

# Check-list of the pycnogonids from Antarctic and sub-Antarctic waters: zoogeographic implications

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**Abstract:** This study contains the current list of the austral pycnogonids together with details of their depth range and distribution. To date 264 species have been recorded, accounting for 19.6% of the 1344 species recorded worldwide. One hundred and eight species are endemic to Antarctic waters, 62 to the sub-Antarctic, 63 are common in both regions, and 55 are circumpolar. The richest genus is *Nymphon*, with 67 species and the richest area is the Scotia Sea. Comparing species lists between the years 2000 and 2007 shows that increased expeditions with more sampling has increased the circumpolarity of species and decreased zonal endemism. The benthic insular refuge hypothesis is proposed as an explanation for the southern distribution of the present pycnogonid fauna, with an origin in the Scotia Arc.

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**Key words:** benthic insular refuge hypothesis, biogeography, circumpolarity, endemism

## Introduction

Pycnogonids (Chelicerata, Arthropoda) from Antarctic and sub-Antarctic waters have been studied more extensively than those from any other ocean of a similar size. Exploration of this area began with the American expedition of Nathaniel Palmer whose naturalist, James Eights (1835), described and drew the first Antarctic pycnogonid *Decolopoda australis* on a serolid and some fossils. Pycnogonids have been collected by many scientists but the main monographs are by Hoek (1881), Möbius (1902), Hodgson (1907, 1927), Bouvier (1913), Calman (1915), Gordon (1932, 1938, 1944), Fry & Hedgpeth (1969), Pushkin (1993) and Child (1994a, 1994b, 1995a, 1995b, 1995c). The most detailed information about the historical background of several families is contained in the Child papers, whilst the Pushkin monograph shows the geographical distribution of many species. The two latest Antarctic species to be described are *Ammothe bigibossa* Munilla, 2005 and *Ammothea victoriae* Cano & López-Gonzalez, 2007 from the Antarctic Peninsula and the Ross Sea respectively. The aim of this paper is to provide a complete up-to-date list of austral pycnogonids and, using zoogeographical information consider hypotheses describing their geographical distribution.

## Material and methods

This paper is an analysis of published data. The works mentioned above, as well as the Müller catalogue (1993) and many others (Hoek 1898, Hodgson 1902, 1904, 1908, 1914, 1915, Bouvier 1905, 1906, Loman 1923, Calman 1933, Stephensen 1947, Hedgpeth 1950, Fage 1952a, 1952b, Utinomi 1959, Stock 1965, Arnaud 1972a, 1972b, Pushkin 1974, 1975a, 1975b, 1976, 1977, 1982, 1984a, 1984b, 1990, Turpaeva 1974, 1990, 1998, 2000, Krapp 1980, Child 1987,

1998, Pushkin 1988, Munilla 1989, 1991, 2000, 2001b, 2002, 2005, Stiboy-Risch 1992, 1993, 1994, Bamber 1995, 2007, Bamber *et al.* 2001, Chimenz & Gravina 2001), were used to compile the species list. The main zoogeographical works about pycnogonids are those of Fry (1964), Fry & Hedgpeth (1969), Hedgpeth (1969a, 1969b, 1971) and Munilla 2001a. Other works (Clarke & Crame 1989, 1997, Barnes & De Grave 2000, Clarke & Johnston 2003, Arntz *et al.* 2005, 2006, Barnes 2005, 2006, Clarke *et al.* 2005, Moyano 2005, Thatje *et al.* 2005, Gili *et al.* 2006, Linse *et al.* 2006), contain particular zoogeographical reviews of some zoological groups or global and evolutionary reviews of benthos. A total of 98 papers were consulted.

## Results and discussion

### *Historical research and specific richness*

This analysis of the austral pycnogonids covers 172 years, 16 countries and more than 42 ships or expeditions. So far 40 000 specimens have been found in the Antarctic and sub-Antarctic waters, (termed the Austral Ocean by Jacques & Treguer 1986, p. 133) at about 2100 sampled stations. The Southern Ocean usually contains the Antarctic waters south of the Polar Front and does not include sub-Antarctic localities between this front and the Subtropical Convergence (D. Barnes, personal communication 2007). This sub-Antarctic zone contains many islands with pycnogonids (see legend, Table I) and the South American zone (Magellan and Falkland zones). Bouvet Island is just south of the Polar Front, but given its isolation and that it acts as a link between sub-Antarctic and Antarctic fauna (Arntz *et al.* 2006), I consider it as another sub-Antarctic island. Moreover, the general composition of the actual

**Table I.** Genera and species recorded in Antarctic (A) and sub-Antarctic (S) waters with regard to their depth and various geographical zones. W.sp = number of world species. Antarctic waters: C = circumpolar, Sc = Scotia Sea, p = Antarctic Peninsula, a = Amundsen Sea, b = Bellingshausen Sea, r = Ross Sea, w = Weddell Sea, e = East Antarctic zone. sub-Antarctic waters: s = South America, k = Iles Kerguelen, c = Ile Crozet, n = New Zealand Plateau, t = Tristan da Cunha, b = Bouvet Is., M + PE = Marion & Prince Edwards Is., St.P + A = Saint Paul & Amsterdam Is.

Genera/species	W. sp.	A + S sp. & % of W.sp	Depth (m)	Antarctic zone	sub-Antarctic zone	Remarks and synonyms
<i>Achelia</i>	80	12 (15.4)				
<i>A. assimilis</i> (Haswell, 1875)			0–903		s,n	also west Pacific and Australia
<i>A. communis</i> (Bouvier, 1906)			0–714	C	s,t	<i>A. brucei</i> Calman, 1915
<i>A. dorhni</i> (Thompson, 1884)			0–192		n	
<i>A. hoekii</i> (Pfeffer, 1889)			5–256	Sc,p,b	s	
<i>A. lagena</i> Child, 1994a			23–137		s	
<i>A. megacephala</i> (Hodgson, 1915)			shallow water		k	
<i>A. parvula</i> (Loman, 1923)			0–267	p	s	also in Peru-Ecuador-Argentina
<i>A. quadridentata</i> (Hodgson, 1910)			0–21		St.PI + A	
<i>A. serratipalpis</i> (Bouvier, 1911)			64–361	Sc,p,b,e		also on Angola coast
<i>A. spicata</i> (Hodgson, 1915)			0–1138	C		described as <i>Austrothea</i>
<i>A. sufflata</i> Gordon, 1944			0–300	w,e		e: 40–100°E
<i>A. transfuga</i> Stock, 1954			2–10		n	muddy bottom
<i>Ammothea</i>	40	25 (62.5)				Magnammothea and Biammothea
<i>A. adunca</i> Child, 1994a			185–800	w	k	
<i>A. allopodes</i> Fry & Hedgpeth, 1969			210–2000	C	b	<i>A. bicorniculata</i> Stiboy-Risch, 1992
<i>A. antipodensis</i> Clark, 1972			0–24		n	
<i>A. armentis</i> Child, 1994a			230–380		k	
<i>A. bentartica</i> Munilla, 2001			167–335	Sc		Livingston. Island, mud
<i>A. bigibbosa</i> Munilla, 2005			517	p		
<i>A. calmani</i> Gordon, 1932			99–1408	Sc,p,b,r,w		
<i>A. carolinensis</i> Leach, 1814			3–670	C	b	
<i>A. clausi</i> Pfeffer, 1889			3–860	C	s	
<i>A. cooki</i> Child, 1987			1463–2992		n	
<i>A. dubia</i> (Hedgpeth, 1950)			106	r		described as <i>Boehmia</i>
<i>A. gibbosa</i> Bouvier, 1913			439–567		b	recorded as <i>Colossendeis gibbosa</i> Möbius, 1902
<i>A. gigantea</i> Gordon, 1932			99–1116	C		145°E–178°W. <i>Magnammothea gigantea</i> Fry & Hedgpeth, 1969
<i>A. glacialis</i> (Hodgson, 1907)			0–640	C		
<i>A. gordonae</i> Child, 1994a)			348–732	Sc,r		
<i>A. hesperidensis</i> Munilla, 2000			30–439	Sc		Livingston. Island, mud
<i>A. longispina</i> Gordon, 1932			57–1454	C	s	
<i>A. meridionalis</i> (Hodgson, 1915)			10–454	C		
<i>A. minor</i> (Hodgson, 1907)			8–473	C		
<i>A. sextarticulata</i> Munilla, 1989			5–516	C		also on South Georgia, <i>Biammothea brevipalpa</i> Puskin, 1993
<i>A. spinosa</i> Hodgson, 1907			76–1679	Sc,p,w,r	s	also in Argentine Basin
<i>A. striata</i> Möbius, 1902			72–567	C	b	
<i>A. stylirostris</i> Gordon, 1932			165–494	Sc,w,p	s	
<i>A. tetrapora</i> Gordon, 1932			105–303	Sc	s	
<i>A. tibialis</i> Munilla, 2002			710	Sc		
<i>A. victoriae</i> Cano & López, 2007			360–366	r		
<i>Ascorhynchus</i>	75	6 (8.0)				
<i>A. antipodus</i> Child, 1987			5340		n	
<i>A. cooki</i> Child, 1987			1463–2992		n	
<i>A. cuculus</i> Fry & Hedgpeth, 1969			993–4008	Sc		also in Argentine Basin
<i>A. hedgpheti</i> Turpaeva, 1974			3700–3910	Sc		
<i>A. inflatum</i> Stock, 1963			2743–6070	Sc		also in Peru–Chile trench, South Africa, Kurile trench
<i>A. ornatum</i> (Helfer, 1938)			90–108		k	also in South Africa

