 genera of gastropods were present, with the dominant families being struthiolariid, buccinid, conoid, and epitoniid gastropods. Only 13 genera of this fauna are still represented in the Southern Ocean (SO), while most of the remaining ones now occur in the seas north of the Polar Front. On the whole, it appears that little more than 15% of the Paleocene taxa and 30% of the Early – Middle Eocene could be referred to modern genera (Beu 2009).

During the early Cenozoic, seawater temperatures cooled down and an ice cap covered most of the Antarctic continent. This major event conditioned also marine species and the continental shelf gastropod fauna underwent further compositional shifts and extinction events. In particular, the establishment of a strong seasonality seems to have been one of the major drivers in the evolution of polar marine assemblages, a role that is still important even nowadays for the structure and function of contemporary ecosystems (Crame 2013).

Taxa which are typically adapted to warmer, temperate waters, such as struthioloariids, ficids and mitrids, disappeared from the SO, while other taxa like buccinids and turrids *sensu lato* underwent extensive radiation (Crame 1996). Pliocene fossils from Cockburn Island (5.3 to 1.8 Ma) comprise two gastropod species of which *Nacella polaris* (Hombron & Jacquinot 1841) (formerly known as *N. concinna* (Strebel, 1908)) is still extant (Stilwell 2002). More recently, the molecular analysis of phylogeny and historical biogeography of *Nacella* in the Southern Hemisphere showed a end Miocene (<15 Ma) origin and diversification of the group followed by a Pleistocene radiation in the Magellan region (González-Wevar *et al*. 2010) (Map 3).

In the SO, scientific work on recent gastropods started in the middle of the 18th century. To date ~600 gastropods have been censused in the Southern Ocean, the bulk being described following the era of international Antarctic exploration and discovery, in the late nineteenth and early twentieth centuries (Clarke *et al*. 2007) (Maps 1 and 2). Over the last two decades the number of newly discovered and described species has significantly increased again following the recent international expeditions, especially those held in previously not sampled areas like the southern Bellingshausen and Amundsen seas or in the abysses (Brandt *et al*. 2007, Schwabe *et al*. 2007, Aldea & Troncoso 2008). Currently ongoing molecular phylogenetic and population genetic work is likely to identify new species and cryptic lineages as occurred for *Doris kerguelenensis* (Bergh, 1884) (Wilson *et al*. 2009) (Map 4 and Photo 1e) and Antarctic solariellids (Williams *et al*. 2012). In the first case, the apparent circumpolar species *D. kerguelenensis* turned out to be formed by a mosaic of ~30 different haplotypes (some also occurring sympatrically) determined by repeated glacial cycles which promoted isolations and divergence of populations. (Wilson *et al*. 2009). In the case of solariellids, taxonomic revision was up to the family level and several Antarctic representatives previously placed in the species-rich and 'catch-all' Family Trochidae were moved into newly erected families and subfamilies (Williams 2012).

The current gastropod taxonomic diversity comprises over 70 families of which the Buccinidae (Photo 1i), a taxon of generalists, is the most speciose, with over 75 species in 18 genera. The dominance of this group can be traced back in both polar regions more than 60 MY (Crame 2013). Other species-rich groups are Turridae *sensu lato* (now splitted into 13 Families of Conoidea, see Bouchet *et al*. 2011) (~36 species/14 genera), Naticidae (34 species/10 genera) (Photo 1j), and Eatoniellidae with 15 species in 1 genus (Clarke *et al*. 2007, Brandt *et al*. 2009). The recent Southern Ocean gastropod species share prominent characteristics with the other SO shelled molluscs (chitons, bivalves and scaphopods): more than half of the species are less than 10 mm in size and more than 90% of the species have very thin and fragile shells. In his revision of Antarctic Mollusca, Dell (1990) underlined an apparent lack of Antarctic micromolluscs in museums' collections, a fact that the author explained with the gears and sampling protocols in use at that time, which were not specifically designed to retain the smaller fraction (Dell 1990: 264). A recent analysis of Ross Sea molluscs collected with a 'Rauschert dredge' which, instead, is specifically designed to retain more minute life forms, having a mesh size of 0.5 mm, revealed an unexpected number of new records and new species, especially in gastropods, confirming that great part of the diversity is in the small fraction (Schiaparelli *et al*. submitted).

