

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

CHAPTER 5.25. SOUTHERN OCEAN CRINOIDS.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.25. Southern Ocean Crinoids

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1. Introduction

The first crinoid species described from the Southern Ocean were dredged during the Challenger expedition (1872-1876). Carpenter (1884, 1888) was the first crinoid expert to study the Southern Ocean crinoid fauna. Immediately following the Antarctic expeditions of the late 19th and early 20th centuries, Clark (1915), Mortensen (1917), John (1938, 1939) and Clark & Clark (1967), among others, have substantially added to the known crinoid diversity in the Southern Ocean. More recently, Speel & Dearborn (1983) studied the comatulid specimens collected by the USNS Eltanin between 1962 and 1968. Marr (1963) gave the first overview of the comatulid species distribution on the Antarctic continental shelf, and Hedgepeth (1969) gave the first broad study of the crinoid biogeography in the Southern Ocean. Eléaume (2006) added substantially to this overview and produced the first comprehensive review of the comatulid diversity in the Southern Ocean. This review was updated by Améziane et al. (2011) for the Kerguelen Plateau, Hemery (2011) and Hemery et al. (2011, 2012). New crinoid species have been recently described and added to the known diversity by Eléaume et al. (2011, 2012), and Roux (in prep.) is currently revising the USNS Eltanin stalked crinoid collection



Photo 1 Dumetocrinus aff. antarcticus (Bather, 1908). Det. M. Roux, Larsen B (*Polarstern* ANT-XXIII/8, st. 710-1, 137–209 m). Image: J. Gutt © AWI/Marum, University of Bremen. Germany.



Photo 2 Promachocrinus kerguelensis Carpenter, 1879. Det. M. Eléaume, Larsen B (*Polarstern* ANT-XXIII/8, st. 720-1, 228–233 m). Image: J. Gutt © AWI/Marum, University of Bremen, Germany.

2. Methods

The northern geographical limits used here generally follow the limits described in De Broyer & Danis (2011, Fig. 2). However, benthic data collection is highly dependent on bathymetry, ice conditions, distance to research stations and substrate type (Griffiths 2010). The species collected and their occurrences are therefore mainly restricted to the shelves and near the research stations.

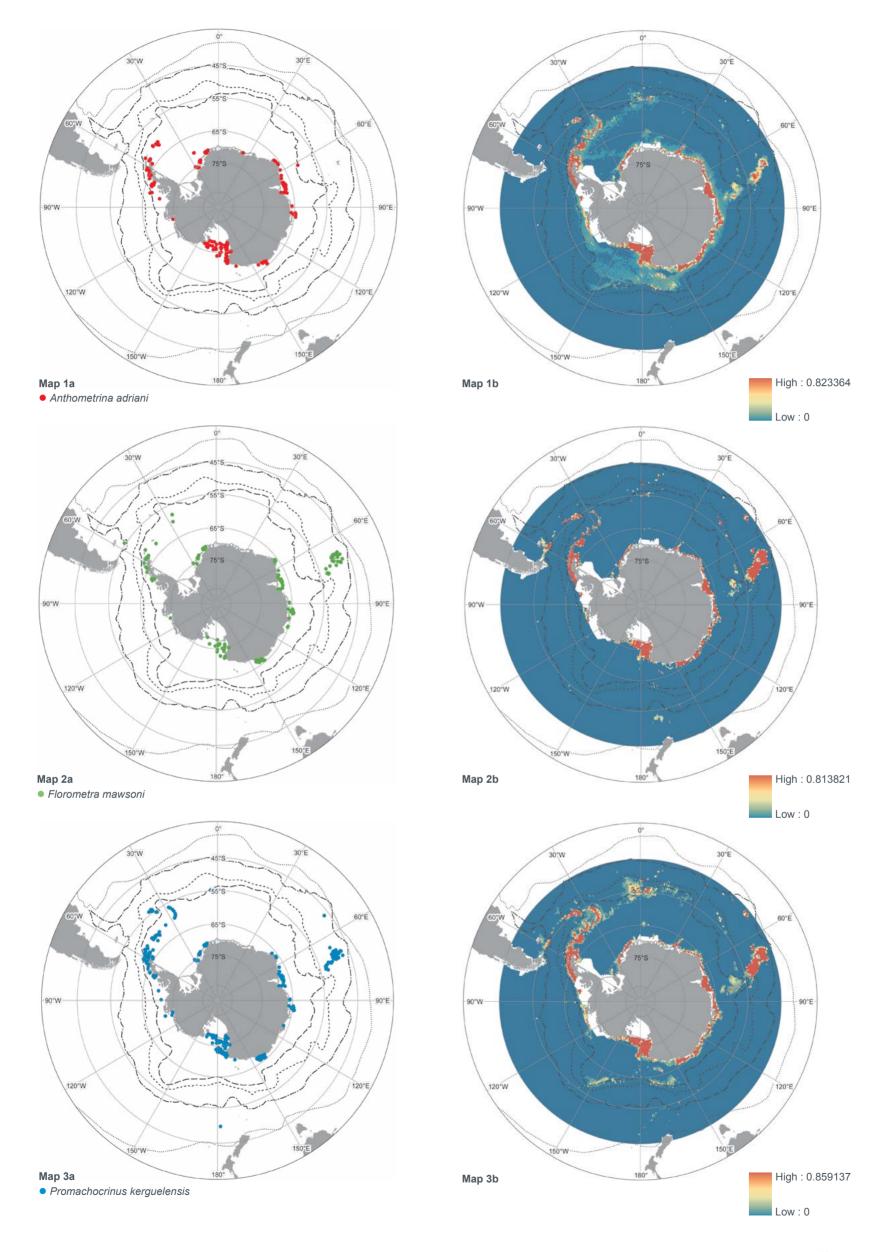
Species occurrences are derived from published sources (indicated when relevant) and from museums and other conservation institutions databases. Most comatulids from older collections were re-examined and their taxonomic attribution checked by Eléaume; new comatulid collections were identified and barcoded by Eléaume, Hemery and Améziane; all stalked crinoids re-examined and their taxonomic attribution checked by Roux.