Continued

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Genera/species	W. sp.	A + S sp. & % of W.sp	Depth (m)	Antarctic zone	sub-Antarctic zone	Remarks and synonyms
<i>Austroraptus</i>	5	5 (100)				
<i>A. calcaratus</i> Gordon, 1944			143–219	r,e		e: 65°E
<i>A. juvenilis</i> Calman, 1915			3–500	C		e: 92°E, 145°E
<i>A. polaris</i> Hodgson, 1907			10–569	Sc,p,b,r,e		e: 78°E. Possibly C
<i>A. praecox</i> Calman, 1915			6–260	C		
<i>A. sicarius</i> Fry & Hedgpeth, 1969			220–380	Sc,r		
<i>Cilunculus</i>	31	4 (12.9)				
<i>C. acanthus</i> Fry & Hedgpeth, 1969			2440–2818	b		also in Argentine Basin
<i>C. cactoides</i> Fry & Hedgpeth, 1969			38–540	Sc,p,e	n	
<i>C. kravcovi</i> Pushkin, 1973			255–309		c,M + PE	
<i>C. spinicristus</i> Child, 1987			476–540		n	
<i>Dromedopycnon</i>	2	1 (50)				
<i>D. acanthus</i> Child, 1982			124–903		s	also in Brazilian slope
<i>Eurycyde</i>	21	1 (4.8)				
<i>E. antarctica</i> Child, 1987			527–714	r		
<i>Sericosura</i>	6	1 (16.7)				
<i>S. mitrata</i> (Gordon, 1944)			106–2154	r		also in Walvis Ridge (South Africa)
<i>Tanystylum</i>	45	10 (22.2)				
<i>T. antipodum</i> Clark, 1977			shallow water		n	
<i>T. brevicaudatum</i> (Fage & Stock, 1966)			0–15		St.P + A	also in Cape Verde Island
<i>T. brevipes</i> (Hoek, 1881)			45–100		p,St + A	also in South Africa
<i>T. bueroisi</i> Arnaud, 1974			80–100		St.P + A.	
<i>T. cavidosum</i> Stock, 1957			0–245	Sc	s,M + PE,c,n	also in southern Chile
<i>T. pfefferi</i> Loman, 1923			2–100	Sc		<i>T. dohrni</i> Schimkewitsch, 1889
<i>T. neorhetum</i> Marcus, 1940			0–410	Sc	s,k,n,t	
<i>T. oedinotum</i> Loman, 1923			0–183		s,k	
<i>T. ornatum</i> Flynn, 1928			46–560		M + P.E	
<i>T. stylicherum</i> Myers, 1875			0–200	p	s,k,n	
<i>Austrodecus</i>	42	22 (52.4)				
<i>A. breviceps</i> Gordon, 1938			0–298	Sc	k,n	
<i>A. calcaricauda</i> Stock, 1957			73–1373	Sc,p	s	
<i>A. cestum</i> Child, 1994b			86–207		n	
<i>A. crenatum</i> Child, 1994b			1–360	Sc,p		
<i>A. curtipes</i> Stock, 1957			0–903	Sc,w	s,k	
<i>A. elegans</i> Stock, 1957			99–606		M + PE	
<i>A. fagei</i> Stock, 1957			26–3400	C		
<i>A. fryi</i> Child, 1994b			112–859		n	
<i>A. glabrum</i> Stock, 1957			18–277	Sc		
<i>A. glaciale</i> Hodgson, 1907			0–2100	C		
<i>A. goughense</i> Stock, 1957			42–120		St.P + A	also in Gough Island
<i>A. kelpi</i> Pushkin, 1977			shallow water	Sc		among kelps
<i>A. longispinum</i> Stock, 1957			91–325		k	
<i>A. macrum</i> Child, 1994b			1442–2350	r		
<i>A. profundum</i> Stock, 1957			920	p		mud & stones, Graham Land
<i>A. pushkini</i> Child, 1994b			60–903		s	southern Argentina
<i>A. serratum</i> Child, 1994b			79–124		n	Macquarie Island
<i>A. simulans</i> Stock, 1957			91–545	b,w	k	
<i>A. sinuatum</i> Stock, 1957			shallow water		n	
<i>A. tristanense</i> Stock, 1955			0–70		M + PE,t	
<i>A. varum</i> Child, 1994b			443–549		n	Macquarie Island
<i>Pantopipetta</i>	20	4 (20.0)				

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Genera/species	W. sp.	A + S sp. & % of W.sp	Depth (m)	Antarctic zone	sub-Antarctic zone	Remarks and synonyms
<i>P. australis</i> (Hodgdon 1914)			680–5340	Sc,r	M + PE,n	
<i>P. buccina</i> Child 1994b			3193–3423	Sc		also in Concepción waters, Chile
<i>P. lata</i> Stock 1981			523–3655	b,w		also in Cape Basin, South Africa
<i>P. longituberculata</i> Turpaeva, 1985			567–6700	Sc		also in SW Africa, Pacific & all Atlantic
						<i>P. brevicauda</i> Stock, 1963
Austropallene	11	10 (90.9)				
<i>A. brachyura</i> Bouvier, 1913			85–920	C		<i>A. spicata</i> Hodgson, 1915 <i>Pseudopallene brachyura</i> Bouvier, 1911 holotype without figures
<i>A. buccina</i> Pushkin, 1993			3–280	Sc,e		
<i>A. calmani</i> Gordon, 1944			163–2955	C		
<i>A. cornigera</i> (Möbius, 1902)			3–1180	C	b,c	
<i>A. cristata</i> Bouvier, 1911			104–2100	C		
<i>A. gracilipes</i> Gordon, 1944			45–645	C		
<i>A. spinicornis</i> Pushkin, 1993			1200–1280	Sc		holotype without figures
<i>A. tcherniaii</i> Fage, 1952			50–580	C		
<i>A. tenuicornis</i> Pushkin, 1993			580–1180	e		holotype without figures
<i>A. tibicina</i> Calman, 1915			45–550	Sc,r	n	
Callipallene	35	1 (2.9)				
<i>C. margarita</i> Gordon, 1932			73–578	p	s	also at 23°S (off Brazil)
Cheilopallene	7	1 (14.3)				
<i>Ch. gigantea</i> Child, 1987			581–3777	P,w		
Oropallene	6	3 (50)				
<i>O. dimorpha</i> (Hoek, 1898)			3–415		k,n	
<i>O. dolichodera</i> Child, 1995c			112–2612		n	
<i>O. metacaula</i> Child, 1995c			1586		n	
Pseudopallene	16	2 (12.5)				
<i>P. centrotus</i> Pushkin, 1990			250	Sc		
<i>P. glutus</i> Pushkin, 1975			320		c	
Seguapallene	6	1 (16.7)				
<i>S. insignatus</i> Pushkin, 1975			3–30		k	
Pallenopsis	86	18 (20.9)				
<i>P. boehmi</i> Schimkewitsch, 1930			35–383	Sc	s	also in waters of Uruguay, Brazil and Argentine e: 69°S–14°E
<i>P. bupthalmus</i> Pushkin, 1993			104–830	Sc,w,p,e		also in Surinam & W. Atlantic
<i>P. candidoi</i> Mello-Leitao, 1949			0–430	Sc		
<i>P. gurjanovi</i> Pushkin, 1993			65–600	Sc		
<i>P. kupei</i> Clark, 1971			146–1530	w	n	
<i>P. latefrontalis</i> Pushkin, 1993			115–260	Sc,p		
<i>P. lateralia</i> Child, 1995c			2273–2421	r		
<i>P. lattina</i> Pushkin, 1993			117–430	Sc		Holotype with figures
<i>P. leiopus</i> Pushkin, 1993			15–275	Sc,w,e		
<i>P. longiseta</i> Turpaeva, 1958			1228–3060	Sc	n	also Subarctic & Gulf of Panama
<i>P. macronix</i> Bouvier, 1911			100–1138	Sc,p,r,w		<i>P. knipovitchi</i> Turpaeva, 1974
<i>P. obliqua</i> Thompson, 1884			0–400		n	rock & algal bottoms
<i>P. patagonica</i> (Hoek, 1881)			3–4540	C	s	described as <i>Phoxichilidium patagonicum</i> <i>P. hiemalis</i> Hodgson, 1907 <i>P. glabra</i> Möbius, 1902 <i>P. möbiusi</i> Pushkin, 1975 <i>P. meridionalis</i> Pushkin, 1975
<i>P. pilosa</i> (Hoek, 1881)			25–3650	C	b	<i>P. hodgsoni</i> Gordon, 1938
<i>P. spicata</i> Hodgson, 1914			25–549	C		<i>Cheilopallene spicata</i> Stock, 1955, <i>Clavigeropallene spicata</i> Pushkin, 1974
<i>P. tumidula</i> Loman, 1923			42–270	Sc		also in Uruguay, Brazil, Argentina
<i>P. vanhoeffeni</i> Hodgson, 1915			3–889	C	s	<i>P. gatlssiana</i> Hodgson, 1914

