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 endemicity. 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, endemicity

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
Achelia	80	12 (15.4)				
A. assimilis (Haswell, 1875)			0–903		s,n	also west Pacific and Australia
A. communis (Bouvier, 1906)			0–714	C	s,t	*A. brucei* Calman, 1915
A. dorhni (Thompson, 1884)			0–192		n	
A. hoekii (Pfeffer, 1889)			5–256	Sc,p,b	s	
A. lagena Child, 1994a			23–137		s	
A. megacephala (Hodgson, 1915)			shallow water		k	
A. parvula (Loman, 1923)			0–267	p	s	also in Peru-Ecuador-Argentina
A. quadridentata (Hodgson, 1910)			0–21		St.Pl + A	
A. serratipalpis (Bouvier, 1911)			64–361	Sc,p,b,e.		also on Angola coast
A. spicata (Hodgson, 1915)			0–1138	C		described as *Austrothea*
A. sufflata Gordon, 1944			0–300	w,e		e: 40–100ºE
A. transfuga Stock, 1954			2–10		n	muddy bottom
Ammothea	40	25 (62.5)				Magnammothea and Biammothea
A. adunca Child, 1994a			185–800	w	k	
A. allopodes Fry & Hedgpeth, 1969			210–2000	C	b	*A. bicorniculata* Stiboy-Risch, 1992
A. antipodensis Clark, 1972			0–24		n	
A. armentis Child, 1994a			230–380		k	
A. bentartica Munilla, 2001			167–335	Sc		Livingston. Island, mud
A. bigibbosa Munilla, 2005			517	p		
A. calmani Gordon, 1932			99–1408	Sc,p,b,r,w		
A. carolinensis Leach, 1814			3–670	C	b	
A. clausi Pfeffer, 1889			3–860	C	s	
A. cooki Child, 1987			1463–2992		n	
A. dubia (Hedgpeth, 1950)			106	r		described as *Boehmia*
A. gibbosa Bouvier, 1913			439–567		b	recorded as *Colossendeis gibbosa* Möbius, 1902
A. gigantea Gordon, 1932			99–1116	C		145ºE–178ºW. *Magnammothea gigantea* Fry & Hedgpeth, 1969
A. glacialis (Hodgson, 1907)			0–640	C		
A. gordonae Child, 1994a)			348–732	Sc,r		
A. hesperidensis Munilla, 2000			30–439	Sc		Livingston. Island, mud
A. longispina Gordon, 1932			57–1454	C	s	
A. meridionalis (Hodgson, 1915)			10–454	C		
A. minor (Hodgson, 1907)			8–473	C		
A. sextarticulata Munilla, 1989			5–516	C		also on South Georgia, *Biammothea brevipalpa* Puskin, 1993
A. spinosa Hodgson, 1907			76–1679	Sc,p,w,r	s	also in Argentine Basin
A. striata Möbius, 1902			72–567	C	b	
A. stylirostris Gordon, 1932			165–494	Sc,w,p	s	
*A. tetra*pora Gordon, 1932			105–303	Sc	s	
*A. tibiali*s Munilla, 2002			710	Sc		
A. victoriae Cano & López, 2007			360–366	r		
Ascorhynchus	75	6 (8.0)				
A. antipodus Child, 1987			5340		n	
A. cooki Child, 1987			1463–2992		n	
A. cuculus Fry & Hedgpeth, 1969			993–4008	Sc		also in Argentine Basin
A. hedgpheti Turpaeva, 1974			3700–3910	Sc		
A. inflatum Stock, 1963			2743–6070	Sc		also in Peru–Chile trench, South Africa, Kurile trench
A. ornatum (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
Austroraptus	5	5 (100)				
A. calcaratus Gordon, 1944			143–219	r,e		e: 65ºE
A. juvenilis Calman, 1915			3–500	C		e: 92ºE, 145ºE
A. polaris Hodgson, 1907			10–569	Sc,p,b,r,e		e: 78ºE. Possibly C
A. praecox Calman, 1915			6–260	C		
A. sicarius Fry & Hedgpeth, 1969			220–380	Sc,r		
Cilunculus	31	4 (12.9)				
C. acanthus Fry & Hedgpeth, 1969			2440–2818	b		also in Argentine Basin
C. cactoides Fry & Hedgpeth, 1969			38–540	Sc,p,e	n	
C. kravcovi Pushkin, 1973			255–309		c,M + PE	
C. spinicristus Child, 1987			476–540		n	
Dromedopycnon	2	1 (50)				
D. acanthus Child, 1982			124–903		s	also in Brazilian slope
Eurycyde	21	1 (4.8)				
E. antarctica Child, 1987			527–714	r		
Sericosura	6	1 (16.7)				
S. mitrata (Gordon, 1944)			106–2154	r		also in Walvis Ridge (South Africa)