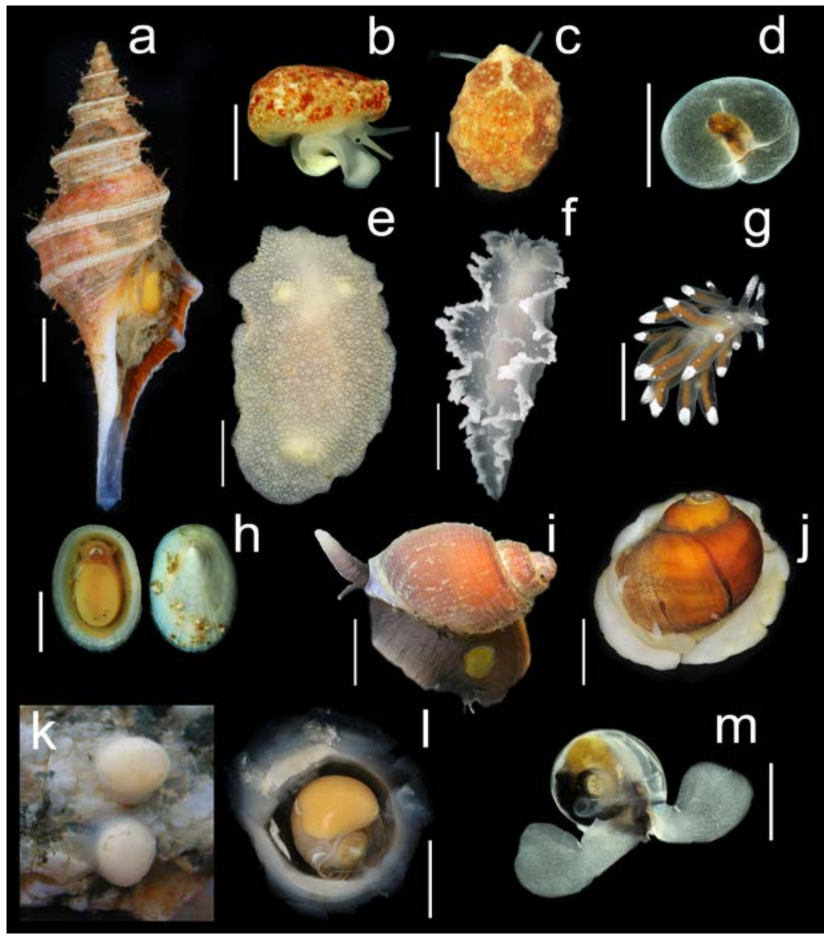
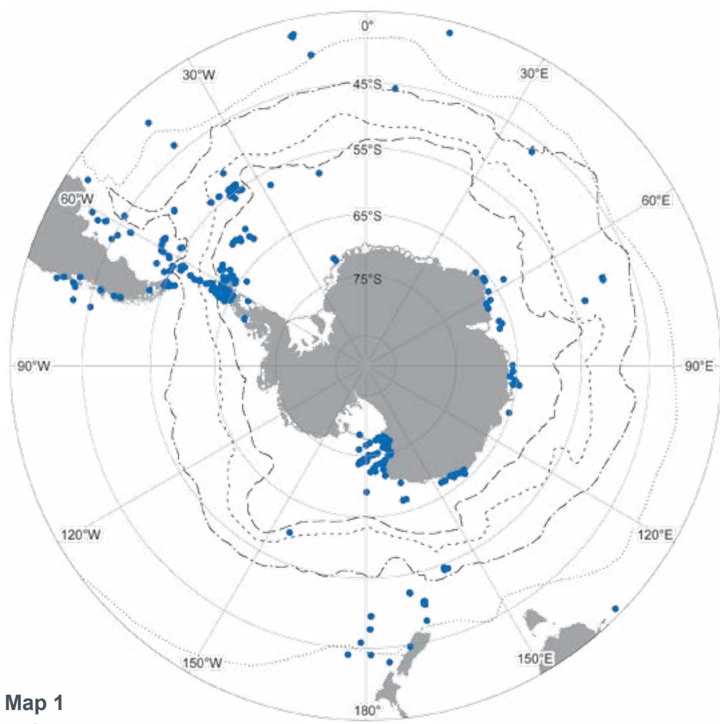
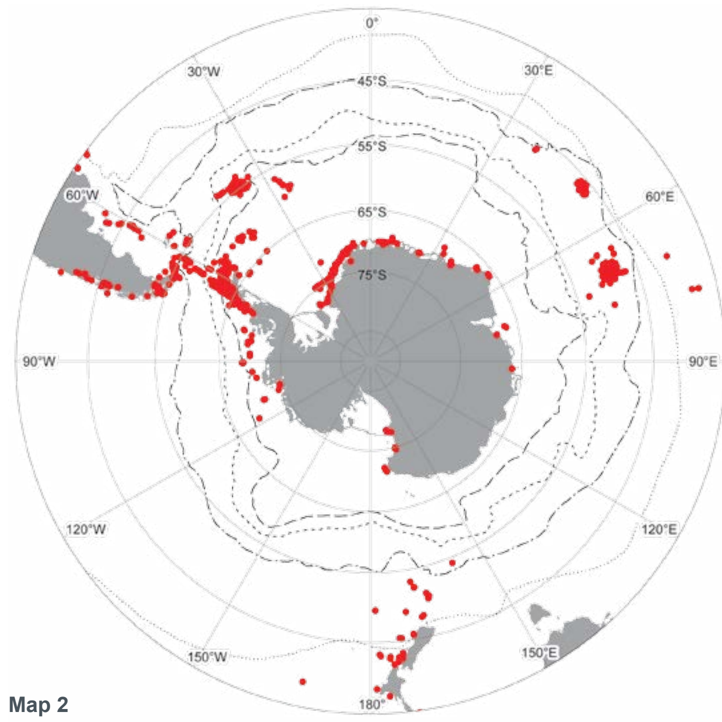