Continued

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Genera/species	W. sp.	A + S sp. & % of W.sp	Depth (m)	Antarctic zone	sub-Antarctic zone	Remarks and synonyms
						<i>P. setigera</i> Hodgson, 1914
<i>P. villosa</i> Hodgson, 1907			160–2804	C		
Colossendeis	75	36(48.0)				
<i>C. adelpha</i> Child, 1998			333–341	e		Prydz Bay
<i>C. angusta</i> Sars, 1877			22–5480	Sc		cosmopolitan
						<i>C. gracilis</i> Hoek, 1881
<i>C. arundorostri</i> (Fry & Hedpeth, 1969)			610	r		
<i>C. australis</i> Hodgson, 1907			15–3935	C	k	also in Chile & Argentina
<i>C. avidus</i> Pushkin, 1970			270–426	p,w,e		<i>C. acuta</i> Stiboy-Rich, 1993
<i>C. belekurovi</i> Pushkin, 1993			150–377		c	
<i>C. brevirostris</i> Child, 1995b			5449–604	a		
<i>C. colossea</i> Wilson, 1881			425–4140	Sc,w		cosmopolitan
<i>C. concedis</i> Child, 1995b			2248–2907	Sc,r		
<i>C. drakei</i> Calman, 1915			3–3000	C	s	also in southern Tasmania
						<i>C. smirnovi</i> Pushkin, 1988
<i>C. elephantis</i> Child, 1995b			2384–4795	Sc,e		
<i>C. enigmatica</i> Turpaeva, 1974			315–335	Sc		
<i>C. ensifer</i> Child, 1995b			3250–3285	Sc		
<i>C. fragilis</i> Pushkin, 1992			3–830	Sc,e	s	
<i>C. grassus</i> Pushkin, 1993			315–435	Sc		
<i>C. hoecki</i> Gordon, 1944			120–3112	Sc,w,r	k,n	
<i>C. insolitus</i> Pushkin, 1993					s	47°S, Argentina
<i>C. korotkevischi</i> Pushkin, 1984			132–660	w	k,c	
<i>C. kurtchatovi</i> Turpaeva, 1993			4700		s	
<i>C. leniensis</i> Pushkin, 1993			250–432		52°S–43°E	south of Iles Crozet
<i>C. lepthorynchus</i> Hoek, 1881			561–3675		M + PE,s	cosmopolitan
						<i>C. pennata</i> Pushkin, 1970
<i>C. longirostris</i> Gordon, 1932			2–3700	C	n	also in southern Tasmania
<i>C. macerrima</i> Wilson, 1881			2010–2100		n	cosmopolitan.
						<i>C. japonica</i> , Hoek, 1898, <i>C. spei</i>
<i>C. media</i> Hoek, 1881			3386–5798	Sc		also in Argentina
						<i>C. brevipes</i> Hoek, 1881
<i>C. megalonix</i> Hoek, 1881			7–4900	C	s,k,n	also in South Africa, Madagascar & E. Argentina
						<i>C. rugosa</i> Hodgson, 1907
						<i>C. frigida</i> Hodgson, 1907
						<i>C. orcadense</i> Stock, 1963
<i>C. mica</i> Pushkin, 1970			1400		37°S–22°E	Sub-Antarctic Indian Ocean
<i>C. notialis</i> Child, 1995b			260–380		k	
<i>C. pseudochelata</i> Pushkin, 1993			125–180	Sc,e		e: 69°S, 11°E
<i>C. robusta</i> Hoek, 1881			0–3610	C	b,k	<i>C. lilliei</i> Calman, 1915
<i>C. glacialis</i> Hodgson, 1907						<i>C. gracillipes</i> Bouvier, 1911
						<i>C. rostrata</i> Turpaeva, 1994
<i>C. scoresbii</i> Calman, 1915			130–5227	Sc,w,r	s	
<i>C. scotti</i> Calman, 1915			35–352	C		
<i>C. stramendi</i> Fry & Hedpeth, 1969			645–3806		s	
<i>C. tenuipedis</i> Pushkin, 1993			250–860	C	s	also in E. Argentina
<i>C. tethya</i> Turpaeva, 1974			318	Sc,w		
<i>C. tortipalpis</i> Gordon, 1932			160–4026	C	s,k	
<i>C. wilsoni</i> Calman, 1915			60–801	Sc,w,r		also in Adélie Land
Decolopoda	2	2 (100)				
<i>D. australis</i> Eights, 1835			0–1890	Sc,p,b,w,r	k	possibly C
						<i>D. antarctica</i> Bouvier, 1905
<i>D. quasami</i> Sree et al., 1993			150	e		

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**Table I.** (Continued) Genera and species recorded in Antarctic (A) and sub-Antarctic (S) waters with regard to their depth and various geographical zones. W.sp = number of world species. Antarctic waters: C = circumpolar, Sc = Scotia Sea, p = Antarctic Peninsula, a = Amundsen Sea, b = Bellingshausen Sea, r = Ross Sea, w = Weddell Sea, e = East Antarctic zone. sub-Antarctic waters: s = South America, k = Iles Kerguelen, c = Ile Crozet, n = New Zealand Plateau, t = Tristan da Cunha, b = Bouvet Is., M + PE = Marion & Prince Edwards Is., St.P + A = Saint Paul & Amsterdam Is.

Genera/species	W. sp.	A + S sp. & % of W.sp	Depth (m)	Antarctic zone	sub-Antarctic zone	Remarks and synonyms
Dodecolopoda	1	1 (100)				
<i>D. mawsoni</i> Calman & Gordon, 1933			160–549	C		
Heteronymphon	7	1 (14.3)				
<i>H. exiguum</i> (Hodgson, 1927)			3–415	C	n	described as Nymphon
Nymphon	268	67 (25.0)				Chaetonymphon
<i>N. adareanum</i> Hodgson, 1907			1–903	Sc,p,r,e	s	also in SE Argentina, possibly C
<i>N. andriashevi</i> Puskin, 1993			116–135	p		
<i>N. arcuatum</i> Child, 1995a			38–157		s	
<i>N. articulare</i> Hodgson, 1908			18–910	Sc,p,w	s	
<i>N. australe</i> Hodgson, 1902			8–4136	C	s,n,b	also Indian Ocean & off Argentine–Chilean coasts
<i>N. stylops</i> Bouvier, 1913						
<i>N. biarticulatum</i> Hodgson, 1907			35–889	C	k	
<i>N. bouvieri</i> Gordon, 1932			158–583	Sc,p,e		
<i>N. brachyrhynchum</i> Hoek, 1881			82–430		k	also in Heard Island
<i>N. brevicaudatum</i> Miers, 1875			27–1100	C	k	
<i>N. bucuspidum</i> Child, 1995a			1262		n	
<i>N. chaetodir</i> Utinomi, 1971			995–1110		n	
<i>N. charcoti</i> Bouvier, 1911			3–1200	C		
<i>N. clarencei</i> Gordon, 1932			65–342	Sc		
<i>N. compactum</i> Hoek, 1881			731–3246	Sc	n	also in South Africa
<i>N. eltaminae</i> Child, 1995a			467–1233	Sc,r		
<i>N. forticulum</i> Child, 1995a			438–548		s	s: SE Argentine
<i>N. frigidum</i> Hodgson, 1907			227	r		
<i>N. galathea</i> Fage, 1956			3111–5798	w		
<i>N. gerlachei</i> Giltay, 1937			460–578	p,b		
<i>N. glabrum</i> Child, 1995a			55	Sc		
<i>N. gracilipes</i> Miers, 1875			3–3055	w,e	k	also in Kermadec Trench, (SW Pacific Ocean)
<i>N. gruzovi</i> Pushkin, 1993			250	p,w		holotype is a juvenile
<i>N. hadale</i> Child, 1982			3010–5798	Sc		also in Argentine basin
<i>N. hamatum</i> Hoek, 1881			2502–3400	Sc	c	
<i>N. hiemale</i> Hodgson, 1907			30–1435	C		<i>N. gracillimum</i> Calman, 1915
<i>N. inferum</i> Child, 1995a			2450–3873	Sc, Palmer Is.		
<i>N. inornatum</i> Child, 1995a			513	w		
<i>N. isabellae</i> Turpaeva, 2000			333–571	w		
<i>N. isaenki</i> Pushkin, 1993			500–700		k	
<i>N. lanare</i> Hodgson, 1907			60–848	C		
<i>N. lomani</i> Gordon, 1944			112–714	C	n	
<i>N. longicolum</i> Hoek, 1881			68–4600	C	n	also in Chilean Basin & New Zealand
<i>N. longicoxa</i> Hoek, 1881			318–2998	Sc,b,r	n	also in Argentine Basin
<i>N. longisetosum</i> Hodgson, 1915			385–2450	e		
<i>N. macquarensis</i> Child, 1995a			112–124		n	
<i>N. macrochelatum</i> Pushkin, 1993			540	68°S–32°E,w		
<i>N. mendosum</i> (Hodgson, 1907)			15–555	C		
<i>N. microgracilipes</i> Pushkin, 1993			150–309	B	c	c: 46°S–49°E
<i>N. monotrix</i> Child, 1995a			3495–3514	r		
<i>N. multidentis</i> Gordon, 1944			40–260	Sc,p,b	b	
<i>N. multituberculatum</i> Gordon, 1944			180–640	w,Sc,e		e: 20–140°E
<i>N. neelovi</i> Pushkin, 1993			65–240	Sc	c	
<i>N. neumayeri</i> Gordon, 1932			160–403	Sc,p	s	
<i>N. orcadense</i> (Hodgson, 1908)			18–163	Sc,p	s	