Tanystylum	45	10 (22.2)				
T. antipodum Clark, 1977			shallow water		n	
T. brevicaudatum (Fage & Stock, 1966)			0–15		St.P + A	also in Cape Verde Island
T. brevipes (Hoek, 1881)			45–100		p,St + A	also in South Africa
T. bueroisi Arnaud, 1974			80–100		St.P + A.	
T. cavidorsum Stock, 1957			0–245	Sc	s,M + PE,c,n	also in southern Chile
T. pfefferi Loman, 1923			2–100	Sc		*T. dohrni* Schimkewitsch, 1889
T. neorhetum Marcus, 1940			0–410	Sc	s,k,n,t	
T. oedinotum Loman, 1923			0–183		s,k	
T. ornatum Flynn, 1928			46–560		M + P.E	
T. styligerum Myers, 1875			0–200	p	s,k,n	
Austrodecus	42	22 (52.4)				
A. breviceps Gordon, 1938			0–298	Sc	k,n	
A. calcaricauda Stock, 1957			73–1373	Sc,p	s	
A. cestum Child, 1994b			86–207		n	
A. crenatum Child, 1994b			1–360	Sc,p		
A. curtipes Stock, 1957			0–903	Sc,w	s,k	
A. elegans Stock, 1957			99–606		M + PE	
A. fagei Stock, 1957			26–3400	C		
A. fryi Child, 1994b			112–859		n	
A. glabrum Stock, 1957			18–277	Sc		
A. glaciale Hodgson, 1907			0–2100	C		
A. goughense Stock, 1957			42–120		St.P + A	also in Gough Island
A. kelpi Pushkin, 1977			shallow water	Sc		among kelps
A. longispinum Stock, 1957			91–325		k	
A. macrum Child, 1994b			1442–2350	r		
A. profundum Stock, 1957			920	p		mud & stones, Graham Land
A. pushkini Child, 1994b			60–903		s	southern Argentina
A. serratum Child, 1994b			79–124		n	Macquarie Island
A. simulans Stock, 1957			91–545	b,w	k	
A. sinuatum Stock, 1957			shallow water		n	
A. tristanense Stock, 1955			0–70		M + PE,t	
A. varum Child, 1994b			443–549		n	Macquarie Island
Pantopipetta	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
P. australis (Hodgdon 1914)			680–5340	Sc,r	M + PE,n	
P. buccina Child 1994b			3193–3423	Sc		also in Concepción waters, Chile
P. lata Stock 1981			523–3655	b,w		also in Cape Basin, South Africa
P. longituberculata Turpaeva, 1985			567–6700	Sc		also in SW Africa, Pacific & all Atlantic
						P. brevicauda Stock, 1963
Austropallene	11	10 (90.9)				
A. brachyura Bouvier, 1913			85–920	C		*A. spicata* Hodgson, 1915
						Pseudopallene brachyura Bouvier, 1911
A. bucera Pushkin, 1993			3–280	Sc,e		holotype without figures
A. calmani Gordon, 1944			163–2955	C		
A. cornigera (Möbius, 1902)			3–1180	C	b,c	
A. cristata Bouvier, 1911			104–2100	C		
A. gracilipes Gordon, 1944			45–645	C		
A. spinicornis Pushkin, 1993			1200–1280	Sc		holotype without figures
A. tcherniai Fage, 1952			50–580	C		
A. tenuicornis Pushkin, 1993			580–1180	e		holotype without figures
A. tibicina Calman, 1915			45–550	Sc,r	n	
Callipallene	35	1 (2.9)				
C. margarita Gordon, 1932			73–578	p	s	also at 23ºS (off Brazil)
Cheilopallene	7	1 (14.3)				
Ch. gigantea Child, 1987			581–3777	P,w		
Oropallene	6	3 (50)				
O. dimorpha (Hoek, 1898)			3–415		k,n	
O. dolichodera Child, 1995c			112–2612		n	
O. metacaula Child, 1995c			1586		n	
Pseudopallene	16	2 (12.5)				
P. centrotus Pushkin, 1990			250	Sc		
P. glutus Pushkin, 1975			320		c	
Seguapallene	6	1 (16.7)				
S. insignatus Pushkin, 1975			3–30		k	
Pallenopsis	86	18 (20.9)				
P. boehmi Schimkewitsch, 1930			35–383	Sc	s	also in waters of Uruguay, Brazil and Argentine
P. buphthalmus Pushkin, 1993			104–830	Sc,w,p,e		e: 69ºS–14ºE
P. candidoi Mello-Leitao, 1949			0–430	Sc		also in Surinam & W. Atlantic
P. gurjanovi Pushkin, 1993			65–600	Sc		
P. kupei Clark, 1971			146–1530	w	n	
P. latefrontalis Pushkin, 1993			115–260	Sc,p		
