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ORIGINAL PAPER

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Synopsis of the pycnogonids from Antarctic and Subantarctic waters

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Abstract This work summarizes existing knowledge on the faunal history, biodiversity and biogeography of the Antarctic and Subantarctic pycnogonids. It refers to material sampled between 1829 and 1999 from more than 40 expeditions run by 14 countries, and published in 75 papers. Up to now, 31 genera and 25 species have been recorded from a total of about 38,000 specimens captured at 2,000 stations. They constitute 38.75% and 21.5%, respectively, of the 80 genera and 1,164 species recorded worldwide. One hundred and twenty species have been found in Antarctic, 71 in Subantarctic waters, and 60 species in both zones, yielding an endemicity for the entire area of over 80%. Fifty five species revealed a circumpolar distribution and 161 were found mainly on the shelf. The Antarctic Ocean is suggested to be a centre of pycnogonid speciation and dispersion.

Introduction

The pycnogonids (Cheliceriformes, Arthropoda) from Antarctic and Subantarctic waters have been studied more extensively than those from any other world ocean of similar size. Exploration of this area began with the American Expedition of Nathaniel Palmer (Palmer Archipelago, 1829–1830). The naturalist of this cruise, James Eights, described (Eights 1835) and drew the first Antarctic pycnogonid *Decolopoda australis*, on a serolid and some fossils. Later on, many countries were to send their own "National Antarctic Expedition", which produced numerous monographs, the main ones being the works of Hoek (1881), Möbius (1902), Hodgson (1907, 1927), Bouvier (1913), Calman (1915), Gordon (1932, 1938, 1944), Fry and Hedgpeth (1969), Pushkin (1993) and Child (1994a, b, 1995a, b, c). The Child papers mentioned contain more detailed information about the historical background of distinct families.

The goal of this work is to extract inferences (about historical research, biodiversity, zoogeography and ecology) on the Austral pycnogonids by analysing the consulted literature.

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Materials and methods

This is a bibliographic paper. On the biodiversity and history I have consulted the above mentioned works, the Müller catalogue (Müller 1993) and 42 others. The main ecological and zoogeographical works examined are those of Fry (1964), Fry and Hedgpeth (1969), Hedgpeth (1969a, b, 1971), Arntz et al. (1994), Arntz (1997), Clarke (1990) and Clarke and Crame (1989, 1997). In total, 75 papers have been consulted.

Results and discussion

Historical research and biodiversity

The chronological and synoptic faunal histories of the Austral pycnogonids captured on different expeditions and in different decades are shown in Tables 1 and 2, respectively. This research involves 165 years, 14 countries and more than 40 ships or expeditions. The main results are that at present 38,000 specimens have been found at about 2,000 stations in the Southern Ocean.

These individuals belong to 31 genera and 251 species of pycnogonids, 1,164 being the total number of species in the world. They represent 21.5% of the actual world species, which were captured in Austral waters, that is to say, in 21% of the ocean areas (Jacques and Tréguer 1986). Nymphonidae is the most abundant family (69 species), the first genus is *Nymphon* (66 species), and *N. australe* the most frequently recorded species. In short, 101 species are endemic in the Antarctic area, 60 are present only in the Subantarctic zone and 42 species

Table 1 Chronological history of discovery of pycnogonids from Antarctic and Subantarctic waters. *N* Number of specimens, *STS*. number of stations, *S* number of species, *N. SP*. number of new species