Continued



**Table I.** (Continued) Genera and species recorded in Antarctic (A) and sub-Antarctic (S) waters with regard to their depth and various geographical zones. W.sp = number of world species. Antarctic waters: C = circumpolar, Sc = Scotia Sea, p = Antarctic Peninsula, a = Amundsen Sea, b = Bellingshausen Sea, r = Ross Sea, w = Weddell Sea, e = East Antarctic zone. sub-Antarctic waters: s = South America, k = Iles Kerguelen, c = Ile Crozet, n = New Zealand Plateau, t = Tristan da Cunha, b = Bouvet Is., M + PE = Marion & Prince Edwards Is., St.P + A = Saint Paul & Amsterdam Is.

Genera/species	W. sp.	A + S sp. & % of W.sp	Depth (m)	Antarctic zone	sub-Antarctic zone	Remarks and synonyms
<i>N. pagophylum</i> Child, 1995a			265–1170	Sc,p,w		
<i>N. paucidens</i> Gordon, 1932			22–334	Sc	c	also SE Argentina
<i>N. paucituberculatum</i> Gordon, 1944			180–219	w,e		
<i>N. pfefferi</i> Loman, 1923			12–250	Sc	s	
<i>N. phasmatoides</i> Böhm, 1879			13–94	p,w		also in South Africa; <i>P. capense</i> Hodgson, 1908
<i>N. polare</i> Hodgson, 1915			350	e		
<i>N. premordicum</i> Child, 1995a			2597–3215	Sc		
<i>N. proceroides</i> Bouvier, 1913			91–1180	Sc,p,e		
<i>N. procerum</i> Hoek, 1881			2450–6135	Sc		cosmopolitan
<i>N. proximum</i> Calman, 1915			40–1555	C		<i>N. banzare</i> Gordon, 1944
<i>N. pseudogracilipes</i> Pushkin, 1993			195–216		k	
<i>N. punctum</i> Child, 1995a			415		n	
<i>N. rybakovi</i> Pushkin, 1993			220	Sc,w		
<i>N. sabellum</i> Child, 1995			2872–2928	r		62°S–160°W
<i>N. scotiae</i> Stock, 1981			2960–2980	Sc		<i>N. stocki</i> Turpaeva, 1974
<i>N. subtile</i> Loman, 1923			13–304		s,k	also SE Argentina
<i>N. tenuimanum</i> Hodgson, 1914			1903–3398	r		
<i>N. tenuipes</i> Bouvier, 1911			122–1180	C		also in S. Australia <i>N. soyae</i> Utinomi, 1953
<i>N. trituberculum</i> Child, 1995a			3200–3259	e		
<i>N. typhops</i> (Hodgson, 1915)			2450–2815	Sc,p,w,e		
<i>N. unguiculatum</i> Hodgson, 1927			168–450	Sc		
<i>N. villosum</i> (Hodgson, 1915)			13–636	C		also 10°E
<i>N. zundiamum</i> Pushkin, 1993			160		s	s: near Falkland Islands
Pentanympion	1	1 (100)				
<i>P. antarcticum</i> Hodgson, 1904			3–3227	C		<i>P. minutum</i> Gordon, 1944
Sexanympion	1	1 (100)				
<i>S. mirabilis</i> Hedgpeth & Fry, 1964			1687–2897	Sc,p		
Anoplodactylus	140	9 (6.4)				
<i>A. australis</i> (Hodgson, 1914)			15–616	C	t	also in Tasmania
<i>A. californicus</i> Hall, 1912			0–100		s	cosmopolitan; <i>C. projectus</i> Hilton, 1942, <i>C. portus</i> Sawaya 1950
<i>A. lacinosus</i> Child, 1995c			456–540		n	also in Antipodes Island
<i>A. laminifer</i> Arnaud, 1974			80–100		St.P+A	
<i>A. petiolatus</i> (Kröyer, 1844)			0–1180		s	also in Atlantic–Mediterranean
<i>A. speculus</i> Child, 1995c			1586–1640		n	
<i>A. typhlops</i> Sars, 1888			915–3620	Sc	c,n,PE	cosmopolitan <i>A. pelagicus</i> Flynn, 1908 <i>A. neglectus</i> Hoek, 1898
<i>A. vema</i> Child, 1982			90–676		s	
<i>A. virescens</i> (Hodge, 1864)			0–16		St.P+A	also in Atlantic–Mediterranean
Phoxichilidium	14	1 (7.1)				
<i>P. pigordum</i> Child, 1995c			79–124		n	
Endeis	17	2 (11.8)				
<i>E. australis</i> (Hodgson, 1907)			3–1570	C	n,b	
<i>E. viridis</i> Pushkin, 1976			3–377		k,c,M+PE	
Pentapycnon	3	2 (66)				
<i>P. bouvieri</i> Puskin, 1993			90–419	Sc,w		<i>P. bouvieri</i> Child (1993) <i>P. magnum</i> Siboy-Rish (1994)
<i>P. charcoti</i> Bouvier, 1910			240–1420	Sc,p,r		
Pycnogonum	69	10 (14.5)				

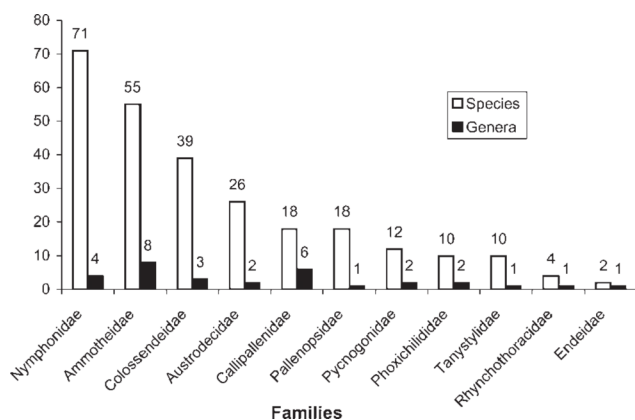
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**Table I.** (Continued) Genera and species recorded in Antarctic (A) and sub-Antarctic (S) waters with regard to their depth and various geographical zones. W.sp = number of world species. Antarctic waters: C = circumpolar, Sc = Scotia Sea, p = Antarctic Peninsula, a = Amundsen Sea, b = Bellingshausen Sea, r = Ross Sea, w = Weddell Sea, e = East Antarctic zone. sub-Antarctic waters: s = South America, k = Iles Kerguelen, c = Ile Crozet, n = New Zealand Plateau, t = Tristan da Cunha, b = Bouvet Is., M + PE = Marion & Prince Edwards Is., St.P + A = Saint Paul & Amsterdam Is.

Genera/species	W. sp.	A + S sp. & % of W.sp	Depth (m)	Antarctic zone	sub-Antarctic zone	Remarks and synonyms
<i>P. calculum</i> Bamber, 1955			littoral	Sc	s	rock with algae
<i>P. rhinoceros</i> Loman, 1923			30–1115	C		<i>P. diceros</i> Marcus, 1940
<i>P. gaini</i> Bouvier, 1910			24–2495	C	k	
<i>P. gordonae</i> Pushkin, 1984			219–400	w,e		
<i>P. magellanicum</i> Hoek, 1898			85–548		s	
<i>P. magniroste</i> Möbius, 1902			3–309		k,c	
<i>P. paragaini</i> Munilla, 1989			205–440	Sc		
<i>P. platylophum</i> Loman, 1923			0–903	Sc,e	k,c	
<i>P. sivertseni</i> Stock, 1955			102–141		t	
Rhynchothorax	19	4 (21.1)				
<i>R. australis</i> Hodgson, 1907			60–900	C	s,k,n	
<i>R. oblongus</i> (Pushkin, 1977)			100–140		k	described as <i>Austrodecus</i>
<i>R. percivali</i> Clark, 1976			0–101		S,n	also in Mexico
<i>R. philopsammum</i> Hedgpeth, 1951			0–77		s	also in Caribbean Sea, E. Pacific Ocean, Azores, Mediterranean Sea
Total species		264		192	137	

Bouvet fauna is more similar to the Magellan area than the high Antarctic region (Arntz *et al.* 2006).