P. lateralia Child, 1995c			2273–2421	r		
P. lattina Pushkin, 1993			117–430	Sc		Holoptype with figures
P. leiopus Pushkin, 1993			15–275	Sc,w,e		
P. longiseta Turpaeva, 1958			1228–3060	Sc	n	also Subarctic & Gulf of Panama
P. macronix Bouvier, 1911			100–1138	Sc,p,r,w		*P. knipovitchi* Turpaeva, 1974
P. oblicua Thompson, 1884			0–400		n	rock & algal bottoms
P. patagonica (Hoek, 1881)			3–4540	C	s	described as *Phoxichilidium patagonicum*
						P. hiemalis Hodgson, 1907
						P. glabra Möbius, 1902
						P. möbiusi Pushkin, 1975
						P. meridionalis Pushkin, 1975
P. pilosa (Hoek, 1881)			25–3650	C	b	*P. hodgsoni* Gordon, 1938
P. spicata Hodgson, 1914			25–549	C		*Cheilopallene spicata* Stock, 1955,
						Clavigeropallene spicata Pushkin, 1974
P. tumidula Loman, 1923			42–270	Sc		also in Uruguay, Brazil, Argentina
P. vanhöffeni Hodgson, 1915			3–889	C	s	*P. gaüssiana* 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
						P. setigera Hodgson, 1914
P. villosa Hodgson, 1907			160–2804	C		
Colossendeis	75	36(48.0)				
C. adelpha Child, 1998			333–341	e		Prydz Bay
C. angusta Sars, 1877			22–5480	Sc		cosmopolitan
						C. gracilis Hoek, 1881
C. arundorostris (Fry & Hedpeth, 1969)			610	r		
C. australis Hodgson, 1907			15–3935	C	k	also in Chile & Argentina
C. avidus Pushkin, 1970			270–426	p,w,e		*C. acuta* Stiboy-Rich, 1993
C. belekurovi Pushkin, 1993			150–377		c	
C. brevirostris Child, 1995b			5449–604	a		
C. colossea Wilson, 1881			425–4140	Sc,w		cosmopolitan
C. concedis Child, 1995b			2248–2907	Sc,r		
C. drakei Calman, 1915			3–3000	C	s	also in southern Tasmania
						C. smirnovi Pushkin, 1988
C. elephantis Child, 1995b			2384–4795	Sc,e		
C. enigmatica Turpaeva, 1974			315–335	Sc		
C. ensifer Child, 1995b			3250–3285	Sc		
C. fragilis Pushkin, 1992			3–830	Sc,e	s	
C. grassus Pushkin, 1993			315–435	Sc		
C. hoecki Gordon, 1944			120–3112	Sc,w,r	k,n	
C. insolitus Pushkin, 1993					s	47ºS, Argentina
C. korotkevischi Pushkin, 1984			132–660	w	k,c	
C. kurtchatovi Turpaeva, 1993			4700		s	
C. leniensis Pushkin, 1993			250–432		52ºS–43ºE	south of Iles Crozet
C. lepthorynchus Hoek, 1881			561–3675		M + PE,s	cosmopolitan
						C. pennata Pushkin, 1970
C. longirostris Gordon, 1932			2–3700	C	n	also in southern Tasmania
C. macerrima Wilson, 1881			2010–2100		n	cosmopolitan.
						C. japonica, Hoek, 1898, *C. spei*
C. media Hoek, 1881			3386–5798	Sc		also in Argentina
						C. brevipes Hoek, 1881
C. megalonix Hoek, 1881			7–4900	C	s,k,n	also in South Africa, Madagascar & E. Argentina
						C. rugosa Hodgson, 1907
						C. frigida Hodgson, 1907
						C. orcadense Stock, 1963
C. mica Pushkin, 1970			1400		37°S–22°E	Sub-Antarctic Indian Ocean
C. notialis Child, 1995b			260–380		k	
C. pseudochelata Pushkin, 1993			125–180	Sc,e		e: 69ºS, 11ºE
C. robusta Hoek, 1881			0–3610	C	b,k	*C. lilliei* Calman, 1915
C. glacialis Hodgson, 1907						*C. gracillipes* Bouvier, 1911
						C. rostrata Turpaeva, 1994
C. scoresbii Calman, 1915			130–5227	Sc,w,r	s	
C. scotti Calman, 1915			35–352	C		
C. stramendi Fry & Hedgpeth, 1969			645–3806		s	
C. tenuipedis Pushkin, 1993			250–860	C	s	also in E. Argentina
C. tethya Turpaeva, 1974			318	Sc,w		
C. tortipalpis Gordon, 1932			160–4026	C	s,k	
C. wilsoni Calman, 1915			60–801	Sc,w,r		also in Adélie Land
Decolopoda	2	2 (100)				
D. australis Eights, 1835			0–1890	Sc,p,b,w,r	k	possibly C
						D. antarctica Bouvier, 1905
D. quasami Sree *et al.*, 1993			150	e		

