

Article

## Research on sea spiders (Chelicerata; Pycnogonida) in the era of single-ship oceanographic voyages (1870-1915)

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### Abstract

The study of pycnogonid diversity and biogeography began in the late nineteenth century with a series of 13 single ship cruises between 1870 and 1915. The rapid expansion of research on sea spiders was made possible by the availability of research ships with powered winches or capstans and the wealth either private or governmental necessary to fund major oceanographic research expeditions. The 13 ships and cruise dates were *Voringen* (1875), *HMS Challenger* (1873-1876), *Blake* (1875-1878), *Willem Barents* (1878 and 1879), *Ingolf* (1895-1896), *George W. Elder* (1899), *Southern Cross* (1899-1900), *Siboga* (1899-1900), *RRS Discovery* (1901-1904), *Scotia* (1902-1904), *Albatross* (1900 & 1906), *Terra Nova* (1910-1914) and *Aurora* (1911-1914). The results of these cruises identified 13 families of Pycnogonida. Modern taxonomic systems based in part on molecular traits still recognize 10 of the original families recognized by the scientists who analyzed the collections of the earlier workers. Their distribution in the Arctic, Antarctic, Tropical and Boreal seas was established. The vertical abundance and distribution of seven families of Pycnogonida was elucidated from the results of the *HMS Challenger* expedition.

**Keywords** benthic fauna; biogeography; *Pycnogonida*; sea spiders.

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### 1 Introduction

The Pycnogonida Latreille, 1810 were first described in the scientific literature in the first decade of the nineteenth century (Latreille, 1810). Their distribution and diversity were not well studied before the 1880s. The biogeography and taxonomic richness of Pycnogonida in the World Oceans was revealed by a series of scientific expeditions conducted between 1870 and 1915. In this paper we attempt to document the process and major factors which resulted in this rapid increase of our understanding of the diversity and biogeography of sea spiders.

The advancement of science is in part a series of trends, initiated by the development of and/or the

availability of innovative technologies. One such trend was the rapid expansion of data relating to the benthic fauna and flora made possible by the availability of seagoing ships with steam powered winches or capstans which could be used to haul bottom dredges and large plankton nets for the collection of marine animals from the world's oceans. A second factor was the financial capacity and willingness of individuals and governments to fund basic research projects on a large scale. These two factors made possible a series of single ship research expeditions spanning the world's oceans. This era of single ship research expeditions between 1870 and 1915 led to a rapid growth in our knowledge of marine benthic fauna (Wöst, 1964). Much was learned about marine animals and algae from the collections of these cruises. In this survey, we will focus on the contributions to the study of marine chelicerates, specifically sea spiders (Chelicerata; Pycnogonida). The contributions of 13 oceanic collecting expeditions from 1870 to 1915 are examined to illuminate their contributions to the study of the sea spiders (Wöst, 1964; Nelson, 1971; Rice, 1986). The results of these cruises were published between 1881 and 1949.

The scientific findings of the following research ship cruises are included in this study: (1) The Norwegian *Voringen* (1875) (Lead Scientist G. O. Sars); (2) The British *HMS Challenger* (1873-1876) (Capt. G. S. Nares/ Lead scientist C. W. Thomson); (3) The Coast Survey Steamer *Blake* (1875-1878) (lead scientist L. Agassiz); (4) The Dutch *Willem Barents* (1878 and 1879) (Captain A. De Bruyne, Schiffs-Lieutenant der Nieder Ländischeu Marine); (5) The Danish *Ingolf* (1895-1896); (6) The privately funded American *George W. Elder* (1899); (7) The privately funded British *Southern Cross* (1899-1900) (Capt. W. Colbeck/ zoologist Nicolai Hanson); (8) The Dutch *Siboga* (1899-1900); (9) The British *RRS Discovery* (1901-1904) (Capt. R. F. Scott and lead scientist P. P. C. Hoek); (10) The United Kingdom *Scotia* (1902-1904) (Capt. T. Robertson/ lead scientist W. Spiers); (11) The U. S. Fish Commission *Albatross* (1900 and 1906) (One of the first ships built in America specifically for Oceanographic Research); (12) The British *Terra Nova* (1910-1914); and (13) The Australian *Aurora* (1911-1914) (Capt. J. K. Davis/Lead scientist D. Mawson) (Sars, 1891; Hoek, 1881a, 1881b; Meinert, 1899; Cole, 1904; Hedgepeth, 1948, 1949; Nelson, 1971; Rice, 1986).

The Naval vessels *HMS Challenger*, *William Barents* and *Siboga*, were used on three of the expeditions. Government owned and or funded ships, *Voringen*, *Blake*, *Ingolf*, *RRS Discovery*, *Scotia*, *Albatross*, *Terra Nova*, and *Aurora* were used on eight of the expeditions. Two of the expeditions, *George W. Elder* and *Southern Cross*, were funded by scientifically minded wealthy individuals. Three of these ships, *Albatross*, *Blake* and *RRS Discovery* were among the first ships specifically constructed for research (Table 1).

The scientific findings of these cruises were not in many cases published in the scientific literature until many years after the end of the cruise. For example, the results of Coast Survey Steamer *Blake* (1875-1878) were published in 1949, 71 years after the end of the cruise and the U. S. Fish Commission *Albatross* (1900 and 1906) results were published in 1948, 42 years after the end of the expedition. The results and analysis being conducted and reported by the Smithsonian Institution curator, Joel Hedgepeth (Hedgepeth, 1948, 1949). In other cruises, The British *Southern Cross* (1899-1900), and The Dutch *Willem Barents* (1878 and 1879), the time from completion of the field work to publication was as little as two years (Hoek, 1881b; Hodgson, 1902). The results of The British *HMS Challenger* (1873-1876) were analyzed and published by Hoek five years after the end of the cruise (Hoek, 1881a).