These individuals belong to 31 genera and 264 different species of pycnogonids (Table I), out of a total number of species worldwide of 1344. They thus represent 19.6% of the actual world species that have been recorded in 21% of the ocean areas (Jacques & Treguer 1986). Figure 1 shows the richness of species and genera for each family. Nymphonidae is the most abundant family (71 species), with *Nymphon* the major genus (67 species), and *N. australe* the most frequently recorded species. Of these 264 species, 108 are endemic in the Antarctic area, 62 are present only in the sub-Antarctic zone and 63 are common to both. Table I shows the current list of the Antarctic and sub-Antarctic species, their synonyms (47), the percentage



**Fig. 1.** Richness of species and genera from austral pycnogonid families.

of species per genus with respect to their number worldwide, their geographical distribution and bathymetric range. The majority of synonyms have been proposed or recorded in the Child (1994a, 1994b, 1995a, 1995b, 1995c), Pushkin (1993) and Müller (1993) papers. The richest zone, with 89 recorded non-circumpolar species, is the Scotia Sea, followed by the sub-Antarctic islands with 64 species. The circumpolarity criterion is that a species

**Table II.** Variation in the austral pycnogonid species between 2000 and 2007.

Differences between seven years	2000	2007
Species in the world	1165	1344
Species in the Southern Ocean ( <i>sensu lato</i> )	251	264
Species reported in Antarctic waters	180	192
Species reported in sub-Antarctic waters	131	138
Endemic species in Antarctic waters	101	108
Endemic species in sub-Antarctic waters	59	62
Common species	60	63
Circumpolar species	45	55
Circumpolar genera	13	15
Cosmopolitan species	5	7
Endemicity of species from Antarctic zones	2000	2007
Scotia Sea	26	22
Antarctic Peninsula	4	3
Bellingshausen Sea	1	0
Amundsen Sea	1	1
Ross Sea	8	9
Weddell Sea	4	3
East Antarctica	8	4
Total	52	42
Endemicity of species from sub-Antarctic zones		
South America (Magellan region)	10	10
New Zealand Plateau	21	23
sub-Antarctic Islands + Bouvet Island	24	24



was recorded on one or more occasions in each of the waters to the north, south, east and west of the Antarctic continent, with the east zone the largest one and least sampled (it contains 24 species of which only four are endemic).

### Zoogeography

The Antarctic benthos has evolved as a consequence both of the abiotic environmental conditions in the past and of biotic interactions (Arntz *et al.* 1994). The distribution of most of the benthic Antarctic fauna is considered as circumpolar (Hedgpeth 1971, Arntz & Gallardo 1994, Clarke & Crame 1997), almost certainly due to the powerful Antarctic Circumpolar Current (Clarke & Johnston 2003). The circumantarctic element is also the most frequent pattern for pycnogonids (Fry & Hedgpeth 1969, Hedgpeth 1969a, Munilla 2001a), since at present 55 of the 192 (28.7%) Antarctic recorded species are circumpolar.

The comparative data in Table II, based on cruise data and literature dealing with austral pycnogonids over a period of seven years, shows that the number of endemic species for each Antarctic zone is low, with the exception of the Scotia Sea, which could be considered as a sub-centre of speciation. Moreover, this table shows that the circumantarctic pattern for the pycnogonid species has increased over the seven years, and the endemicity of the species from each zone has consequently decreased. In other words, increased sampling has shown more circumpolarity and less zonal endemicity.

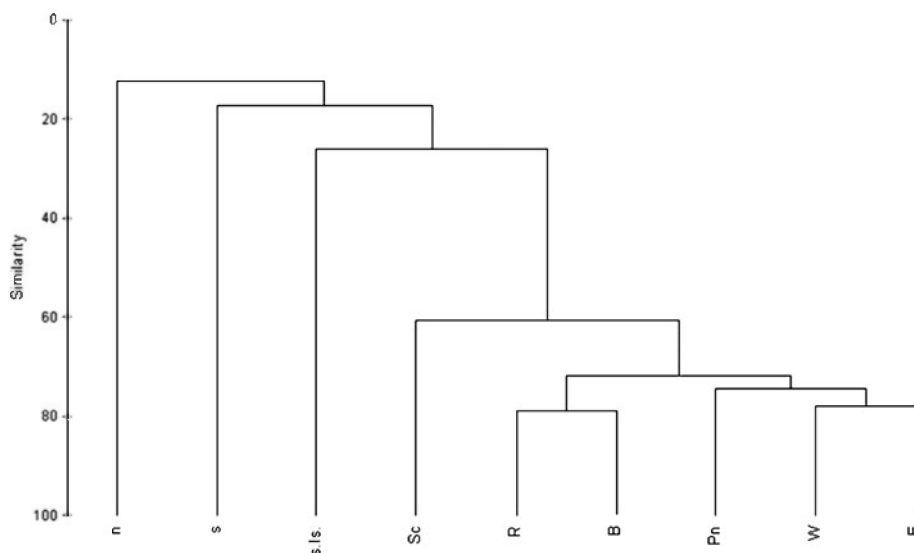
Only 10 genera are exclusively from austral waters and four of them (*Dodecolopoda*, *Pentanympyon*, *Sexanympyon*, *Austroraptus*) are endemic to Antarctic waters. Other genera (*Decolopoda*, *Austropallene*) which were considered by Hedgpeth (1969b) as typically Antarctic, have already been found in sub-Antarctic waters, including in the Kuril Islands (*Austropallene likinii* Turpaeva, 2002); the same is true for some species. The genera with the most species in austral

waters are: *Ammothea* (25 species out of 40 in the world; 62.5%), *Colossendeis* (36 out of 75; 48%), *Austrodecus* (22 out of 42; 52.4%), *Nymphon* (67 out of 268; 25.0%) and *Pallenopsis* (18 out of 86; 20.9%). There are not endemic families.

The sub-Antarctic pycnogonid fauna shows origins in the Antarctic fauna at genus level (Arnaud & Bamber 1987). For example, this is true of *Colossendeis* and *Ammothea*, two genera with more than half of their species in the Austral Ocean. Like other genera with abundant species, both have more species in Antarctic than in sub-Antarctic waters. We therefore view the Southern Ocean as a centre of speciation (suggested by Hedgpeth 1969b, and Munilla 2001a) but also of geographic dispersion and evolutive radiation, because of its high relative endemicity (108 Antarctic species versus 62 of sub-Antarctic ones).

The dendrogram (Fig. 2), based on the presence-absence data of the 264 austral species, shows that the Antarctic species form a large zoogeographic group linked to circumpolarity (55 species). Three trends are clear:

- The Scotia Sea is closely linked to other southern zones (60.75% of similarity), indicating some peculiarity of the former.
- Two branches of the Circumpolar Current (with 71% of similarity) have been differentiated: the north-eastern (Antarctic Peninsula–Weddell–East zones) and the southern (Bellingshausen–Ross zones). This supports the geographical proximity of the species distribution to the direction of the Circumpolar Current.
- Each sub-Antarctic zone is separate, and the three zones (Magellan region, New Zealand and sub-Antarctic islands), present low levels of similarity (< 30%, Fig. 2) to Antarctic waters. The suites of organisms in the seas surrounding the sub-Antarctic islands, have long been considered sufficiently dissimilar to



**Fig. 2.** Similarity of Antarctic and sub-Antarctic zones (Bray-Curtis Index, complete linkage), based in presence-absence data. CircumAntarctic species are included. n = New Zealand Plateau, s = South America, s.Is = sub-Antarctic islands, Sc = Scotia Sea, R = Ross Sea, B = Bellingshausen Sea, Pn = Antarctic Peninsula, W = Weddell Sea, E = East zone.

constitute a different zone (Hedgepeth 1969a), with 63 species at present. Recent multivariate analysis of the bryozoan component of benthos south of 47°S supports the categorization of Patagonia, the sub-Antarctic islands and Antarctica into separate zones (Barnes & De Grave 2000).

Two complementary hypotheses (Clarke & Johnston 2003) may explain the possible origin of today's Antarctic benthic fauna:

1. It comes from an *in situ* stock in Cretaceous waters (141–65 Ma), from the coastal fauna of Gondwana, when the present Antarctic continent was part of the supercontinent. This is supported by the Gasteropoda (Clarke 1990), two Isopoda families (Brandt 1992) and some sessile groups (Alcyonarians and sponges, Gili *et al.* 2006) among others.
2. There was subsequent interchange with the deep fauna of the contiguous oceans, as is the case with Tanaidacea and Amphypoda (Brandt 1999). One possibility is that the Magellan region provided Antarctic benthic fauna across the Drake Passage or the Scotia Arc. This may be the case in some groups such as Serolidae (Held 2000), Polychaeta (Montiel *et al.* 2004) and Bryozoa (Moyano 2005, Barnes 2006). The Scotia Arc and Bouvet Island are clearly undersampled, if they are considered as transitory areas between the Magellan region and the Antarctic Peninsula or the Weddell Sea (Arntz *et al.* 2005). Modern Antarctic communities are thus composed of a mixture of Palaeozoic taxa, which migrated from the deep ocean during interglacial periods, and a component of fauna that evolved from common Gondwana Cretaceous ancestors (Gili *et al.* 2006).

