

SMITHSONIAN MISCELLANEOUS COLLECTIONS

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OF THE PYCNOGONIDA

(WITH ONE PLATE)

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Marine Biologist, Texas Game, Fish and Oyster Commission



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## INTRODUCTORY NOTE

The Pycnogonida, or sea spiders, are an anomalous class or sub-phylum of marine arthropods, unknown except by name to most zoologists. They are of no economic importance to man, and of little discernible significance in the natural order of things. Yet within the last 10 years more than 50 papers dealing with these creatures have been published, and the complete bibliography now comprises several hundred titles. More than 500 species have been described, but there are relatively few parts of the world in which the pycnogonid fauna is adequately known, and the actual number of extant species may be considerably larger.

Also known as Pantopoda, the Pycnogonida have often been considered an "appendix" to the Arachnida in comprehensive treatises, but they have no real relationship to the arachnids, since at no stage in their development do they have a cephalothorax or prominent abdomen. Their relationship to the Crustacea is even more tenuous, for they do not have biramous appendages, and their own peculiar larval stage, the protonymphon, is distinct from all other arthropod larvae. They are characterized by an extreme reduction of the body, very long legs, which house the sex glands and diverticulae of the gut, and a subsidiary pair of egg-bearing legs, or ovigers, which are present in all males but lacking in the females of some genera. In addition to the walking legs, which are usually 8 in number, but may occasionally be 10 or 12, and the ovigers, there may be a pair of chelate appendages (chelifores) and sensory palpi. The presence or absence of these accessory appendages constitutes the basis of classification within the group. There is a simple nervous system of ventral ganglia, and a rudimentary circulatory system. There is no respiratory system or any specialized excretory organ, although in the males of many species there is a specialized cement gland which is believed to be of use in attaching the eggs to the ovigers of the male, who carries them around

until they are hatched. Shortly after hatching, the larvae of many species become encysted in hydroids, sea anemones or small medusae, where they live as parasites for a time. Some species are found in holothurians and at least one species spends its early life in the mantle cavity of bivalve mollusks.

Pycnogonids are found from the littoral zone to depths of more than 2,000 fathoms, in all oceans. Some live on sargassum at the surface while others appear to be bathypelagic. They vary in size from a span of 3 mm. for small littoral species to about 50 cm. in some of the abyssal forms.

In the course of my taxonomic studies of the collections of Pycnogonida in the United States National Museum, the Museum of Comparative Zoology, and the Peabody Museum at Yale, I have examined several hundred specimens, including examples of many of the known 10-legged forms, and in this paper I shall attempt to bring together in a coherent manner some of the speculations inspired by this large mass of material. Unfortunately, little is known about these creatures, especially the deep-sea forms, other than that which can be surmised from their pickled corpses. The following discussion, therefore, is not intended to blaze new paths in invertebrate morphology and evolution, but simply to suggest some directions in which future investigators might profitably set out. In other words, I have gathered together some speculations on the possible causes of some observed effects, for, as Aristotle said, "Nature does nothing which lacks purpose."<sup>1</sup>

I wish to acknowledge with thanks the generosity of Dr. Waldo L. Schmitt, Head Curator of Biology of the United States National Museum, in loaning me material and literature, and I also wish to thank Dr. Isabella Gordon, of the British Museum, for her patient answers to my persistent correspondence at a time when the British Museum was in the front line of battle (and suffered accordingly) and for the gift of a specimen of *Nymphon hiemale* from the *Discovery* collections.

## I. PHYLOGENY AND PATTERNS OF VARIATION

From time to time attempts have been made to divide the Pycnogonida into orders, but the families are so closely related, and their boundaries so broken down by transitional generic forms, that none of these attempts have been successful. An attempt to separate the families on the basis of the presence of ovigers in both sexes, or in the

<sup>1</sup> Gen. Anim. II, v. (741 b, 4-5), Loeb Classics ed., p. 207.

males only, for example, breaks down in the genus *Pallenopsis*, which has well-developed ovigers in the male and rudimentary ones in the female. Some workers have assigned this genus to the Phoxichilidiidae, others consider it a member of the Pallenidae. Diagnoses based on the retention or loss of chelifores in the adult cannot even be applied at the generic rank, particularly in the predominantly achelate genus *Achelia*, which has several chelate species. Hence, when one comes to draw a family tree, it looks more like a tangled web, or a bush with anastomosed branches, as in figure 1.



FIG. 1.—Hypothetical family tree of the Pycnogonida. (Transitional genera in backhand lettering.)

It will be noted that this family tree—or bush—rises from a hemispherical base. This base is the quantitative diagram of the families represented in figure 2, together with diagnostic drawings of the most common types of pycnogonids. Most of the forms illustrated in this diagram represent the type genera of the families concerned.

Such attempts as this to erect a family tree naturally bring up the problem of the roots, that is, the phylogenetic relationships of the Pycnogonida with other arthropod groups. This is probably the most difficult problem connected with these animals and may never be solved. Snodgrass, in the most recent and lucid discussion of arthropod evolution (1938) is none too certain of the affinities of the Pycnogonida, beyond placing them in the Chelicerata together with the Arachnida and Xiphosurida. But, if we accept his restriction

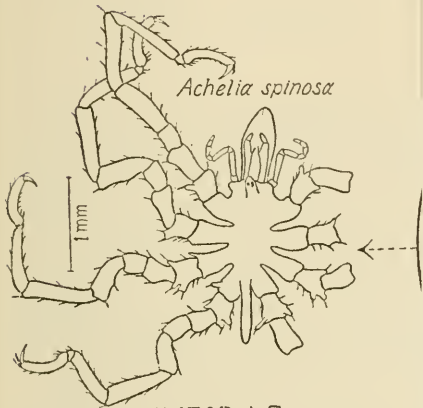
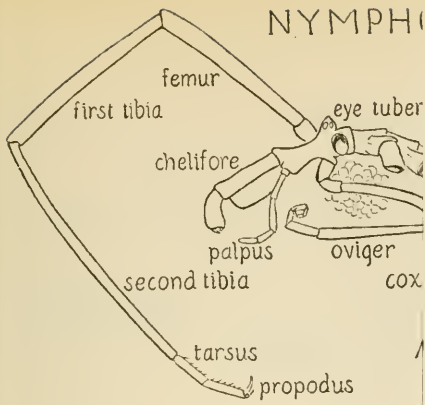