In this study the cruises will be taken up in order of the date of publication of the results, and not the cruise dates themselves.

Hoek (1881a) analyzed the worldwide collections brought back by *HMS Challenger* (1873-1876) which included 410 specimens representing 7 families, 8 genera and 42 species (See Tables 2-4). As can be seen the Pycnogonida were found most often in the upper 915 m. Also known as the euphotic zone. The frequency of occurrence decreased to less than one third on the continental rise. There is a second peak of frequency of

occurrence at 3660 m to 5500 m, that is, the depth range of the abyss. They are least abundant at Hadal depths ( $\geq 6000$  m). The Pycnogonida, thus display a bimodal peak abundance on the continental shelf and on the abyssal plane (Table 2). This was the only research cruise which produced a significant data set based on depth for collections in the North and South Atlantic, Southern Ocean and North Pacific Ocean (Hoek, 1881a).

**Table 1** A Chronological listing of the research cruises.

Nationality	Date(s)	Ship	Geographic Region	Publication
Norwegian	1875	<i>Voringen</i>	North-Atlantic, North Sea, Barents Sea and Kara Seas	1891
British	1873-1876	<i>HMS Challenger</i>	World Cruise-Shallow-Abyss	1881
U.S.A.	1875-1878	<i>Blake</i>	N. W. Atlantic and Caribbean	1948
Dutch	1878 & 1879	<i>Williem Barents</i>	N. Atlantic & Arctic Oceans, North Sea & Barents Sea	1881
Danish	1895-1896	<i>Ingolf</i>	Davis Strait, Iceland, Jan Mayan, Faroe Islands & Kara Sea.	1899
U.S.A.	1899	<i>George W. Elder</i>	Coastal Alaska, Coastal Siberia	1904
British	1899-1900	<i>Southern Cross</i>	Southern Ocean	1902
Dutch	1899-1900	<i>Siboga</i>	8° S to 6°N & 110°E to 133° E East Indies Islands	1908
British	1901-1904	<i>RRS Discovery</i>	Southern Ocean	1907
British	1902-1904	<i>Scotia</i>	Southern Ocean	1908
U. S. A.	(1900 & 1906)	<i>Albatross</i>	Japanese coastal waters, Kamchatka Peninsula	1949
Australia	(1910-1914)	<i>Aurora</i>	Southern Ocean	1938
British	(1910-1914)	<i>Terra Nova</i>	Ross Sea	1915

Hoek (1881a) also provided a depth range for the species in the *HMS Challenger* collections (Table 3). The members of the Family Ammotheidae were confined to shallow waters. Members of the Family Ascorhynchidae were found from the shore to 5351 m, that is intertidal to the upper part of the abyss. Members of the Family Phoxichilidiidae ranged in depth from 12 m to 3567 m, from the continental shelf to the abyss. The Family Pallenidae was limited to 69 m to 219 m, the continental shelf to the upper shelf break. Members of the families Nymphonidae and Colossendeidae are found from the continental shelf to the abyss.

**Table 2** The families, genera, and species from *HMS Challenger*.

Families	Genera and species
Ascorhynchidae	genus <i>Ascorhynchus</i> -2 species.
Ammotheidae	genus <i>Discoarachne</i> -1 species, genus <i>Dicoarachne (Tanystylum)</i> -1 species.
Colossendeidae	genus <i>Colossendeis</i> -8 species.
Nymphonidae	genus <i>Nymphon</i> -16 species.
Pallenidae	genus <i>Pallene</i> -4 species.
Phoxichilididae	genus <i>Phoxichilidium</i> -8 species.
Pycnogonidae	genus <i>Pycnogonum</i> -2 species.

**Table 3** Number of specimens as a function of depth in the *HMS Challenger* samples (Hoek, 1881b).

Number of specimens	Depth Range
99	0 to 914 m
30	915 m to 1830 m (Continental Rise)
47	1831 m to 2750 m
47	2751 m to 3660 m
93	3660 m to 4575 m
83	4575 m to 5500 m
11	5599 m to 8368 m

In the same year as the publication of the *HMS Challenger* expedition results, Hoek also published his analysis of the collections returned by the two cruises of the *Willem Barents* in the years 1878 and 1879 (Hoek, 1881b). As in the case of the *HMS Challenger* results Hoek did not actually participate as a member of the scientific party on the *Willem Barents*. This work includes specimens from the *Willem Barents* (1878 and 1879) as well as reports from earlier cruises. Hoek's list of species which came from Sub-Arctic North American coast to the Arctic Ocean, and the Barents Sea is given in Table 5. The collections included 6 families, 8 genera and 25 species (Table 5) (Hoek, 1881b).

Sars (1891) described the collections from the Norwegian North-Atlantic Expedition (1876-1878) on the steamer *Voringen*. This publication includes the Pycnogonida collected in the named expedition plus specimens collected from the Kara Sea by the Nordenskjold Expedition of 1875 (Sars, 1891). The Atlantic specimens are from the Northeastern Atlantic (60°N to 80°N and 15° W to 38°E), northern part of the North Sea and Barents Sea. All the collections analyzed by Sars are arctic specimens. He noted that the Pycnogonida from his collections were typically larger than those from the Mediterranean Sea reported by Dohrn (1881). Sars (1891) reported 7 families, 13 genera and 51 species. The family Nymphonidae accounted for 25 of the 51 species found in his collections (See Table 6).

