

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN



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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.9. Sipuncula and Echiura

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1. Introduction

In Zoology, the groups of marine worms named Sipuncula and Echiura, experienced a long history of common discoveries, since their representatives, coincidentally, were lacking an obvious external character such as segmentation. This attribute was heavily weighted in the animal classification during the last century, and both groups of marine worms were proposed as separate phyla for a long time. From the other side, sipunculans and echiurans exhibit relatively low numbers of species in their global diversification (with about 150 species described each one), especially when compared with other prominent invertebrate groups such as the phyla Annelida or Mollusca. Moreover, the same taxonomic authorities often identified sipunculan and echiuran species in collections they received (Stephen & Edmonds 1972). In this way, it is worth mentioning that Edmonds (1969) dealt with both phyla in the same chapter of the Antarctic Map Folio Series 11; both phyla were dealt together in the most comprehensive monograph ever published (Stephen & Edmonds 1972); and finally, sipunculans and echiurans were the common topic of the 1st International Symposium devoted to both phyla (Rice 1975-76). Thus, both groups of marine worms keep on being considered once more together in the present chapter.

Sipunculans and echiurans are soft-bodied, defenceless, sedentary marine invertebrates lacking hard structures to help in their classification (Stephen & Edmonds 1972). With this morphological constraint, they are often reported from cryptic habitats, such as burrows, crevices, tubes and discarded shells from sediments and rocky bottoms. They occur widely along oceans, from polar to the tropical seas. Their bathymetric range is also extensive from the intertidal zone down to the large deep sea bottoms. Once they are collected, they are easy to differentiate from each other, especially dealing with living specimens. Sipunculans exhibit a retractable introvert, whereas echiurans have a contractile proboscis (never retracted within the body). Other external character is setation, still present in echiurans, completely absent in sipunculans. Finally, the details of their internal anatomy separate radically the two involved phyla. Echiurans, for example, exhibit mouth and anus in a regular way at both ends of the trunk. By contrast, mouth in sipunculans is placed at the tip of the introvert, whereas the position of the anus is highly modified, remaining dorsal at the anterior trunk end.



Photo 1 Unidentified echiuran, about 80 mm long, Larsen B (*Polarstern* ANT-XXII1/8). Image: C. d'Udekem d'Acoz © RBINS.

The view of two minor phyla of marine worms has dramatically changed during the last decade by the application of new molecular techniques (Struck et al. 2007). The main conclusion is that segmentation in annelids appears to be a weak anatomical character, with a strong need of conceptual re-definition (Dordel et al. 2010). Several studies of molecular analysis are indicating that echiurans are nested within the phylum Annelida, whereas the placement of sipunculans is more contentious, but closely related to Annelida (Dunn et al. 2008, Struck et al. 2011). In the meantime, the phyletic taxonomic rank for both minor groups of marine worms is still used here (Hickman et al. 2011), pending conclusive evidence.

Little more than taxonomy is known about these two small phyla of invertebrates in cold waters around Antarctica. In general, both phyla (Murina 1975, Biseswar 1985) are rather thermophilic in their global distribution, however some selected species remain noticeably abundant around the Southern Ocean. The credit for the first published description of representatives of these two small phyla from localities close to the Antarctic Polar Front (Antarctic Convergence), should perhaps go to the Swiss naturalist Théophile Rudolphe Studer (1879, 1889), who took part in the German "Gazelle" Expedition during the years 1874–76 and named the echiuran worm Thalassema verrucosa [now Maxmuelleria verrucosum (Studer, 1879)] from Kerguelen Islands. Apparently, the first sipunculan collections from localities south of the Antarctic Convergence were taken by the German "Deutschen Polarkommission", which wintered at South Georgia during the years 1882

to 1883, the sipunculans being described by Michaelsen (1889). Next, the "Swedish Antarctic Expedition" of 1901 to 1903 made important collections. *Echiurus antarcticus* was the only species described by Spengel (1912), whereas a rich collection of sipunculans was described by Théel (1911), who also discussed the phenomenon of bipolarity. While a few more species were collected by several further expeditions, the most extensive collections were made mainly during the scientific cruises of several British and Russian research vessels (Dell 1972). The 'Antarctic Map Folio Series' was a major step forward in summarising in 4 maps all the knowledge of sipunculans and echiurans (Edmonds 1969) from both the sub-Antarctic and Antarctic regions. More recently, large additions of sipunculan and echiuran collections were performed by several European and US expeditions, which completed the current geographical distribution of both phyla south of the Polar Front (Saiz *et al.* 2000, Cutler *et al.* 2001).