For greater clarity we used in this work a classification and a nomenclature of extant crinoids anterior to the first molecular analyses, mainly based on Roux *et al.* (2002) for stalked crinoids, and Messing (1997) for comatulids. However, molecular phylogeny (Hemery *et al.* 2013b) and phylogeography (Hemery 2011, Hemery *et al.* 2012) have been used to help understand intravs. inter-specific variability, and placement of taxa within the Crinoidea.

3. Biodiversity

The new conception of the Antarctic and sub-Antarctic crinoid diversity presented here results from a significant increase in the number of described species, the recognition of taxonomic issues, and the recognition of suspected cryptic species. We recognise 43 crinoid species (Table 1). They represent around 7% of all known extant species. Thirty-one species are endemic to the Southern Ocean, five of them are restricted to the slope, 15 to the shelf, and eight to depths >2000 m. A total of 19 (43%) species of comatulids are described as brooders and all others are thought to have planktonic larvae

Crinoidea Maps 1–3 Crinoidea Map 1a. Distribution pattern of Anthometrina adriani. The dataset is derived from published literature and institutional databases. Anthometrina adriani is exclusively found on the high Antarctic shelf, south of the Polar Front. This species has never been reported from the Burdwood Bank, Bouvet Island, or the sub-Antarctic islands. Map 1b. Potential distribution of Anthometrina adriani. Habitat suitability map generated using Maxent following the methods described in Pierrat et al. (2012). The 'suitable area' encompasses all pixels for which probability is over the minimal probability value assigned to a true occurrence (100% of occurrence data are included in this area). The 'highly suitable area' corresponds to a threshold that excludes the 5% of true occurrences that show the lowest probability values (95% of true occurrences are still included in this second area). Hatched areas correspond to areas where data are missing for at least one environmental variable. According to this method, Anthometrina adriani highly suitable habitat is restricted to the high Antarctic shelf and the Scotia Arc. Other suitable habitats are found in deeper areas and around the sub-Antarctic islands mostly south of the Polar Front. This is congruent with our direct observations. Anthometrina adriani was observed in depths ranging from 55 to 1156 m with a mean around 411 m and most specimens collected from depths ranging from 200 to 650 m. Specimens observed in areas deeper than 1000 m (four specimens in the Davis Sea) are rare. — Map 2a Distribution pattern of Florometra mawsoni. The dataset is derived from published literature and institutional databases. Florometra mawsoni is found on the high Antarctic shelf, the Kerguelen Plateau, the Scotia Arc and south of the Falkland Islands. Map 2b. Potential distribution of Florometra mawsoni. Habitat suitability map generated using Maxent following the methods described in Pierrat et al. (2012). The 'suitable area' encompasses all pixels for which probability is over the minimal probability value assigned to a true occurrence (100% of occurrence data are included in this area). The 'highly suitable area' corresponds to a threshold that excludes the 5% of true occurrences that show the lowest probability values (95% of true occurrences are still included in this second area). Hatched areas correspond to areas where data are missing for at least one environmental variable. According to this method, Florometra mawsoni highly suitable habitat is found on the high Antarctic shelf, the Scotia Arc, Burdwood Bank, the Kerguelen Plateau and some sub-Antarctic islands. This is congruent with our direct observations. Florometra mawsoni was observed in depths ranging from 50 to 2355 m with a mean around 420 m and most specimens collected from depths ranging from 200 to 650 m. However, 56 specimens have been dredged from depths deeper than 1000 meters in the Weddell and Davis Seas. One specimen is also known from over 2000 m in the Weddell Sea. — Map 3a. Distribution pattern of Promachocrinus kerguelensis. The dataset is derived from published literature and institutional databases. Promachocrinus kerguelensis is very abundant locally and is found on the high Antarctic shelf, the sub-Antarctic islands, and was also dredged from the Campbell Plateau. Map 3b. Potential distribution of Promachocrinus kerguelensis. Habitat suitability map generated using Maxent following the methods described in Pierrat et al. (2012). The 'suitable area' encompasses all pixels for which probability is over the minimal probability value assigned to a true occurrence (100% of occurrence data are included in this area). The 'highly suitable area' corresponds to a threshold that excludes the 5% of true occurrences that show the lowest probability values (95% of true occurrences are still included in this second area). Hatched areas correspond to areas where data are missing for at least one environmental variable. According to this method, Promachocrinus kerguelensis highly suitable habitat is found on the high Antarctic shelf, the Scotia Arc, Burdwood Bank, the Kerguelen Plateau and some sub-Antarctic islands. This is congruent with our direct observations. Promachocrinus kerguelensis was observed in depths ranging from <20 to 2100 m with a mean around 350 m and most specimens collected from depths ranging from 100 to 800 m. However, two specimens have been dredged from depths deeper than 2000 meters near the Campbell Plateau. Almost 50 specimens are known from over 1000 m in various localities all around the continental shelf.