Specimens from the Russian owned Arctic Ocean archipelago known as Franz-Josef Land (Centered at

81°N 55°E) collected by Mr. S.W. Bruce on an unnamed vessel were described by Carpenter (1898). The specimens reported from Franz-Josef Land are listed in Table 7. The collections included 3 families, 3 genera and 11 species.

The Danish *Ingolf* Expedition (Fig. 1) consisting of two voyages in 1895 and 1896, included collections made in the Davis Strait between Greenland and Canada, the coastal waters of Iceland, Jan Mayan Island, the Faroe Islands, and the far Western Kara Sea (Table 8). Four families, 9 genera and 33 species are reported including 8 new to science. The contribution to new taxa is small, but the increase in geographic distribution is significant (Table 8) (Meinert, 1899).

The *Southern Cross* (Fig. 2) Expedition, also named the British Antarctic Expedition, 1899-1900 was privately funded by Sir George Newness. The expedition leader was Carsten Egeberg Borchgrevink, and the ship's captain was William Colbeck (Rice, 1986). This cruise produced only one pycnogonid species, *Nymphon australe* Hodgson, 1902 in the family Nymphonidae (Hodgson, 1902). It should be noted that *N. austral* is a common species with a circumpolar distribution in the Antarctic seas. This expedition was a precursor to the much more ambitious and productive expeditions to the Antarctic in the first decades of the twentieth century.

Pycnogonida were collected from the northern Pacific on a steam ship named the *George W. Elder* (Cole, 1904). This vessel was chartered by Edward Harriman for a privately funded expedition of two months duration starting May 31, 1899. Harriman, a railroad tycoon, brought twenty-six experts along including two photographers, an artist, and a writer. The expedition studied the coastal waters of Alaska and the East coast of Siberia. One hundred and eight specimens of pycnogonids were collected including 3 families, 10 genera and 25 species (see Table 9).

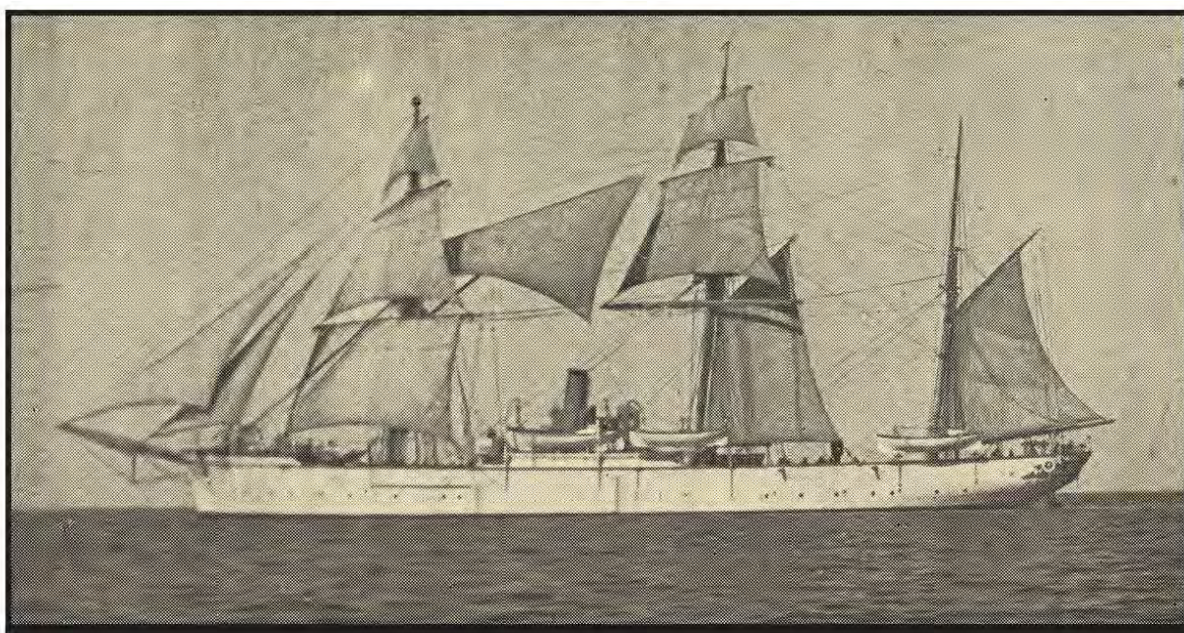
In the years 1901 to 1904 Robert Falcon Scott led an expedition to the Antarctic to locate the South Magnetic pole, which at that time was located on the Antarctic continent west of The Ross Sea and South of Australia (Hodgson, 1902, 1907; Rice, 1986). The expedition party included the biologist T. V. Hodgson, who collected pycnogonids from the sea near the *RRS Discovery* (Fig. 3). During the expedition, the ship was frozen in from the austral autumn of 1902 until being cut free in the summer of 1904 (Hodgson, 1908; Rice, 1986).

Hodgson's analysis of his collections from the Ross Sea on *RRS Discovery* included 10 families, 22 genera and 67 species (see Table 10). These also included collections from the *Southern Cross* Expedition (Table 10). In addition to the taxa listed in Table 10, two genera *Austrodecus*-1 species, and not *Austrodecus*-1 species, are not currently recognized in World Register of Marine Species WoRMS (Hodgson, 1902, 1908; WoRMS Editorial Board, 2023).