The objective of this work is (1) to update the geographical distribution of all sipunculan and echiuran species south of the Polar Front and (2) to detect spatial (both vertical and horizontal) preferences of the species around the investigated area.

2. Methods

The data used herein represent a final compilation of all the works published previously by Saiz (1995, 1996), Saiz *et al.* (2000) and Cutler *et al.* (2001) on both phyla. An updated list of all Antarctic sipunculan and echiuran records are summarised in Tables 1 and 2. The distribution of the sipunculan and echiuran species north of the Polar Front corresponds to databases already registered on the OBIS webpage (www.iobis.org). Moreover, the recent reviews of Biseswar (2009, 2010, 2012) concerning the global distribution of echiurans have been used. Classification and coding of the higher taxa of sipunculans follow the one suggested by Cutler (1994), with the recent amendments of Kawauchi *et al.* (2012). Echiurans follow that summarised by Biseswar (2010), which included the changes introduced previously by Nishikawa (1998, 2002).

3. Biodiversity and Biogeography

In Tables 1 and 2 a taxonomic list of all species of sipunculans and echiurans recorded south of the Polar Front is given. Bathymetric and global distribution data are also included for each species. Distribution of all sipunculan and echiuran species recorded south of the Polar Front are displayed in Maps 1–9. The most ubiquitous Antarctic species is the sipunculan *Golfingia margaritacea*. Other two global widespread golfingiid species are *G. anderssoni* and *G. muricaudata*. The three involved species have been plotted across the world oceans (Map 1). Whereas *G. margaritacea* shows practically a cosmopolitan distribution, *G. anderssoni* has been reported mainly from the far southern latitudes, although some other disjunct areas appear in the northern Pacific and central Atlantic Ocean. Concerning the third species, *G. muricaudata*, the majority of its records come from the Atlantic Ocean (few Pacific and Indian) at deep waters (Map 1).

South of the Polar Front, *G. margaritacea* comprises 60% of the total records of sipunculans. The species is present along almost the entire coastline of Antarctica with a few gaps such as off 'Dronning Maud Land' (between longitude 0°–45° E) and 'Marie Byrd Land' (120°–150° W). Several other common species (*G. anderssoni, G. muricaudata, Nephasoma diaphanes, Phascolion lutense* and *P. hedraeum*) appear more restricted to those areas heavily sampled by oceanographic vessels such as the Antarctic Peninsula, the Ross and Weddell Seas (Maps 1–3). The remaining species are represented by few specimens from widely scattered locations (Maps 2–3). With regard to the vertical distribution, most sipunculan species (around 85% of the records) were found at sublittoral (1–200 m) and bathyal (200–3000 m) depths, whereas only two species, *Phascolion lutense* and *P. pacificum,* showed a preference for deeper water (>2000 m).

By contrast, echiuran records are noticeably scarce in Antarctic waters, with only a 10% of the total records for both phyla. From this small percentage, almost half of the records belong to the ubiquitous Echiurus antarcticus, and when combined with the bonelliid Alomasoma belyaevi, they achieve the 65% of all echiuran records (Map 4). The remaining species are scarce around the Southern Ocean (Maps 5-9). The only echiuran endemic species restricted to Antarctic waters by now is Ikeda sp. (previously known as Prashadus sp.) (Map 5). Other basic taxonomic metrics, such as species richness and especially generic richness, show higher absolute numbers than sipunculans, with 13 species organised in 11 genera. However, when relativised to the global figures of echiurans, the Antarctic echiurans display surprisingly similar percentages (7% for species and about 25 % for genera) as referred to sipunculans. In relation to the vertical distribution, only 4 species are found at depths less than 200 m, whereas 12 species were collected at depths greater than 200 m. Whereas the numbers of representatives of family Bonelliidae increases at greater depths (2 sublittoral species, 1-200 m; 5 bathyal species,

