Fld Stud. (1971), 3, 455-480

LITTORAL PYCNOGONIDS OF THE BRITISH ISLES

By P. E. KING and G. B. CRAPP*

Department of Zoology, University College, Swansea and Marine Science Laboratories, Menai Bridge, Anglesey

1. Keys to the littoral pycnogonids of the British Isles are presented.

2. Brief notes concerning distribution, possible food sources and the validity of each species are included. The Nymphonidae are considered in relation to the species which occur in other parts of the Atlantic and evidence presented to demonstrate the validity of the three species *Nymphon gracile*, *N. rubrum* and *N. brevirostre*.

INTRODUCTION

THE Pycnogonida are a group of marine arthropods often referred to as sea-spiders. Although various affinities have been ascribed to the group, it is now generally agreed that they should have Class status. They are characterized by a body which is narrow and composed of a number of distinct segments. The front end bears the head or cephalon which has anteriorly a proboscis (Fig. 1), and on its dorsal surface there is a tubercle bearing four eyes. The first trunk segment is fused with the cephalon and the last segment has an anal process or abdomen. The appendages consist of palps, chelifores, ovigerous legs and ambulatory or natatory legs. The first two are not present in all species and the ovigerous legs usually only in the male, though in some species both sexes have them. Each body segment has a prominent lateral process with which the legs articulate. The legs, which in British species are eight in number, consist of three coxae, a femur, two tibias, a tarsus, a propodus and a terminal claw, with sometimes auxiliary claws associated with it or the propodus. The general biology of the class has been reviewed by Thompson (1909), Helfer and Schlottke (1935) and Fage (1949).

Hedgpeth (1954) divided the Class Pycnogonida (Latreille) into two orders, the Order Palaeopantopoda (Broili) containing the fossils *Palaeopantopus maucheri* and *Palaeoisopus problematicus*, and the Order Pantopoda (Gerstaecker) containing all the extant forms. This classification has the advantage that it recognizes the priority of Latreille's name, whilst retaining Gerstaecker's "Pantopoda", which has been widely adopted. The name "Podosomata", given by Leach (1815), has never found favour.

Hedgpeth divides the Pantopoda into eight families (Hedgpeth, 1947) and this basic division has been adopted in this study. Six of these families are represented in the fauna of British coasts.

Bouvier (1923) produced a key to the pycnogonids of the French coast, Giltay (1928) produced one for the coast of Belgium, and Schlottke (1932) for Heligoland. Hodge (1864), Thompson (1909), Hodgson (1910) and Halhed (1896) produced lists of species from various parts of the British Isles. Carpenter (1905) listed the species occurring on the coast of Ireland and Norman (1908) published a list of species from the temperate Atlantic and Arctic oceans. Pycnogonid records are included in the fauna lists from the Clare Island Survey (Carpenter, 1912), the Isle

* Present address: Department of Agriculture and Fisheries, Fisheries Division, 3 Cathal Brugha Street, Dublin 1.

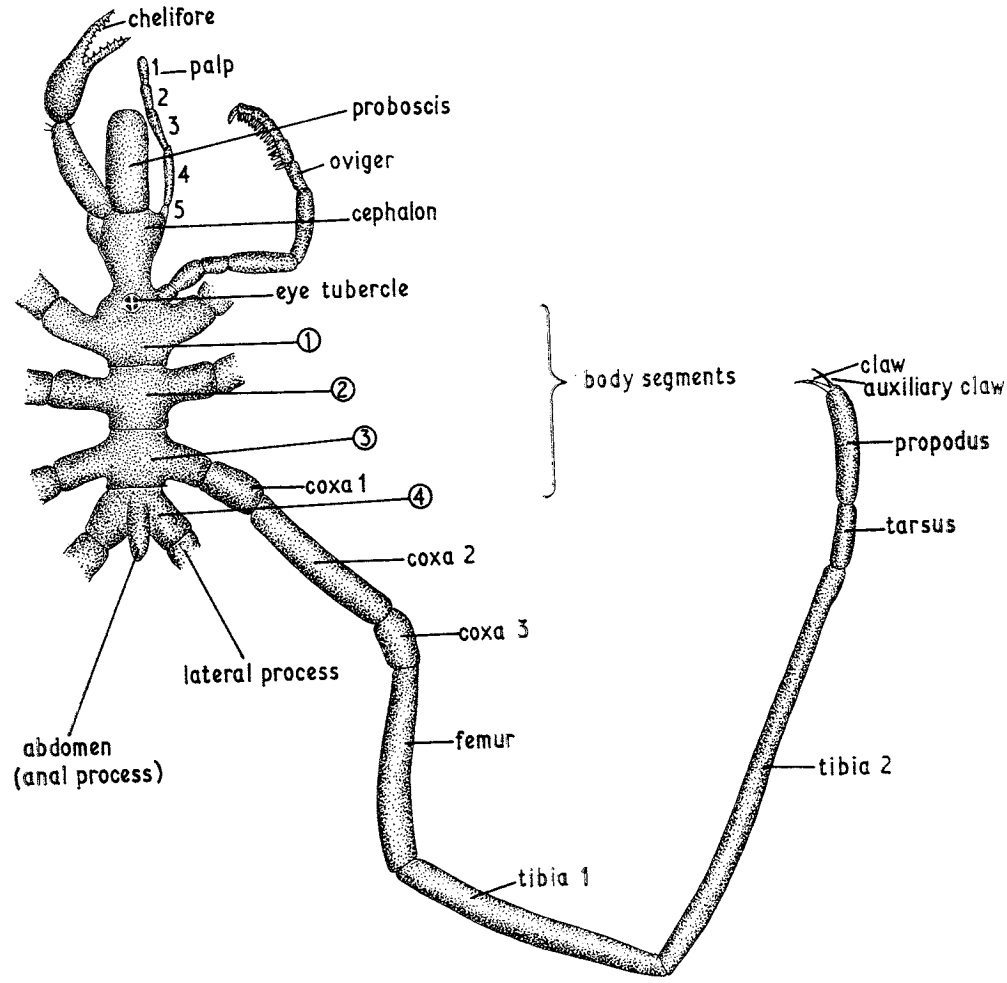

FIG. 1.
Diagram of a Pycnogonid with all legs except one removed, and only one of the paired ovigers, palps and chelifores represented. The parts used in the key are labelled. Specimens will be presented in this form in subsequent diagrams.

of Man (Bruce, Colman and Jones, 1963), Milford Haven (Crothers, 1966) and Plymouth (Marine Biological Association, 1957).

Eales (1950) produced a key covering some of the British species and Lebour (1947) reviewed the Phoxichilidiidae but no comprehensive key exists dealing with the British species alone. The purpose of the present work is to remedy this. The keys of Bouvier (1923), Lebour (1947) and Hedgpeth's (1948) key to the families have been consulted. The key presented in this study deals only with those species likely to be encountered on the shore and is accurate for adult forms only.

Pycnogonids were collected by scraping small seaweeds, hydroids, polyzoans and algal holdfasts from the shore. These were allowed to stand in bowls for several hours, then sorted in the laboratory and examined with a binocular microscope. Pycnogonids were most often found by their characteristic, sluggish movements.

Specimens were narcotized with a few drops of ethyl acetate added to the water

and dropped after 5–10 minutes into hot Bouin's fixative. In this way they were preserved in an extended condition, and could be kept in 70 per cent alcohol.

Slides were made by passing the animals through 90 per cent and absolute alcohol, and mounting in euparal or canada balsam.

Caution must be exercised in identifying some species, if the male specimens are not bearing eggs or larvae on their ovigers, or the females do not have eggs visible in their femurs. For an accurate identification of many species it is advisable to make a microscope-slide mount of them. In species such as *Achelia echinata* the use of a soft camel-hair brush before mounting, to remove adhering detritus is desirable, and makes the diagnostic characters easier to determine.

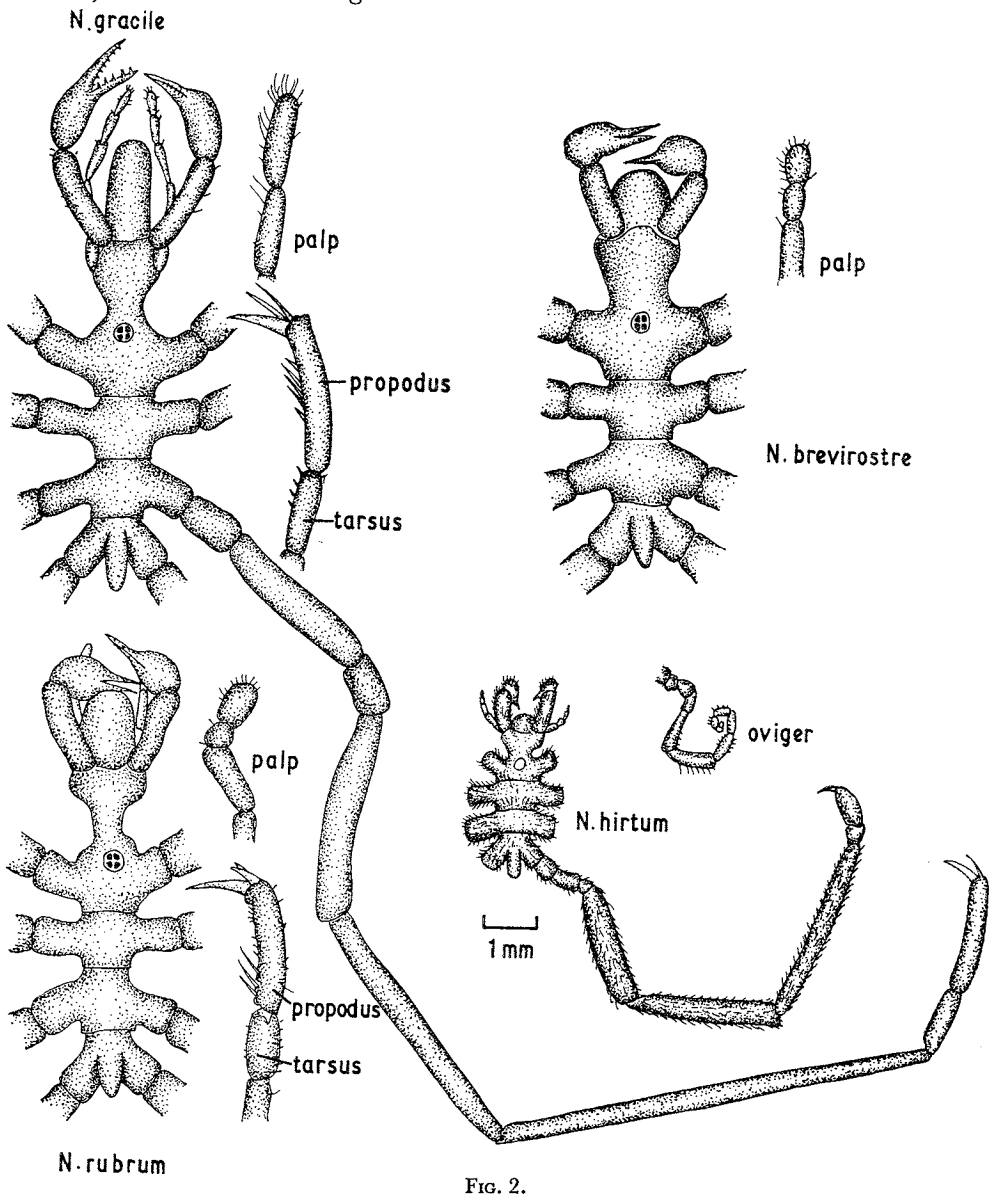

FIG. 2.
Diagrams showing diagnostic features of the Nymphonidae.