The *Siboga* (Fig. 4) Expedition (March 7, 1899 to February 27, 1900) (Captain Gustaaf Frederik Tydeman was in command) surveyed benthic and planktonic flora and fauna in the East Indies (8°S to 6°N and 110°E to 133°E including the coastal waters of the Dutch owned islands in this area, Java, Sumbawa, Flores, Soemba, Timor, Roma, Boeroe, Ceram, Misroi, New Guinea, Soela Eilanden, Celebes, Tawi, Soeloe, and Borneo (Lowman, 1908; van Aken, 2005).

**Table 4** the depth distribution of Families, genera and species of the Pycnogonida from *HMS Challenger* and the paddle steamer *Knight Errant* (Hoek, 1881b).

Shore	Family Ammotheidae <i>Tanystylum brevipes</i> Hoek.
Shore	Family Ascorhynchoidea <i>Hannonia typica</i> Hoek.
12 to 36 m	Family Phoxichilidiidae <i>Phoxichilidium Fluminense</i> Kröyer.
33 to 219 m	Family Nymphonidae <i>Nymphon brachyrhynchus</i> Hoek.
46 to 219 m	Family Nymphonidae <i>Nymphon fuseum</i> Meirs.
69 m	Family Ascorhynchidae <i>Ascorhynchus minutus</i> Hoek.
69	Family Pallenidae <i>Pallene longuida</i> Hoek.
69 m	Family Pallenidae <i>Pallene laevis</i> Hoek.
69 to 219 m	Family Pallenidae <i>Pallene australiensis</i> Hoek.
82, 101, 320 m	Family Phoxichilidiidae <i>Phoxichilidium patagonicum</i> Hoek.
97 m	Family Pycnogonidae <i>Pycnogonium litoralae</i> Hoek.
101, 128, 219 m	Family Colossendeidae <i>Colossendeis Megalonyx</i> Hoek.
151 m	Family Nymphonidae <i>Nymphon brevicollum</i> Hoek.
151 to 987 m	Family Nymphonidae <i>Nymphon grossipes</i> Hoek.
219 m	Family Colossendeidae <i>Colossendeis robusta</i> Hoek.
274 m	Family Ascorhynchidae <i>Ascorhynchus orthorhynchus</i> Hoek.
653 to 988 m	Family Nymphonidae <i>Nymphon robustum</i> Hoek.
732 to 2926 m	Family Colossendeidae <i>Colossendeis leptorhynchus</i> Hoek.
942, 969, 988 m	Family Nymphonidae <i>Nymphon strömii</i> Kröyer.
988 m	Family Nymphonidae <i>Nymphon macronyx</i> G. O. Sars.
988 m	Family Colossendeidae <i>Colossendeis proboscidea</i> Sab., sp.
1097 m	Family Phoxichilidiidae <i>Phoxichilidium patagonicum</i> var. <i>elagans</i> , Hoek.
1097 m	Family Phoxichilidiidae <i>Phoxichilidium insigne</i> Hoek.
1280 m	Family Pallenidae <i>Oorhynchus aucklandia</i> Hoek.
1509 m	Family Nymphonidae <i>Nymphon perliicidum</i> Hoek.
2012 m	Family Nymphonidae <i>Nymphon lonjicoxa</i> Hoek.
2012 m	Family Nymphonidae <i>Nymphmi compadum</i> Hoek.
2286 m	Family Colossendeidae <i>Colossendeis minuta</i> Hoek.
5215 m	Family Ascorhynchidae <i>Ascorhynchus glaber</i> Hoek.
2515 to 2926 m	Family Nymphonidae <i>Nymplion hamatum</i> Hoek.
3064 m	Family Colossendeidae <i>Colosaendeis gigas</i> Hoek.
3064 m	Family Colossendeidae <i>Colossendeis gracilis</i> Hoek.
2926 to 3567 m	Family Phoxichilidiidae <i>Phoxichilidium pilosium</i> Hoek.
3064 m	Family Nymphonidae <i>Nymphon meridionale</i> Hoek.
3064 m	Family Phoxichilidiidae <i>Phoxichilidium oscitans</i> Hoek.
3429 M	Family Phoxichilidiidae <i>Phoxichilidium mollissimum</i> Hoek.
3951 m	Family Nymphonidae <i>Nymphon procerum</i> Hoek.
4070 m	Family Nymphonidae <i>Nymphon longicollum</i> Hoek.
4070 m	Family Colossendeidae <i>Colossendeis media</i> Hook.
4847 m	Family Colossendeidae <i>Colossendeis hrevipes</i> Hoek.



***Danish Ingolf***

**Fig. 1** The Danish *Ingolf* used in studying the fauna in the seas between Canada and Greenland as well as the fauna of Iceland. Pycnogonida. From *The Danish Ingolf Expedition 3, Buscano Luna* (F. Duyer), Printers to the Crown (1899), Copenhagen, Denmark.



***Southern Cross***

**Fig. 2** The *Southern Cross* on the Derwent River. Unknown author. From the State Library of Tasmania - Image Number: AUTAS001126071802.

**Table 5** The families, genera, and species from the *Williem Barents* (Hoek, 1882b).

Families	Genera and species
Ascorhynchidae	genus <i>Ascorhynchus</i> -1 species, genus <i>Zetes</i> -1 species.
Colossendeidae	genus <i>Colossendeis</i> -2 species,
Pallenidae	genus <i>Pallene</i> -4 species.
Nymphonidae	genus <i>Nymphon</i> -13 species.
Phoxichilidiidae	genus <i>Phoxichilidium</i> -2 species, genus <i>Phoxichilus</i> -1 species.
Pycnogonidae	genus <i>Pycnogonum</i> -1 species.