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Genera/species	W. sp.	A + S sp. & % of W.sp	Depth (m)	Antarctic zone	sub-Antarctic zone	Remarks and synonyms
Dodecolopoda	1	1 (100)				
D. mawsoni Calman & Gordon, 1933			160–549	C		
Heteronymphon	7	1 (14.3)				
H. exiguum (Hodgson, 1927)			3–415	C	n	described as Nymphon
Nymphon	268	67 (25.0)				Chaetonymphon
N. adareanum Hodgson, 1907			1–903	Sc,p,r,e	s	also in SE Argentina, possibly C
N. andriashevi Puskin, 1993			116–135	p		
N. arcuatum Child, 1995a			38–157		s	
N. articulare Hodgson, 1908			18–910	Sc,p,w	s	
N. australe Hodgson, 1902			8–4136	C	s,n,b	also Indian Ocean & off Argentine–Chilean coasts
N. stylops Bouvier, 1913						
N. biarticulatum Hodgson, 1907			35–889	C	k	
N. bouvieri Gordon, 1932			158–583	Sc,p,e		
N. brachyrhynchum Hoek, 1881			82–430		k	also in Heard Island
N. brevicaudatum Miers, 1875			27–1100	C	k	
N. bucuspidum Child, 1995a			1262		n	
N. chaetodir Utinomi, 1971			995–1110		n	
N. charcoti Bouvier, 1911			3–1200	C		
N. clarencei Gordon, 1932			65–342	Sc		
N. compactum Hoek, 1881			731–3246	Sc	n	also in South Africa
N. eltaninae Child, 1995a			467–1233	Sc,r		
N. forticulum Child, 1995a			438–548		s	s: SE Argentine
N. frigidum Hodgson, 1907			227	r		
N. galatheae Fage, 1956			3111–5798	w		
N. gerlachei Giltay, 1937			460–578	p,b		
N. glabrum Child, 1995a			55	Sc		
N. gracilipes Miers, 1875			3–3055	w,e	k	also in Kermadec Trench, (SW Pacific Ocean)
N. gruzovi Pushkin, 1993			250	p,w		holotype is a juvenile
N. hadale Child, 1982			3010–5798	Sc		also in Argentine basin
N. hamatum Hoek, 1881			2502–3400	Sc	c	
N. hiemale Hodgson, 1907			30–1435	C		*N. gracillimum* Calman, 1915
N. inferum Child, 1995a			2450–3873	Sc, Palmer Is.		
N. inornatum Child, 1995a			513	w		
N. isabellae Turpaeva, 2000			333–571	w		
N. isaenki Pushkin, 1993			500–700		k	
N. lanare Hodgson, 1907			60–848	C		
N. lomani Gordon, 1944			112–714	C	n	
N. longicolum Hoek, 1881			68–4600	C	n	also in Chilean Basin & New Zealand
N. longicoxa Hoek, 1881			318–2998	Sc,b,r	n	also in Argentine Basin
N. longisetosum Hodgson, 1915			385–2450	e		
N. macquarensis Child, 1995a			112–124		n	
N. macrochelatum Pushkin, 1993			540	68ºS–32ºE,w		
N. mendosum (Hodgson, 1907)			15–555	C		
N. microgracilipes Pushkin, 1993			150–309	B	c	c: 46ºS–49ºE
N. monotrix Child, 1995a			3495–3514	r		
N. multidens Gordon, 1944			40–260	Sc,p,b	b	
N. multituberculatum Gordon, 1944			180–640	w,Sc,e		e: 20–140ºE
N. neelovi Pushkin, 1993			65–240	Sc	c	