KEY TO FAMILIES

1. Chelifores and palpi present — 2
   Chelifores or palpi, or both, lacking — 3
2. Palpi 5-jointed: chelae conspicuous, over-reaching proboscis — *Nymphonidae* (Fig. 2)
   Palpi 8–9 jointed: chelae small, chelifores shorter than proboscis — *Ammotheidae* (Fig. 3)
3. Chelifores present, palpi lacking — 4
   Both chelifores and palpi lacking — 5
4. Ovigers 10-jointed, in both sexes — *Pallenidae* (Fig. 4)
   Ovigers 5–6 jointed, in male only — *Phoxichilidiidae* (Fig. 5 and 6)
5. Body slender, legs about twice as long as body. Auxiliary claws present. Ovigers 7-jointed, in male only — *Endeidae* (Fig. 7)
   Body stout; legs short, little longer than body. Auxiliary claws absent. Ovigers 9-jointed, in male only — *Pycnogonidae* (Fig. 8)

KEY TO SPECIES

Nymphonidae

1. Anal process longer than fourth pair of lateral processes. Body and legs covered with a thick pilosity (Fig. 2) — *Nymphon hirtum.* (Fabr.)
   Anal processes not longer than fourth pair of lateral processes. Body bare. Legs provided with spines — 2
2. Terminal and subterminal segments of palps equal in length (Fig. 2) — *Nymphon gracile* (Leach)
   Terminal segment of palp approximately twice as long as subterminal segment — 3
3. Length of segment 2 or 3 of trunk slightly greater than width (Fig. 2) — *Nymphon rubrum* (Hodge)
   Length of segment 2 or 3 of trunk slightly smaller than width (Fig. 2) — *Nymphon brevirostre* (Hodge)

Ammotheidae

1. Palps with nine segments. No coxal projections in male (Fig. 3) — *Achelia longipes* (Hodge)
   Palps with eight segments. Coxal projections present on the second coxae of the third and fourth pairs of legs in the male — 2
2. No articulations or sutures visible on the trunk (Fig. 3) — *Achelia laevis* (Hodge)
   Articulations or sutures separate at least two trunk segments — 3
3. Second trunk segment separated from first and third segments by articulations. Lateral processes and legs with spine-bearing projections (Fig. 3) — *Achelia echinata* (Hodge)
   Second trunk segment separated from the first and third by articulations with a feebly distinct suture between third and fourth segments. No spine-bearing projections on lateral processes and legs (Fig. 3) — *Achelia simplex* (Giltay)

Pallenidae

Central part of trunk segments two and three nearly as wide as long. Anterior part of cephalon almost twice as wide as neck (Fig. 4)
Callipallene brevirostris (Johnston)

Central part of trunk segments two and three nearly twice as long as wide. Anterior part of cephalon more than twice as wide as neck (Fig. 4)
Callipallene phantoma (Dohrn)

Phoxichilidiidae

1. Eye tubercle not projecting beyond cephalon. No protuberances on lateral processes. Propodus without cutting lamella. Ovigers with five or six segments (Fig. 5) 2

   Eye tubercle projects beyond cephalon. Protuberances present on lateral processes. Propodus with cutting lamella. Ovigers with six segments 5
2. Auxiliary claws fairly large and dorsally placed. Proboscis rounded at end, without angles (Fig. 5) 3

   Auxiliary claws small and laterally placed. Proboscis straight at end, with more or less distinct angles at corners 4
3. Abdomen about the same length as the lateral processes of last trunk segment. Heel of propodus armed with three or four large single teeth, and one pair of smaller teeth (Fig. 5)
   Phoxichilidium femoratum (Rathke)

   Abdomen about twice as long as the lateral processes of the last trunk segment. Heel of propodus armed with two large single teeth, and one pair of smaller teeth: occasionally with a third large single tooth on the proximal part of the heel, very close to the adjacent tooth (Fig. 5)
   Phoxichilidium tubulariae (Lebour)
4. Ovigers with five segments. Proboscis straight at the end with slight angles at the corners. Abdomen slightly longer than fourth pair of lateral processes (Fig. 6) *Phoxichilidium virescens* (Hodge)

   Ovigers with six segments. Proboscis with conspicuous angles at corners. Abdomen more than twice the length of the lateral processes of the last trunk segment (Fig. 6) *Anoplodactylus angulatus* (Dohrn)

   Anterior part of cephalon long and narrow, overhanging posterior half of proboscis. Auxiliary claws small and mounted laterally. Protuberances on lateral processes without spine at apex. Cutting lamella of propodus short, preceded by 4–6 small teeth (Fig. 6) *Anoplodactylus petiolatus* (Kröyer)

   Cephalon short and wide, does not overhang proboscis. Auxiliary claws absent. Protuberances on lateral processes with spine at apex. Cutting lamella of propodus long, preceded by 1–2 small teeth (Fig. 6)
   Anoplodactylus pygmaeus (Hodge)

Endeidae

Only one British species: *Endeis spinosus* (Montagu) (Fig. 7)

Pycnogonidae

Only one British species: *Pycnogonum littorale* (Ström) (Fig. 8)

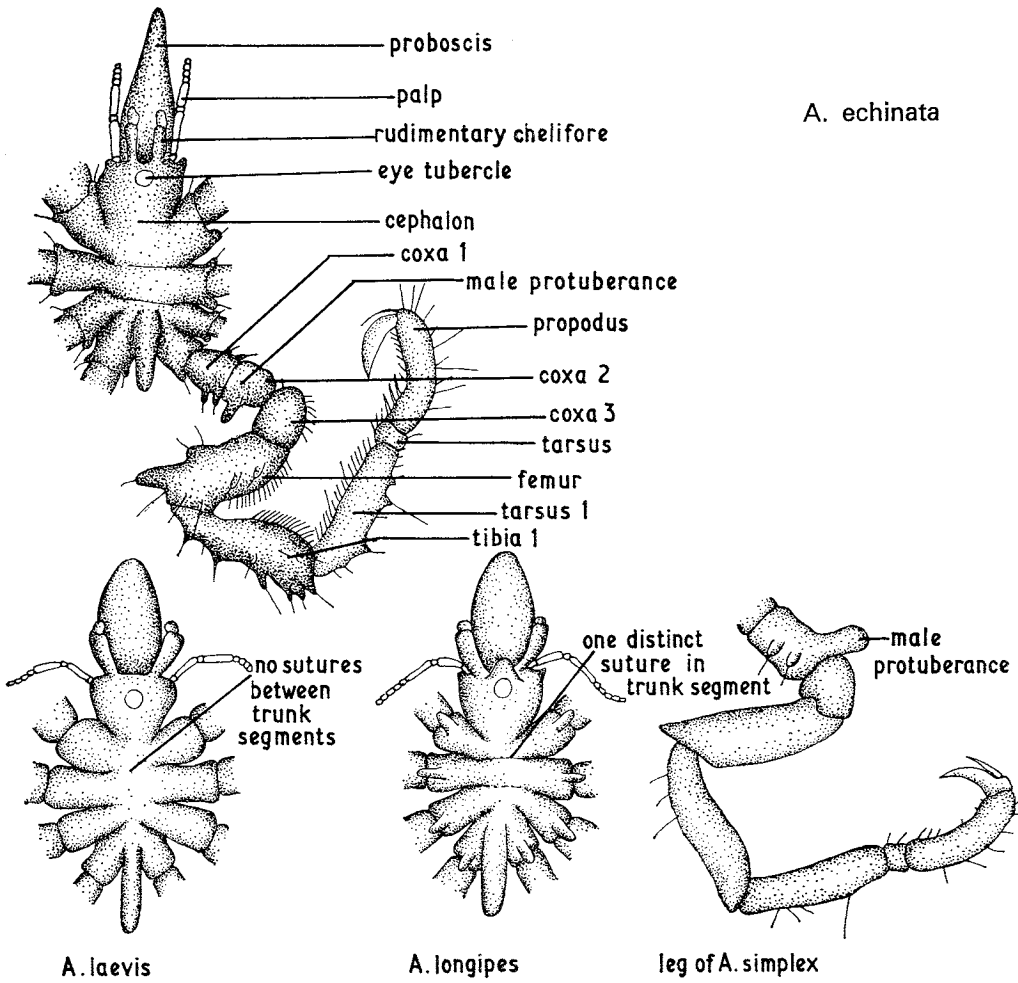

FIG. 3.
Diagram to show the diagnostic characters of the Ammotheidae.