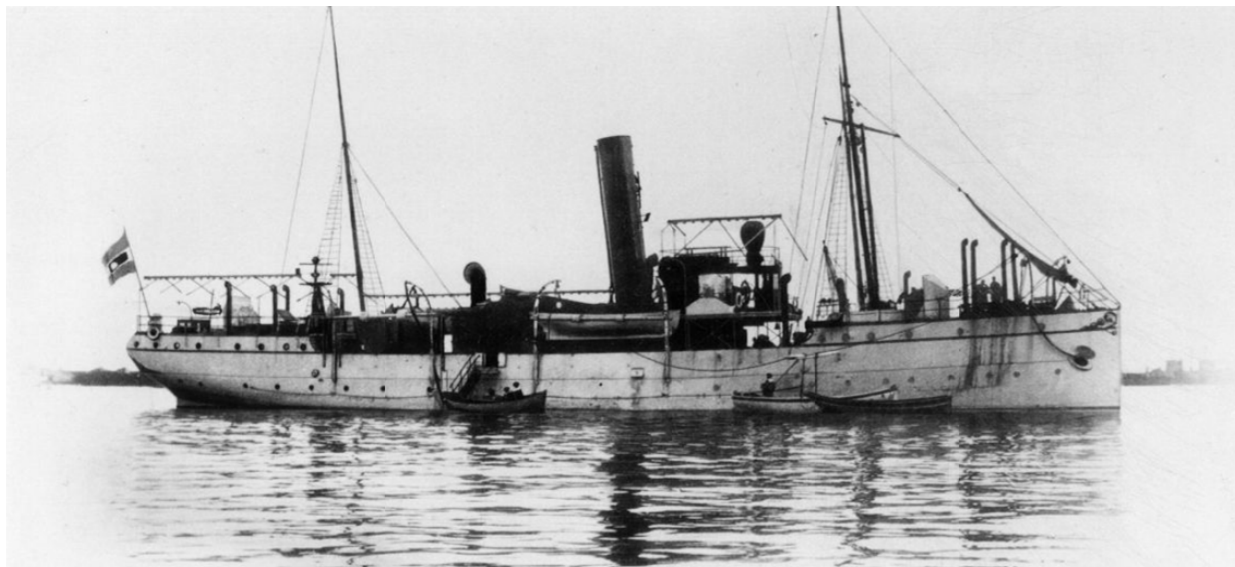
The expedition lead scientist was Max Webber. It should also be noted that this vessel's survey was one of the most thorough samplings of tropical forms and produced many families and genera. Only the *RRS Discovery*, *Albatross*, and *Blake* collections in the Ross Sea, the coastal waters of Japan and the western North Atlantic respectively exceeded it in terms of number of families and genera (Lowman, 1908; Hedgepeth, 1948, 1949). The collections from 323 stations which included 8 families 15 genera and 62 species are listed in (Table 11) (Lowman, 1908; van Aken, 2005).

The Scottish National Antarctic Expedition was conducted on the auxiliary barque-rigged steam ship *Scotia* from 1902 to 1904 in the Waddell Sea. The *Scotia* was under the command of Captain Thomas Robertson and the expedition lead scientist was William Spiers Bruce. The collections included pycnogonids from 8 families, 19 genera and 73 species (Table 12) (Hodgson, 1908; Rice, 1986).



**Fig. 3** The *RRS Discovery* in Australia in the 1920s. Source: John Oxley Library, State Library of Queensland. Black and white negative Number: 130494.





*The Dutch Siboga*

**Fig. 4** The Dutch cruiser *Siboga* as she appeared in 1899. From Lowman, J. C. C. 1908. Die Pantopoden Der Siboga Expedition. Buchhandlung und druckerei vormals E. J. Brill, Leiden.

The *Terra Nova* (Captain M. Mackay in command) transported Robert Falcon Scott to West Victoria Land, Antarctica. This was Scott's unsuccessful and fatal attempt to be the first to reach the South Geographic Pole. The *Terra Nova* transported Scott's team to the Antarctic continent in the austral summer of 1910 and recovered the survivors in the austral summer of 1913 (Calman, 1915; Rice, 1986). The collections of the *Terra Nova* Expedition, 1910 to 1913, came almost exclusively from the Ross Sea. The only exception was one specimen (*Colossendeis megalonyx* Hoek, 1881) from the Falkland Islands. The collections (Table 13) included 7 families, 11 genera and 42 species (Calman, 1915; Rice, 1986).

**Table 6** The families, genera, and species from the *Voringen* (Sars, 1891).

Families	Genera and species
Ammotheidae	genus <i>Ammothea</i> -2 species.
Colossendeidae	genus <i>Colossendeis</i> -2 species.
Eurycyidae	genus <i>Eurycyde</i> -1 species, genus <i>Ascorhyncus</i> -1 species.
Nymphonidae	genus <i>Nymphon</i> -19 species, genus <i>Chaetonymphon</i> -5 species, genus <i>Boreonymphon</i> -1 species.
Pallenidae	genus <i>Pallene</i> -2 species, genus <i>Pseudopallene</i> -2 species, genus <i>Cordylochele</i> -3 species.
Phoxichilidae	genus <i>Phoxichilidum</i> -1 species, genus <i>Anoplodactylus</i> -2 species.
Pycnogonidae	genus <i>Pycnogonum</i> -2 species.