Author	Country	Ships or expedition	Years of cruises	N	STS.	S	N. SP.
Eights 1835	USA	Palmer Exp.	1829–1830	4	3	1	1
Hoek 1881, 1898	UK	Challenger	1872–1876	78+	17	24	17
Möbius 1902	Germany	Valdivia	1898–1899	85	17	26	14
Hodgson 1902, 1904, 1907, 1908, 1914, 1915, 1927	UK, Germany	Southern Cross Discovery, Siboga Gauss	1898–1904	?	?	94	43
Bouvier 1905, 1906, 1913	France	Francais, Pourquoi-pas	1903–1910	500 approx.	41	34	18
Calman 1915, 1933	UK	Terranova	1915–1933	600	16	44	11
Loman 1923	Sweden	Swedish Antarct.	1901–1903	1,000 approx.	31	32	5
Gordon 1932, 1938, 1944	UK, Australia New Zealand	Discovery I, II Australian Antarct. Banzare	1911–1931	3,820 approx.	158	105	28
Stephensen 1947	Norway	Norwegian Antarct. Exp.	1927–1928	109	37	17	0
Hedgpeth 1950	USA	USA Navy	1947–1948	192	19	24	1 ?
Fage 1952a, b	France	Commandant Chargot	1950	74	24	18	0
Utinomi 1959	Japan	Japanese Antarct. Research	1955–1958	3	3	3	1
Stock 1965	Belgium	Antarctique 1960–1961	1960–1961	46	9	13	0
Fry and Hedgpeth 1969	New Zealand, USA	Endeavour, Eltanin Glacier	1956–1964	600	118	49	7
Arnaud 1972a, b	France	Terre Adélie, Kerguelen	1961–1970	961	121	41	0
Turpaeva 1974, 1990	Soviet Union	Akademic Koerstschatov	1965–1971	729	16	34	4
Krapp 1980	Belgium		1965–1967	37	17	16	0
Child 1987, 1994a, b, 1995a, b, c	USA, New Zealand	Eltanin, Aurora australis, Hero, Endeavour, Islas Orcadas, Vema Prof. Siedlecki 7 Coastguard	1956–1986	20,203	600 approx.	168	42
Munilla 1989, 1991, 2000 , 2001	Spain	Pescapuerta IV Hespérides (Bentart)	1986, 1994–1995	1,435	46	72	4
Bamber 1995	Canada		1970–1994	198	9	18	1
Stiboy-Risch 1992, 1993	Germany	Polarstern	1984–1985	674	81	50	2[a]
Pushkin 1993+ 10 papers	Soviet Union	Soviet Antarct. Exps.	1956–1987	5,813	616	162	25
Others							27
TOTAL	14	40+	1829–1999	38,000 approx.	2,000 approx.		251

[a] *Ammothea bicorniculata* Stiboy-Risch 1992 is probably a junior synonym for *A. allopodes*

Table 2 History of pycnogonid new species published by decades, indicating the importance of the expeditions around 1900. The Russian and USA cruises (1956–1987) published their data in the last decade. The influence of the Second World War (and the post-war) is notorious. Some species have been synonymized

Decades	New species
1835–1880	22
1881–1898	17
1900–1909	20
1910–1919	51
1920–1929	20
1930–1939	17
1940–1949	11
1950–1959	2
1960–1969	7
1970–1979	4
1980–1989	7
1990–1998	67

were recorded as endemic from Austral oceans (Table 3). Detailed data for the 251 austral species can be obtained from the author on request.

Finally, the comparison of percentages from Antarctic-living species of the main animal groups (Table 4) is relatively high for the pycnogonids: 15% versus 14.2% of the amphipods (the other most abundant group). More studies will be necessary in order to expand the knowledge of the specific biodiversity of this and other groups, mainly in the South African, Australian and Bellinghausen zones.

Ecology

Fluctuations of the abiotic parameters of the Weddell Sea (temperature, salinity, O_2, phosphates, nitrates) as an example of Antarctic environmental conditions are

Table 3 Endemicity and species richness of pycnogonid species in Antarctic and Subantarctic waters

Living in...	Total spp. number	% of spp. known worldwide (1,164 in total)	Endemics there of (no. spp.)	% of endemic spp. in respective zone	Other waters (no. spp.)
Antarctic only	120	10.3	101	84.2	19
Subantarctic only	71	6.1	60	84.5	11
Antarctic and Subantarctic	60	5.1	42	70.0	18
Total	251	21.5	203		48

Table 4 Number and percentages of recorded Antarctic species in relation to worldwide ones (main zoological groups). Sources: Arntz 1997; Brusca and Brusca 1990; Hickman et al. 1990; Wilson 1994; Corbera 1999

Zoological group	World species	Antarctic species	Percentage
Pycnogonida	1,164	180	15.5
Amphipoda	6,000	850	14.2
Polychaeta	5,500	670	12.2
Isopoda	4,000	350	8.7
Porifera	5,000	310	6.2
Crustacea	30,500	1,800	5.9
Cumacea[a]	1,200+	68	5.6
Echinodermata	6,100	300	4.9
Cnidaria	9,000	360	4.0
Mollusca	50,000	900	1.8
Pisces	23,000	300	1.3

[a] In the Southern hemisphere

very low, except for silicates (between 73 and 115 g m^{-3}) and depth (0–4,500 m; Jacques and Tréguer 1986). Apparently, the silicates are not important for the pycnogonids because they have no silicates as structural components. In respect to depth, San Vicente et al. (1997) mention that it is the only important abiotic factor of six tested in waters around Livingston Island.