TABLE 1.—Synopsis of the families of Pycnogonida

| Family                                  | Ovigers   | Chelifores   | Palpi  | Trunk segs. | Principal genera   |
|---|---|--|--|-------------|--|
| NYMPHONIDAE<br>Wilson, 1878             | ♂, ♀;<br>10 jt., with<br>compound<br>spines           | present,<br>chelate  | 5 jt.  | 4-5         | <i>Nymphon</i><br><i>Heteronymphon</i><br>[ <i>Pentanymphon</i> ]  |
| PALLENIDAE<br>Wilson, 1878              | ♂, ♀;<br>10 jt., with<br>compound<br>spines           | present,<br>chelate  | absent, or<br>knoblike,<br>or 3-4 jt.                  | 4           | <i>Callipallene</i><br><i>Pseudopallene</i><br><i>Cordylochele</i><br><i>Austropallene</i><br><i>Oropallene</i><br><i>Propallene</i><br><i>Hannonia</i><br><i>Pycnothea</i><br><i>Decachela</i><br><i>Pigrogromitus</i><br><i>Pallenopsis</i>  |
| PHOXICHILIDIIDAE<br>G. O. Sars,<br>1891 | ♂;<br>5-9 jt., with<br>simple<br>spines               | present,<br>chelate  | absent, or<br>knoblike                                 | 4           | <i>Phoxichilidium</i><br><i>Anoplodactylus</i><br><i>Halosoma</i><br><i>Hodgsonia</i><br><i>Pycnosoma</i>  |
| ENDEIDAE<br>Norman, 1908                | ♂;<br>7 jt., with<br>simple<br>spines                 | absent   | absent   | 4           | <i>Endeis</i>  |
| AMMOTHEIDAE<br>Dohrn, 1881              | ♂, ♀;<br>9-10 jt.,<br>spines<br>simple or<br>compound | present,<br>usually<br>achelate,<br>but some-<br>times with<br>small<br>chelae | 6-10 jt.<br>( <i>Nympho-<br/>nella</i> ,<br>17-20 jt.) |             | <i>Ammothea</i><br><i>Achelia</i><br><i>Ammothella</i><br><i>Nymphopsis</i><br><i>Ascorhynchus</i><br><i>Nymphonella</i><br><i>Eurycyde</i><br><i>Cilunculus</i><br><i>Bohemia</i><br><i>Ephyrogymna</i><br><i>Pycnofragilia</i><br><i>Heterofragilia</i><br><i>Austroraptus</i><br><i>Lecythorhynchus</i><br><i>Ainigma</i><br><i>Paranymphon</i> |
| TANYSTYLIDAE<br>Schimkewitsch,<br>1913  | ♂, ♀;<br>10 jt., with<br>compound<br>spines           | achelate   | 4-6  | 4           | <i>Tanystylum</i><br><i>Clotenia</i><br><i>Austrodecus</i><br><i>Rhynchothorax</i><br><i>Discoarachne</i><br><i>Dorhynchus</i><br><i>Trygaeus</i><br><i>Scipiolus</i>  |

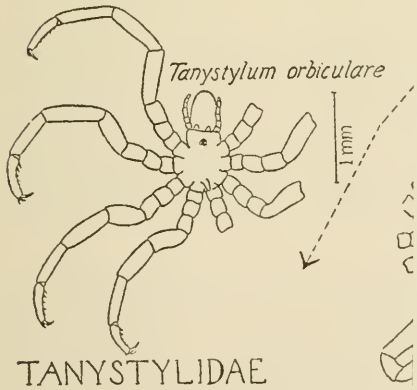


NYMPH



*Achelia spinosa*

AMMOTHEIDAE



*Tanystylum orbiculare*

TANYSTYLIDAE

FIG. 2.—Dia







TABLE 1.—*Synopsis of the families of Pycnogonida*—Continued

| Family                       | Ovigers                                     | Chelifores   | Palpi  | Trunk segs. | Principal genera  |
|------------------------------|---|--|--------|-------------|---|
| COLOSSENDEIDAE<br>Hoek, 1881 | ♂, ♀;<br>10 jt., with<br>compound<br>spines | absent, or<br>deciduous,<br>or chelate<br>in extra-<br>legged form | 8-10   | 4-6         | <i>Colossendeis</i><br><i>Rhopalorhynchus</i><br>[ <i>Pentacolossendeis</i><br><i>Decolopoda</i><br><i>Dodecolopoda</i> ]<br>? <i>Pipetta</i> |
| PYCNOGONIDAE<br>Wilson, 1878 | ♂;<br>6-9 jt., no<br>spines                 | absent   | absent | 4-5         | <i>Pycnogonum</i><br>[ <i>Pentapycnon</i> ]   |

(p. 137) of the Chelicerata to forms in which the genital openings occur always on the eighth postoral somite, the Pycnogonida occupy an anomalous position, since in several forms there are genital openings only on the last pair of legs. If we assign two postoral segments to the proboscis, as some do, this places the genital openings on the ninth postoral segment. This difficulty is recognized by Snodgrass himself (p. 138), and it would seem best not to attempt to include the Pycnogonida with any other group, but to leave it on a limb of its own somewhere between the Annelida and Arachnida.