**Table 7** The families, genera, and species of the Pycnogonida from Franz-Josef Land (Carpenter, 1898).

Families	Genera and species
Colossendeidae	<i>Anomorayncrus</i> -1 species.
Nymphonidae	Nymphon-9 species.
Pallenidae	<i>Pseudopallene</i> -1 species.

**Table 8** The families, genera, and species of the Pycnogonida from the Danish *INGOLF* (Meinert, 1899).

Families	Genera and species
Ascorhynchidae	genus <i>Ascorhynchus</i> -1 species.
Colossendeidae	genus <i>Colossendeis</i> -5 species.
Nymphonidae	genus <i>Nymphon</i> -17 species, genus <i>Paranymphon</i> -1 species. genus <i>Pallene</i> -3 species; <i>Cordylochele</i> -2 species, genus <i>Pseudopallene</i> -1 species, genus <i>Pallenopsis</i> -2 species.
Pycnogonidae	genus <i>Pycnogonum</i> -1 species.

Chronologically the last scientific expedition included in this study was the Australian Antarctic Expedition from 1911-1914. The scientific results of this expedition were published twenty-four years after the completion of the collecting voyage (Gordon, 1938). This expedition was organized and led by D. Mawson, who was transported from Australia to Antarctica on the barque-rigged auxiliary stemmer *Aurora* where he intended to explore the region of Antarctic claimed by Australia from Cape Adare westward to Gaussberg. At the same time, the *Aurora* cruised along the Antarctic coast making biological collections and oceanographic observations (Gordon, 1938; Rice, 1986).

The collections on this research project came from Commonwealth Bay, King George Land and Macquari Land. Pycnogonida from 6 families, 11 genera and 37 species were included in the collections of the Australian Antarctic Expedition. The genus *Colossendeis* is represented by 11 species, one of which is new (Table 14). The genus *Ammothea*, represented by 6 species is the second most diverse genus.

Alexander Agassiz an Ichthyologist and the son of the Harvard University naturalist, Jean Louis Randolph Agassiz, was the lead scientist on a research cruise to study the western North Atlantic Ocean Atlantic [20° N to 40°N and 30°W to 90° W] in the 1870s on the Coast and geodetic Survey steamer *Blake* (Hedgepeth, 1948).

**Table 9** The families, genera, and species from the *George W. Elder* (Cole, 1904).

<b>Families</b>	<b>Genera and species</b>
Ammotheidae	<i>Ammothea</i> -4 species, genus <i>Achelia</i> -4 species, <i>Ammothella</i> -4 species, <i>Tanystylum</i> -2 species, <i>Clotenia</i> -1 species, <i>Lecythorhynchus</i> -2 species.
Phoxichilidiidae	<i>Phoxichilidium</i> -5 species, <i>Holosoma</i> -1 species, <i>Anoplodactylus</i> -1 species.
Pycnogonidae	<i>Pycnogonum</i> -1 species.

**Table 10** The families, genera, and species of Pycnogonida from the *RRS Discovery*.

<b>Families</b>	<b>Genera and species</b>
Ammotheidae	<i>Ammothea</i> -7 species, <i>Achelia</i> -3 species, <i>Austroaptus</i> -2 species, <i>Astrodecus</i> -1 species, <i>Austroraptus</i> -1 species.
Callipallenidae	<i>Pseudopallene</i> -2 species.
Colossendeidae	<i>Colossendeis</i> -10 species, genus <i>Colossendeis</i> -4 species.
Endeidae	<i>Endeis</i> -1 species.
Pallenidae	<i>Austropallene</i> -3 species.
Pallenopsisidae	<i>Pallenopsis</i> -4 species.
Nymphonidae	<i>Nymphon</i> -9 species, <i>Chaetonymphon</i> -4 species, <i>Pentanymphon</i> -1 species, <i>Leionymphon</i> -5 species.
Phoxichilidae	<i>Pallenopsis</i> -4 species, <i>Phoxichilidium</i> -1 species, <i>Phoxichilus</i> -1 species.
Pycnogonidae	<i>Pycnogonium</i> -1 species.
Rhynchothoracidae	genus <i>Rhynchothorax</i> -1 species.

The Pycnogonids collected by Agassiz were archived in the U. S. National Museum of Natural History (NMNH). Some seventy years later Joel Hedgepeth, a Curator at the NMNH analyzed the collections (Hedgepeth, 1948). The collections of the *Blake* made between 1875 to 1878 came from the western North Atlantic and the Western Tropical Atlantic, Gulf of Mexico and Hudson's Bay (Table 15). A total of 8 families, 24 genera and 74 species were reported (Hedgepeth, 1948).

In the years 1900 and 1906 the U.S. Commission of Fish and Fisheries (a predecessor of the National Marine Fisheries Service) Steamer *Albatross*, collected samples of the marine life in the coastal waters of Japan, the Kamchatka Peninsula, the Sea of Japan (East Sea), and Russian coastal waters (Table 16). As in the case of the collections made by the steamer *Blake* in the 1880s, the pycnogonid specimens were archived in the National Museum of Natural History (NMNH) in Washington, DC. Joel Hedgepeth, a curator of the NMNH who did not participate in the cruise analyzed the collections. This publication appeared 43 years after the date of the last collections of sea spiders in Japanese waters. A total of 9 families, 23 genera and 71 species were reported (Table 16) (Hedgepeth, 1949). It was, however, along with the brief publication by Cole (1904) one of the earliest English language publications on the Pycnogonida in the Western Pacific Ocean (Hedgepeth, 1949).