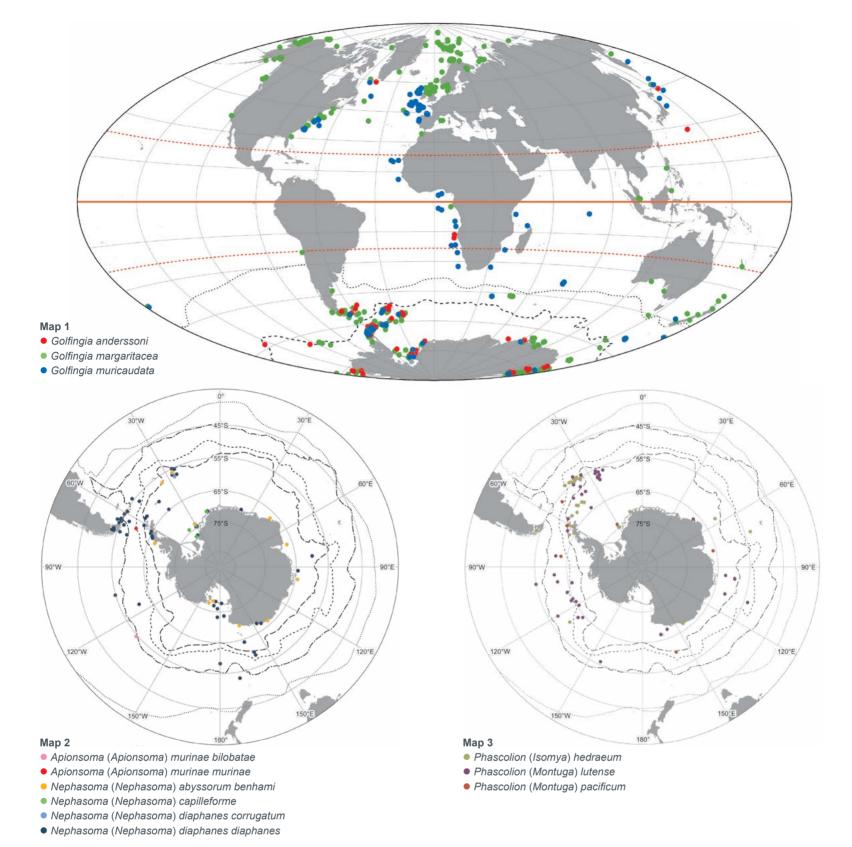


 Table 1
 List of sipunculans reported from the Southern Ocean with bathymetric data (south of the Polar Front) and global distribution. (> = mostly).

	Bathymetry (South PF)	Global distribution
Phylum Sipuncula Sedgwick, 1898		
Class Sipunculidea Cutler & Gibbs, 1985		
Order Golfingiiformes Cutler & Gibbs, 1985		
Family Golfingiidae Stephen & Edmonds, 1972		
Genus Golfingia Lankester, 1885		
1. Golfingia (Golfingia) anderssoni (Théel, 1911)	28–2975 m	disjunct
2. Golfingia (Golfingia) margaritacea (Sars, 1851)	1–4886 m	cosmopolitan
3. Golfingia (Golfingia) muricaudata (Southern, 1913)	20–2975 m	> Atlantic Ocean
Genus Nephasoma Pergament, 1946		
4. Nephasoma (Nephasoma) abyssorum benhami (Stephen, 1948)	460–4606 m	Southern Hemisphere
5. Nephasoma (Nephasoma) capilleforme (Murina, 1973)	650–2037 m	Pacific, Atlantic Oceans
6.1. Nephasoma (Nephasoma) diaphanes diaphanes (Gerould, 1913)	1–6150 m	cosmopolitan
6.2. Nephasoma (Nephasoma) diaphanes corrugatum Cutler & Cutler, 1986	1779 m	Pacific, Atlantic Oceans
Genus Phascolion Théel, 1875		
7. Phascolion (Isomya) hedraeum Selenka & De Man, 1883	70–4375 m	> Southern Hemisphere
8. Phascolion (Montuga) lutense Selenka, 1885	1820–6150 m	> Southern Hemisphere
9. Phascolion (Montuga) pacificum Murina, 1957	2965–5600 m	widespread
Class Phascolosomatidea Cutler & Gibbs, 1985		
Order Phascolosomatiformes Cutler & Gibbs, 1985		
Family Phascolosomatidae Stephen & Edmonds, 1972		
Genus Apionsoma Sluiter, 1902		
10.1. Apionsoma (Apionsoma) murinae murinae (Cutler, 1969)	3687 m	> Atlantic, Pacific Oceans
10.2. Apionsoma (Apionsoma) murinae bilobatae (Cutler, 1969)	1035 m	> North Atlantic