This is essentially the view of those early students of the group, Dohrn and Hoek, who argued in favor of an independent origin for the Pycnogonida (cf. Hoek, 1881, as translated by Morgan, 1891, pp. 26-28). Morgan, however, believed that the Pycnogonida shared a common, albeit remote, origin with the Arachnida, and supported his view by pointing out embryological parallels between marine and terrestrial spiders, as well as such anatomical similarities as the diverticulae of the gut and the occurrence of chelae on the first pair of appendages. The most recent statement in favor of an independent position for the Pycnogonida is that of Marcus, (1940b, p. 129):

The Pantopoda do not in any phase possess the crustacean biramous limbs nor the arachnomorphous body composed of cephalothorax (prosoma) with six pairs of appendages and abdomen (opisthosoma). Therefore it seems advisable to consider them as a separate class of the Arthropoda—or the Euarthropoda, if the Malacopoda (Onychophora and Tardigrada) are left aside—and not to include them in Crustacea or Arachnomorpha (Merostomata and Arachnoidea) and thereby make diagnoses for these classes impossible.

The argument in favor of arachnid affinities for the Pycnogonida still has its supporters, however. In the imposing monograph for the Bronn's Tierreich series, Helfer and Schlotke (1935) consider the Pycnogonida a subclass of the Chelicerata, nearer to the Arachnoidea

than to any other group. But they are none too sure on the point, and conclude their discussion of affinities with this escape clause (p. 179): "Aber darüber ist das letzte Wort noch nicht gesprochen." Calman and Gordon (1933) are more positive in their view of the arachnid affinities of the Pycnogonida, and advance the theory that discrepancies between the Pycnogonida and the Arachnida might be accounted for by metameric instability in the cephalic region of the Pycnogonida. It does not seem to be that this is a tenable view, for although there is

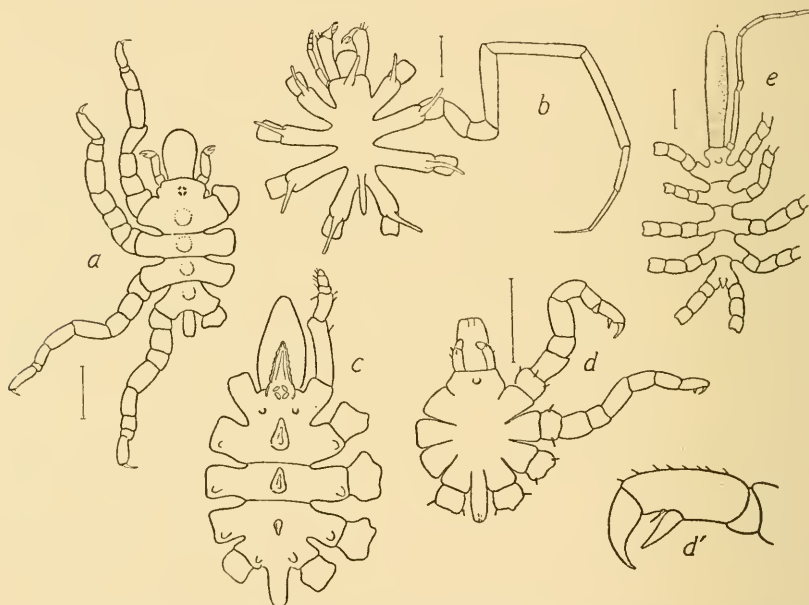


FIG. 3.—Some transitional forms of pycnogonids. a, *Pigrogromitus timsanus* (after Calman, 1927); b, *Paranympyon spinosum*; c, *Rhynchothorax mediterraneus* (after Dohrn, 1881); d, *Decachela discata*; d', tarsus and propodus; e, *Pentacolossendeis reticulata*. The line indicates 1 mm.

evidence of instability in the Pycnogonida, I am inclined to believe that it is too recent to be of phylogenetic significance, and is of a different character than Calman and Gordon apparently believed.

However, I do agree with these authors that certain fossil forms from the Lower Devonian are not pycnogonids, and I further suspect that the group is a fairly recent one, and is still undergoing active evolution.

Certainly an inspection of the transitional and anomalous genera (see fig. 3) lends support to this view, for they present examples of missing links which would delight and confuse a paleontologist. This occurrence of diversified forms connected by numerous transitional



types suggests youth rather than age, for we would expect a loss of transitional and experimental forms in an old group.

There is, for example, the curious genus *Pigrogromitus* Calman (1927) from the Suez Canal.<sup>2</sup> The body type of this genus is the same as that of *Pycnogonum*, the type and only genus of the family Pycnogonidae, which is without chelifores and palpi and lacks ovigers in the female. But *Pigrogromitus*, with its 10-jointed ovigers in both sexes and chelate chelifores, must be placed in the Pallenidae. Nor is it the only transitional genus in this family; it represents but one of the extremes of variation.

Most members of the Pallenidae are of the long-legged, extended type, but there are several compact disciform genera, such as *Pseudopallene*, which suggest affiliation with the Tanystylidae. Without its peculiar propodus, which Hilton (1939a) considered to be a family character, *Decachela* appears to be another transitional form between the Tanystylidae and Pallenidae. The possession of a large spine on the sole, which is opposable to the terminal claw, the two forming a subchelate structure, cannot be considered a character entitling this form to family status, although it may be a variation *sui generis*. There are the usual eight joints in the leg instead of the seven suggested by Hilton's statement, "legs apparently seven jointed."

The genus *Pallenopsis*, a transitional form between the Pallenidae and the Phoxichilidiidae, has already been referred to. The phoxichilidiid characters of this genus are the possession of femoral cement glands in the male and the overhanging prolongation of the cephalic segment. Because of its 10-jointed ovigers, present in both sexes but reduced in the female, I consider it a pallenid.