**Table 11** The families, genera, and species of Pycnogonida from the Dutch gunboat *Siboga* (Lowman, 1908; Van Akin, 2005).

Families	Genera and species
Ammonotheidae	<i>Nymphopsis</i> -3 species, <i>Scipiolous</i> -1 species, <i>Ammonothea</i> -5 species, <i>Cilunculus</i> -2 species.
Ascorhynchidae	<i>Ascorhynchus</i> -5 species.
Callipallenidae	<i>Parapallene</i> -10 species.
Colossendeidae	<i>Colossendeis</i> -5 species, <i>Eurycyde</i> -2 species, <i>Rhopalorhynchus</i> -1 species.
Pallenidae	<i>Pallene</i> -6 species.
Pallenopsidae	<i>Pallenopsis</i> -6 species.
Phoxichilidiidae	<i>Phoxichilidium</i> -2 species, genus <i>Phoxichilus</i> -3 species <i>Anoplodactylus</i> -6 species.
Pycnogonidae	<i>Pycnogonum</i> -5 species.

**Table 12** The families, genera, and species of Pycnogonida from the *Scotia* (Hodgson, 1908).

Families	Genera and species
Ammonotheidae	<i>Nymphopsis</i> -3 species, <i>Scipiolous</i> -1 species, <i>Ammonothea</i> -5 species, <i>Cilunculus</i> -2 species.
Ascorhynchidae	<i>Ascorhynchus</i> -5 species.
Callipallenidae	<i>Parapallene</i> -10 species.
Colossendeidae	<i>Colossendeis</i> -5 species, <i>Eurycyde</i> -2 species, <i>Rhopalorhynchus</i> -1 species.
Pallenidae	<i>Pallene</i> -6 species.
Pallenopsidae	<i>Pallenopsis</i> -6 species.
Phoxichilidiidae	<i>Phoxichilidium</i> -2 species, <i>Phoxichilus</i> -3 species, <i>Anoplodactylus</i> -6 species.
Pycnogonidae	<i>Pycnogonum</i> -5 species.

## 2 Discussion

The results from the era of single ship research projects established a framework on which our current knowledge is based. Research on taxonomic diversity and biogeography of the Pycnogonida continues to this day and much has been learned since 1949 when the last analysis of the earlier data was published.

The taxonomy of the Pycnogonida was developed to include 13 families based solely on external morphology. This we should remember was state-of-the-art taxonomy in the period 1870 to 1948. Navigation was at best good to a few nautical miles under ideal conditions, so geographic distribution was rarely better than to a regional sea or an island (Table 17).

In the course of describing the specimens collected by the thirteen cruises covered in this report, biologists proposed thirteen families in the Order Pycnogonida Latreille, 1810. Ten families, Ammonotheidae Dohrn 1881,

Ascorhynchidae Hoek 1881, Colossendeidae Hoek, 1881, Callipallenidae Hilton 1942, Endeidae Norman, 1908, Nymphonidae Wilson 1878, Pallenopsidae Fry 1978, Phoxichilidiidae Sars 1891, Pycnogonidae Wilson 1881, and Rhynchothoracidae Thompson 1909 are recognized by twenty-first century researchers who employ external morphology as well as molecular data such as mitochondrial DNA and Cladistics (Table 17) (Arango and Wheeler, 2007; WoRMS Editorial Board, 2023).

**Table 13** The families, genera, and species of Pycnogonida from the *Tera Nova* (Calman, 1915).

<b>Families</b>	<b>Genera and species</b>
Ammotheidae	<i>Ammothea</i> -1 species, <i>Achelia</i> -3 species, <i>Pallenopsis</i> -4 species, <i>Phoxichilidiwn</i> -1 species, <i>Austroraptus</i> -1 species, <i>Tanystylum</i> -12 species.
Austrodecidae	<i>Austrodecus</i> -1 species, <i>Ascorhynchus</i> -1 species, <i>Rhynchothorax</i> -1 species.
Callipallenidae	<i>Pallene</i> -1 species, <i>Pseudopallene</i> -2 species, <i>Pallenopsis</i> -7 species.
Colossendeidae	<i>Colossendeis</i> -4 species, <i>Decolopoda</i> -3 species <i>Austroraptuspolaris</i> -2 species, <i>Austrodecus</i> -1 species, <i>Rhynchothorax</i> -1species.
Endeidae	<i>Phoxichilus</i> -1 species.
Nymphonidae	<i>Pentanymphton</i> -1 species, <i>Nymphon</i> -15 species.
Pycnogonidae	<i>Pycnogonum</i> -4 species, <i>Chetonymplicn</i> -6 species, <i>Chmtonymphton</i> -2 species, <i>Pentanymphton</i> -1 species, <i>Leionymphmi</i> -8 species, <i>Chsetonymplicn</i> -6 species, <i>Austropallene</i> -3 species, <i>Phoxichilidium</i> -1 species, <i>Endeis</i> -1 species.
Phoxichilidae	<i>Anoplodactylus</i> -2 species.

**Table 14** The families, genera, and species from the *Aurora* (Gordon, 1938).

<b>Families</b>	<b>Genera and species</b>
Ammotheidae	<i>Ammothea</i> -6 species, <i>Achelia</i> -4 species, <i>Austroraptus</i> -2 species.
Colossendeidae	<i>Colossendeis</i> -11 species (One new to science).
Endeidae	<i>Endeis</i> -1 species.
Nymphonidae	<i>Pentanymphton</i> -1 species, <i>Nymphon</i> -2 species, <i>Heteronymphton</i> -1 species.
Phoxichilidae	<i>Austropallene</i> -3 species.
Phoxichilidiidae	<i>Pallenopsis</i> -5 species (One new to science), <i>Phoxichilidium</i> -1 species.