N. neumayeri Gordon, 1932			160–403	Sc,p	s	
N. orcadense (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
N. pagophylum Child, 1995a			265–1170	Sc,p,w		
N. paucidens Gordon, 1932			22–334	Sc	c	also SE Argentina
N. paucituberculatum Gordon, 1944			180–219	w,e		
N. pfefferi Loman, 1923			12–250	Sc	s	
N. phasmatoides Böhm, 1879			13–94	p,w		also in South Africa; *P. capense* Hodgson, 1908
N. polare Hodgson, 1915			350	e		
N. premordicum Child, 1995a			2597–3215	Sc		
N. proceroides Bouvier, 1913			91–1180	Sc,p,e		
N. procerum Hoek, 1881			2450–6135	Sc		cosmopolitan
N. proximum Calman, 1915			40–1555	C		*N. banzare* Gordon, 1944
N. pseudogracilipes Pushkin, 1993			195–216		k	
N. punctum Child, 1995a			415		n	
N. rybakovi Pushkin, 1993			220	Sc,w		
N. sabellum Child, 1995			2872–2928	r		62ºS–160ºW
N. scotiae Stock, 1981			2960–2980	Sc		*N. stocki* Turpaeva, 1974
N. subtile Loman, 1923			13–304		s,k	also SE Argentine
N. tenuimanum Hodgson, 1914			1903–3398	r		
N. tenuipes Bouvier, 1911			122–1180	C		also in S. Australia *N. soyae* Utinomi, 1953
N. trituberculum Child, 1995a			3200–3259	e		
N. typhops (Hodgson, 1915)			2450–2815	Sc,p,w,e		
N. unguiculatum Hodgson, 1927			168–450	Sc		
N. villosum (Hodgson, 1915)			13–636	C		also 10ºE
N. zundiamum Pushkin, 1993			160		s	s: near Falkland Islands
Pentanymphon	1	1 (100)				
P. antarcticum Hodgson, 1904			3–3227	C		*P. minutum* Gordon, 1944
Sexanymphon	1	1 (100)				
S. mirabilis Hedgpeth & Fry, 1964			1687–2897	Sc,p		
Anoplodactylus	140	9 (6.4)				
A. australis (Hodgson, 1914)			15–616	C	t	also in Tasmania
A. californicus Hall, 1912			0–100		s	cosmopolitan; *C. projectus* Hilton, 1942, *C. portus* Sawaya 1950
A. laciniosus Child, 1995c			456–540		n	also in Antipodes Island
A. laminifer Arnaud, 1974			80–100		St.P+A	
A. petiolatus (Kröyer, 1844)			0–1180		s	also in Atlantic–Mediterranean
A. speculus Child, 1995c			1586–1640		n	
A. typhlops Sars, 1888			915–3620	Sc	c,n,PE	cosmopolitan *A. pelagicus* Flynn, 1908 *A. neglectus* Hoek, 1898
A. vemae Child, 1982			90–676		s	
A. virescens (Hodge, 1864)			0–16		St.P+A	also in Atlantic–Mediterranean
Phoxichilidium	14	1 (7.1)				
P. pigordum Child, 1995c			79–124		n	
Endeis	17	2 (11.8)				
E. australis (Hodgson, 1907)			3–1570	C	n,b	
E. viridis Pushkin, 1976			3–377		k,c,M+PE	
Pentapycnon	3	2 (66)				
P. bouvieri Puskin, 1993			90–419	Sc,w		*P. bouvieri* Child (1993) *P. magnum* Stiboy-Rish (1994)
P. charcoti Bouvier, 1910			240–1420	Sc,p,r		
Pycnogonum	69	10 (14.5)				