Thus, in one family alone, there are transitional forms indicating affinities with three diverse groups considered worthy of family rank. If we consider the Tanystylidae, which is related to the Pallenidae through such genera as *Pseudopallene* and *Decachela*, we find that it in turn is related to the Pycnogonidae through the genus *Rhynchothorax*, which has a body form approximating that of *Pycnogonum*. Inasmuch as the Tanystylidae are almost inseparable from the Ammotheidae, observations on the relationships between either of these families and the other families are mutually applicable. The principal differences between the two families are that the proboscis is usually large and bulbous in the Ammotheidae and that the palpus has more

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<sup>2</sup> Hilton's (1942c) *Pigrogromitus robustus* from Unalaska is actually *Pycnosoma strongylocentroti* Losina-Losinsky, and constitutes an extension of range for that species from its type locality (48° 58.2' N., 140° 35.3' E.) to Alaskan waters.



joints. The Ammotheidae (and Tanystylidae) comprise a diverse group of forms whose common characters are the reduction of the chelifores (or, when chelate, the chelae are small and lack teeth on the fingers), well-developed palpi, and ovigers in both sexes, usually with compound spines on the terminal segments.

Among the interesting genera in the Ammotheidae are *Cilunculus* Loman (1908), the male of which has femoral cement glands opening through a prominent dorsal tube as in *Pallenopsis* and some species of *Anoplodactylus* (Phoxichilidiidae), and *Paranymphon* Caullery (1896), which has heretofore been referred to the Nymphonidae. In *Paranymphon* the palpi are seven-jointed, whereas in *Nymphon* they are always five-jointed, but the principal reason for removing this genus from the Nymphonidae is the discovery of a somewhat similar form, *Ainigma* Helfer (1938), in which the ammotheid affinities are more clearly marked, and which in turn seems to be more closely related to *Paranymphon* than to any other genus. These two curious forms are very similar in body form, with high dorsal tubercles on the well-separated lateral processes, and simple tarsal joints.

In contrast to the diversity of form in the Ammotheidae, Tanystylidae, Pallenidae, and Phoxichilidiidae, the families Nymphonidae, Colossendeidae, Pycnogonidae, and Endeidae are remarkably uniform. The Pycnogonidae and Endeidae are monogeneric families, and there are but two indubitable genera in the Nymphonidae and Colossendeidae, apart from the extra-legged forms, which are a special case. These latter families, however, possess large numbers of closely related species.

The most conspicuous thing about this pattern of variation is the way in which it is correlated with extra-legged forms. It will be noted, from an examination of figure 2, that in families where variation is manifested at generic rank (as indicated by the high proportion of genera to species), 10-legged forms do not occur (so far as we know), whereas in those families in which variation is more active at the species rank, several 10-legged forms have appeared. The only exception to this generalization is the Endeidae, a small monogeneric family which may actually be an offshoot of the Pycnogonidae.

It will be noted that I have not attempted to indicate the comparative ages of the various families or branches in my diagram. It is usually contended that the Pycnogonidae are the most specialized family, and the Nymphonidae the most generalized group, retaining more of the primitive attributes than the Pycnogonidae. The Colossendeidae are intermediate, according to this view, and the other families branch out from the tree more or less according to individual

fancy or taste. When 10-legged forms were first discovered, it was suggested that they were the primitive types, and should be at the base of the tree (Cole, 1905), but this suggestion was made before these forms were well known. It now seems more reasonable to suggest that they are recent innovations in form, at least as far as the present pattern of variation is concerned. The occurrence of these 10-legged forms in three widely divergent branches suggests a common origin for these branches. For that matter, none of the families are actually different enough to enable one to assign any to a higher or lower place on a vertical scale, and the pattern of variation in the Pycnogonida is not amenable to a lineal or two-dimensional interpretation, but is three-dimensional, the various families or branches diverging in all directions from a central or nuclear type.

How such a structure might be bound into relationship with the other groups of the Arthropoda, is difficult to say. However, it is probably no more difficult to visualize a relationship of three-dimensional structures than it is to decide just where, in a simple branching pattern, the Pycnogonida stem out from the remaining Arthropoda. All phylogenetic trees and speculations are influenced by honest errors in evaluating characters, but as Snodgrass said in his concluding remark (1938, p. 149): "Every biologist must have a working creed of phylogeny, but he should not too implicitly believe its tenets."

## II. TEN-LEGGED FORMS

Forty years ago, most zoologists who interested themselves in the matter believed that the Pycnogonida possessed but four pairs of walking legs, and considered that feature one of the diagnostic characters of the group. Although the first 10-legged form had been collected by James Eights on a voyage to the South Shetlands in 1829 and described, with an adequate figure, in 1835 under the name *Decolopoda australis*, it was generally ignored by naturalists.<sup>3</sup> For ex-

<sup>3</sup> For the melancholy story of Dr. James Eights (M. D.) and his Antarctic travels, see *The Reincarnation of James Eights, Antarctic explorer*, by John M. Clark (Sci. Month., vol. 2, No. 2, pp. 189-202, 1916), and *James Eights, a pioneer Antarctic naturalist*, by W. T. Calman (1937a). The latter paper is based on the earlier one, but a bibliography of Eights' writings has been added and the discussion of his zoological discoveries is more extended. There is also an interesting diagram of extra-legged pycnogonids, and a facsimile of the original figure of *Decolopoda australis*. Unfortunately the color of the copy from which the facsimile was made is poor; it should be red instead of slate brown. Further information on Eights and his contemporaries will be found in a brief paper by Lawrence Martin, *Early explorations and investigations in southern South America and adjacent Antarctic waters by mariners and scientists from*

ample, Hoek, in his monograph on the *Challenger* Pycnogonida (1881, p. 6), dismissed Eight's *Decolopoda* with these words: ". . . I have not been able to ascertain whether this is a good genus, nor where it has been found." Apparently he did not see Eight's paper. When the Rev. T. R. R. Stebbing wrote a series of popular articles on pycnogonids for *Knowledge* in 1902, he considered *Decolopoda* an amateurish blunder and denied that there could be such a thing as a 10-legged pycnogonid. A few years later, Dr. J. C. C. Loman, a well-known Dutch zoologist and author of several papers on the Pycnogonida, published a paper to the effect that *Decolopoda* must have been a monstrosity. Hardly had the ink dried on these contributions when the South Polar expeditions began to return with not one but two species of 10-legged pycnogonids!