NOTES

Nymphonidae

Bouvier (1932) listed six species of *Nymphon* from the French coast, *N. rubrum* (Hodge), *N. megalops* (Sars), *N. grossipes* (Fabr), *N. stromii* (Kröyer), *N. gracile* (Leach) and *N. brevirostris* (Hodge). Giltay (1928) published a key for the Belgian species and listed *N. gracile*, *N. rubrum* and *N. brevirostre*. Schlottke (1932) wrote a key for the pycnogonids of Heligoland and included *N. grossipes*, *N. rubrum* and *N. brevirostre*. Lists of species from parts of the British Isles have been produced. Sars (1888) published a list entitled "Pycnogonida borealia and arctica" in which he listed *N. gracile*, *N. rubrum*, *N. brevitarse* (Kröyer), *N. gracile* (Lilljeborg), *N. grossipes* (Fabr.), *N. nixtum* (Kröyer), *N. microrhynchum* (Sars), *N. slinteri* (Hoek), *N. longitarse* Kröyer, *N. leptocheles* (Sars), *N. stromii*, *N. gracilipes* (Heller), *N. elegans* (Hansen), *N. macrum* (Wilson), *N. micronyx* (Sars), *N. longimanum* (Sars), *N. serratum* (Sars), *N. megalops* (Sars), *N.* (*Chaetonymphon*) *hirtum* (Fabr.). Norman (1908) pro-

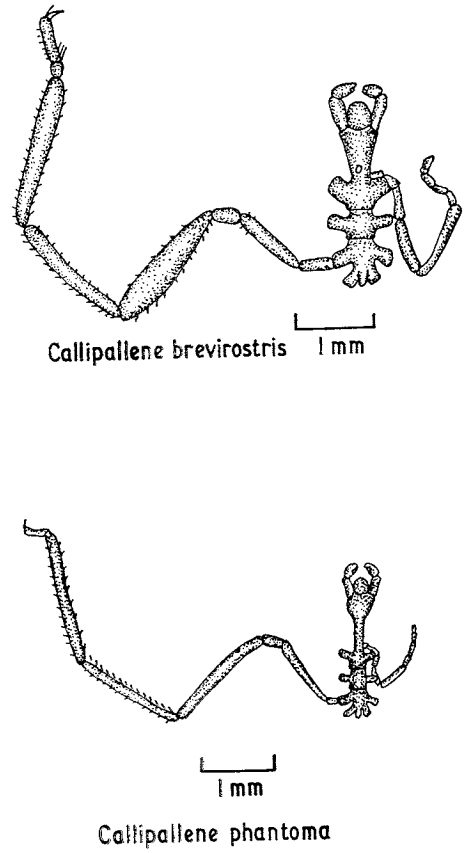

FIG. 4.
Diagram of the diagnostic features of the Pallenidae.

duced a list from the Temperate Atlantic and Arctic oceans which added several species to that of Sars (1888). Stephenson (1935) dealt with the Pycnogonida from Norway and adjacent waters and Carpenter (1901, 1912) with those of the Irish coast. Other fauna lists have been produced by Hodge (1864), Halhed (1896), Thompson (1909), Bruce, Colman and Jones (1963), Crothers (1966), and by the Marine Biological Association for Plymouth (1957).

Many of these lists were compiled with the keys listed, with assistance perhaps from keys by Eales (1950) and Helfer and Schlottke (1935). However, Sars (1888) noted some confusion between *N. gracile* and *N. rubrum* and Giltay (1928) also commented on this.

Mobius (1901) grouped a number of Nymphon species together. These were *N. grossipes*, *N. gracile*, *N. mixtum*, *N. glaciale*, *N. rubrum* and *N. piliferum* (Carpenter). Giltay (1928) basing his evidence on (a) the proportions of the palp segments, (b) the ratio of the length of the tarsus and propodus and (c) the arrangement of spines on the propodus stated that on the Belgian coast *N. gracile*, *N. rubrum* and *N. brevirostre* are distinct species.

Working on pycnogonids from the Polar seas of the U.S.S.R. Losina-Losinsky (1935) considered that *Nymphon brevirostre* was an especially strongly varying species and that *N. glaciale*, *N. rubrum* and *N. brevirostre* represent forms of the same species

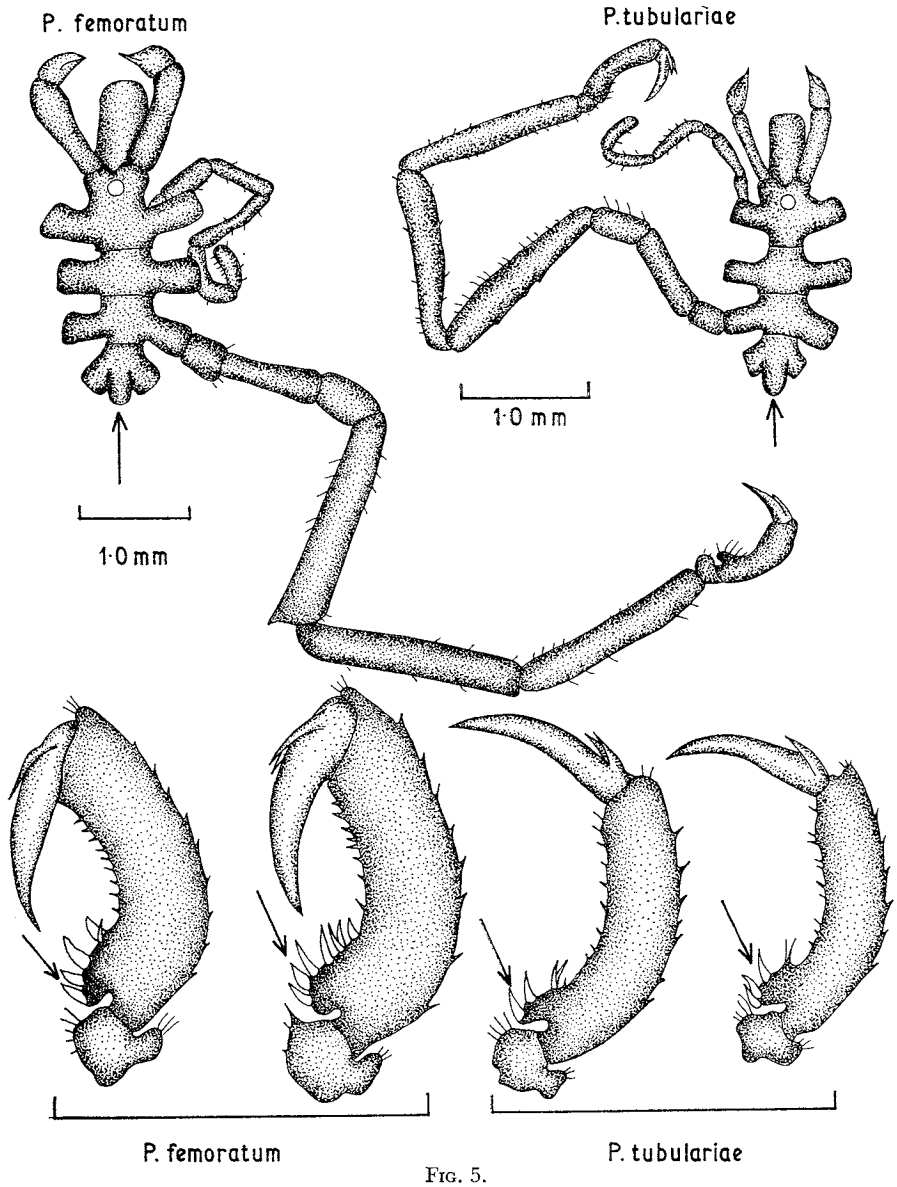

FIG. 5.
Diagnostic characters of some members of the Phoxichilidiidae: *Phoxichilidium femoratum*, *P. tubulariae*.

to which he left the name *N. brevirostre*. All specific characters in these specimens transgressed, there was a pronounced variability of the age character and the different stages of development in the separate forms may be similar to each other. It was claimed that the open sea forms, which live at great depths on slime bottoms, grow to a larger size than the coastal ones which settle in the littoral or immediate sublittoral zones on different bottoms with a rich fixed fauna. The open sea forms are said to retain the characters peculiar to the young individuals of the species. It is believed that the variation could be the result of (a) stunted development of the post-larval stadium, (b) differential acceleration of some characters, or (c) an unequal ratio of growth in some parts of the animal.

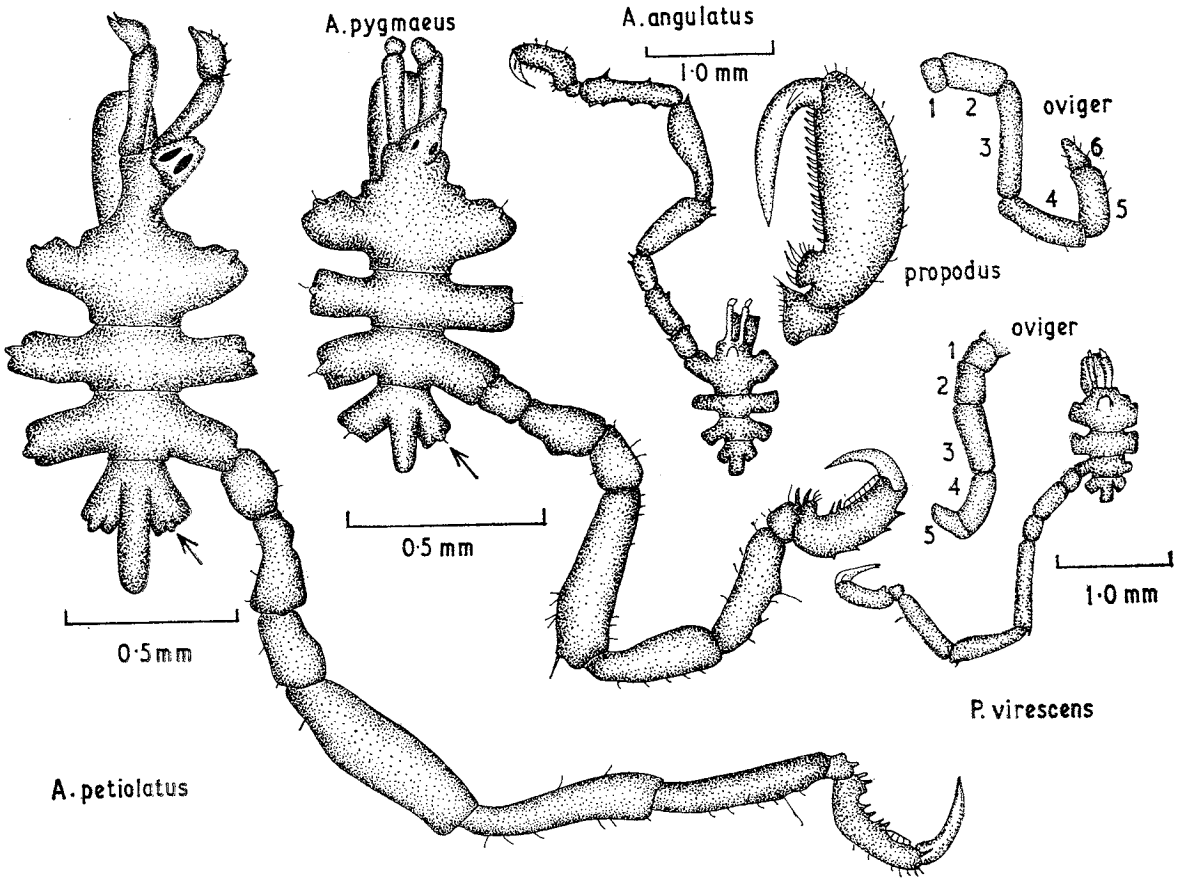

FIG. 6.
Diagnostic characters of some members of the Phoxichilidiidae: *Anoplodactylus petiolatus, A. pygmaeus, A. angulatus, Phoxichilidium virescens.*