**Table 15** The Families, genera and species of Pycnogonida from the Coast and Geodetic Survey vessel *Blake* (Hedgepeth, 1949).

<b>Families</b>	<b>Genera and Species</b>
Ammonotheidae	<i>Achelia</i> -5 species, <i>Ammothella</i> -2 species, <i>Nymphopsis</i> -2 species, <i>Paranymphon</i> -1 species, <i>Ascorhynchus</i> -4 species, <i>Eurycyde</i> -1 species, <i>Ephyrogymna</i> -1 species, <i>Heterofragilia</i> -1 species, <i>Calypsopyenon</i> -1 species.
Colossendeidae	<i>Colossendeis</i> -6 species, <i>Pentacrossendeis</i> -1 species.
Endeidae	<i>Endeis</i> -1 species.
Nymphonidae	<i>Nymphon</i> -13 species.
Pallenidae	<i>Callipallene</i> -4 species, <i>Pseudopallene</i> -1 species, <i>Cordylochele</i> -2 species, <i>Pallenopsis</i> -4 species, <i>Pigrogromitus</i> -1 species.
Phoxichilidiidae	<i>Phoxichilidium</i> -1 species, <i>Halosoma</i> -1 species, <i>Anaplodactylus</i> -15 species.
Pycnogonidae	<i>Pycnogonum</i> -3 species, <i>Pentapycnon</i> -1 species.
Tanystylidae	<i>Tanystylum</i> -2 species.

**Table 16** The families, genera, and species of Pycnogonida from the Fisheries Biology Research Ships *Albatross* (Hedgepeth, 1948).

<b>Families</b>	<b>Genus and species</b>
Amotheidae	<i>Achelia</i> -8 species, <i>Ammothella</i> -2 species.
Ascorhynchidae	<i>Ascorhynchus</i> -6 species, genus <i>Nymphonella</i> -1 species; <i>Nymphopsis</i> -1 species, <i>Cilunculus</i> -1 species, <i>Cilunculus</i> -1 species.
Colossendeidae	<i>Colossendeis</i> -7 species.
Endeidae	<i>Endeis</i> -1 species.
Nymphonidae	<i>Nymphon</i> -20 species.
Pallenidae	<i>Callipallene</i> -1 species, <i>Pallenopsis</i> -3 species, <i>Decachela</i> -1 species, <i>Callipallene</i> -2 species, <i>Propallene</i> -1 species, <i>Pallenopsis</i> -4 species, <i>Decachda</i> -1 species (2 species in this family were new to science).
Phoxichilidiidae	<i>Phoxichilidium</i> -1 species, <i>Anoplodactylus</i> -2 species, <i>Halosoma</i> -1 species, <i>Pycnosoma</i> -1 species.
Pycnogonidae	<i>Pycnogonum</i> -5 species (Hedgepeth, 1949).
Tanystylidae	<i>Tanystylum</i> -1 species.

Three additional families Tanystylidae (Hedgepeth, 1949), Pallenidae (Hoek, 1881b), and Eurycyidae (Sars, 1891) were also proposed, but are not now recognized as valid taxa (Arango and Wheeler, 2007; WoRMS Editorial Board, 2023). The Tanystylidae are now included in the Ammonotheidae, the Pallenidae are now included in the Callipallenidae, and the Eurycyidae are now in the family Ascorhynchidae (WoRMS Editorial Board, 2023).

Two families, Phoxichilidiidae, and Colossendeidae are found in all seas and both coastal and abyssal depths. The families Callipallenidae, Endeidae, Pallenopsidae, Rhynchothoracidae, and were absent from the

collections made by *HMS Challenger* thus their vertical distribution had not been documented by the early twentieth century.

**Table 17** Summarizing the geographic distribution of thirteen Pycnogonid families originally described from the 13 cruises included in this review. The Asterisk indicates the family is currently recognized as valid in WoRMS.

Family	Arctic	Antarctic	Boreal Seas	Tropical Seas	Abyss Sea	Continental Shelf
Ammotheidae*	X	X	X	X		X
Ascorhynchidae*	X		X	X		X
Callipallenidae*	X					
Colossendeidae*	X	X	X	X	X	X
Endeidae*	X	X				
Eurycyidae	X					
Nymphonidae*	X	X	X	X		X
Pallenidae	X	X	X	X	X	X
Pallenopsidae*					X	
Pycnogonidae*	X	X	X	X		X
Phoxichilidiidae*	X	X	X	X	X	X
Rhynchothoracidae*			X			
Tanystylidae		X				

The Family Nymphonidae are cold water animals being found in all seas except the shallow tropical waters. They make-up a sizable portion of the Pycnogonida in Arctic and Antarctic areas (Tables 2-4). The sampling techniques and survey areas covered by each cruise in this history were too varied to allow any meaningful comparisons to be made on relative geographic abundance. Only the *HMS Challenger* data on vertical abundance and occurrence allow any such conclusions to be drawn (Table 1 and 3).

The Laptev Sea, East Siberian Sea, Chukchi Sea, the Pacific west coast of North America, south of Alaska, Central America, and the West Coast of South America were not sampled during this epoch of single ship expeditions. The *HMS Challenger* transited the Pacific principally north of the equator from Japan to Hawaii and south through the Polynesian Islands of the central Southeast Pacific.

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