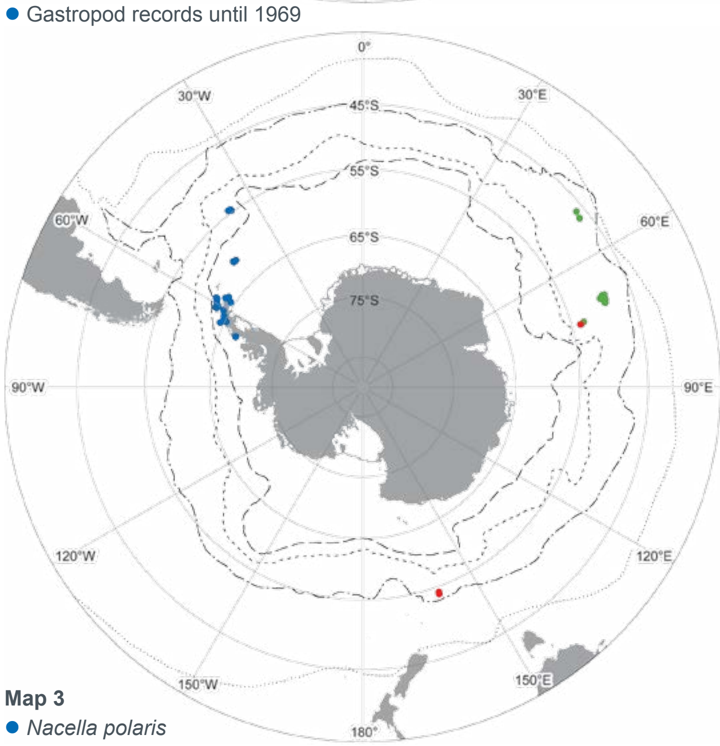
Photo 1 Antarctic gastropods. (a) The large cochlespirid *Aforia magnifica* (Strebel, 1908) (Supfam. Conoidea) is one of the largest Antarctic gastropods; ANT-XXIX/3 (2013) Bransfield Strait, Joinville Island (~400 m depth); scale bar: 1 cm; image: © M.C. Alvaro. (b) An unidentified *Marseniopsis* in lateral view, showing the foot, the cephalic tentacles with the eye and the brightly coloured mantle containing the internal shell. XXVIII PNRA Expedition, Terra Nova Bay (Sample-511, BAMBi Project); scale bar: 5 mm; image: S. Schiaparelli © PNRA. (c) *Marseniopsis* cf. *conica* (E.A. Smith, 1902) viewed from above; this species is characterised by the presence of flattened areas on the mantle; XXVIII PNRA Expedition, Terra Nova Bay (Sample-081, BAMBi Project); scale bar: 5 mm; image: S. Schiaparelli © PNRA. (d) A 'limacosphaera' larva of *Marseniopsis* sp. (see Hain & Arnaud 1992 for an anatomical description) which enables long-term transport of propagules of Velutinidae; XXVIII PNRA Expedition, Terra Nova Bay (Sample-761, BAMBi Project); Scale bar: 1 cm; image: S. Schiaparelli © PNRA. (e) The nudibranch *Doris kerguelenensis* (Bergh, 1884); XXVII PNRA Expedition, Terra Nova Bay; scale bar: 1 cm; image: S. Schiaparelli © PNRA. (f) The nudibranch *Tritoniella belli* Eliot, 1907; XIX PNRA Expedition, Terra Nova Bay. Scale bar: 1 cm; image: S. Schiaparelli © PNRA. (g) The nudibranch *Cuthona georgiana* (Pfeffer in Martens & Pfeffer, 1886) is one of the few Aeolidida species present in Antarctica; XXV PNRA Expedition, Terra Nova Bay. Scale bar: 5 mm; image: S. Schiaparelli © PNRA. (h) *Iothia emarginuloides* (Philippi, 1868); XXVIII PNRA expedition, Terra Nova Bay (Sample-1204, BAMBi Project); scale bar: 5 mm; image: S. Schiaparelli © PNRA. (i) *Chlanidota signeyana* Powell, 1951; BIOROSS TAN0402 Expedition, Stn 102, Ross Sea; Scale bar: 1 cm: image: S. Schiaparelli © NIWA. (j) The naticid *Amauropsis rossiana* E.A. Smith, 1907 is a common finding in shelf samples; VII PNRA expediton, Terra Nova Bay (Sample-173, BAMBi Project, MNA 3573) Scale bar: 1 cm; image: S. Schiaparelli © PNRA. (k) Egg capsules of the buccinid *Neobuccinum eatoni* (E.A. Smith, 1875) laid on a granitic boulder; XVII PNRA Expedition, Terra Nova Bay (diving, 25 m depth); image: S. Schiaparelli © PNRA. (l) One of the capsules of Photo 1m dissected to show the larva which is at the end of the intracapsular development; note the presence of the operculum and the large yolk reserve; scale bar: 5 mm; image: S. Schiaparelli © PNRA. (m) *Limacina rangii* f. *antarctica* Woodward, 1854. XXVIII PNRA Expedition, Terra Nova Bay (Sample-751, BAMBi Project); scale bar: 5mm; image: S. Schiaparelli © PNRA.