The new species was *Pentanympyon antarcticum*, whose generic name indicates that it differs from the well-established octopodous *Nympyon* only in the possession of an additional pair of legs. Another species, *P. minutum*, has recently been described (Gordon, 1944). Shortly after the discovery of *Pentanympyon*, a third type, related to the octopodous *Pycnogonum*, was found, one species in the Antarctic and another, strangely enough, from French Guiana, and a second species of *Decolopoda* was collected in the Antarctic. As if this were not enough, a 12-legged specimen, which has been named *Dodecolopoda mawsoni*, was found by the recent British, Australian, and New Zealand Antarctic Research Expedition on the edge of the Antarctic south of Kerguelen. Finally, among the material belonging to the United States National Museum, I found several specimens of still another form of 10-legged pycnogonid, which I have named *Pentacolossendeis reticulata*, collected as early as 1872 off the Florida Keys. It is something of a mystery why this species remained undescribed so long, since it was first collected by William Stimpson,

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the United States of America (*Nature*, vol. 146, pp. 238-239, 1940), and Congressional Record, vol. 86, Appendix, pp. 3194-3195, 1940.

Now, after more than a hundred years, one of Eight's original specimens of *Decolopoda* has been found among the collections in the Museum of Comparative Zoology. Although the only information available concerning this specimen is a cryptic "Parchment No. 952" and a catalog entry, "South Shetlands," the circumstances indicate that this is one of the long-lost types. It is possible that it was presented to Dr. Amos Binney, together with the manuscript and plate referred to in the letter from Eight to Dr. Binney (included in Calman's paper), and eventually found its way to the Museum of Comparative Zoology. The specimen is lacking a few of the terminal joints of some of the legs and one of the ovigers is detached, but it is otherwise in good condition. Accordingly, the specimen has been designated "Neoholotype, ♂, M.C.Z. No. 12271."

author of several species of pycnogonids, and although he died before finding time to study his material, the species was collected again in 1893 by the State University of Iowa expedition, and three more specimens were collected by the *Fish Hawk* in 1902.<sup>4</sup>

There are, then, seven, or perhaps eight (there may be a third species of *Decolopoda*), species of decapodous pycnogonids, and one dodecapodous species. They are so far known only from the Antarctic and American tropical regions, and several of them are common, to the extent that every expedition manages to collect several specimens. They are neither isolated freaks nor monstrosities, but relatively stable forms.

The most curious thing about these extra-legged pycnogonids is their close resemblance to certain "normal" genera, a resemblance which in some cases extends to a particular species. *Pentanympyon* is simply a *Nympyon* with an extra pair of legs, *Pentapycnon* a 10-legged *Pycnogonum*, and *Pentacolossendeis* would be *Colossendeis* without its extra legs. *Decolopoda*, however, is somewhat different from the thick-set species of *Colossendeis* which it resembles in that it possesses chelifores, but since chelifores are occasionally retained through the last moult stage in some individuals of the genus, the difference is not as great as it seems. *Dodecolopoda* is merely an extra-legged *Decolopoda*, and is so far known only from a single specimen.

The most conspicuous example of resemblance between a decapodous and an octopodous form is that of *Pentapycnon charcoti* Bouvier and *Pycnogonum gaini* Bouvier. Both of these are Antarctic forms: *P. charcoti* occurs in the South Shetlands, and *P. gaini* has been collected from the Palmer Archipelago, Ross Sea, and eastward to 54° E. Bouvier, who described both species, commented upon the similarities

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<sup>4</sup> William Stimpson, M. D. (1832-1872), was "a naturalist of no mean capacity" who gathered a fine collection, wrote largely in Latin and was director of the Chicago Academy of Sciences from 1865 to 1872. He lost all his work and collections (including the Pourtalès collection from the Florida Keys) in the Chicago fire of 1871, and never recovered from the shock. In April 1872 he went to the Keys on the *Bache*, but even this did not revive him and he died on May 26. Nathaniel Southgate Shaler, in his *Autobiography*, pp. 128-129, has an interesting little story about Stimpson. It happened in those days when Agassiz père reigned at Harvard and "that Darwinian hypothesis" was not to be mentioned except in private. According to Shaler, Stimpson "was much puzzled by the transitional varieties between many of the species of molluscs he was studying, especially those occurring among the fresh water gastropods. On one occasion I saw him throw one of these vexatious shapes upon the floor, after he had studied it for a long time, put his heel upon it and grind it to powder, remarking, 'That's the proper way to serve a damned transitional form.'"