► Echinodermata: Crinoidea

(John 1938, Clark & Clark 1967, Dearborn & Rommel 1969, Speel & Dearborn 1983, McClintock & Pearse 1987). However, the early larval development of stalked species remains unknown. All crinoid species are thought to be suspension feeders. A number of comatulid crinoids have been observed actively swimming (e.g. *Promachocrinus kerguelensis*), demonstrating the possibility of an alternative mode of dispersion. A number of species have been observed remaining still either perched on other organisms (e.g. *Florometra mawsoni*) or sitting close to the seabed (e.g. *Anthometrina adriani*).

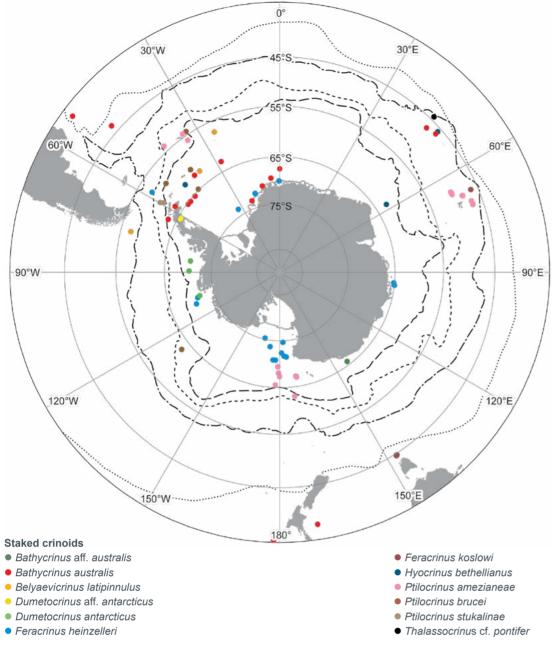
The total crinoid diversity is probably underestimated. New remarkable species have been recently described from under-sampled regions: *Ptilocrinus* (*Ptilocrinus*) *amezianeae* (see Eléaume *et al.* 2011) from seamounts off the Ross Sea, *Feracrinus heinzelleri* (see Eléaume *et al.* 2012) from Antarctic shelf slopes, *F. koslowi* (see Améziane & Roux 2011) from seamounts. Other species recently dredged from previously inaccessible environments are currently being described: *Thalassometra* n. sp., *Pentametrocrinus* n. sp., *Thalassocrinus* n. sp., and *Dumetocrinus* n. sp. (see Eléaume *et al.* 2012 for details). Other species show a high genetic diversity that suggests a cryptic diversity: *Promachocrinus kerguelensis* may represent six (Wilson *et al.* 2007), two (Hemery *et al.* 2012) or a single species, *Notocrinus* spp. may represent more than the two known species, and *P. amezianeae* is thought to represent

two distinct populations (Hemery 2011). Results associated to the analysis of *Isometra* and *Eumorphometra* spp. also seem to indicate a very high genetic diversity that still need to be correlated to morphological variability. Some species have rarely been collected and are considered rare: *Anisometra frigida*, *Balanometra* sp., *Eometra* spp., *Eumorphometra* spp., *Kempometra grisea* and *Thaumatocrinus renovatus*. This may be due to the deep / remote / inaccessible environments where most of them occur (see Table 1). The small size of some species may also explain their scarcity in samples either because they may be washed through the trawl mesh or overlooked during sorting (see Eléaume 2013).