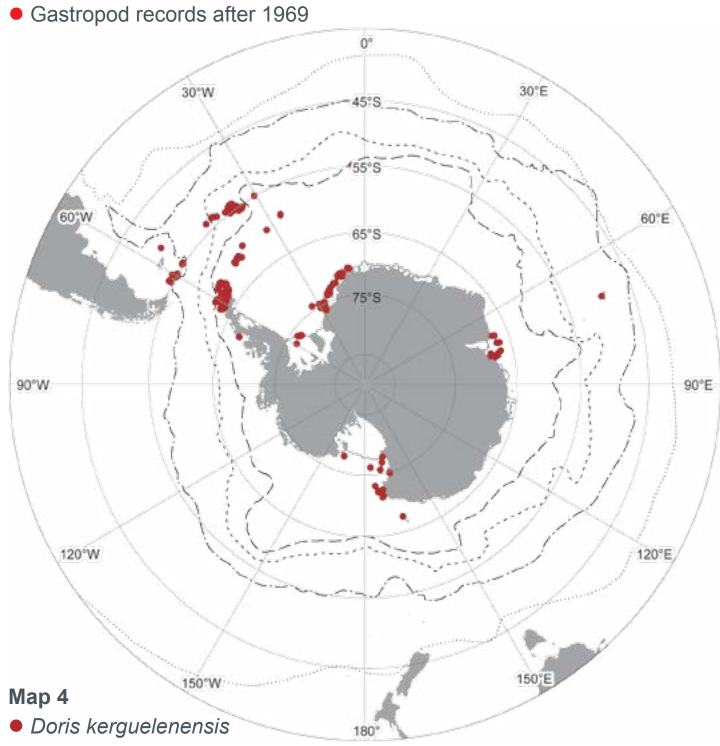
Map 1
● Gastropod records until 1969



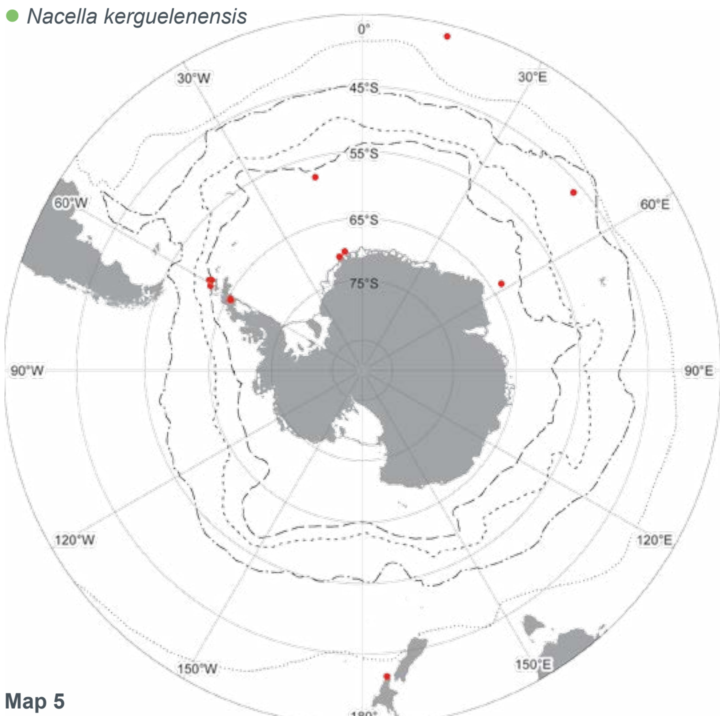
Map 2
● Gastropod records after 1969



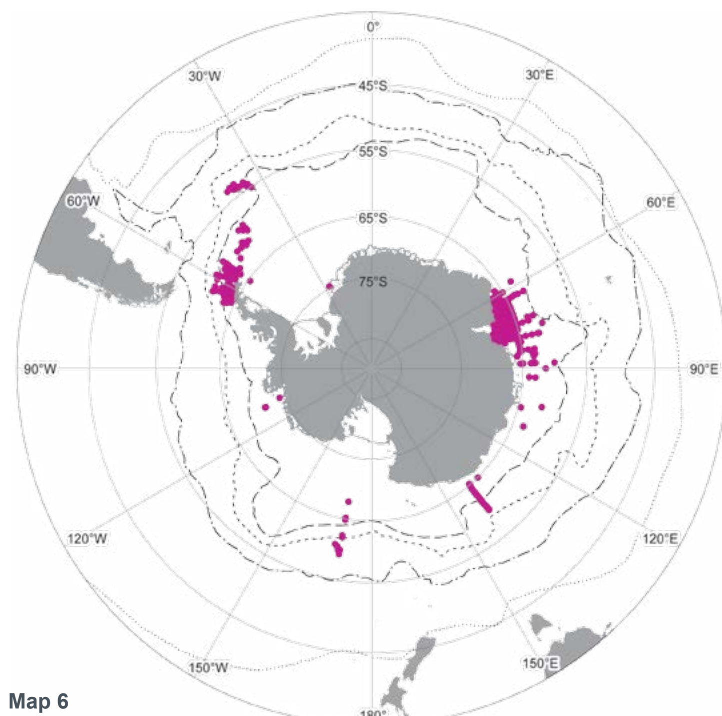
Map 3
● *Nacella polaris*
● *Nacella macquariensis*
● *Nacella kerguelenensis*



Map 4
● *Doris kerguelenensis*



Map 5
● *Seguenzia antarctica*



Map 6
● *Limacina rangii* f. *antartica*

Gastropoda Maps 1–6 Map 1. Gastropod species records at the time of Hedgpeth (1969). Map 2. Gastropod species records since of Hedgpeth (1969) up to March 2012. Map 3. Distribution of the most common *Nacella* species in the Southern Ocean: *Nacella polaris* (Hombron & Jacquinot, 1841), typically found along the Antarctic Peninsula and along the islands of the Scotia Arc; *N. macquarensis* (Finlay, 1926) and *N. kerguelenensis* (Smith, 1877) which are instead restricted to few sub-Antarctic islands. Few other species of uncertain status are known, but lacking a sound molecular framework about their real status are here omitted. Map 4. The nudibranch *Doris kerguelenensis* (Bergh, 1884) has an apparent wide and circumpolar distribution, with records extending also in the South America. However, a recent molecular study (Wilson *et al*., 2009) has pointed out the existence of up to 30 distinct haplotypes, likely originated through isolation during glacial events combined with limited subsequent dispersal. Map 5. *Sequenzia antarctica* Thiele, 1925 is a deep-sea species having a wide depth range of occurrence, larger than 2500 m. Map 6. *Limacina rangii* f. *antarctica* Woodward, 1854 is a pteropod species believed to have a bipolar distribution. Recent molecular work (Hunt *et al*., 2010) demonstrated that Arctic and Antarctic representatives belong to different species despite a very similar external morphology.

On the other hand, there are some exceptions of large species, such as the large cochlespirid *Aforia magnifica* (Strebel, 1908) (Photo 1a), attaining a height up to 15 cm, and the deep-sea buccinulid *Germonea rachelae* Harewych & Kantor, 2004 with up to 6.7 cm shell height.