The final connection between South America and the Antarctica was broken just over 25 Ma ago. The result was the formation of the Circumpolar Current, causing the oceanographic and geographical isolation of the Antarctic continent. The continental remains of the ancient isthmus today form many of the islands adjacent to the Antarctic

**Table III.** Specimens and species of pycnogonids from islands and the open Bellingshausen Sea, in the Bentart-03 Cruise.

Zones Bentart-03	Thurston + Peter I islands	Bellingshausen Sea
Stations (st.)	8	9
Latitude S	68–70°	68–70°
n	187	12
S	13	10
n/S mean	14.4	1.2
S/st. mean	1.6	1.1
n/st. mean	23.4	1.3
Depth (m)	86–726	492–1947

n = number of specimens, S = number of species

**Table IV.** Number of species recorded in each zone (in bold) and common species between different zones. Circumpolar species are excluded.

	S	Sc	Pn	R	W	B	E	n	s.Is.	Tot
s	<b>46</b>	14	10	3	5	1	1	8	10	52
Sc	14	<b>89</b>	24	18	20	8	16	11	12	123
Pn	10	24	<b>35</b>	7	14	5	8	2	3	73
R	3	18	7	<b>27</b>	8	3	4	4	3	50
W	5	20	14	8	<b>35</b>	4	11	2	7	71
B	1	8	5	3	4	<b>12</b>	2	1	3	27
E	1	16	8	4	11	2	<b>24</b>	0	2	44
n	8	11	2	4	2	1	0	<b>47</b>	11	39
s.Is	10	12	3	3	7	3	2	11	<b>64</b>	49

s = South America, Sc = Scotia Sea, Pn = Antarctic Peninsula, R = Ross Sea, W = Weddell Sea, B = Bellingshausen Sea, E = East zone, n = New Zealand Plateau, s.Is = sub-Antarctic islands. Tot = sum of the common species for each zone and the remaining ones.

Peninsula, but the main topographical obstacle between South America and Antarctica is the Scotia Arc, through which the Circumpolar Current passes.

Two main probable dispersion routes of pycnogonids are proposed, coming from the ancient Cretaceous fauna and principally along the bottom (since they have benthic larvae):

1. From Western Antarctica to the Eastern zone by means of the Circumpolar Current. In support of this, there are 15 common non-circumpolar species between the Scotia Arc–Antarctic Peninsula couplet and the Eastern Antarctic zone. Moreover, a branch of the dendrogram (Pn–W–E, Fig. 2) also supports this suggestion.
2. From South America to western Antarctica going along the route from the Scotia Arc. This is supported by 17 common non-circumpolar species between the Scotia Arc–Antarctic Peninsula couplet and the Magellan zone; moreover, 13 of 48 austral species recorded in other waters have been also found in the Argentine and Brazilian zones (the Brazil current versus circumpolar one).

#### *The benthic insular refuge hypothesis*

The submerged zones of the Peter I and Thurston islands in the Bellingshausen Sea are sheltered areas and optimal zones for the settlement and protection of pycnogonid fauna from the surrounding open seas, similar to oases in the desert. They are species rich and the densities of animals are here higher than on open bottoms (Table III), probably because of more feeding possibilities. Animals can be transported from them by deep currents, including by hitchhiking on a moving animal or debris or by simply drifting to other waters. This trend, observed in the Bellingshausen Sea, is extensive in other waters, and occurs in Bouvet Island, which act as stepping stones (Arntz *et al.* 2006) to Antarctic waters.

The benthic insular refuge hypothesis suggests that the islands serve as a home, accumulating a rich benthic fauna, and subsequently acting as migration points. This is similar to the reserve effect of a marine protected zone. This theory needs to be confirmed using more quantitative data about species richness, densities and biomass in pycnogonids and many other zoological groups. Far from any island, deep waters of under 1000 m, have few species and specimens (Munilla 2001a). Moreover, no circumpolar species have been recorded (Table IV) and the number of endemic species (Table II) in each austral zone is much more important at islands (Scotia Sea, New Zealand Plateau and sub-Antarctic ones) than at the benthic bottoms of the open seas. There also seems to be no decreasing latitudinal decline of species richness if the sub-Antarctic islands are included (Table II and IV), because there are more species in Antarctic waters than in sub-Antarctic ones.

#### *Possible stages in the origin and dispersion of the Antarctic pycnogonids*

1. *In situ* origin (Munilla 2001a), from the Cretaceous Gondwana fauna (141–65 Ma). This possibility is supported by the two most ancient families of the sea spiders (Colossendeidae and Austrodecidae, (Arango & Wheeler 2007, Bamber 2007), morphological and molecular data, having 48% and 42% respectively of their species in southern waters. This hypothesis has been suggested previously for Austrodecidae genera (Stock 1957, Child 1995b).
2. Many archipelagos in the Scotia Arc are the tips of an almost continuous subsurface mountain chain linking the Andes and the Antarctic Peninsula (Barnes 2005). All the Scotia Sea islands sheltered the existing fauna at the time of its creation and they still retain the ancient Cretaceous fauna that the Antarctic Circumpolar Current (ACC) subsequently carries, because the Scotia Arc is the only major barrier to the circulation of this current. Many more species remain on its islands than in other waters, as shown by the large number of species that have been captured in this zone (Table IV): 89 non-circumpolar species plus 55 circumpolar ones, that is the 75% of the 192 recorded Antarctic species.
3. From the Scotia Arc waters, the fauna was, and today still is, actually exported towards the East Antarctic zone thanks to the Circumpolar Current, which also distributes some species to the sub-Antarctic islands. A similar trend happens with the benthic larvae of cheilostome bryozoa (Bouvet Island, Barnes 2006). Moreover, the Scotia Arc pycnogonid fauna also arrive at the southern branch of the Circumpolar Current (Bellinghausen–Ross Sea, Fig 2). This link is shown in the cluster in Fig. 2, where the Scotia Sea branch is closely related to other Antarctic zones. The large number of common species between the Scotia Sea Arc and remaining zones (123, Table IV) support this movement of pycnogonids.

The low water temperature is the main factor that isolates the Antarctic species, leading to high endemism in various groups (108 of 192, 56.3% in pycnogonids). With the warming of global oceans, the colonization of the Antarctic waters will be greater in the future. The number of species will increase and the relative Antarctic endemism will decrease. This trend will be favoured by the increasing passive transport of animals or algae on various ships, swimming animals and floating debris. Eddies and currents are factors that also contribute to passive transport (Barnes *et al.* 2006).

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#### **References**

- ARANGO, C. & WHEELER, W.C. 2007. Phylogeny of the sea spiders (Arthropoda, Pycnogonida) based on direct optimization of six loci and morphology. *Cladistics*, **23**, 255–293.
- ARNAUD, F. 1972a. 9 Pycnogonides. Invertébrés marins. XIIème et XVème expéditions antarctiques françaises en Terre Adélie. *Téthys*, **4**, 135–156.
- ARNAUD, F. 1972b. Pycnogonides des îles Kerguelen (Sud Océan Indien); matériel nouveau et révision des spécimens du Muséum National d'Histoire Naturelle de Paris. *Bulletin du Museum National d'Histoire Naturelle*, **3**, 801–815.
- ARNAUD, F. & BAMBER, R.N. 1987. The biology of Pycnogonida. *Advances in Marine Biology*, **24**, 1–96.
- ARNTZ, W. & GALLARDO, V.A. 1994. Antarctic benthos: present position and future prospects. In HEMPEL, C., ed. *Antarctic science: global concerns*. Berlin: Springer, 243–277.
- ARNTZ, W., BREY, T. & GALLARDO, V.A. 1994. Antarctic zoobenthos. *Oceanographic Marine Biology Annual Review*, **32**, 241–304.
- ARNTZ, W., THATJE, S., GERDES, D., GILL, J.M., GUT, J., JACOB, U., MONTIEL, A., OREJAS, C. & TEIXIDÓ, N. 2005. The Antarctic–Magellan connection: macrobenthos ecology on the self and upper slope, a progress report. *Scientia Marina*, **69**, 237–269.
- ARNTZ, W., THATJE, S., LINSE, K., AVILA, C., BALLESTERROS, M., BARNES, D., COPE, T., CRISTOBO, F., DE BROUYER, C., GUT, J., ISLA, E., LOPEZ GONZALEZ, P., MONTIEL, A., MUNILLA, T., RAMOS ESPLÁ, A., RAUPACH, M., RAUSCHERT, M., RODRIGUEZ, E. & TEIXIDÓ, N. 2006. Missing link in the Southern Ocean: sampling the marine benthic fauna of remote Bouvet Island. *Polar Biology*, **29**, 83–96.
- BAMBER, R.N. 1995. A new species of *Pycnogonum* Brünnich 1764 (Arthropoda, Pycnogonida) with other pycnogonid records from the Falkland and South Shetland Islands. *Ophelia*, **40**, 199–205.
- BAMBER, R.N. 2007. A holistic re-interpretation of the phylogeny of the Pycnogonida Latreille, 1810. *Zootaxa*, **1668**, 295–312.