Nesis (1960) does not agree with the synonymy of *N. brevirostre* and *N. rubrum* because of a difference in the pattern of the spines in specimens he examined. Stock (1955) considers *N. brevirostre* and *N. rubrum* to be distinct and well characterized species. He recognized *N. gracile* as a synonym of *N. rubrum* however. Hedgpeth (1963) agrees that, with the possible exception of *N. rubrum*, these various forms and species are obviously part of a large, variable species-complex of a type common among certain widely distributed pycnogonids. He points out that the nomenclature proposed by Losina-Losinsky (1935) and followed by later Soviet workers does not agree with the international rules and that Krøyer's name *brevitarse* is the oldest and must be used for the stem species. Obviously considerable local variation occurs in these species to have led to this confusion. Since keys dealing with other faunas have been used to identify specimens in British fauna lists it was considered worthwhile to examine the validity and distinctness of the British species *N. gracile*, *N. rubrum* and *N. brevirostre*. Using specimens collected from a number of locations measurements were made of the terminal and subterminal palp segments, the length and width of the second trunk segment, the length of the propodus and tarsus of the hind legs, the length and width of the proboscis and the length

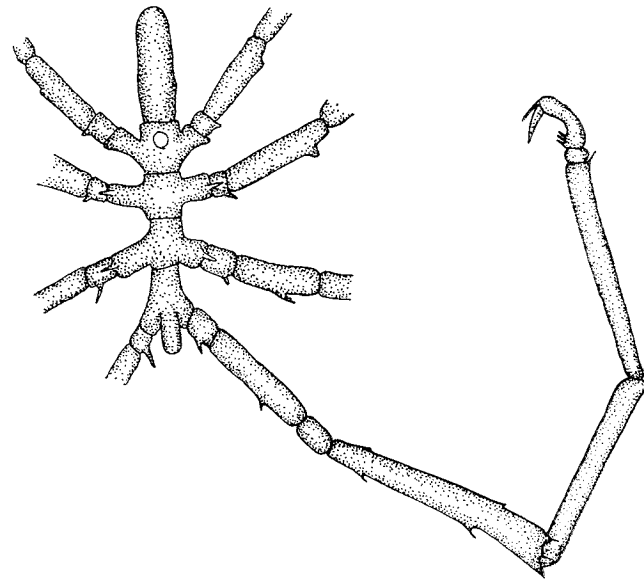

FIG. 7.
Diagrammatic representation of the only British representative of the Endeidae—*Endeis spinosus*.

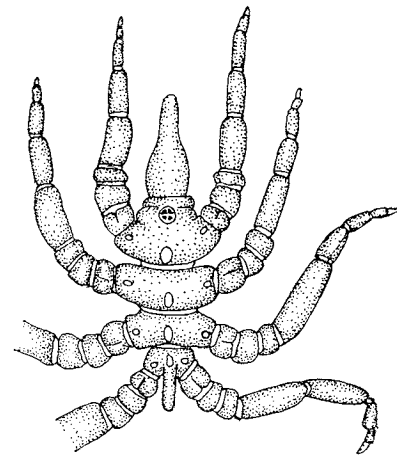

FIG. 8.
Diagrammatic representation of the only British representative of the Pycnogonidae—*Pynogonum littorale*.

of the body from the tip of the proboscis to the end of trunk segment 4. The abdomen points in a postero-dorsal direction which cannot be consistently flattened on a slide, so that a measurement taken from the tip of the proboscis to the tip of the abdomen would have a considerable error. The measurements taken were then expressed as ratios of one to the other, so that possible size variation between individuals was not significant. These results were then expressed as histograms (Figs. 9, 10, 11, 12 and 13). The results show that the ratio of the distal to the penultimate palp segments separates *N. gracile* from *N. rubrum* and *N. brevirostre* which on this character cannot be distinguished from each other (Fig. 8). The ratio of length to breadth of the second trunk segment separates *N. brevirostre* from *N. rubrum* and

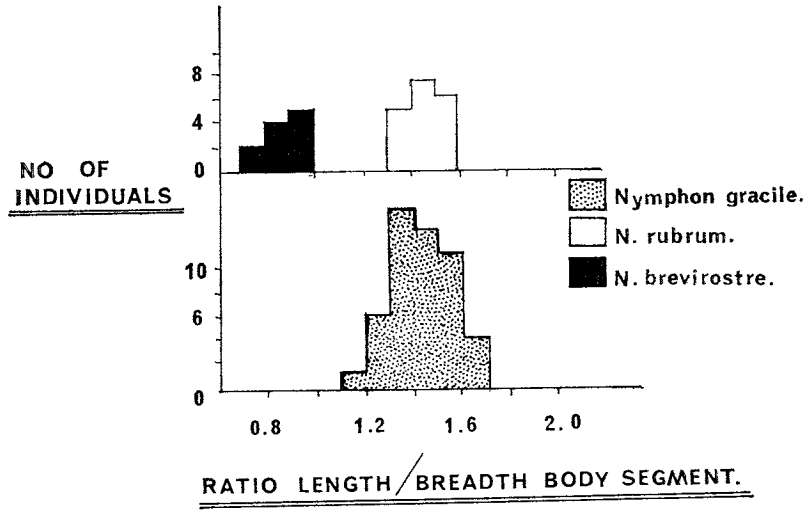

FIG. 9.
Distribution of ratios of length to breadth of the body segments for *Nymphon gracile*, *N. rubrum* and *N. brevirostre*.

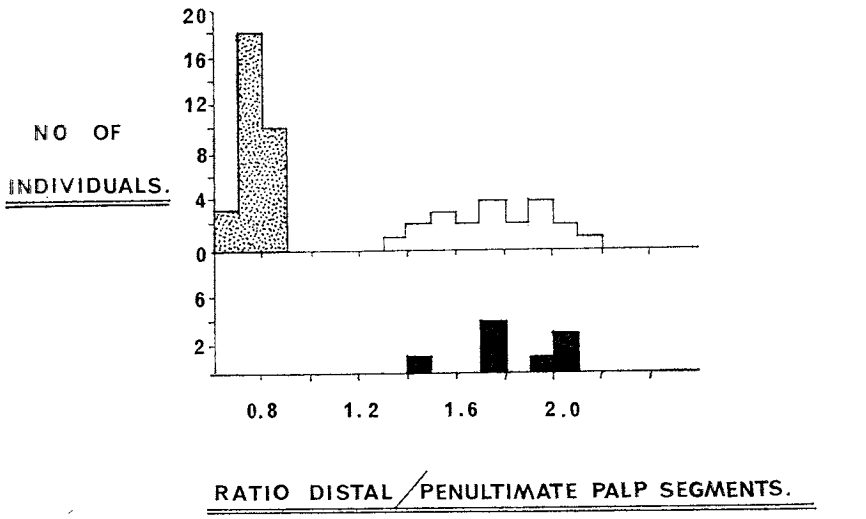

FIG. 10.
Distribution of ratios of length of distal to penultimate palp segments of *Nymphon gracile*, *N. rubrum* and *N. brevirostre*. (Shading of histograms as Fig. 9.)

N. gracile which, in turn, are not separable from each other on this character (Fig. 9). The other ratios used, length of propodus to length of tarsus, length to the width of the proboscis and the length of the proboscis to the total body length, did not give complete separation of any of the species though the majority of specimens of each were distinct from each other. These characters can thus be useful in some specimens in a confirmatory capacity. The characters were only used on adult specimens.

Thus although the species *N. gracile*, *N. rubrum* and *N. brevirostre* are not distinct in the Russian Arctic (Losina-Losinsky (1935)), in common with those occurring on the Belgian coast (Giltay (1928)) the species are distinct on the British coasts.

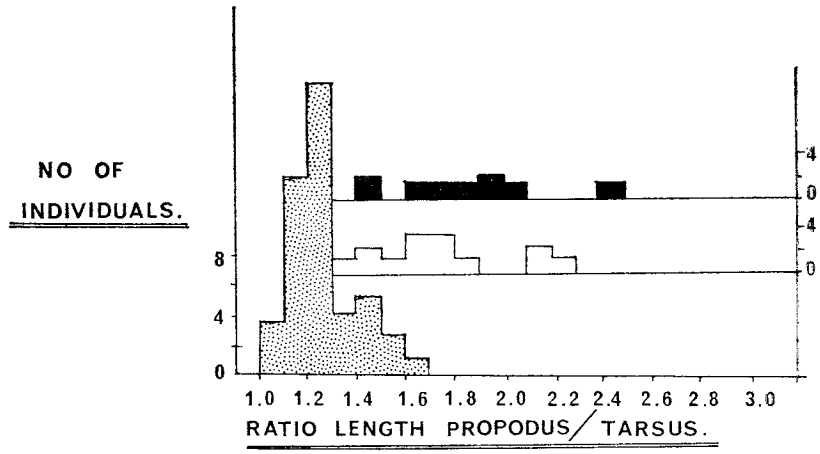

FIG. 11.
Distribution of ratios of length of propodus to tarsus for *Nymphon gracile*, *N. rubrum* and *N. brevirostre*. (Shading of histograms as Fig. 9.)