Most Antarctic gastropod species lay egg capsules where a intracapsular metamorphosis occur leading to a very long embryonic development (Photo 1km–ln). On the contrary while meropelagic, planktotrophic larvae are rare (Hain & Arnaud 1992). For example the limpet *Nacella polaris* has external fertilisation and is a broadcast spawner with pelagic larvae (Picken & Allen 1983; González-Wevar *et al*. 2010). Meroplanktonic larvae have been described for *Capulus subcompressus* Pelseneer, 1903 (see Map 14 and Photo 1m in Schiaparelli 2013, this book), *Marseniopsis conica* (Smith, 1902) and *M. mollis* (Smith, 1902) (Hain & Arnaud 1992) (Photo 1b–d). Late veliger stages with large yolk deposits hatching from egg masses were observed for *Philine alata* Thiele, 1912 (Hain & Arnaud 1992). The brood protection mode by laying egg masses is likely to limit active larval/juvenile dispersal and to favour the separation of populations enhancing speciation processes. Adult gastropods have considerable movement capabilities and are able to actively search for food sources, e.g. the grazers, scavengers and predators. More limited in their active movements are endo- and ectoparasites like members of the eulimids and or the pycnogonid-ectoparasite *Dickdellia labioflecta* (Dell, 1990) (see Photo 1c in Schiaparelli 2013, this volume), which are passively moved by their hosts (Schiaparelli et al. 2007, 2008).

2. Gastropod bathymetry

Recently, the bathymetric distributions of Antarctic shelled gastropods have been reviewed by Brandt *et al.* (2009), analysing the distribution records of 566 species from 0 to 5000 m. The characteristic phenomenon of the Antarctic benthos, eurybathy, is less common feature in Antarctic gastropod species and only 81 species have depth ranges of over 1000 m. The discovered pattern showed the highest species richness on the shelf with sharply dropping species numbers to around 1000 m and then more or less constant low species numbers in bathyal and abyssal depths. The shallow, in near shore waters (0–100 m) down to 300 m depth on the upper continental shelf, hosts gastropod richness of >250 species per analysed depth zone (Brandt *et al.* 2009). More than 80% of the discovered Antarctic gastropod species occurred on the shelf and upper slope. In depths deeper than 1000 m the species richness dropped to around 40 species per depth interval and below 4000m no more than 20 species were found. The Cerithopsidae, Cingulopsidae, Eatoniellidae, Nacellidae and Mathildidae were examples for numerous families with a shelf bound depth range. The speciose groups Muricidae, Rissoidae and Conoidea were recorded from the shelf to lower slope depth. Fewer families, e.g. the Buccinidae, Cyclostrematidae, Diaphanidae, Eulimidae, Naticidae, Sequenziidae and Trochidae occurred from the shelf to abyssal depth. A representative for a shallow-water gastropod with a narrow depth distribution from the intertidal to mid shelf depth is *Nacella polaris* (Map 3) while *Sequenzia antarctica* Thiele, 1925 (Map 5) is a typical deep-sea species with a wide eurybathic range of more than >2500 m.

3. Gastropod endemism

Shelled gastropods are a taxon with high species level endemism within the Antarctic and Southern Ocean with approximately 74% in the Antarctic and 79 in the SO (Griffiths *et al.* 2009). At the generic and familial levels, this is reduced to 15% and 0% respectively, indicating that, in the cold Antarctic environment, adaptive radiation influenced species and, to a certain degree, genera but not families (Linse *et al*. 2006). In the Nudipleura (Photos 1e–g), the Antarctic species level endemism is even higher, reaching about 83% (Schrödl 1999, 2003). While most Antarctic genera and families can be found at both poles, no bipolar gastropod species are known to date. Until recently, pelagic gastropods like the sea butterfly *Limacina rangii* f. *antarctica* Woodward, 1854 (formerly known as *Limacina helicina antarctica* Woodward, 1854) (Map 6 and Photo 1m) were listed as bipolar, but Hunt *et al*. (2010) were able to show significant genetic differences at the species level. Comparison of regional endemism within and outside the SO showed that several sub-Antarctic and high Antarctic areas had endemism rates of >20–39.6%, with 59 endemic species (39.6%) reported from South Georgia. Interestingly no endemic nudibranch is present at South Georgia. A representative for Antarctic endemism is the whelk genus *Chlanidota* Martens, 1878 (Map 7 and Photo 1i), belonging to the globally distributed and diverse family Buccinidae, which has seen significant diversification in the SO and development on multiple endemic species.