- BAMBER, R.N., MITCHELL, N.J. & FERRERO, T.J. 2001. Rediscovery of *Nymphon gerlachei* Giltay, 1935 (Arthropoda, Pycnogonida). *Antarctic Science*, **13**, 237–239.
- BARNES, D.K.A. & DE GRAVE, S. 2000. Biogeography of southern polar bryozoans. *Vie et Milieu*, **50**, 261–273.
- BARNES, D.K.A. 2005. Changing chain: past, present and future of the Scotia Arc's and Antarctica's shallow benthic communities. *Scientia Marina*, **69**, 65–89.
- BARNES, D.K.A. 2006. A most isolated benthos: coastal bryozoans of Bouvet Island. *Polar Biology*, **29**, 114–119.
- BARNES, D.K.A., HODGSON, D.A., CONVEY, P., ALLEN, C.S. & CLARKE, A. 2006. Incursion and excursion of Antarctic biota: past, present and future. *Global Ecology and Biogeography*, **15**, 121–142.
- BOUVIER, E.L. 1905. Observations préliminaires sur les Pycnogonides recueillis dans la région antarctique par la mission du "Français". *Bulletin Museum National d'Histoire Naturelle*, **11**, 294–298.
- BOUVIER, E.L. 1906. Nouvelles observations sur les Pycnogonides recueillis dans les régions antarctiques au cours de la campagne dirigée par M. Jean Chargot. *Comptes Rendus des Séances Hebdomadaires Académie Sciences*, **142**, 15–22.
- BOUVIER, E.L. 1913. Pycnogonides du "Pourquoi Pas?". *Deuxième Expédition Antarctique Française (1908–1910)*, **6**, 1–169.
- BRANDT, A. 1992. Origin of Antarctic Isopods (Crustacea, Malacostracea). *Marine Biology*, **113**, 415–423.
- BRANDT, A. 1999. On the origin and evolution of Antarctic Peracarida (Crustacea, Malacostraca). *Scientia Marina*, **63**, 261–274.
- CALMAN, W.T. 1915. Pycnogonida. *British Antarctic (Terra Nova) Expedition, 1910 Natural History Reports, Zoology*, **3**, 1–74.
- CALMAN, W.T. 1933. A dodecapodous pycnogonid. *Nature*, **131**, 242.
- CANO, E. & LÓPEZ-GONZÁLEZ, J.P. 2007. Ammonotheidae (Arthropoda, Pycnogonida) collected during the Victoria Land Transect Cruise (Ross Sea, Antarctica) with a description of a new species of Ammonothea. *Marine Biological Research*, **3**, 438–445.
- CHILD, C.A. 1987. New and little known Pycnogonida from Antarctic and Subantarctic waters. *Proceedings Biological Society Washington*, **100**, 902–916.
- CHILD, W.A. 1994a. Antarctic and Subantarctic Pycnogonida. I. The Family Ammonotheidae. *Antarctic Research Series*, **63**, 1–48.
- CHILD, W.A. 1994b. Antarctic and Subantarctic Pycnogonida II. The Family Austrodecidae. *Antarctic Research Series*, **63**, 49–99.
- CHILD, W.A. 1995a. Antarctic and Subantarctic Pycnogonida III. The Family Nymphonidae. *Antarctic Research Series*, **69**, 1–68.
- CHILD, W.A. 1995b. Antarctic and Subantarctic Pycnogonida IV. The Families Colossendeidae and Rhynchtoraxidae. *Antarctic Research Series*, **69**, 69–112.
- CHILD, W.A. 1995c. Antarctic and Subantarctic Pycnogonida V. The Families Pycnogonidae, Phoxichilidiidae, Endeidae, and Callipallenidae, including the genus Pallenopsis. *Antarctic Research Series*, **69**, 113–165.
- CHILD, W.A. 1998. Pycnogonida from Prydz Bay, East Antarctica. *Records of the South Australian Museum*, **31** (1), 5–7.
- CHIMENZ, C. & GRAVINA, M.F. 2001. Faunistic and biological traits of some Antarctic Pycnogonida. *Italian Journal of Zoology*, **68**, 335–344.
- CLARKE, A. 1990. Temperature and evolution: southern ocean cooling and the Antarctic marine fauna. In KERRY, K.R. & HEMPEL, G., eds. *Antarctic ecosystems: ecological change and conservation*. Berlin: Springer, 9–22.
- CLARKE, A. & CRAME, J.A. 1989. The origin of the Southern Ocean marine fauna. In CRAME, J.A., ed. *Origins and evolution of the Antarctic biota. Geological Society of London Special Publication*, No. 47, 253–268.
- CLARKE, A. & CRAME, A.C. 1997. Diversity, latitude and time: patterns in the shallow sea. In ORMOND, R., GAGE, J. & ANGEL, M.V., eds. *Marine biodiversity: patterns and processes*. Cambridge: Cambridge University Press, 122–147.
- CLARKE, A. & JOHONSTON, N. 2003. Antarctic marine benthic diversity. *Oceanography and Marine Biology*, **41**, 47–104.
- CLARKE, A., BARNES, D.K.A. & HODGSON, D.A. 2005. How isolated is Antarctica? *Trends in Ecology and Evolution*, **20**, 1–3.
- EIGHTS, J. 1835. Description of a new animal belonging to the Arachnides of Latreille, discovered in the sea along the shores of the New South Shetland Islands. *Boston Journal of Natural History*, **1**, 203–206.
- FAGE, L. 1952a. Pycnogonides. Missions du bâtiment polaire Commandant Chargot, récoltes faites en Terre Adélie (1950). *Bulletin du Museum National d'Histoire Naturelle*, **2** (24) 2, 180–186.
- FAGE, L. 1952b. Pycnogonides de la Terre Adélie. *Bulletin du Museum National d'Histoire Naturelle*, **2** (24) 3, 263–273.
- FRY, W.G. 1964. The pycnogonid fauna of the Antarctic continental shelf. In CARRICK, R., HOLDGATE, M.W. & PROVOST, J., eds. *Biologie Antarctique*. Paris: Hermann, 263–269.
- FRY, W.G. & HEDGPETH, J.W. 1969. Pycnogonida. 1. Colossendeidae, Pycnogonidae, Endeidae and Ammonotheidae. Fauna of the Ross Sea, 7. *Memoirs of the New Zealand Oceanographic Institute*, **49**, 1–149.
- GILL, J.M., ARNTZ, W., PALANQUES, A., OREJAS, C., CLARKE, A., DAYTON, P.K., ISLA, E., TEIXIDÓ, N., ROSSI, S. & LÓPEZ-GONZÁLEZ, P.J. 2006. A unique assemblage of epibenthic sessile suspension feeders with archaic features in the high-Antarctic. *Deep Sea Research II*, **53**, 1029–1052.
- GORDON, I. 1932. Pycnogonida. *Discovery Reports*, **6**, 1–138.
- GORDON, I. 1938. Pycnogonida. *Scientific Reports of the Australasian Antarctic Expedition, Zoology & Botany*, **2** (8), 1–40.
- GORDON, I. 1944. Pycnogonida. *Reports of the British, Australian and New Zealand Expedition*, **B5** (1), 1–72.
- HEDGPETH, J.W. 1950. Pycnogonida of the United States Navy Expedition, 1947–48. *Proceedings U.S. National Museum*, **100**, 147–160.
- HEDGPETH, J.W. 1969a. Introduction to Antarctic zoogeography. *Antarctic Map Folio Series*, **11**, 1–9.
- HEDGPETH, J.W. 1969b. Pycnogonida. *Antarctic Map Folio Series*, **11**, 26–28.
- HEDGPETH, J.W. 1971. Perspectives in benthic ecology in Antarctica. In QUAM, L.O., ed. *Research in the Antarctic*. Washington, DC: American Association for the Advancement of Science, Publication No. 93, 93–136.
- HELD, C. 2000. Phylogeny and biogeography of serolid isopods (Crustacea, Isopoda, Serolidae) and the use of ribosomal expansion segments in molecular systematics. *Molecular Phylogeny and Evolution*, **15**, 165–178.
- HODGSON, T.V. 1902. Crustacea (Pycnogonida). *Report on the collections of natural history made in the Antarctic Regions during the voyage of the "Southern Cross"*. London: British Museum, 256–258.
- HODGSON, T.V. 1904. On a new pycnogonid from the South Polar regions. *Annals and Magazine of Natural History*, **7**, 458–462.
- HODGSON, T.V. 1907. Pycnogonida. *Natural History Reports of the National Antarctic Expedition 1901–1904*, **3**, 1–72.
- HODGSON, T.V. 1908. The Pycnogonida of the Scottish National Antarctic Expedition. *Transactions of the Royal Society of Edinburgh*, **46**, 159–188.
- HODGSON, T.V. 1914. Preliminary report of the German South Polar Expedition, 1901–1903. *Zoologische Anzeiger*, **45** (4), 158–165.
- HODGSON, T.V. 1915. The Pycnogonida collected by the Gauss in the Antarctic regions, 1901–1903; preliminary report. *Annals and Magazine of Natural History* (series 8), **15**, 141–149.
- HODGSON, T.V. 1927. Die Pycnogoniden der Deutschen Südpolar-Expedition 1901–1903. *Deutsche Südpolar-Expedition, Zoologie*, **19**, 303–358.
- HOEK, P.P.C. 1881. Report on the Pycnogonida dredged by HMS Challenger 1873–1876. *Reports of the Scientific Results of the Exploring Voyage HMS Challenger*, **3**, 1–167.
- HOEK, P.P.C. 1898. On four pycnogonids dredged during the cruise of the Challenger. *Tijdschrift der Nederlandsche Dierkundige Vereeniging*, **5**, 190–301.
- JACQUES, G. & TREGUER, P. 1986. *Écosystèmes pélagiques marins*. Paris: Masson, 130–161.