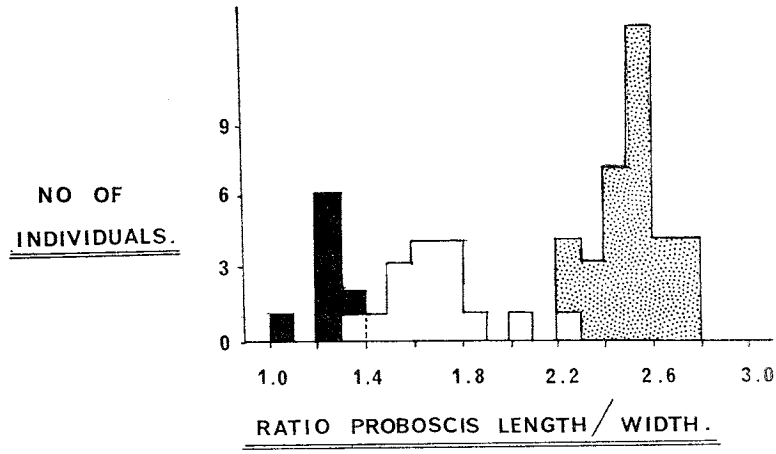

FIG. 12.
Distribution of ratios of proboscis length to width for *Nymphon gracile*, *N. rubrum* and *N. brevirostre*. (Shading of histograms as Fig. 9.)

Nymphon hirtum can easily be distinguished from the others by the pilosity covering its limbs. It has similar proportions to *N. brevirostre* and is characteristic of the Arctic or Subarctic and extends to below 200 metres. Although usually occurring in the cold seas of the North Atlantic, Iceland, Greenland and Spitzbergen, though infrequent west of Iceland (Hedgpeth, 1963), it sometimes reaches the northern parts of the British Isles having been recorded in Shetland, Northumberland and parts of Scotland. The nearest record to the collecting sites, used in the present study, was the Isle of Man. It is not normally, however, a littoral species.

Ammotheidae

A. echinata and *A. longipes* are clearly defined species. *A. simplex* has only been recorded from the shore on the Isle of Man (Giltay, 1934; Bruce, Colman and Jones, 1963). Immature forms of all Ammotheids have fewer palp segments than the adults,

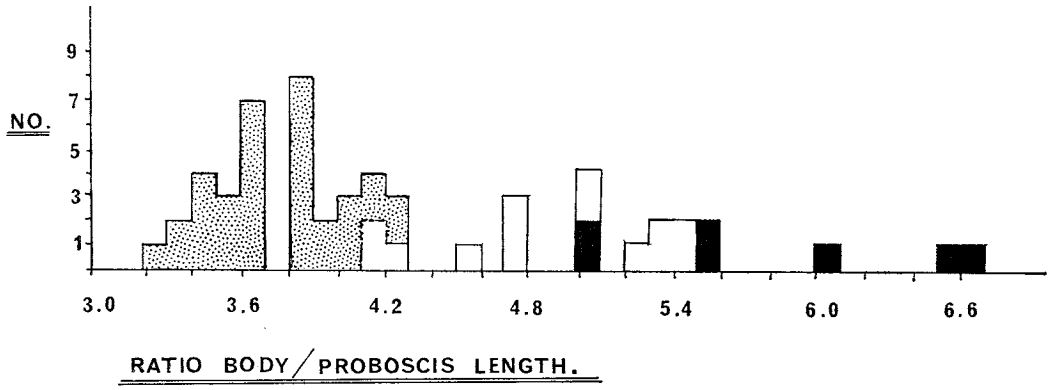

FIG. 13.
Distribution of ratios of body length to proboscis length for *Nymphon gracile*, *N. rubrum* and *N. brevirostre*. (Shading of histograms as Fig. 9.)

have chelae on their cheliphores and lack segmentation of the body. *A. laevis* has rarely been recorded and has the immature Ammotheid character of no body segmentation. Until a study is made of the family as a whole, it will not be possible to determine the validity of *A. laevis* and caution must thus be exercised. *Trygaeus communis* (Dorhn) has only been recorded once (Crothers, 1966) and since this is normally a Mediterranean species it is not considered to be a normal member of the British Pycnogonida.

Pallenidae

Apart from *Nymphon hirtum* and *Phoxichilidium virescens*, *Caillipallene brevirostris* and *C. phantoma* are the only species included in the key which we have not found in the course of our collecting. *Pallenopsis* sp. has been recorded from Milford Haven (Crothers, 1966). This may, however, be *Callipallene* sp. but to date, we have not been able to locate the specimens.

C. spectrum (Dohrn), which is remarkably similar to *C. brevirostris*, has only been recorded twice, one of these records is a British one (Norman, 1908). This species has therefore been omitted from the key.

Phoxichilidiidae

P. tubulariae is a recently established species (Lebour, 1947), and has only been recorded from Plymouth, Millport and Anglesey. An earlier record exists from Holland when it was identified initially as *P. femoratum*. Its great similarity to *P. femoratum* led Hedgpeth (1948) to suggest that it was merely a variety of *P. femoratum*, but Crapp (1967), working with specimens of both species, concluded that *P. tubulariae* was sufficiently different to merit specific rank. It is probably a specialized form derived from *P. femoratum*.

Nymphon gracile (Leach)

Nymphon gracile Hoek, 1881
N. gallicum Hoek 1881
N. gracile Halhed, 1886

N. gracile Carpenter, 1905
N. gracile Norman, 1908
N. gracile Hodgson, 1910
N. gracile Bouvier, 1923
N. gracile Giltay, 1928
N. gracile Lebour, 1947
N. gracile Eales, 1950

Body about 8 mm. with legs three or four times as long. Slender smooth body and limbs. The body segments longer than wide. Proboscis elongate, twice as long as wide. Cephalon has a slender neck. The ultimate segment of the palp longer than the penultimate segment. The propodus and tarsus are subequal in length. The propodus has a number of spines and usually three slightly larger ones half way along it. The alimentary canal usually a pink or red colour but the rest of the body is translucent.

N. gracile is a shore and shallow water species occurring higher up the beach than the other species on most of the European Atlantic coasts from Norway to Morocco and parts of the English Channel.

Nymphon rubrum (Hodge)

Nymphon rubrum Hodge, 1867
N. rubrum Sars, 1891
N. rubrum Carpenter, 1905
N. rubrum Norman, 1908
N. rubrum Hodgson, 1910
N. rubrum Bouvier, 1923
N. rubrum Giltay, 1928
N. rubrum Lebour, 1947
N. rubrum Hedgpeth, 1948
N. rubrum Wolff, 1958

Body 4–5 mm. with legs four times longer. Smooth and elongate the trunk segments being longer than wide. The neck of the cephalon slender. The ultimate segment of the palp shorter than the penultimate segment. The propodus longer than the tarsus. Usually with three or four spines near the heel and a shorter one half-way along. Sometimes rosy-coloured or may be white. Young specimens frequently resemble *N. brevirostre* in being broader in the body segments and, unless adults are present, determination is sometimes doubtful. Littoral and sublittoral species to a depth of 60 metres on hydroids. Occurs from the Russian Arctic, Norway, Britain, Ireland, Holland.

Nymphon brevirostre (Hodge)

Nymphon brevirostre Hodge, 1863
Nymphon gracile Sars, 1891
N. brevirostre Norman, 1908
N. brevirostre Hodgson, 1910
N. brevirostre Bouvier, 1923
N. brevirostre Lebour, 1947
N. brevirostre Hedgpeth, 1949

Body 2·5–3 mm. long with legs three and a half times as long as the body. Short stout proboscis. Cephalon broad, abdomen stout and conical. Thoracic segments broader than long. Palpi five jointed, the ultimate segment shorter than the penultimate which is approximately the same length as the antipenultimate. The other two segments are of equal length and equal to the terminal three segments. The propodus longer than the tarsus, is slightly bent and has along its inner margin a few short spines with three longer ones near the heel and terminally with a large claw and two small ones.

Occurs in littoral and sublittoral zone, amongst algae on hydroids to a depth of 60 metres, white or translucent sometimes with violet bands. Perhaps extends from the arctic to the south of Brittany (Losina-Losinsky, 1935).

Achelia longipes (Hodge, 1864)

Ammothea longipes Hodge, 1864
Achelia hispida Hodge, 1864
A. hispida Hoek, 1881
Ammothea longipes Hoek, 1881
Achelia hispida Halhed, 1886
Ammothea hispida Norman, 1908
Achelia hispida Hodgson, 1910
Ammothella longipes Bouvier, 1923
Ammothea longipes Lebour, 1947

The body is approximately 2 mm. long and the legs are three times as long. It has the same basic shape as *A. echinata* except that the body has smoother contours, is not spiny and the joint between segments 2 and 3 is frequently indistinct. There is a prominent pointed dorsal tubercle on each lateral projection. The proboscis has its widest point near the middle of its length, the palps usually point in a lateral direction and have nine segments and the cheliphore are more laterally inclined than in *A. echinata* (Fig. 3).

This has a more southern distribution than *A. echinata* occurring on the Atlantic and Mediterranean coast of France, Portugal and Naples.

Achelia laevis (Hodge, 1864)

Achelia laevis Hodge, 1864
A. laevis Hoek, 1881
Ammothea laevis Sars, 1891
A. laevis Norman, 1908
Achelia laevis Hodgson, 1910
A. laevis Bouvier, 1923
Ammothea laevis Maiseuheimer, 1928
A. laevis Giltay, 1928
A. laevis Stephenson, 1937
A. laevis Lebour, 1947

The body of this species is 1·5 mm. long. The most important character is the lack of visible trunk segmentation. This species has not been recorded as frequently as either *A. echinata* or *A. longipes* and, since the absence of segmentation is a juvenile

character of the other species and the juveniles of *A. echinata* are not as spiny as the adults, there is a possibility that some at least of the records for this species represent specimens in which the chelae have already atrophied but segmentation has not yet appeared. This has been discussed at greater length by King (1971).