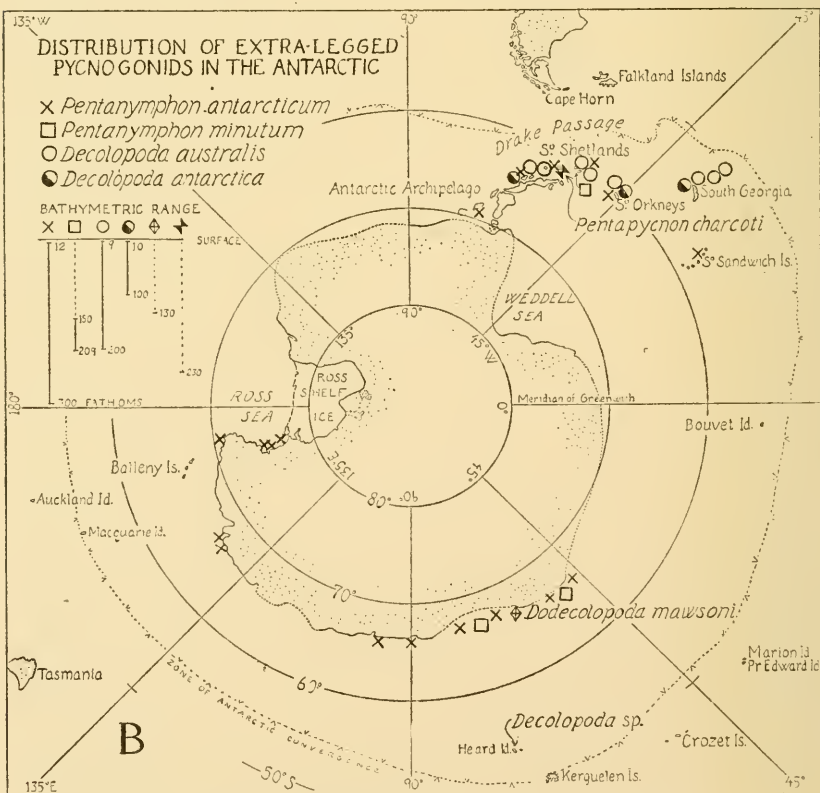
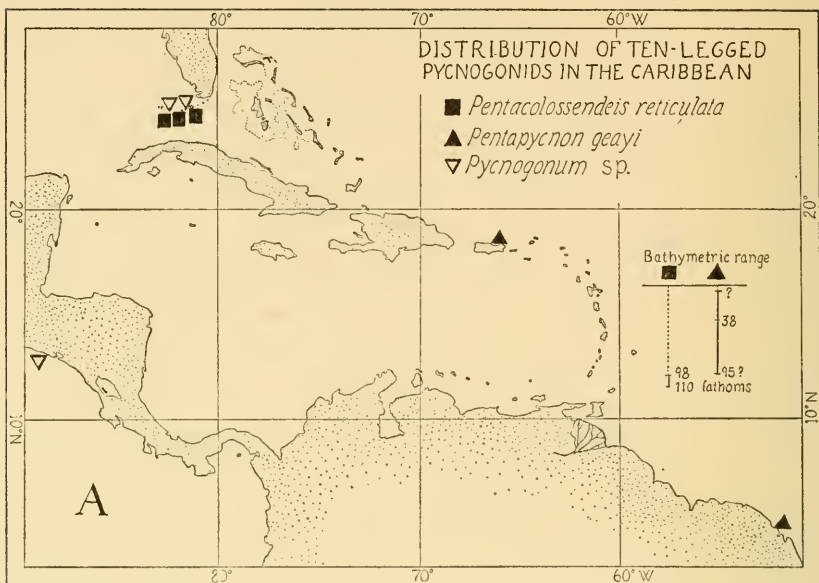


FIG. 4.—Distribution maps of polymerous pycnogonids.

between them at some length (1913, pp. 157-160), but placed stress on the last dorsal trunk tubercle of *P. gaini* as a vestigial remnant of the lost fourth somite, in support of his theory that the 10-legged species were the primitive forms. The essential difference between these two forms, according to Bouvier's figures, is the dilated proboscis, adorned with a dorsal tubercle, of *Pentapycnon charcoti*. According to Gordon (1944, p. 69), the proboscis of *Pycnogonum gaini* is sometimes dilated at the tip and may also bear a noticeable tubercle. It would seem, then, that these two forms are closely similar, with essentially the same range of variation, and that it would be impossible to refer a specimen lacking the posterior segments to its "genus."

This same parallelism is evident, but not as pronounced, between the tropical American *Pentapycnon geayi* Bouvier and a West Indian species, *Pycnogonum* sp.<sup>5</sup> Here again the most conspicuous difference between the two forms is the shape of the proboscis, which is longer and more tapered in the decapodous form. Also, its dorsal tubercles are taller. The ovigers are almost identical and could not be told apart if separated from the specimens. Unfortunately there is not enough material available of either species to determine the range of variation.

Turning to the 10-legged nymphons, we find similar examples of paired species. Although it might be protested that the genus *Nymphon* is such a large and complex one that it would be easy to find an approximate counterpart of a 10-legged form, the case is strengthened by the existence of a double parallel, in which the two decapodous forms are closely related to a pair of octopodous species, *Nymphon hiemale* Hodgson and *Nymphon gracillimum* Calman.

The most widely distributed decapodous form, *Pentanympyon antarcticum*,<sup>6</sup> differs from its cognate "normal" species, *Nymphon hie-*

<sup>5</sup> This is an unpublished species. I regret that this discussion necessitates mention of this species before its formal description in my forthcoming monograph of Western Atlantic and Caribbean species.