Recent recognition of some taxonomic problems (Eléaume 2006, Roux & Lambert 2011, Eléaume et al. 2012, Hemery et al. 2013b) partly counterbalances the diversity patterns. Solanometra antarctica sensu Clark & Clark (1967) is probably not a valid species. As A.M. Clark stated (Clark & Clark 1967) S. antarctica resembles F. mawsoni (sensu Clark & Clark 1967) and may constitute an ecomorph or an ontogenetic stage. Florometra mawsoni has proved to be closely related to P. kerguelensis, and belongs to a lineage only distantly related to other Florometra representatives (Eléaume 2006, Hemery et al. 2013b).

Table 1 AP = Antarctic Peninsula, AS = Amundsen Sea, CA = circum-Antarctic, CaP = Campbell Plateau, CrI = Crozet Islands, DS = Davis Sea, EA = East Antarctic, HI = Heard Island, KP = Kerguelen Plateau, MI = Marion Island, PO = Pacifique Ocean, RS = Ross Sea, SA = Scotia Arc, sAO = South-Atlantic Ocean, sAU = South Australia; SGI = South Georgia Island, sNZ = South New-Zealand, SOI = South Orkney Islands, sSAm = South America, SSI = South Shetland Islands, WA = West Antarctic, WS = Weddell Sea. Brooding species are indicated by a star. 0 = this study; 1 = Bohn 2009; 2 = Speel & Dearborn 1983; 3 = Clark & Clark 1967; 4 = Eléaume *et al.* 2004; 5 = Eléaume *et al.* 2012; 6 = Eléaume *et al.* 2011; 7 = Améziane & Roux 2011; 8 = Roux & Lambert 2011; 9 = Mironov & Sorokina 1998; 10 = Hemery 2011; 11 = Hemery *et al.* 2013a; 12 = Eléaume 2013. * = Hyocrinus bethellianus subsp. n. Mironov & Sorokina 1998 was mistakenly recorded as *Hyocrinus bethellianus* in Eléaume et al. (2012), but Roux (2004) attributed this taxon to *Hyocrinus foelli* Roux & Pawson, 1999.

Family	Genus/Species	Distribution	Depth (m)	Ref.
Antedonidae	Anthometrina adriani (Bell, 1908)	CA	55–1156	10
	Florometra magellanica (Bell, 1882)	sSAm	20–594	1
	Florometra mawsoni A.H. Clark, 1937	CA/KP	50–2355	10
	Promachocrinus kerguelensis Carpenter, 1879	CA/KP/CaP	20–2100	2/11
	Solanometra antarctica (Carpenter, 1881)	Н	137–274	3
	*Isometra challengeri (A.H. Clark, 1907)	sAO/AP	300–1097	3/12
	*Isometra flavescens John, 1938	SGI	170–2044	2
	*Isometra graminea John, 1938	CA	59–714	2
	*Isometra hordea John, 1938	SA/RS	117–641	2
	*Isometra johanni A.M. Clark in A.H. & A.M. Clark, 1937	EA	180-300	3
	*Isometra vivipara Mortensen, 1917	sSAm/SA	79 –1228	0
	*Phrixometra exigua (Carpenter, 1888)	MI/sNZ	91–540	3
	*Phrixometra longipinna (Carpenter, 1888)	SA	200–610	3
	*Phrixometra nutrix (Mortensen, 1918)	sSAm/SA	137–485	2
	*Phrixometra rayneri John, 1938	SGI/RS	177–1444	2
	Thaumatometra abyssorum (Carpenter, 1888)	MI/CrI	2925	3
	Tonrometra remota (Carpenter, 1888)	SOI/MI/CrI	2925–3426	3
	Tonrometra spinulifera (John, 1939)	EA	1266	3
	Anisometra frigida (John, 1939)	EA/RS/AP	219–503	2/12
	Balanometra sp.	SA	142–3093	2
	*Kempometra grisea John, 1938	SSI/AP	660–1120	2/12
	*Eumorphometra aurora John, 1938	SA/EA	177–426	2
	*Eumorphometra concinna Clark, 1915	EA	380–400	3
	*Eumorphometra hirsuta (Carpenter, 1888)	MI/sNZ	256–951	2
	*Eumorphometra fraseri John, 1938	SSI/RS	311–440	2
	*Eumorphometra marri John, 1938	SSI/sNZ	220–4218	2
	*Eometra antarctica (A.H. Clark, 1915)	EA	2725	3
	*Eometra weddelli John in Vaney & John, 1939	SA/WS	3426–3806	2
Notocrinidae	*Notocrinus mortenseni John, 1938	AP/WS/EA	93–677	0/12
	*Notocrinus virilis Mortensen, 1917	CA/KP	65–1120	0/12
Thalassometridae	Thalassometra bispinosa (Carpenter, 1888)	MI/CrI/PO	2925–4965	4
	Thalassometra villosa (A.H. Clark, 1907)	PO/sNZ	1860–1940	4
Pentametrocrinidae	Thaumatocrinus renovatus Carpenter, 1884	EA/MI/Crl/sAU	1638–3290	2
Zenometridae	Psathyrometra sp.	sSAm/WA/AP	2355–3621	2
Hyocrinidae	Dumetocrinus antarcticus (Bather, 1908)	AP/AS	480–581	5/10
	Dumetocrinus aff. antarcticus	WS	193–449	10
	Ptilocrinus amezianeae Eléaume, Hemery, Bowden & Roux, 2011	RS/KP	455–1680	6
	Feracrinus heinzelleri Bohn in Eléaume, Bohn, Roux & Améziane, 2012	AS/DS/RS/WS	577–3697	0/10
	Belyaevicrinus latipinnulus (Mironov & Sorokina, 1998)	PO/SA	3056–5530	0/9
	Feracrinus koslowi Améziane & Roux, 2011	PO/KP	1310–1815	7
	Ptilocrinus brucei (Vaney, 1908)	AP	2718–5474	0/9
	Ptilocrinus stukalinae Mironov & Sorokina, 1998	AP/sNZ/PO	4664–6145	9
	Hyocrinus bethellianus Thomson, 1876	AP/EA/Crl/sAO	2926–5037	5 *
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Crinoidea Map 4 Distribution pattern of Southern Ocean stalked crinoids. The dataset is derived from published literature and institutional databases. The East Antarctic area displays five different species of stalked crinoids whereas the West Antarctic area displays ten species. The Peninsula and Scotia Arc area is particularly rich with eight different species recorded.