The distribution of this "species" is similar to that of *A. echinata* and most specimens have been obtained from amongst algae and Bryozoans which is the usual habitat for *A. echinata*. More work is needed to establish the validity of this species.

Achelia echinata (Hodge)

Achelia echinata Hodge, 1864
A. echinata Hoek, 1881
A. echinata Halhed, 1886
Ammothea echinata Sars, 1891
A. echinata Carpenter, 1905
A. echinata Norman, 1908
Achelia echinata Hodgson, 1910
A. echinata Bouvier, 1923
Ammothea echinata Meisenheimer, 1928
A. echinata Giltay, 1928
A. echinata Giltay, 1929
A. echinata Giltay, 1934
A. echinata Lebour, 1947
Achelia echinata Utinomi, 1954

The body length of this species is 1·5–2 mm. with the legs three times as long. The cephalon is fused with the first trunk segment which has a distinct suture between it and the second trunk segment. This in turn is clearly distinct from the third trunk segment though posterior to this the segmentation is not visible externally. The proboscis is approximately as long as the body being broadest one-third of the distance from its proximal end and gradually tapering from that point (Fig. 3). The chelifores have atrophied pincers and are directed anteriorly as are the eight segmented palps. The legs have a number of spines with characteristically one pair on each lateral process and two pairs on each first coxa situated at the end of protuberances. These are better developed in the male which also has a prominent coxal projection on the coxa.

The immature form, as in other membranes of the genus Achelia lacks segmentation and has chelate chelifores. The palps also have fewer segments. The only character which may enable an identification to take place is the shape of the proboscis.

This species is of wide occurrence and may be part of a large complex in the northern hemisphere spreading from the Arctic almost to the Equator (Hedgpeth, 1963).

Achelia simplex (Giltay)

Ammothea simplex Giltay, 1934
Achelia simplex Bruce *et al.*, 1963

According to Giltay (1934) this species has a body length of 1·5 mm. and legs three times as long as this. The cephalon is fused with the first trunk segment which

has a distinct suture between it and the second trunk segment which, in turn, is distinct from the third trunk segment. Posterior to this the segmental divisions are indistinct. The proboscis is slightly longer than the body and is elongately ovoid in shape. The chelofores are equal to one-third the length of the proboscis and have atrophied pincers. The palps have eight segments, the terminal one being one and a half times longer than the penultimate. The ovigers have ten segments.

This species has only been recorded from Port Erin, Isle of Man. Considering the great variability in spines exhibited by *A. echinata*, it is possible that *A. simplex* is a local variety of *A. echinata*.

Callipallene brevirostris (Johnston)

Pallene brevirostris Hodge, 1864
P. brevirostris Hoek, 1881
P. brevirostris Halhed, 1886
P. brevirostris Sars, 1891
P, brevirostris Cole, 1901
P. brevirostris Carpenter, 1905
P. brevirostris Norman, 1908
P. brevirostris Hodgson, 1910
P. brevirostris Bouvier, 1923
P. brevirostris Giltay, 1928
P. brevirostris Lebour, 1947
Callipallene brevirostris Hedgpeth, 1948

Body 1–1·5 mm. long, legs four times as long. Proboscis short and rounded at tip. Cephalon long, slightly wider anteriorly. Segment 2 of trunk short and wide abdomen reduced. Segments 3 and 4 fused, femur equal in length to tibia 2, tibia 1 considerably shorter than this. Ovigers with 10 segments, all segments short except numbers 4 and 5. Sublittoral and occasionally a littoral species occurring from Scandinavia to the Mediterranean and on the Atlantic coast of N. America.

Callipallene phantoma (Dohrn)

Pallene producta Sars, 1891
P. phantoma Norman, 1908
P. producta Norman, 1908
P. phantoma Bouvier, 1923
P. producta Bouvier, 1923
Callipallene phantoma Hedgpeth, 1948

Body 2 mm. long, legs four times this length. Proboscis cyclindrical with blunt but rounded end. Neck long, narrow, widens considerably at anterior end, segments 2 of trunk considerably longer than wide, segments 3 and 4 fused, with short abdomen. Femur shorter than tibia 2, but longer than tibia 1. Ovigers with ten segments, all short except segments 3, 4 and 5, but with segment 3 shorter than either segments 4 or 5.

A predominantly sublittoral but occasionally littoral species found from Norway to Naples, the Black Sea, the Azores and Florida.

Phoxichilidium femoratum (Rathke)

Phoxichilidium coccineum Hodge, 1861
P. femoratum Hoek, 1881
P. femoratum Halhed, 1886
P. femoratum Sars, 1891
P. femoratum Norman, 1908
P. femoratum Hodgson, 1910
P. femoratum Bouvier, 1923
P. femoratum Meisenheimer, 1928
P. femoratum Giltay, 1928
P. femoratum Stephensen, 1933
P. femoratum Stephensen, 1937
P. femoratum Lebour, 1947
P. femoratum Hedgpeth, 1948
P. femoratum Wolff, 1958

Body length 2–3 mm., with legs almost three times as long. Proboscis cyclindrical, almost the same width throughout its length, anterior end almost straight. Five segmented oviger, short cephalon, short ocular process (and well-developed auxiliary) cement glands opening in a series of depressions along the femur. Abdomen short, hardly as long as last lateral processes. Propodus at base with three or four large single, and one pair of teeth, which are usually smaller, number slightly variable, well-developed auxiliary claws dorsally situated.

Colour varies from pale straw to dark red. A shallow water species, ubiquitous in North Atlantic from Greenland and Norway to France and Long Island Sound, also Pacific coast of North America. Feeding habits unknown, larvae have been recorded from cysts in *Syncoryne eximia.*

Phoxichilidium tubulariae (Lebour)

P. femoratum Loman, 1907
P. tubulariae Lebour, 1947

Body length 1·4–1·7 mm., legs three to four times as long. Lebour described the proboscis as being wider anteriorly, shorter than in *P. femoratum*, with the end rounded, but Crapp (1967) found that this feature is variable and in some specimens is very similar to that of *P. femoratum.* Five segmented oviger, short cephalon, short ocular process, often with a marked constriction near the base of the 3rd segment. Cement glands opening by very inconspicuous pores of the femur and abdomen long, twice the length of the lateral processes. Propodus armed at its base with two large single teeth, and one pair of smaller teeth: occasionally a third large single tooth is present on the proximal part of the heel, very close to the adjacent tooth: well developed auxiliary claws placed dorsally.

Colour usually pale straw. A shallow water species recorded from Holland and the British Isles. To date it has only been found living amongst and feeding on *Tubularia* spp. in the polyps of which the young develop.

Phoxichilidium virescens (Hodge)

Phoxichilidium virescens Hodge, 1864
Anaphia virescens Norman, 1908

A. virescens Hodgson, 1910
Anoplodactylus virescens Bouvier, 1923
Phoxichilidium virescens Lebour, 1947

Body length 1 mm., legs three times as long. Proboscis bluntly truncate, showing signs of angles at the corners. Five segments in oviger, last of which is flat and terminally pointed. Broad cephalon with extremely blunt ocular process, very inconspicuous cement glands opening by pores on dorsal surface of femur. Body segments broad, with thick lateral processes, abdomen a short rounded knob reaching obliquely slightly beyond the very short last lateral processes. Few setae on legs and propodus is armed with two or three large spines at base and a row of teeth on the sole, small auxiliary claws placed laterally.

The colour is usually dull green, with bright green intestinal fluid. A littoral species recorded from the British Isles and France. Larvae have been found in cysts on *Syncoryne eximia* (Dogiel, 1913) and *Coryne muscoides* (Bourdillon, 1952).

Anoplodactylus angulatus (Dohrn)

Phoxichilidium virescens Hoek, 1881
Anaphia angulata Norman, 1908
A. angulatus Bouvier, 1923
Anoplodactylus angulatus Giltay, 1929
A. angulatus Lebour, 1947

Body length 1–2 mm., with legs three times as long. Proboscis stout, cylindrical, with conspicuous angles anteriorly. Ovigers similar to those of *P. virescens*, but with a short terminal segment. Short, broad cephalon with short, rounded ocular tubercle with a small point at tip. Very inconspicuous cement glands opening on femur. Body segments broad, with thick lateral processes, but not so compact as *P. virescens*. Last segment very reduced, with abdomen more than twice the length of the very short last lateral processes. Few setae on legs, propodus armed with two large teeth and three setae preceding a row of teeth on the sole. Small auxiliary claws placed laterally. Colour is normally green. A shallow-water species recorded from Naples, France and southern Britain.

Anoplodactylus petiolatus (Krøyer)

Pallene attenuata Hodge, 1864
Phoxichilidium petiolatum Hodge, 1864
P. mutilatum Semper, 1874
P. petiolatum Hoek, 1881
Anoplodactylus petiolatus Sars, 1891
A. petiolatus Carpenter, 1905
A. petiolata Norman, 1908
A. petiolata Hodgson, 1910
A. petiolata Lebour, 1916
A. petiolatus Bouvier, 1923
A. petiolatus Meisenheimer, 1928
A. petiolatus Giltay, 1928
A. petiolatus Giltay, 1929
A. petiolatus Lebour, 1947
A. petiolatus Hedgpeth, 1948

Very slender form 1–1·5 mm. body length, with legs three times as long. Proboscis cylindrical, rounded at end. Ovigers with six segments, with third very long, about twice the length of the second. Very long neck, with long ocular process. Cement glands open through conspicuous funnel on dorsal side of femur. Body segments broad, with fairly wide lateral processes. Abdomen long and narrow, reaching well beyond the last lateral processes. Conspicuous dorsal protuberances without spines on lateral processes. Propodus armed with two large spines and a smaller pair, with four to six spines and a short cutting lamella on the sole. Small auxiliary claws placed laterally.

Colour usually off-white or colourless. A shallow-water species found from Norway to the Mediterranean: it has also been recorded from the Caribbean, and may extend to the western coast of S. America. The larvae have been recorded living parasitically in polyps of *Hydractinia echinata*, *Podocoryne carnea* and *Campanularia flexuosa*, as well as in a number of medusae.

