CHAPTER 5.10. GASTROPODA.
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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN


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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 SO, the gastropods were found for the first time in Late Cretaceous deposits (~499–488 Ma) but were less common in Paleozoic deposits then bivalves and often also poorly preserved. During the Mesozoic (~250–65 Ma) the ancestors of the recent gastropod clades evolved and underwent a radiation in the SO (Steele et al. 2007). In the last two decades the number of newly discovered and described species has significantly increased again (Aldea et al. 2013). Currently ongoing molecular phylogenetic and population genetic work in the abysses (Brandt et al. 2010) (Maps 1 and 2) is still going on today. Concurrent 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. 2009).

The first gastropod fossils in Antarctica are reported from Upper Cambrian deposits in Northern Victoria Land (Sitwell & 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 Paleocene fauna of Seymour Island (northern Antarctic Peninsula) comprises 5 species of fossils 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 one hand, 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 associated also marine species and the continental shelf gastropods 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).

Taxis which are typically adapted to warmer, temperate waters, such as struthiolariids, fucids and nitrids, disappeared from the SO, while other taxa like turrids and turrid sensu lato underwent extensive radiation. Gastropods display different from the one known today and, by following the K-T boundary (65 Ma), the gastropod composition and richness changed significantly. The Early Paleocene fauna of Seymour Island (northern Antarctic Peninsula) comprises 5 species of fossils 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 one hand, 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).

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Photo 1. Antarctic gastropods. (a) The large coelacanthid Afrosia magnifica (Strebel, 1908) (Supfam. Conoidea) is one of the largest Antarctic gastropods; ANT-XIX/3 (2013) Bransfield Strait, Joinville Island (~400 m depth); scale bar: 1 cm; image: © M.C. Alvaro. (b) An unidentified Marenziosopsis in lateral view, showing the foot, the cephalic tentacles with the eye and the brightly coloured mantle containing the internal shell. XXVII PNRA Expedition, Terra Nova Bay (Sample-511, BAMBi Project); scale bar: 5 mm; image: S. Schiaparelli & PINRA. (c) Marenziosopsis cf. conica (E.A. Smith, 1902) viewed from above; this species is characterised by the presence of flattened areas on the mantle; XXVII PNRA Expedition, Terra Nova Bay (Sample-081, BAMBi Project); scale bar: 5 mm; image: S. Schiaparelli © PINRA. (d) A limacosphera larva of Marenziosopsis sp. (see Hain & Amoud 1992 for an anatomical description) which enables long-term transport of propagules of Velutinidae; XXVII PNRA Expedition, Terra Nova Bay (Sample-761, BAMBi Project); Scale bar: 1 cm; image: S. Schiaparelli © PINRA. (e) The nudibranch Doris kerguelenensis (Bergh, 1884); XXVII PNRA Expedition, Terra Nova Bay; scale bar: 1 cm; image: S. Schiaparelli © PINRA. (f) Loha emarginoloides (Philippi, 1868); XXVII PNRA expedition, Terra Nova Bay (Sample-1204, BAMBi Project); scale bar: 5 mm; image: S. Schiaparelli © PINRA. (g) The nudibranch Cuthona georgiana (Pfeffer in Martens & Pfeffer, 1880) is one of the few Aeolididae species present in Antarctica; XXV PNRA Expedition, Terra Nova Bay; Scale bar: 5 mm; image: S. Schiaparelli © PINRA. (h) Chitoniidae signeyana Powell, 1951; BiOBIOSS TAN0402 Expedition, Stn 102, Ross Sea; Scale bar: 1 cm; image: S. Schiaparelli © PINRA. (i) Egg capsules of the buccinid Neobuccinum eatoni (E.A. Smith, 1875) laid on a gratic boulder: XVII PNRA Expedition, Terra Nova Bay (diving, 25 m depth); image: S. Schiaparelli © PINRA. (j) One of the rastus of Photo 1 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 © PINRA. (m) Limacinina rangii f. antarctica Woodward, 1854; XVII PNRA Expedition, Terra Nova Bay (Sample-751, BAMBi Project); scale bar: 5mm; image: S. Schiaparelli © PINRA.
Gastropoda Maps 1–6


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. macquariensis (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 coelothorax Aforia magna (Strebel, 1908) (Photo 1a), attaining a height up to 15 cm, and the deep-sea bivalvulid Gemmarea rachaelae Hewrych & Kantor, 2004 with up to 6.7 cm shell height.

Most Antarctic gastropod species lay egg capsules where a intracapsulic development is the larval leading to a very long embryonic development (Photo 1km–ln). On the contrary while meroplanktonic, planktotrophic larvae are rare (Hain & Arnaud 1992). For example the limpet Crenatella eulimidoidea (Smith, 1902) has 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 or more 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 4000 m no more than 20 species were found. The Cerithiopsidae, Cipangopidae, Eucyclotidae, Littorinidae, Nacellidae and Mathildidae were examples for numerous families with a shelf bound depth range. The species groups Munidopsidae, Rissoidae and Conidae were with recorded from the shelf to lower slope depth. Fewer families, e.g. the Buccinidae, Cypraeommatidae, 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 shelf and upper slope was the gastropod Nacella polaris (Map 3) and Sequencia antarctica Thiele, 1925 (Map 5) is a typical deep-sea species with a eurybathic range of more than >2500 m.

2. Gastropod bathymetry

Recently, the bathymetric distributions of Antarctic shellened 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 bathymetry is that very few species are endemic to the deep-sea. As a result, only 81 species have depth ranges of over 1000 m.

The distribution patterns of gastropods in the Southern Ocean area have been recently reviewed by the early twentieth-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 shellened gastropods and by Wägele (1991 and Schrödl 2003) for nudibranchs (Map 2). These lists included 27 areas in the Southern Ocean and adjacent regions and 566 shellened 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 (222 species/87 genera/42 families), ii) the Ross Sea (148/53/37) and iii) South Georgia (147/75/40). Most species were identified as having species 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 depth forms a separate faunal zone with transitional elements of the High Antarctic and sub-Antarctic (Wägele 1991).

An analysis of species richness in families and genera revealed that most species were encompassed by five overall patterns: i) the Weddell and Ross Seas as centres of taxon richness (for the families Cyclostomatidae, 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; ii) a richness centre (comprising the Rissoidae, Eucyclidae and Antartic Trochidae) spanning the Weddell Sea to Magellanic areas, through the Scotia Arc; iii) a high Southern Ocean richness coupled with low richness in the sub-Antarctic and other northern areas in the calliostomatid genus Pseudomargarita Powell, 1951 and the buccinoid genus Prospho Thiele, 1912; iv) 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 v) a centre of richness in the Weddell Sea for Cancellariidae and Cerithiopsidae.

Most Antarctic gastropods show very limited bathymetric 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 Arenicola marina (Map 4) and Domararginella bertesi and Dorsis 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 species with very limited depth 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 pumilid siphonariid Koenenommus latreillii is a representative species with a sub-Antarctic distribution, Dickellidae labiofacta (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 circum-Antarctic distributions will turn out to be different networks of haplotypes.

2.4. Antarctic gastropod biogeography

The distribution patterns of gastropods in the Southern Ocean area have been recently reviewed by the early twentieth-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 shellened gastropods and by Wägele (1991 and Schrödl 2003) for nudibranchs (Map 2). These lists included 27 areas in the Southern Ocean and adjacent regions and 566 shellened 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)
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. The wide distribution of Lothia 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.


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.ai) 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 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. 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.

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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 station in Antarctica. He has been involved in the ecological responses 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.