 Table 2
 List of echiurans reported from the Southern Ocean with bathymetric data (south of the Polar Front) and global distribution.

	Bathymetry (South PF)	Global distribution
Phylum Echiura Newby, 1940		
Order Echiuroinea Bock, 1942		
Family Echiuridea de Blainville, 1827		
Subfamily Echichiurinae Quatrefages, 1847		
Genus Echiurus Guérin-Méneville, 1831		
1. Echiurus antarcticus Spengel, 1912	1–770 m	SW Atlantic, SE Pacific, Antarctic
Subfamily Thalassematinae Forbes & Goodsir, 1841		
Genus Thalassema Lamarck, 1801		
2. Thalassema antarcticum Stephen, 1941	389 m	SW Atlantic, Antarctic
Genus Ikeda Wharton, 1913		
3. Ikeda sp.	40–99 m	endemic
Family Bonelliidae Lacaze-Duthiers, 1858		
Genus Alomasoma Zenkevitch, 1958		
4. Alomasoma belyaevi Zenkevitch, 1964	74–2947 m	circumtropical, Antarctic
5. Alomasoma chaetifera Zenkevitch, 1958	5847–6275 m	Central Atlantic, W Pacific, Antarctic
Genus Hamingia Danielssen & Koren, 1881		
6. Hamingia arctica Danielssen & Koren, 1881	740 m	Arctic, Antarctic
Genus Jakobia Zenkevitch, 1958		
7. Jakobia birsteini Zenkevitch, 1958	7280 m	W Pacific, Antarctic
Genus Maxmuelleria Bock, 1942		
8. Maxmuelleria faex (Selenka, 1885)	525 m	Atlantic, Antarctic
9. Maxmuelleria verrucosum (Studer, 1879)	1–3500 m	NE Atlantic, Antarctic
Genus Prometor Fisher, 1948		
10. Prometor grandis (Zenkevitch, 1957)	3102–3500 m	W Pacific, Antarctic
Genus Protobonellia Ikeda, 1908		
11. Protobonellia nikitini Murina, 1976	1437 m	W Pacific, Antarctic
Genus Sluiterina Monro, 1927		
12. Sluiterina flabellorhynchum Murina, 1976	2240–5895 m	Central E Atlantic, Antarctic
Genus Pseudoikedella Murina, 1978		
13. Pseudoikedella achaeta (Zenkevitch, 1958)	1300–3490 m	W Pacific, NE Atlantic, Antarctic



Sipuncula Maps 1–3 Map 1. Global distribution of *Golfingia anderssoni* (Théel, 1911), *G. margaritacea* (Sars, 1851), and *G. muricaudata* (Southern, 1913). Map 2. Distribution of *Apionsoma* (*Apionsoma*) *murinae bilobatae* (Cutler, 1969), *A.* (*A.*) *murinae murinae* (Cutler, 1969), *Nephasoma* (*Nephasoma*) *abyssorum benhami* (Stephen, 1948), *N.* (*N.*) *capilleforme* (Murina, 1973), *N.* (*N.*) *diaphanes corrugatum* Cutler & Cutler, 1986 and *N.* (*N.*) *diaphanes diaphanes* (Gerould, 1913) around the Southern Ocean. Map 3. Distribution of *Phascolion* (*Isomya*) *hedraeum* Selenka & De Man, 1883, *P.* (*Montuga*) *lutense* Selenka, 1885 and *P.* (*M.*) *pacificum* Murina, 1957 around the Southern Ocean.