4. Biogeographic patterns

The Southern Ocean crinoid phylogenetic diversity may be described using the recent high-resolution phylogeny developed by Hemery *et al.* (2013b). Only seven over 32 extant families are represented in the Southern Ocean. The Southern Ocean lineages are not monophyletic, indicating multiple colonisation events (Hemery 2011). Some lineages appear to have diversified *in situ*: the *Promachocrinus*, *Notocrinus*, *Isometra*, and *Eumorphometra* complexes (Hemery 2011). *Dumetocrinus antarcticus* (Photo 1) seems to constitute a good example of Antarctic emergence with subsequent *in situ* divergence probably after reproductive isolation took place on both sides of the Antarctic Peninsula, and *Bathycrinus australis* may constitute a case of Antarctic submergence (Eléaume *et al.* 2012).

4.1. Patterns of geographic distribution

Because only five species were known from more than ten occurrences, Hedgepeth (1969) failed to identify clear zoogeographic provinces for the Antarctic and sub-Antarctic crinoids. The recent improvements in crinoid sampling and identification tools provide a better understanding of the crinoid biogeographic patterns, and indicate that these patterns are much more diverse than expected. A number of species are found in the Southern Ocean as well as other ocean basins. *Bathycrinus australis* is well represented in the Atlantic sector from the Antarctic Peninsula to the Walvis Ridge (Eléaume *et al.* 2012) at bathyal to abyssal depths (Table 1). *Feracrinus koslowi* occurs from the Kerguelen Plateau to the Tasmanian seamounts (Améziane & Roux 2011, see Map 4). *Thaumatocrinus renovatus* was collected from the Indian and Pacific sectors of the Southern Ocean and from southern Australia at abyssal depths (Clark & Clark 1967).

Some species are endemic to the Southern Ocean. *Promachocrinus kerguelensis* (Maps 3a-b, Photo 2) and *Florometra mawsoni* (Maps 2a-b) are well distributed over the whole Antarctic and sub-Antarctic regions.

The genus *Dumetocrinus* is known from Antarctic slopes and the shelf of the eastern Weddell Sea. *Ptilocrinus* (*Ptilocrinus*) *amezianeae* is also found in Antarctic and sub-Antarctic localities, but seems to be restricted to seamount or slopelike environments (Map 4). *Notocrinus virilis* (*sensu* Mortensen 1917) was

collected from all around the high-Antarctic shelf and from the Scotia Arc. *Anthometrina adriani* is circumpolar in distribution and restricted to the high-Antarctic shelf (Maps 1a–b). *Feracrinus heinzelleri* (Map 4) also is circumpolar in distribution and restricted to the high-Antarctic, but mainly occurs on the slopes.