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
P. calculum Bamber, 1955			littoral	Sc	s	rock with algae
P. rhinoceros Loman, 1923			30–1115	C		*P. diceros* Marcus, 1940
P. gaini Bouvier, 1910			24–2495	C	k	
P. gordonae Pushkin, 1984			219–400	w,e		
P. magellanicum Hoek, 1898			85–548		s	
P. magniroste Möbius, 1902			3–309		k,c	
P. paragaini Munilla, 1989			205–440	Sc		
P. platylophum Loman, 1923			0–903	Sc,e	k,c	
P. sivertseni Stock, 1955			102–141		t	
Rhynchothorax	19	4 (21.1)				
R. australis Hodgson, 1907			60–900	C	s,k,n	
R. oblongus (Pushkin, 1977)			100–140		k	described as *Austrodecus*
R. percivali Clark, 1976			0–101		S,n	also in Mexico
R. philopsammum 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 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

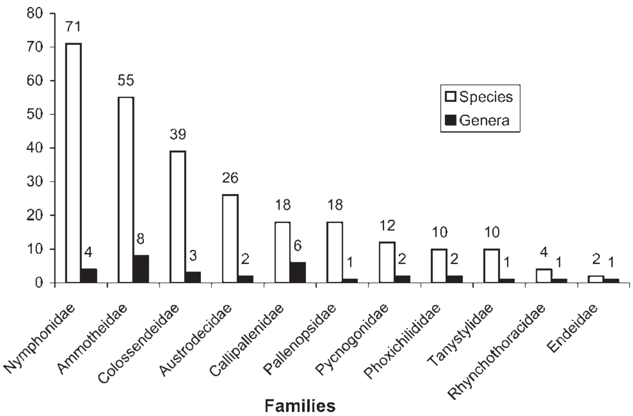

Fig. 1. Richness of species and genera from austral pycnogonid families.