- KRAPP, F. 1980. Neue Pantopodenfunde (Pycnogonida, Arthropoda) nahe der belgischen Antarktis-Station. *Bulletin de l'Institute Royal du Sciences Naturels de Belgique, Bruxelles, Biologie*, **52** (18), 1–8.
- LINSE, K., GRIFFITHS, H.J., BARNES, D.K.A. & CLARKE, A. 2006. Biodiversity and biogeography of Antarctic and Subantarctic Mollusca. *Deep Sea Research*, **53**, 985–1008.
- LOMAN, J.C.C. 1923. The Pycnogonida. *Further Zoological Results of the Swedish Antarctic Expedition*, **1** (2), 1–41.
- MÖBIUS, K. 1902. Die Pantopoden der Deutschen Tiefsee-Expedition, 1898–99. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899*, **3**, 177–196.
- MONTIEL, A., RIOS, C., MUTSCHKE, T. & ROZBACZYLO, N. 2004. Poliquetos de fiordos y canales adyacentes al campo de hielo patagónico sur, Chile (Annelida, Polichaeta). *Ciencia y Tecnología Marina*, **27**, 49–67.
- MOYANO, H. 2005. Scotia Arc bryozoa from the LAMPOS expeditions: a narrow bridge between two different faunas. *Scientia Marina*, **69**, 103–112.
- MÜLLER, H.G. 1993. *World catalogue and bibliography of the recent Pycnogonida*. Wetzlar, Germany: Laboratory for Tropical Ecosystems, 388 pp.
- MUNILLA, T. 1989. Dos nuevas especies de Pycnogónidos antárticos. *Actas II Simposium Español de Estudios de Bentos Antártico*, 74–79.
- MUNILLA, T. 1991. Pycnogónidos capturados en la campaña "Antártida 8811". *Boletín del Instituto Español de Oceanografía*, **7**, 3–44.
- MUNILLA, T. 2000. A new species of *Ammonothea* and other pycnogonids from around Livingston Island, South Shetland Islands, Antarctica. *Antarctic Science*, **12**, 47–51.
- MUNILLA, T. 2001a. Synopsis of the pycnogonids from Antarctic and Subantarctic waters. *Polar Biology*, **24**, 941–945.
- MUNILLA, T. 2001b. A new species of *Ammonothea* (Pycnogonida) and other pycnogonids from around Livingston Island and surrounding waters (South Shetland Islands, Antarctica). *Antarctic Science*, **13**, 144–149.
- MUNILLA, T. 2002. *Ammonothea tibialis*, a new pycnogonid from the Drake passage, Antarctica. *Antarctic Science*, **14**, 171–173.
- MUNILLA, T. 2005. *Ammonothea bigibossa* (Arthropoda, Pycnogonida), a new species of the Antarctic Peninsula waters. *Polar Biology*, **29**, 70–72.
- PUSHKIN, A.F. 1974. Clavigeropallene. A new genus from Antarctic. *Zoologicheskii Zhurnal*, **53**, 938–940.
- PUSHKIN, A.F. 1975a. New species of Callipallenidae (Pantopoda) from the Subantarctic. *Zoologicheskii Zhurnal*, **54**, 1402–1406.
- PUSHKIN, A.F. 1975b. Revision of the Pycnogonids (Pantopoda) of the Pallenopsis patagonica group from Antarctic and adjacent waters. *Byulleten Sovietskoi Antarkticheskoi Ekspedititsii*, **90**, 72–83.
- PUSHKIN, A.F. 1976. New species of Endeidae (Pantopoda) from Subantarctic. *Zoologicheskii Zhurnal*, **55**, 923–925.
- PUSHKIN, A.F. 1977. New species of Austrodecidae from Antarctic. *Explorations of the Fauna of the Seas*, **21**, 54–59.
- PUSHKIN, A.F. 1982. On the species composition of the genus *Decolopoda* (Pantopoda). *Zoologicheskii Zhurnal*, **59**, 1657–1661.
- PUSHKIN, A.F. 1984a. A new species of the genus *Colossendeis* (Pantopoda) from the Antarctic. *Zoologicheskii Zhurnal*, **163**, 1259–1261.
- PUSHKIN, A.F. 1984b. A new species of the genus *Pycnogonum* (Pantopoda, Pycnogonida) from the Antarctic. *Zoologicheskii Zhurnal*, **63**, 1102–1104.
- PUSHKIN, A.F. 1988. On the revision of the *Colossendeis robusta* (Pantopoda) from the Southern Ocean. *Zoologicheskii Zhurnal*, **67**, 953–956.
- PUSHKIN, A.F. 1990. A new species of the genus *Pseudopallene* (Pycnogonida, Callipallenidae) from the Antarctic. *Zoologicheskii Zhurnal*, **69**, 155–157.
- PUSHKIN, A.F. 1993. The pycnogonid fauna of the South Ocean: biological results of the Soviet Antarctic expeditions. Russian Academy of Sciences. *Explorations of the Fauna of the Seas*, **20**, 1–397.
- STEPHENSEN, K. 1947. Tanaidacea, Isopoda, Amphipoda and Pycnogonida. *Science Research Norwegian Antarctic Expeditions, 1927–1928*, **27**, 1–90.
- STIBOY-RISCH, C. 1992. *Ammonothea bicorniculata*, eine neue art der Ammonotheidae aus der Antarktis (Pantopoda, Pycnogonida). *Bonner Zoologische Beiträge*, **43**, 333–338.
- STIBOY-RISCH, C. 1993. Funde antarktischer und subantarktischer Pantopoden einschließlich *Colossendeis acuta* sp.n.- sowie ein Beitrag zur Artbestimmung von *Colossendeis glacialis* Hodgson 1907 und *Colossendeis robusta* Hoek 1881. *Mitteilungen aus dem hamburgischen zoologischen Museum und Institut*, **90**, 251–264.
- STIBOY-RISCH, C. 1994. *Pentapycnon magnum*, eine neue Art der Pycnogonidae aus der Antarktis (Pantopoda, Pycnogonida). *Bonner Zoologische Beiträge*, **45**, 147–151.
- STOCK, J.H. 1957. The pycnogonid family of Austrodecidae. *Beaufortia*, **6**, 1–81.
- STOCK, J.H. 1965. Pycnogonides provenant de la base Antarctique Belge. *Bulletin de l'Institute Royal du Sciences Naturelles Belgium*, **41**, 1–2.
- THATJE, S., HILLEBRANT, C.D. & LARTER, R. 2005. On the origin of Antarctic marine benthic community structure. *Trends of Ecology and Evolution*, **20**, 418–419.
- TURPAEVA, E.P. 1974. The Pycnogonida of the Scotia Sea and surrounding waters. *Trudy Instituta Okeanologii P.P. Shirshov, Akademiya Nauka USSR*, **98**, 277–305.
- TURPAEVA, E.P. 1990. Polypantopoda (Pycnogonida) of Southern part of Atlantic Ocean. *Trudy Instituta Okeanologii P.P. Shirshov, Akademiya Nauk USSR*, **126**, 108–125.
- TURPAEVA, E.P. 1998. Annotated list of Pantopods (Pycnogonida) from eastern part of Weddell Sea. *Benthos of the high latitude regions*. Moscow: VNIRO Publishing, 56–68.
- TURPAEVA, E.P. 2000. New and little-known pycnogonid species of the genus *Nymphon* (Pycnogonida, Nymphonidae) from the Weddell Sea. *Zoologicheskii Zhurnal*, **79**, 669–678.
- TURPAEVA, E.P. 2002. Shallow-water sea spiders (Pycnogonida) from the Kuril, Commander and Yamskii islands. 1. Colossendeidae and Callipallenidae families. *Zoologicheskii Zhurnal*, **81**, 1448–1460.
- UTINOMI, H. 1959. Pycnogonida of the Japanese Antarctic research expeditions 1956–1958. *Special Publications of Seto Marine Biological Laboratory*, **8**, 1–12.