<sup>6</sup> If the future taxonomists act on the suggestion that such decapodous genera as *Pentanympyon*, *Pentapycnon*, and *Pentacolossendeis* cannot stand alone, it should be noted that both *antarcticum* (Miers, 1879), and *minutum* (Goodsir, 1842) have been used for *Nymphon* and that nomina nova might be required for the pentamerous forms, since these names would be unavailable for trinomial designations. As a matter of convenience, the pseudogeneric names should be retained, but in any event, names for new decapodous species should be different from those in the respective octopodous genera. Dr. Hobart M. Smith (Science, vol. 102, No. 2643, pp. 185-189, 1945, Categories of species names in zoology) has proposed an elaborate classification of species names, which does not, however, suggest a solution for this particular problem. It might be feasible, if it

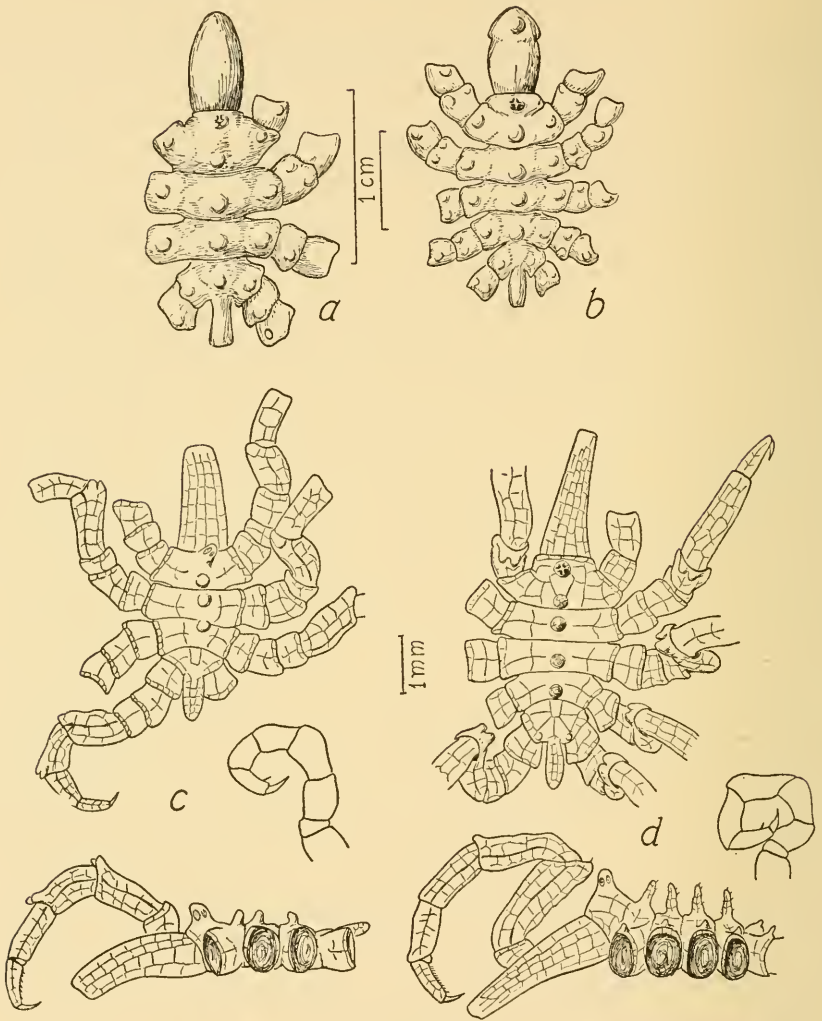


FIG. 5.—a, *Pycnogonum gaini*; b, *Pentapycnon charcoti*; c, *Pycnogonum* sp.; d, *Pentapycnon geayi*. (a and b, and oviger of *P. geayi* after Bouvier, 1913; c and d, original and to same scale.)

*male*, in the following respects: The tarsus of *P. antarcticum* is somewhat shorter than the same joint in *N. hiemale*, the third joint of the palpus may be slightly longer, and the compound spines of the

turns out these forms actually represent the same species, to adopt some sort of exponential notation, such as *Nymphon<sub>3</sub> hiemale [antarcticum]*, or *N. hiemale<sub>3</sub>*, etc. It does not seem to me that these pseudogeneric names can be used as subgeneric categories, as the forms represented do not conform with the usual conception of a subgenus.



oviger are somewhat different (see fig. 6). According to Hodgson's figures, the differences between these compound spines are conspicuous, but in the two specimens I have examined they are not so signifi-