Species distribution may be restricted to relatively small areas. *Notocrinus mortenseni* (sensu John 1938) is only found in the Weddell Sea and was recently collected from Burdwood Bank, indicating that this species is distributed on both sides of the Polar Front in the Drake Passage area (Hemery 2011). *Eometra weddelli* has rarely been collected and only from the Weddell Sea, off the South Orkney Islands at depths >3000 m.

4.2. Patterns of bathymetric distribution

Deep sea species may or may not be found outside the Southern Ocean. Belyaevicrinus latipinnulus, Ptilocrinus (Ptilocrinus) australis, F. koslowi and T. renovatus are found north of the Sub-Antarctic Front (SAF). On the contrary, Eometra weddelli is restricted to very few localities, all in the same area. This may be linked to the lack of deep-sea samples from around Antarctica. Dumetocrinus antarcticus (Photo 1) and Feracrinus heinzelleri are unique in being the only known Southern Ocean stalked crinoid to be found on shelf areas; it was recorded at the shallowest depths known for hyocrinids. Many species (Table 1) may be considered eurybathic because their bathymetric range largely covers the range of depths commonly encountered on the shelf, from coastal areas to deep trenches. However, shelf species are rarely sampled from slope areas. Video footage (CEAMARC) seems to indicate that shelf species become much less abundant on the slopes. Moreover, Hemery et al. (2011) have shown that the shelf species Anthometrina adriani has an ecological niche and suitable habitat preferentially restricted to the shallowest

parts of the available habitat, despite its bathymetric distribution ranging from 55 to 1156 m (Table 1). Here again, the lack of systematic exploration of slope environments may strongly bias our interpretations of available data.

Stalked crinoids are well represented in the Southern Ocean. They display an unusual level of taxonomic diversity in the deep areas around the tip of the Peninsula and South Georgia (Map 4). This stands especially true for the Hyocrinidae. This pattern was already suggested by Brandt *et al.* (2007) on crustacea.

4.3. Connectivity

Several species are not restricted to the Southern Ocean only and have been found north of the Polar Front. Isometra vivipara is recorded from the Chilean fjords as well as from the Antarctic Peninsula and the Weddell Sea (Bohn 2009). Phrixometra nutrix is also recorded from the Magellanic Region and from Burdwood Bank as well as from the Antarctic Peninsula and some sub-Antarctic islands (Bohn 2009). Promachocrinus kerguelensis is recorded from the Magellanic Region (Mutschke & Rios 2006, Bohn 2009) and from the whole Southern Ocean, including the Campbell Plateau (Speel & Dearborn 1983). Thalassometra villosa is recorded from Campbell Island and from the northern Pacific (Eléaume et al. 2004). Ptilocrinus (Ptilocrinus) stukalinae is also recorded from the northern Pacific, and from the South Orkney and Macquarie Islands. This species is a case illustrating bipolarity within the crinoids. Thalassometra bispinosa is recorded from the sub-Antarctic Marion and Crozet Islands and from off Peru in the central Eastern Pacific (Eléaume et al. 2004). Bathycrinus australis is found on both side of the Polar Front: in the Argentine and Walvis Basins in the Southern Atlantic Ocean, the Atlantic sector of the Southern Ocean and the western Antarctic Peninsula (Eléaume et al. 2012). These patterns of connectivity suggest that the Polar Front may not be such a strong barrier to gene flow and dispersion for some crinoid species.



5. Biogeographic processes

The main driving force that is thought to have lead to the observed taxonomic diversity is the cyclical habitat fragmentation due to the cyclical advance of ice-sheets bulldozing the shelf. Broadcast-spawning populations have the ability to stay connected in the whole species distribution area during glacial periods, or to reconnect rapidly after ice retreat. Most of the crinoid species studied to date, including broadcasters, show signal of lack of connectivity in the past between some populations, leading to the suggestion of an isolation into refugia during glacial events (Hemery 2011, Hemery et al. 2012). Promachocrinus kerguelensis is thought to be a complex of several cryptic species, consisting of seven sympatric, eurybathic and circumpolar genetic lineages (Wilson et al. 2007, Hemery et al. 2012). The genetic structure evidenced by Hemery et al. (2012) is interpreted as the result of population isolation during glacial events. During interglacial periods, this broadcaster species was able to recolonise areas left free of ice. The interactions of the glacial history in Antarctica, and the life history traits of P. kerguelensis best explain the observed patterns of distribution.

Brooding species such as Notocrinus spp., Isometra spp. and Eumorphometra spp. are also structured into distinct genetic lineages. These lineages are restricted to specific areas (Hemery 2011). These patterns can be interpreted as being the result of population isolation during glacial events, and poor recolonisation potential during interglacial periods.