201–2000 m; 10 abyssal species, >2001 m), the 3 species of the family Echiuridae are distributed in shallower bottoms of less than 770 m (50% of all Antarctic records are indeed less than 200 m). In contrast, only 4 records (8% of the total) of bonelliids are found at depths less than 200 m. Two species of bonelliids, *Maxmuelleria verrucosum* and *A. belyaevi*, exhibit some degree of emergence towards shallower bottoms in Antarctic waters.

4. Discussion

The main feature concerning the distribution of sipunculans and echiurans in the Southern Oceans is the progressive loss of species richness along a polar gradient from sub-Antarctic waters to the high latitudinal Antarctic regions. The 10 sipunculan species recorded in the Southern Ocean, compared with the total world fauna of 150 species, testify once more the relative poverty of sipunculan species (7%) as a component of the Antarctic benthos. Again, if the generic level is considered, only 4 of a total of 16 genera described for the phylum were able to penetrate into the cold bottoms around Antarctica. Except for the genus *Apionsoma*, the remaining genera belong to the large sipunculan family Golfingiidae, which show many cold deep-water representatives in the world oceans (Murina 1975, Cutler 1994). Obviously, cold-water golfingiid species were physiologically better pre-adapted to the Antarctic conditions and they could radiate better than other warm water species in the bottoms around Antarctica.

A special attention should be paid to the cosmopolitan concept in sipunculans, which is affecting directly to the most common species here recorded, Golfingia margaritacea. In the monograph of Stephen & Edmonds (1972), up to 8 subspecies of G. margaritacea in addition to the nominate form were compiled from the world oceans. Cutler & Cutler (1987) synonymised all subspecies under the nominate form, but related a new subspecies G. margaritacea ohlini for those varieties coming from the Southern Ocean. Saiz (1995) had difficulties in using the subspecific name for a large collection coming from the Weddell Sea. Consequently, Cutler et al. (2001) unified all varieties under a broad plastic concept by only applying the traditional anatomical characters. However, recent analyses using molecular techniques are showing that our concept of cosmopolitism in sipunculans has to be revised. Kawauchi & Giribet (2010) and Schulze et al. (2012) indicated the existence of a complex of cryptic species in other widespread geographically or 'cosmopolitan' species of the phylum. Now G. margaritacea populations, which are rather abundant in some localities across the world oceans, are representing a suitable material for investigating further the cosmopolitan concept on sipunculans.

Before attempting to compare between sipunculan faunas from both sides of the Polar Front, it is necessary to make a comment on old sipunculan names used by Edmonds (1969) in the Antarctic Map Folio Series, especially his groupings (1) and (2) erected for cold water species. They are: *Golfingia*



charcoti, which was considered a posterior synonym of G. elongata by Cutler & Murina (1977), and later related most likely to the broad concept of G. margaritacea (Cutler et al. 2001). In a similar way, G. nordenskjoldi and G. mawsoni, were considered junior synonyms of G. margaritacea by Cutler & Cutler (1987). Another old subspecific name used by Edmonds (1969) was G. eremita australis. In the generic revision of Cutler & Cutler (1986) the subspecific rank was synonymised under the nominal form becoming Nephasoma eremita. Later on (Cutler et al. 2001), the few Antarctic records of N. eremita became suspicious, and they were related likely to other broad taxonomic concept named N. diaphanes. Something similar happens with all the Antarctic records of G. minuta. They were transferred to the broad concept of N. diaphanes by Cutler & Cutler (1986). The case of G. intermedia is also parallel to the above obsolete Edmonds' names, since Gibbs (1977) submerged it under another broad concept named Phascolion strombus. Finally, Cutler et al. (2001) noted that all the Antarctic records of P. strombus were likely pertaining to other Southern Hemisphere species named P. hedraeum.