Anoplodactylus pygmaeus (Hodge)

Pallene pygmaea Hodge, 1864
Phoxichilidium pygmaeum Hoek, 1881
Anoplodactylus petiolatus Sars, 1891
A. pygmaeus Carpenter, 1905
Anaphia petiolata Norman, 1908
Anoplodactylus pygmaeus Bouvier, 1923
A. pygmaeus Meisenheimer, 1928
A. pygmaeus Giltay, 1928
A. pygmaeus Lebour, 1947
A. pygmaeus Hedgpeth, 1948
A. pygmaeus Wolff, 1958

A small species with body 0·7–1 mm. long, legs 2·5 times as long. Proboscis cylindrical, rounded anteriorly, with a constriction encircling the anterior end. Short, broad cephalon, with long ocular process overlapping it in front. Ovigers with six segments, third of which is short and equal in length to second. Cement glands open through dorsal funnel on femur. Body segments wide, with thick lateral processes more compact than in *A. petiolatus*. Abdomen about twice as long as last pair of lateral processes. Small dorsal protuberances on lateral processes, each bearing a spine. Propodus with two spines on heel, and one or two spines before long cutting lamella. Auxiliary claws absent.

Colour usually pale straw, or colourless. A common shallow-water species found from Denmark to the Azores, and also on the south-west coast of N. America. Larvae have been recorded from polyps of *Obelia* sp. and *Podocoryne carnea*, and from galls in *Coryne muscoides*.

Endeis spinosa (Montagu)

Phoxichilus spinosus Halhed, 1881
P. spinosus Sars, 1891
Chilophoxus spinosus Stebbing, 1902
Phoxichilus laevis Carpenter, 1905
Endeis spinosus Norman, 1908

E. spinosus Hodgson, 1910
Chilophoxus spinosus Bouvier, 1923
C. spinosus Meisenheimer, 1928
C. spinosus Giltay, 1928
E. spinosus Lebour, 1947
E. spinosa Hedgpeth, 1948
Chilophoxus spinosus (Stebbing, Bouvier)

This has an elongate, graceful body and similar in proportions to *N. rubrum* but is without both palps and chelifores

This species occurs from Norway to the Mediterranean.

Pycnogonum littorale (Ström)

Pycnogonum littorale Hoek, 1881
P. littorale Halhed, 1886
P. littorale Sars, 1891
P. littorale Carpenter, 1905
P. littorale Norman, 1908
P. littorale Hodgson, 1910
P. littorale Bouvier, 1923
P. littorale Meisenheimer, 1928
P. littorale Giltay, 1928
P. littorale Stephensen, 1937
P. littorale Lebour, 1947
P. littorale Hedgpeth, 1948
P. littorale Wolff, 1958

This species has a sturdy body, with short tubercles on the dorsal surface of each trunk segment and lacks both palps and chelicerae. The proboscis is conical and the abdomen is truncate at its posterior end. The legs are slightly shorter than the body and terminate in a claw. The body is white or cream coloured and the male is smaller than the female and has ovigerous eggs: is often darker, sometimes being pale brown. Considerable variation in adult size occurs and unlike other species, the male carries the eggs as a single ventral pad beneath its body.

The species occurs from the Arctic to Southern Spain. It is not necessarily always littoral and on some shores is usually sublittoral with only occasional occurrence between the tides.

Types of habitat

The pycnogonids are small, relatively inactive predators, often justifiably regarded as ectoparasites, on epizoitic and soft-bodied marine animals. Their feeding habits are partially sucking and partly raptorial. The basic organ of feeding is the proboscis, a large structure armed with three rasping teeth around the mouth, which opens at the anterior end. The proboscis may be simply thrust into the prey, but species which also possess a pair of chelae often use these to tear the food apart, or to thrust it into the mouth. The musculature of the proboscis is able to produce a sucking force, at the posterior end is a complex filter of chitinous bristles which filter out and macerate coarse particles of food.

The range of prey animals available to any pycnogonid species is unknown, but the animal can only feed successfully when three factors relating to predator and prey are favourable (Fry, 1965), these being:

(1) The pycnogonid must be able to attack the food animal without encountering dangerous defensive or offensive mechanisms such as the avicularia of polyzoans, or the tentacles of Actinozoa.

(2) The pycnogonid must be able to cling securely to the prey whilst feeding.

(3) The proboscis must be of the right size and shape to reach to the prey's tissues.

In any area, therefore, a pycnogonid species is likely to be restricted to one or very few species of prey organisms, although little definite information exists on this point. This is an important factor to be considered in relation to pycnogonid habitats.

The group as a whole is characterized by slow and inefficient locomotion, usually a rather clumsy walking, although some of the more slender species are able to swim for a limited period. Little is known regarding their sense organs: the only ones which have been studied at all are the four small compound eyes carried dorsally on the ocular tubercle.

Thus if many pycnogonid species leave the area of their food, they may have difficulty in returning and they do in fact behave in a manner which suggests that they are adapted to avoid being swept away from their food. Highly thigmotactic, they cling tightly to any available substrate, and if dropped into a container of clean sea water, usually adopt a "plummeting" posture with all the legs pressed tightly together and pointing ventrally: this takes the animal rapidly to the bottom with the ventral side uppermost.

Therefore, pycnogonids are unable to range over large distances, unless they are attached to floating organisms, such as medusae, or detached seaweeds and sargassum weed. This applies to the larvae as well, for no pycnogonids are known to have a pelagic larvea phase. The eggs are fertilized externally during copulation, and are then carried around on the ovigers of the male parent. So far as we know, the young either develop completely whilst attached to the parent, or are released to develop parasitically in or on some other animal.

With this mode of life, the habitat of pycnogonids is probably best defined in terms of the potential prey animals, for it is the presence or absence of these that will determine whether or not the pycnogonid species is to be found. A second factor which must be considered is temperature, for there is a considerable mass of data which suggests that each pycnogonid species is adapted to a certain range of water temperature.

Information concerning food of pycnogonids is scarce and frequently all the information available concerns the animals on which the pycnogonids are found. A list of the recorded associations, taken in part from the literature, is as follows:

1. NYMPHONIDAE. Young develop attached to the male and are released resembling miniature adults.

Nymphon gracile	Foraminifera
	Tethys leporina (Merton, 1906)
	*Eggs of *Nucella*
N. brevirostre	Tubularians and Sponges (Giltay, 1928)
	Laminaria (Apellöf, 1916)

N. rubrum — *Clava* (Schlottke, 1933)
Coryne pusilla (Schlottke, 1932, 1933)
Obelia genticulata (Schlottke, 1932)
Sponges (Hoek, 1877)

2. AMMOTHEIDS. Larvae live as parasites on hydroids or hydromedusans. Two records inside bivalve molluscs (Ohshima, 1927; Benson and Chivers, 1960). Juveniles recorded on nudibranchs and holothurians (Ohshima, 1927; 1933). Larva of *A. laevis* inside *Obelia* spp. (Dogiel, 1913).

Achelia echinata — **Flustra*, *Electra pilosa*

3. PHOXICHILIDIIDAE. Larvae of *P. femoratum* in cysts in *Syncoryne exima* (Hodge, 1861; Dogiel, 1913).
Larvae of *P. tubulariae* in polyps *Tubularia*.

Phoxichilidium femoratum — *Bougainvillea*, *Eudendrium*, *Clava*, *Tubularia*, *Syncoryne* and *Coryne* (Giltay, 1928)
Syncoryne (Lebour, 1947)
Aglaophenia latirostris (Ricketts and Calvin, 1960)

P. tubulariae — *Tubularia larynx*

P. virescens — *Sertularia* on bases of *Ascophyllum*
Larvae in galls on *Syncoryne exima* (Dogiel, 1913)
Larvae in galls on *Coryne muscoides* (Bourdillon, 1952)

Anoplodactylus angulatus — *Sertularia* on *Ascophyllum*

A. petiolatus — Larvae parasitic on hydroids
Hydractinia echinata (Semper, 1874)
Podocoryne carnea (Bouvier, 1923)
Campanularia flexuosa (Dogiel, 1911)
Larvae in the medusae of:
Cosmetira pilosella, *Turris pileata*, *Stomotoca dinema*, *Phialidium hemisphericum* (Lebour, 1947)

A. pygmaeus — *Tubularia*, *Obelia*, *Sertularia* (=*Dynamena*) (Schlottke, 1932)
Larvae in polyps of *Obelia* (Dogiel, 1913; Lebour, 1947)
Larvae in polyps of *Coryne muscoides* and *Podocoryne carnea* (Sanchez, 1959)

ENDEIDAE. Larvae in polyps of *Obelia* (Lebour, 1916)

Endeis spinosus — *Obelia dichotoma* (Cole, 1910)
Tubularia larynx

PYCNOGONIDAE. Larvae ectoparasitic on *Clava multicornis* (Dogiel, 1913).
Larvae ectoparasitic on *Taelia multicornis*.

Pycnogonum littorale — *Milne-Edwardsia loweni* (Bouvier, 1923)
Taelia crassicornis (Hedgpeth, 1949)
Lucernaria sp. (Bouvier, 1923)
Metridium sp. (Wolff, 1958)
Cucumaria frondosa (Wolff, 1958)
Clava multicornis (Dogiel, 1913)
Taelia spp. (Sars, 1881; Prell, 1910)

Metridium sp. (Mobius, 1893; Prell, 1910)
Actinian sp. (Hilton, 1915)
Sabellaria sp. (Schlottke, 1932)

Distribution in Pembrokeshire

During the summer months of 1969 collections were made at a variety of localities in Pembrokeshire. The results are presented together with data taken from the Dale Fort fauna list.

Pembrokeshire Records

NYMPHONIDAE

1. *Nymphon gracile*	Haven and Daucleddau Martins Haven, Skokholm Solva, West Angle, Freshwater East, Cwm-Eglys
2. *N. rubrum*	Fort Beach, Cliff Cottages Beach, Tenby
3. *N. brevirostre*	

AMMOTHEIDAE

4. *Achelia echinata*	Sandy Haven, West Blockhouse Point, Dale Point, Skokholm—Hog Bay and Peter's Bay, Skomer, Cwm-Eglys, Fishguard, St. Brides, Watwick, West-Angle, Manorbier, Lydstep Point, Caldy, Tenby, Freshwater West.
5. *A. longipes*	Solva, Little Haven, St. Brides, Watwick, West Angle, Freshwater East, Lydstep Point, Caldy, Tenby.
6. *A. laevis*	Caldy.