4. Antarctic gastropod biogeography

The distribution patterns of gastropods in the Southern Ocean area have been studied since the early nineteenth century, followed by comprehensive analyses by Hedgepeth (1969, Fig. 2) and Dell (1972), which were most recently updated by Linse *et al*. (2006) and Griffiths *et al.* (2009) for shelled gastropods and by Wägele (1991) and Schrödl (2003) for nudibranchs (Map 2). These authors analysed 27 areas in the Southern Ocean and adjacent regions and 566 shelled gastropod species, highlighting the very poor knowledge of the Amundsen and southern Bellingshausen seas as well as of the Southern Ocean deep sea in general. Therefore they examined shelf (0–1000 m depth) patterns, but taxon lists in most areas differed little between shelf and all depths. Gastropod species richness differed between shelf and all depths at the South Shetland and South Sandwich Islands and in the Weddell Sea. The three richest areas of the Linse *et al*. (2006) study were: i) the Weddell Sea (221 species/87 genera/42 families), ii) the Ross Sea (149/83/37) and iii) South Georgia (147/75/40). Areas identified as having the highest taxonomic diversity ('hotspots') differed depending on the taxonomic level of the analysis. For example, Wilkes Land patterns of richness were moderate at species level but high at generic and familial levels. For nudibranchs, the Antarctic Peninsula forms a separate faunal zone with transitional elements of the High Antarctic and sub-Antarctic (Wägele 1991).

Analysis of species richness in families and genera revealed that most were encompassed by five overall patterns: 1) the Weddell and Ross Seas as centres of taxon richness (for the families Cyclostrematidae, Buccinidae and Diaphanidae and its genus Dall, 1902), with richness decreasing towards the Scotia Arc, Antarctic Peninsula region and East Antarctica, and lowest in the sub-Antarctic, Magellanic and other areas; 2) a richness centre (comprising the Rissoidae, Eatoniellidae and Antarctic Trochoidea) spanning the Weddell Sea to Magellanic areas, through the Scotia Arc; 3) a high Southern Ocean richness coupled with low richness in the sub-Antarctic and other northern areas in the calliostomatid genus *Falsimargarita* Powell, 1951 and the buccinid genus *Prosipho Thiele,* 1912; 4) conversely the third distribution type was a high richness north of the PF and low richness south of it, as shown by the family Volutidae and 5) a centre of richness in the Weddell Sea for Cancellariidae and Cerithiidae.

Most Antarctic gastropods show very limited latitudinal ranges of less than 10°, but this could be a reflection of sampling, as the majority of species are recorded for a few times only (Clarke *et al*. 2007). Relatively few species have ranges that take them outside the Southern Ocean and examples are *Iothia emarginuloides* (Philippi, 1868) (Map 8 and Photo 1h) and *Doris kerguelenensis* (Map 4 and Photo 1e) but, as explained above for the latter species, molecular data show the existence of more complex distributional patterns and cryptic lineages. Longitudinal range distributions analysed in the same study were dominated by species with very limited ranges, but this again might be the result of most taxa being represented by few samples, and only a few taxa have latitudinal ranges approaching circumpolar.

At species level, the intertidal limpet-like pulmonate siphonariid *Kerguelenella lateralis* is a representative for a species with a sub-Antarctic distribution, *Dickdellia labioflecta* (see Map 10 in Schiaparelli, Chapter 5.31, this volume) for a circum-Antarctic distribution.

However, when more molecular data will be available for other gastropod species, it is likely that many of the purported examples of circumpolar distributions will turn out to be different networks of haplotypes.

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Photo 1i was taken in 2004 during the TAN0402 BIOROSS biodiversity survey of the western Ross Sea and Balleny Islands, undertaken by NIWA (National Institute of Water & Atmospheric Research) and financed by the former New Zealand Ministry of Fisheries. Photo 1a was taken during the ANT-XXIX/3 Polarstern expedition organised by AWI (Alfred Wegener Institute, Bremerhaven). Dr. Huw Griffiths (BAS, Cambridge) is thanked for the preparation of the maps. This is CAML contribution #108 and BAMBi (Project PNRA 2010/A1.10, "Barcoding of Antarctic Marine Biodiversity) contribution #3.