The affinity of the Antarctic sipunculans with the far Southern Hemisphere fauna remains tenuous, since the latter comprises 11 genera and 32 species. after updating the detailed distribution maps of Edmonds (1969). The indication for a latitudinal diversity gradient of sipunculans is given by the fact that the cold waters around Antarctica appear to be unsuitable for 7 genera and 18 species compiled in sub-Antarctic waters. This is especially true for those taxa belonging to the class Phascolosomatidea, which, in general, show a higher thermophilic distribution across the world oceans.

No doubt, the most striking feature exhibited by the Antarctic fauna of echiurans is the contrasting diversification exhibited by the two basic families of the phylum in the settlement process of the Southern Ocean. Ten species organised in 8 genera belong to the family Bonelliidae, whereas the family Echiuridae has only 3 representatives classified in 3 distinct genera. This marked difference could be explained by the two global opposite strategies of diversification of these echiuran taxonomic groups (Zenkevitch 1966, Stephen & Edmonds 1972) along the world oceans. In general, bonelliids exhibit a higher diversification on deeper bottoms where cold temperatures prevail, whereas the representatives of the family Echiuridae show preferences for shallow warm waters. Sea temperatures in the abyssal zones of the world's oceans and in the Antarctic Ocean (below 30 m) are very similar (Picken 1985), so temperature cannot represent a limiting feature for the distribution of bonelliids below the Polar Front. This would explain the larger success of bonelliids when radiating southwards from the abyssal plains around Antarctica.

The indication of a latitudinal gradient for the family Echiuridae is given by the fact that its diversity is only represented by 3 species, and the genera more thermophilic of the subfamily Thlassematinae (such as the most diversified Ochetostoma) are readily absent. In this way, it is worth mentioning than one species in the family Urechidae (classified in the order Xenopneusta), Urechis chilensis, is well represented in sub-Antarctic waters (Edmonds 1969). It comes close to the Polar Front (51.5°S), but populations of this species seem by now not to have crossed this zoogeographical barrier (Saiz et al. 2000).

All available evidence confirms the absence of endemism at the level of families, genera or species in both invertebrate phyla, with the exception of Ikeda sp. in echiurans. This phenomenon may well be the result of a colonisation by selected species from deep cold waters of the Southern Hemisphere during a time prior to the development of the present zoogeographical barriers. This suggests that the Antarctic sipunculan and echiuran faunas could be derived from adjacent deep-water basins as it has been shown for certain isopods, which have clearly colonised the shallow-waters of Antarctica from the deepsea (Clarke & Crame 1989). In fact, the occurrence of bonelliids at shallower depths in the Antarctic has been regarded as an example of emergence of cold deep-water representatives in polar regions (Zenkevitch 1966)

5. Conclusion

In conclusion, the effects of extremely cold temperatures in waters around Antarctica affects drastically both the sipunculan and echiuran faunas. No latitudinal or longitudinal gradients were detected in the current distribution of the species around the Southern Ocean. Moreover, depth is other important structural factor, which especially differentiates two basic patterns in echiurans: the family Echiuridae with a clear preference for sub-littoral and shallow bathyal bottoms (less than 700 m), whereas the family Bonelliidae, shows a stronger preference for bathyal and abyssal depths. Thus, both invertebrate phyla can be characterised together as depauperate components of the far Southern Hemisphere faunas