Synthetic data about the bathymetric distribution of Austral species are shown in Table 5. Their main features are that two-thirds of the species have been found only on the continental shelf and upper slope (also the most sampled zones) and that the number of species decreases dramatically down to 1,000 m. However, 43.6% of the recorded Austral species have a eurybathy superior to 500 m. This fact could be explained by the stability of the environmental conditions in the water column, mainly temperature and salinity. Another cause of the conspicuous eurybathy could be the great extension of the continental glacial ice plates on the Antarctic shelves, forcing the fauna to survive at great depths.

Finally, it is necessary to carry out more coastal and very deep expeditions for a better knowledge of the biodiversity and bathymetrical distribution of the Austral pycnogonids, because the species found between 0 and 100 m and below 1,000 m are very few.

Zoogeography

The Antarctic benthos has evolved as a consequence of abiotic environmental conditions in the past and of biotic interactions (Arntz et al. 1994). The distribution of most of the benthic Antarctic fauna is circumpolar (Hedgpeth 1971; Arntz and Gallardo 1994; Clarke and Crame 1997). Circumantarctic distribution is also the most abundant with respect to pycnogonids (Fry and Hegdpeth 1969; Hegdpeth 1969a), since 55 of the 251 Austral species are circumpolar (21.9%). Only 5 are cosmopolitan.

The data in Table 3 show a high specific endemicity (81% in Austral waters, 84% and 85% in the Antarctic

Table 5 Number (*N*) of Austral species (*Sp.*) of pycnogonids related to depth and their eurybathy (*A* Antarctic, *S* Subantarctic)

	N	% of 251	Remarks
Sp. recorded exclusively between 0 and 100 m	17	6.8	4A + 13S
Sp. recorded exclusively between 0 and 1,000 m	160	63.8	Continental shelf + upper slope
Sp. recorded between 0 and 1,000 m	218	86.9	
Sp. recorded exclusively below 1,000 m	34	13.6	Very deep species
Sp. recorded below 1,000 m	88	35.2	
Sp. recorded exclusively between 1,000 and 5,000 m	28	11.2	
Sp. recorded exclusively below 5,000 m	6	2.4	2 Pantopipetta, 2 Nymphon, 1 Colossendeis, 1 Aschorynchus
Sp. with eurybathy between 500 and 1,000 m	45	18.0	
Sp. with eurybathy superior to 1,000 m	64	25.6	15 Nymphon, 13 Colossendeis, 5 Pallenopsis, 5 Ammothea + others

and Subantarctic respectively), comparable to the Isopoda (87%, Brandt 1992) or Cumacea (89%, Corbera 1999). The number of endemic species for each individual Austral region is low (10 or less) except in the Scotia Sea (26) and on the New Zealand Plateau (21). These two latter areas might be considered subcentres of speciation as a result of the separation of the Antarctic from South American and Australian continents. However, these two zones are also among those most sampled in the Southern Ocean.

Endemic genera of Antarctic waters are very few (*Dodecolopoda, Pentanymphon*, *Sexanymphon, Austroraptus*). Other genera (*Decolopoda, Austropallene*) which were considered by Hegdpeth (1969b) as typically Antarctic, have recently been found in Subantarctic waters; the same occurs with some species. The Subantarctic pycnogonid fauna shows origins in the Antarctic Ocean at genus level (Arnaud and Bamber 1987); this is true for example with *Colossendeis* or *Ammothea*, two genera with more than half the species in the Southern Ocean. Both, similar to other genera with abundant species, have more species in Antarctic than in Subantarctic waters. Therefore, in my opinion, the Antarctic Ocean should be considered not only as a centre of speciation (suggested by Hedgpeth 1969b) but also of geographic dispersion and evolutionary radiation, because of its great relative endemicity (101 Antarctic species versus 60 Subantarctic).

Three possible routes of migration have been proposed by Fry and Hegdpeth (1969):

1. Direct migration from the Antarctic along the sea bottom (*Colossendeis* species).
2. From Antarctica to Australasia by the Westwind Drift-Western current (*Ammothea* sibling species in both zones).
3. From Antarctica to South America via the Scotia Arc (*Achelia* sibling species in both areas).

This last route appears to be certain in the migration of actual species; 20 of the 48 Austral species recorded in other waters were detected in areas off Argentina and Brazil.

Finally, there is evidence which favours the ''in situ'' origin of much of the Antarctic shelf fauna during the Cretaceous or before, when the ex-Gondwana continents were still connected (Clarke and Crame 1989). Examples proposed are the gastropods (Clarke 1990), the serolid and arcturid isopods (Brandt 1992), and now the pycnogonids. This last group, like echinoderms, ascidians and gastropods, show a particular separation into closely related species, which are almost certainly the product of radiation in situ (Clarke and Crame 1989). Moreover, radiation is always connected with a high level of endemism (Arntz et al. 1994).

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