Within Dumetocrinus antarcticus, two lineages are found on each side of the Antarctic Peninsula. This suggests that divergence events occurred by vicariance that resulted in the recent separation of these two entities.

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References and data sources

Data source institutions: NIWA, MNHN, NHM, ZSM, SMNH, BM, USNM, ZMMSU

- Améziane, N., Eléaume, M., Hemery, L.G., Monniot, F., Hemery, A., Hautecoeur, M., Dettai, A., 2011. Biodiversity of the benthos off Kerguelen Islands: overview and perspectives. *In*: Duhamel, G., Welsford, D. (eds), *The Kerguelen Plateau, Marine Ecosystem and Fisheries*. Paris: Société Française d'Ichyologie, pp. 157–167.

 Améziane, N., Roux, M., 2011. Stalked crinoids from Southern Tasmanian Seamounts. Part 1: Family

- Arneziarie, N., Roux, M., 2011. Stalked Critiolus Irom Southern Tasmanian Seamounts. Part 1: Parnily Hyocrinidae. *Journal of Natural History*, 45(3–4), 137–170.
 Bohn, J., 2009. Crinoidea Sea Illies and feather stars. In: Häussermann, V., Försterra, G., (eds.). *Marine Benthic Fauna of Chilean Patagonia*. Santiago: Nature in Focus, 793–800.
 Brandt A., De Broyer, C., De Mesel, I., Ellingsen, K. E., Gooday, A.J., Hilbig, B., Linse, K., Thomson, M.R.A., Tyler P. A., 2007. The biodiversity of the deep Southern Ocean benthos. *Philosophical Transactions of the Royal Society Biological Sciences* 362, 39–66.
 Carpenter, P.H., 1884. Report on the Crinoidea collected during the voyage of H.M.S. Challenger, during the vears 1873–76. First Part Stalked crinoids. *Report on the Scientific Results of the Voyage of the Voyage of the Scientific Results of the Voyage of the Voyage of the Scientific Results of the Voyage o*
- the years 1873-76. First Part Stalked crinoids. Report on the Scientific Results of the Voyage of

- H.M.S. Challenger, Zoology, London, 11(32), i-xii, 1-442, pls. 1-62.
- H.M.S. Challenger, Zoology, London, 11(32), I–XII, 1–442, pis. 1–62. enter, P.H., 1888. Report on the Crinoidea collected during the voyage of H.M.S. Challenger, during the years 1873–76, Second Part The Comatulae. Report on the Scientific Results of the Voyage of H.M.S. Challenger, Zoology, London, 26(60), i–ix, 1–399, pls. 1–70. ,A.H., Clark, A.M., 1967. A monograph of the existing crinoids, Vol. 1: the comatulids, part 5, Suborders Oligophreata (concluded) and Macrophreata. Bulletin of the United States National Museum, 82, i–xv,
- Dearborn J.H. Rommel J.A. 1969 Crinoidea In: Distribution of selected groups of marine invertebrates in waters south of 35°S latitude. Folio 11, Antarctic Map Folio Series, American Geographical Society, pp. 35-36, pl. 21.
- De Broyer, C., Danis, B., 2011. How many species in the Southern ocean? Towards a dynamic inventory of
- the Antarctic marine species. Deep- Sea Research II, 58, 5–17.

 Eléaume, M., 2006. Approche morphométrique de la variabilité phénotypique: conséquences systématiques et évolutives. Application aux crinoïdes actuels (Crinoidea: Echinodermata). PhD dissertation. Paris,
- Muséum national d'Histoire naturelle, pp. 1–402.

 me, M., 2013. Crinoid and asteroid diversity over ecologically contrasted areas. In: Gutt, J. (ed.). The Expedition of the Research Vessel «Polarstern» to the Antarctic in 2013 (ANT-XXIX/3). Berichte zur
- Polar- und Meeresforschung, **665**, 53–57.
 me, M., Améziane, N., Park, Y.-H., 2004. Re-evaluation of the systematics of two deep-sea species of *Thalassometra* (Echinodermata: Crinoidea) and its biogeographical implications. *Journal of Natural* History, 38, 1949-1968.
- ne, M., Bohn, J.M., Roux, M., Améziane, N., 2012. Stalked crinoids (Echinodermata) collected by the
- R/V Polarstern and Meteor in the south Atlantic and in Antarctica. Zootaxa, 3425, 1–22.