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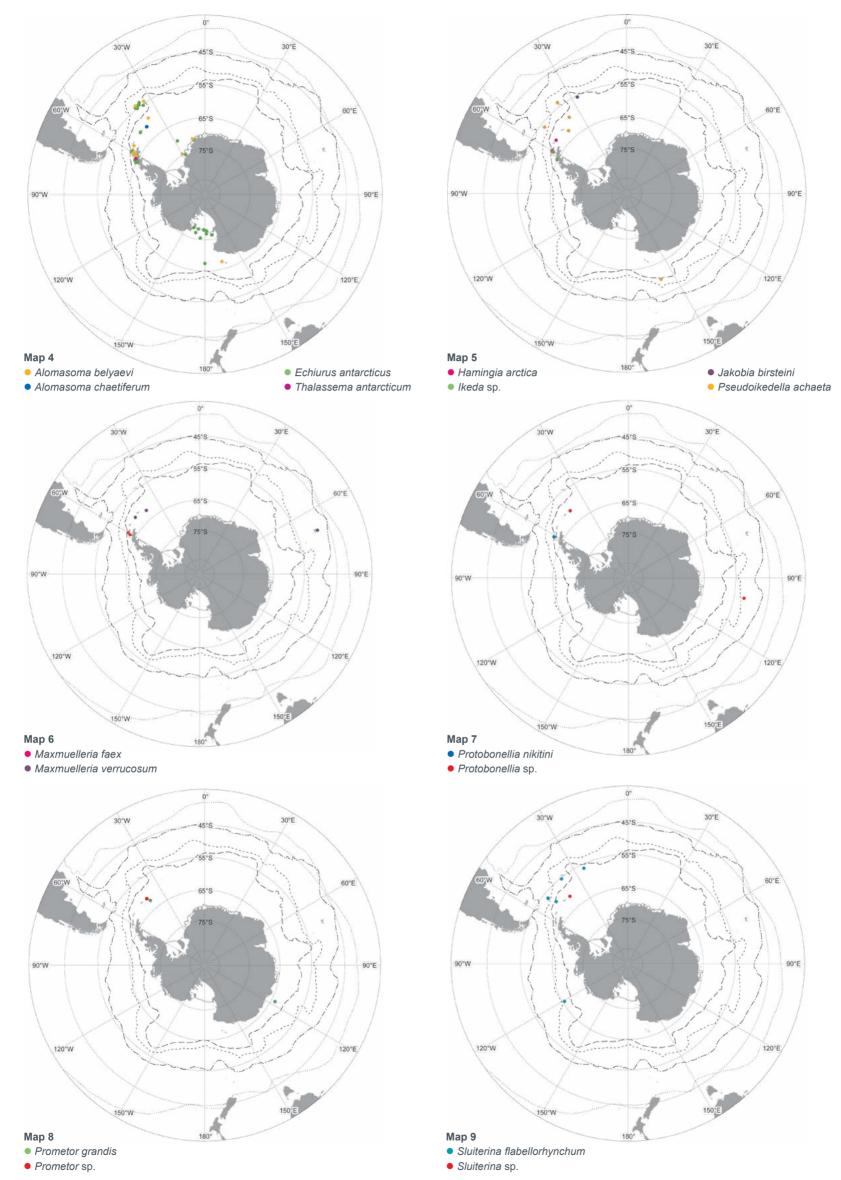
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Echiura Maps 4–9 Map 4. Distribution of Alomasoma belyaevi Zenkevitch, 1964, A. chaetifera Zenkevitch, 1958, Echiurus antarcticus Spengel, 1912 and Thalassema antarcticum Stephen, 1941 around the Southern Ocean. Map 5. Distribution of Hamingia arctica Danielssen & Koren, 1881, Ikeda sp., Jakobia birsteini Zenkevitch, 1958 and Pseudoikedella achaeta (Zenkevitch, 1958) around the Southern Ocean. Map 6. Distribution of Maxmuelleria faex Selenka, 1885 and Maxmuelleria verrucosum (Studer, 1879) around the Southern Ocean. Map 7. Distribution of Protobonellia nikitini Murina, 1976 and Protobonellia sp. around the Southern Ocean. Map 8. Distribution of Prometor grandis (Zenkevitch, 1957) and Prometor sp. around the Southern Ocean. Map 9. Distribution of Sluiterina flabellorhynchum Murina, 1976 and Sluiterina sp. around the Southern Ocean.

THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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

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.

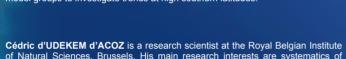
The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)
In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and 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



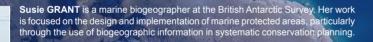
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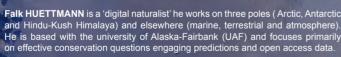


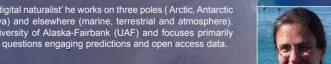


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