PHOXICHILIDIIDAE

7. *Phoxichilidium femoratum*	Castlebeach, Gann Flat, Skomer.
8. *Anoplodactylus angulatus*	Pembroke ferry, Slip Pier Beach, Sandy Haven, St. Brides, West Angle.
9. *A. pygmaeus*	Stack Rock, Sandy Haven, Black Rocks Flat, Tenby, Cwm-Eglys.

ENDEIDAE

10. *Endeis spinosus*	Gann Flat, Musselwick Point, Dale Point, Martins Haven, North Skomer, Mew Stone, Cwm Eglys, Fishguard, Solva, St. Brides, Watwick, Manorbier, Caldy and Tenby.

PYCNOGONIDAE

11. *Pycnogonum littorale*	Slip Pier Beach, Sandy Haven, West Dale Bay, Skokholm.

ACKNOWLEDGEMENTS

We would like to thank Professor E. W. Knight-Jones and Professor D. J. Crisp for providing facilities. Part of the work was carried out whilst one of the authors (G.B.C.) was holding a N.E.R.C. studentship and he would like to thank Mr. W. G. Fry for his valuable advice and assistance.

References

Bourdillou, A. (1952). Note preliminaire sur diverses reactions parastaires d'un Hydroide aux larves de Pycnogonides. *Bull. Stat. Mar. Endoume* (2), 19–26.

Bouvier, E. L. (1923). *Faune de France. 7. Pycnogonides.* Paris.

Bruce, J. R., Colman, J. S., and Jones, N. S. (ed.) (1963). *Marine fauna of the Isle of Man.* Liverpool U.P.

Carpenter, G. H. (1905). The marine fauna of the coast of Ireland, part 6. Pycnogonida. *Scient. Invest. Fish. Brch. Ire.*, **4,** 1–8.

Carpenter, G. H. (1912). Pycnogonida. Clare Island survey. *Proc. Roy. Irish Acad.*, **31,** 1–4.

Cole, L. J. (1910). Notes on the habits of pycnogonids. *Biol. Bull. mar. biol. Lab., Woods Hole* **2** (5), 195–207.

Crapp, G. B. (1967). *The ecology and identification of Anglesey pycnogonids.* M.Sc. thesis, University of Wales.

Crothers, J. H. (ed.) (1966). Dale Fort Marine Fauna (2nd edn.). *Fld. Stud.*, **2** (suppl.), 169 pp.

Dogiel, V. (1913). Embryologische Studien an Pantopoden. *Zeitschr. Wiss. Zool.*, **107** (4), 575–741.

Dohrn, A. (1881). Die Pantopoden des Golfes von Neapel und der angrenzenden Meeresabschnitte. Eine Monographie. Leipzig. Fauna und Flora des Golfes von Neapel, herausg. von de Zoologischen Station zu Neapel. 3 Bd. 4.

Eales, N. B. (1950). *The littoral fauna of Great Britain* (2nd ed.). Cambridge U.P., Cambridge.

Fage, L. (1949). *Traité de Zoologie. 6. Classe des Pycnogonides.* Masson: Paris.

Giltay, L. (1928). Note sur les Pycnogonides de la Belgique. *Bull. Annls. Soc. r. ent. Belg.*, **68,** 193–229.

Giltay, L. (1929). Quelques pycnogonides des environs de Banyuls (France). *Bull. Annls. Soc. r. ent. Belg.*, **69,** 172–176.

Giltay, L. (1934). Remarques sur le genre *Ammothea* Leach, et description d'une espèce nouvelle de la Mer d'Irlande. *Bull. Mus. Hist. nat. Belg.*, **10,** 1–6.

Grube, E. (1871). Mittheilungen über St. Malo ünd Roscoff. *Verh. Schles. Ges.*, 1869–1872.

Halhed, W. B. (1886). Report on the pycnogonida of the L.M.B.C. District. *1st Rep. Fauna Liverpool Bay and Neighbour Seas*, **1,** 227–231.

Halhed, W. B. (1896). Report of the marine zoology, botany and geology of the Irish Sea. List of the Pycnogonida. *Rep. Brit. Ass. advance. Sci.*, p. 442.

Hedgpeth, J. W. (1947). On the evolutionary significance of the Pycnogonida. *Smithson. misc. Collns.*, **106,** p. 53.

Hedgpeth, J. W. (1948). The Pycnogonida of the western North Atlantic and the Caribbean. *Proc. U.S. natn. Mus.*, **97,** 157–342.

Hedgpeth, J. W. (1949). Report on the Pycnogonida collected by the Albatross in Japanese Waters in 1900 and 1906. *Proc. U.S. Natn. Mus.*, **98,** 233–321.

Hedgpeth, J. W. (1954). On the phylogeny of the Pycnogonida. *Acta zool. Stockh.*, **35,** 1–21.

Hedgpeth, J. W. (1963). Pycnogonida of the North American Arctic. *J. Fish. Res. Bd. Can.*, **20,** 1315–1348.

Helfer, H., and Schlottke, E. (1935). Pantopoda. *Bronn's Kl. Ordn. Tierreichs*, **5,** (4), (2).

Hesse, M. (1867). Observation sur des Crustacés rares ou nouveaux des cotes de France. *Ann. soc nat. Zool.*, **VII,** 201.

Hodge, G. (1862). Observations on a species of Pycnogon (Phoxichilidium coccineum, Johnston) with an attempt to explain the order of its development. *Ann. Mag. Nat. Hist.*, **9,** 33–43.

Hodge, G. (1863). Description of two new species of Pycnogonida. *Ann. Nat. Hist.*, **11** (3rd series), 463.

Hodge, G. (1864). List of the British Pycnogonidae, with descriptions of several new species. *Ann. Mag. nat. Hist.*, **13,** series 3, 113–117.

Hodge, G. (1867). Reports of Deep Sea Dredging on the coasts of Northumberland and Durham, 1862–1864. Report on the Pycnogonida. *Nat. Hist. Trans. Northumberland and Durham*, **7,** 41–42.

Hodgson, T. V. (1910). The Pycnogonida of Devonshire. *Rep. Trans. Devon. Ass. Sci. Lit. Art.*, **42,** 425–439.

Hoek, P. P. C. (1877). Ueber Pycnogoniden, *Nied. Arch. Zool.*, **111,** 235.

Hoek, P. P. C. (1881). Nouvelles études sur les Pycnogonides. *Arch. Zool. exp.*, **IX,** 445–542.

Johnston, G. (1837). Miscellanea Zoologica. *Mag. Zool. Bot.*, **1,** 377.

King, P. E. (1971). In preparation.

Leach, W. E. (1814). A tabular view of the external characters of four classes of animals. *Trans. Linn. Soc. Lond.*, **11.**

LEBOUR, M. V. (1916). Notes on the life-history of *Anaphia petiolata* (Krøyer). *J. mar. biol. Ass. U.K.*, **11,** 51–56.

LEBOUR, M. V. (1947). Notes on the Pycnogonida of Plymouth. *J. mar. biol. Ass. U.K.*, **26,** 139–165.

LOMAN, J. C. C. (1907). Biologische Beobachtungen an einem Pantopoden. *Tijdsch. ned. dierk. ver.*, **X,** 255–282.

LOMAN, J. C. C. (1928). *Nymphon brevirostre*. Die Tierwelt Deutschl. Tiel VIII, p. 78.

LOSINA-LOSINSKY, L. K. (1935). Pantopoda arktiches kikh morei S.S.S.R. Pantopoda of the Polar Seas within U.S.S.R. Vsesoiuznyi Arkticheskii Inst. (Materialy lia Izuchenii Arktiki), No. 4, 140 pp.

MARINE BIOLOGICAL ASSOCIATION (1957). *Plymouth marine fauna* (3rd edn.), Plymouth.

MEISNHEIMER, J. (1928). Pantopoda. *Tierwelt N-u Ostsee*. XI.

MONTAGU, G. (1808). Description of several marine animals found on the south coast of Devonshire. *Trans. Linn. Soc. Lond.*, **IX,** 100.

NESIS, K. N. (1960). Pantopoda pribrezhya vostochnogo Murmana. Pantopoda of the coast of eastern Murmansk. Trudy Murmanskogo Biologicheskogo Instituta, **2,** 137–161.

NORMAN, A. M. (1908). The Podosomata (=Pcynogonida) of the temperate Atlantic and Arctic Oceans. *J. Linn. Soc.*, **30,** 98–238.

SARS, G. O. (1891). Pycnogonida. Den Norske Nordhafs-Exped., 20, Bd.

SCHOLTTKE, E. (1932). Die Pantopoden der deutschen Küsten aus der Biologischen Anstalt auf Helgoland und de Zoologischen Institut der Universität Rostock, **XVIII,** 1–10.

SEMPER, C. (1874). Ueber Pycnogoniden und ihre in Hydroiden Schmarotzenden Larvenformen. *Verhandl. physik-medio Gesellsch. Würzb.*, **7,** 264–286.

STEBBING, T. R. R. (1902). The Nobodies, a sea-faring family (*Knowledge*, **XXV,** 37).

STEPHENSON, K. (1933). Pycnogonida. The Godthaab Expedition, 1928. *Medd. om Grønland*, **79** (6).

STEPHENSON, K. (1937). Pycnogonida. *Zoology Iceland*, **3** (58).

STOCK, J. H. (1955). Pycnogonida from the West Indies, Central America and the Pacific coast of North America. *Vidensk. Medd. fra Dansk Naturh. Foren.*, **117,** 209–266.

STRÖM, H. (1762). Physisk og oeconomisk beskrivelse over fogderiet Söndmör.

THOMPSON, D'ARCY W. (1909). *The Cambridge Natural History, Vol. 4. Pycnogonida*, Cambridge University Press: Cambridge.

UTINOMI, H. (1954). The fauna of Akkeshi Bay XIX. Littoral Pycnogonida. *Publ. Akkeshi Mar. Biol. Stat. no.* **3,** 1–28.

WOLFF, T. (1958). Notitser om danske havedderkopper. *Flora, Fauna, Silkeborg*.