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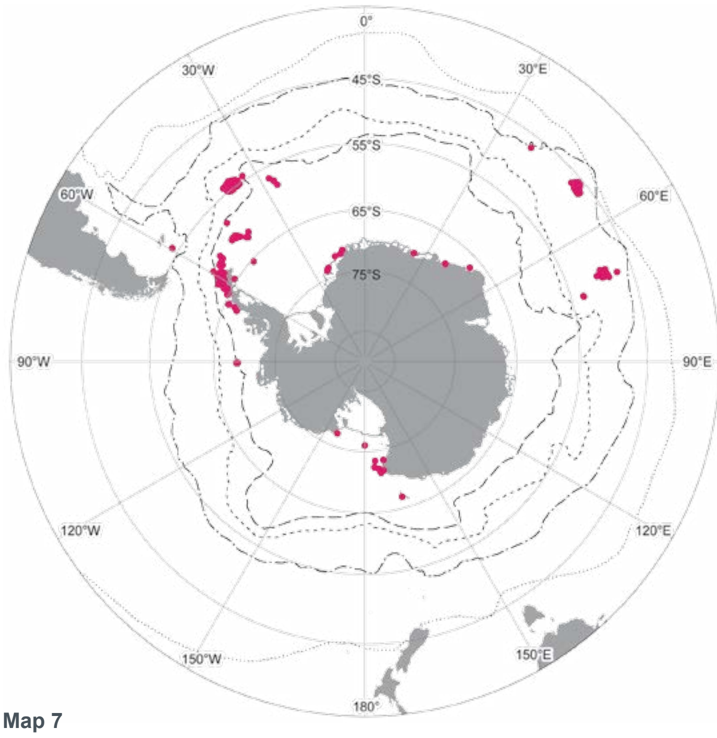
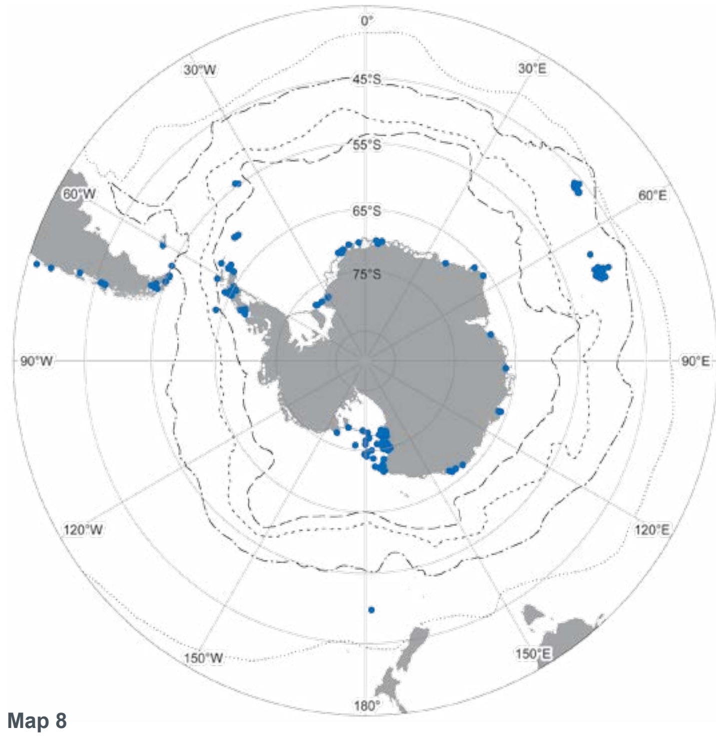


Map 7
● *Chlanidota* spp.



Map 8
● *Lothia emarginuloides*

Gastropoda Maps 7–8 Map 7. The endemic whelk genus *Chlanidota* Martens, 1878 belongs to Buccinidae, a family which underwent an extensive radiation in Antarctic waters. Map 8. The wide distribution of *Iothia emarginuloides* (Philippi, 1868) has still to be verified from a molecular point of view and, as in the case of *D. kerguelenensis*, it is likely that cryptic species are present.

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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.

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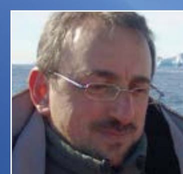

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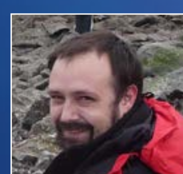

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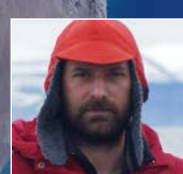
Graham HOSIE is Principal Research Scientist in zooplankton ecology at the Australian Antarctic Division. He founded the SCAR Southern Ocean Continuous Plankton Recorder Survey and is the Chief Officer of the SCAR Life Sciences Standing Scientific Group. His research interests include the ecology and 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.