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 (*sensu lato*)	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 & Hegdpeth 1969, Hegdpeth 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*, *Pentanymphon*, *Sexanymphon*, *Austroraptus*) are endemic to Antarctic waters. Other genera (*Decolopoda*, *Austropallene*) which were considered by Hegdpeth (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:

a) The Scotia Sea is closely linked to other southern zones (60.75% of similarity), indicating some peculiarity of the former.

b) 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.

c) 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

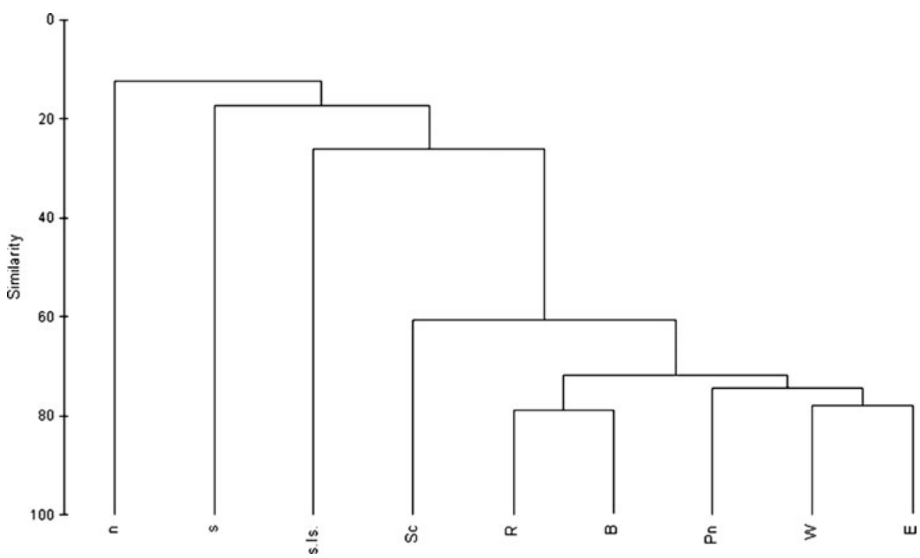

Fig. 2. Similarity of Antarctic and sub-Antarctic zones (Bray-Curtis Index, complete linkage), based in presence-absence data. CircumAntarctic species are included. n = New Zealand Plateau, s = South America, s.Is = sub-Antarctic islands, Sc = Scotia Sea, R = Ross Sea, B = Bellingshausen Sea, Pn = Antarctic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

constitute a different zone (Hedgepth 1969a), with 63 species at present. Recent multivariate analysis of the bryozoan component of benthos south of 47ºS 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 Peninsula, but the main topographical obstacle between South America and Antarctica is the Scotia Arc, through which the Circumpolar Current passes.

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	68–70º	68–70º
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	**46**	14	10	3	5	1	1	8	10	52
Sc	14	**89**	24	18	20	8	16	11	12	123
Pn	10	24	**35**	7	14	5	8	2	3	73
R	3	18	7	**27**	8	3	4	4	3	50
W	5	20	14	8	**35**	4	11	2	7	71
B	1	8	5	3	4	**12**	2	1	3	27
E	1	16	8	4	11	2	**24**	0	2	44
n	8	11	2	4	2	1	0	**47**	11	39
s.Is	10	12	3	3	7	3	2	11	**64**	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.

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 endemicity 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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