 Eléaume, M., Hemery, L.G., Bowden, D.A., Roux, M., 2011. A large new species of the genus Ptilocrinus (Echinodermata, Crinoidea, Hyocrinidae) from Antarctic seamounts, Polar Biology, 34, 1385-1397
- Griffiths, H.J., 2010. Antarctic Marine Biodiversity What Do We Know About the Distribution of Life in the Southern Ocean? *PLoS ONE*, **5(8)**, e11683. doi:10.1371/journal.pone.0011683.
- Hedgpeth, J.W., 1969. Introduction to Antarctic Zoogeography. In: Bushnell, V.C., Hedgpeth, J.W. (eds.). Distribution of Selected Groups of Marine Invertebrates in Waters South of 35°S Latitude. Antarctic Map Folio Series, Folio 11. American Geographical Society, 1–9.

 Hemery, L.G., 2011. Diversité moléculaire, phylogéographie et phylogénie des Crinoïdes (Echinodermes) dans un environnement extrême: l'océan Austral. PhD dissertation. Paris: Muséum national
- d'Histoire naturelle, 381 pp.

 Hemery, L.G., Améziane, N., Eléaume, M., 2013a. Circumpolar dataset of sequenced specimens of *Promachocrinus kerguelensis* (Echinodermata, Crinoidea). *Zookeys*, **315**, 55–64.
- Hemery, L.G., Eléaume, M., Roussel, V., Améziane, N., Gallut, C., Steinke, D., Cruaud, C., Couloux, A., Wilson, N.G., 2012. Comprehensive sampling reveals circumpolarity and sympatry in seven mitochondrial lineages of the Southern Ocean crinoid *Promachocrinus kerguelensis* (Echinodermata).
- Molecular Ecology, 21(10), 2502–2518
 ery, L.G., Galton-Fenzy, B., Améziane, N., Riddle, R.J., Rintoul, S.R., Beaman, R.J., Post, A.L., Eléaume, M., 2011. Predicting habitat preferences for Anthometrina adriani (Echinodermata) on the Antarctic continental shelf. Marine Ecology Progress Series, 441, 105–116.
 ery, L.G., Roux, M., Améziane, N., Eléaume, M., 2013b. High-resolution crinoid phyletic interrelationships: a preliminary study. Proceedings of the 14th International Echinoderm Conference.
 Cahiers de Biologie Marine. 54(4), 511-523.

- John, D.D., 1938. Crinoidea. *Discovery Reports*, **18**, 121–222.

 John, D.D., 1939. Crinoidea. Reports of B.A.N.Z. Antarctic Research Expedition, 1929–1931. Series B (Zoology and Botany), **4(6)**, 189–212.

 Marr, J.W.S., 1963. Unstalked crinoids of Antarctic continental shelf Notes on their natural history
- and distribution. Philosophical Transactions of the Royal Society of London Series B Biological Sciences, 246, 327–379.

 McClintock J.B., Pearse J.S., 1987. Reproductive biology of the common Antarctic crinoid *Promachocrinus*

- kerguelensis (Echinodermata, Crinoidea). Marine Biology **96**, 375–383.

 Messing, C.G., 1997. Living comatulids. In: Waters, J.A., Maples, C.G. (eds.). Geobiology of Echinoderms. Paleontological Society Papers, **3**, 3–30.

 Mironov, A.N., Sorokina, O.A., 1998. Sea lilles of the order Hyocrinida (Echinodermata, Crinoidea). Zoological Museum of Moscow State University, Zoologicheskie Issledovania Moscow **2**, 1–117. [In

- Roux, M., 2004. New hyocrinid crinoids (Echinodermata) from submersible investigations in the Pacific
- Ocean. Pacific Science, **58**(4), 597–613.

 M., Lambert, P., 2011. Two new species of stalked crinoids from the north-eastern Pacific in the genera Gephyrocrinus and Ptilocrinus (Echinodermata, Crinoidea, Hyocrinidae). Effects of ontogeny
- and variability on hyocrinid taxonomy. *Zootaxa*, **2825**, 1–54

 Roux, M., Messing, C.G., Améziane, N., 2002. Artificial keys to the genera of living stalked crinoids (Echinodermata). *Bulletin of Marine Science*, **70**, 799–830
- Speel, J.A., Dearborn, J.H., 1983. Comatulid crinoids from the R/V Eltanin cruises in the Southern Ocean.
- Antartic Research Series, 38, 1–60.

 Wilson N.G., Hunter R.L., Lockhart S.J., Halanych K.M., 2007. Multiple lineages and absence of panmixia in the "circumpolar" crinoid Promachocrinus kerguelensis from the Atlantic sector of Antarctica. Marine Biology 152, 895-904.

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.

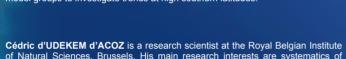
The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)
In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and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



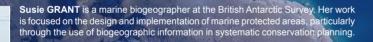
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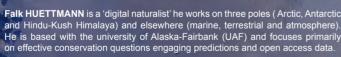


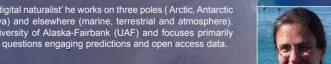


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