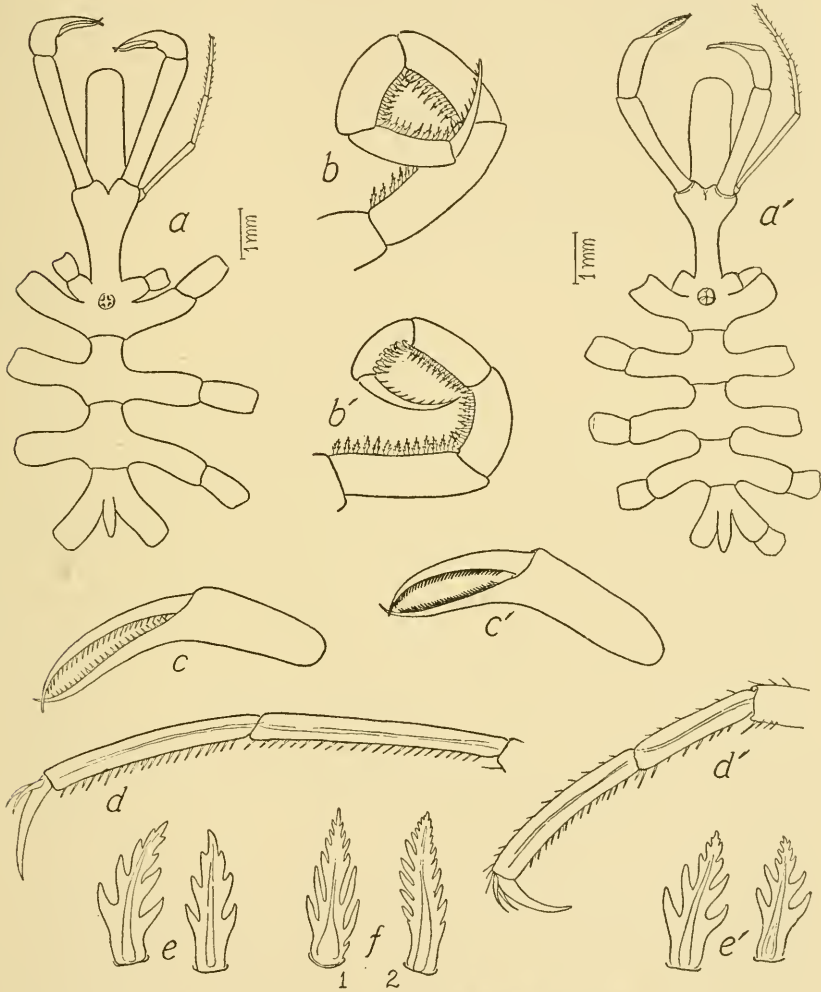


FIG. 6.—*Nymphon hiemale* and *Pentanymphon antarcticum*. a, dorsal view of trunk; b, terminal joints of oviger; c, chela; d, tarsus and propodus; e, compound spines of oviger; f, compound spines of oviger (after Hodgson, 1907): 1, *P. antarcticum*, 2, *N. hiemale*. Scale of magnification for each pair of structures is the same.

cant. Evidently there is some variation in the conformation of these spines with individual specimens, for the differences are too great to be explained by artistic interpretation of a minute structure whose

location renders large-scale camera-lucida drawings impossible. The two species are conspicuously alike in general appearance and conformation of the chelae.

The other decapodous species, *P. minutum*, is a smaller edition of *P. antarcticum*, and is very close to *N. gracillimum*, which in turn appears to be a smaller form of *N. hiemale*. It is closer to *N. gracillimum* than *P. antarcticum* is to *N. hiemale*, especially in the structure of the compound spines and proportions of the tarsal joints. Since all four of these forms are highly variable in these and other details,

TABLE 2.—*Ratios and measurements of Nymphon and Pentanyphon*  
(Compiled principally from Gordon, 1932.)

|                                    | <i>Nymphon hiemale</i> | Sp. from Discovery<br>St. 149 (♂) | <i>Nymphon gracillimum</i> | <i>Pentanyphon antarcticum</i> | Sp. from Neny Fjord,<br>Palmer Land (ov. ♂). | <i>Pentanyphon minutum</i> |
|------------------------------------|------------------------|-----------------------------------|----------------------------|--------------------------------|--|----------------------------|
| Length of trunk, mm....            | 6.-7.2                 | 5.5                               | 4.8                        | 5.8                            | 6.1  | 2.8                        |
| Spinules on chelae.....            | 24/29-36/40            | 25/30                             | 22/24                      | ...                            | 31/33  | 25/29                      |
| Palpus, jts. $\frac{4+5}{2}$ ..... | .81-1.08               | .93                               | .85                        | .96*                           | .66  | 1.*                        |
| Spines on oviger.....              | 31-43                  | 40                                | 33                         | 40                             | 43   | 28-33                      |
| Leg:                               |                        |                                   |                            |                                |  |                            |
| coxa $\frac{2}{1+3}$ .....         | 1.60-2.2               | 1.49                              | 2.1                        | 1.2-2.0                        | 1.78   | 2.14                       |
| tarsus<br>propodus.....            | .83-1.16               | 1.1                               | 1.33                       | .63-1.2                        | .75  | .93                        |
| length, mm.....                    | .....                  | 34.95                             | 41.90                      | ....                           | 27.50  | 15.00                      |
| Leg/trunk ratio.....               | 7.25†                  | 6.4                               | 8.5‡                       | 4.65                           | 4.5  | 5.36                       |

\* Determined from Gordon's (1944) figures.

† Determined from Hodgson's (1907) figures.

‡ Determined from Calman's (1915) figures.

and all are found in the same general regions of the Antarctic, it seems evident that we are dealing with a common racial stock. These relationships are clearly brought out in table 2, from which it will be noted that the most significant deviation between the octopodous and decapodous forms is the ratio of the length of leg to trunk. This, however, is not surprising, but indicates that there has been no material increase in the length of the leg with the addition of an extra somite, which results in a radical reduction of the ratio.

A further interesting fact is brought out by logarithmic plotting of the trunk-leg ratio of these four forms (fig. 7). As is to be expected, the trend is downward, but the much smaller size of the measured

specimen of *Pentanympyon minutum* places it outside this trend. However, if it had happened to be twice as large, its position on the graph would be precisely where expected, namely, in the same relation to *Pentanympyon antarcticum* as *Nymphon gracillimum* is to *N. hiemale*. Therefore it can be assumed that the trend of the leg-trunk ratio of *Pentanympyon minutum* is parallel to that of the other three forms.

This close relationship between decapodous and octopodous forms is not so evident for the species of *Decolopoda*, since the retention of the chelifores sets them apart from *Colossendeis* at the outset. However, the *Colossendeis* most closely resembling *Decolopoda*, *C.*

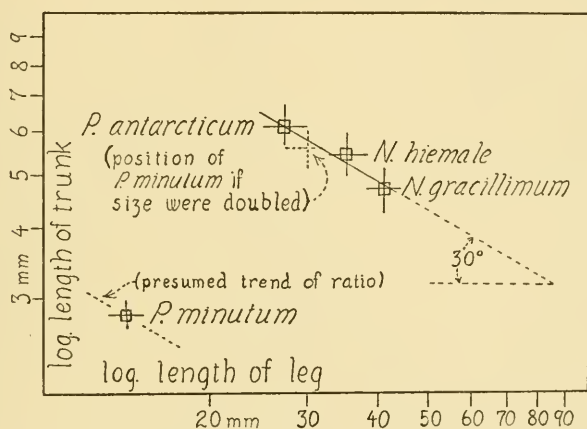


FIG. 7.—Logarithmic graph of the ratios of *Nymphon* and *Pentanympyon*.

*wilsoni*, shows a close agreement in proportions with *D. antarctica*, and this resemblance is further emphasized by the fact that *C. wilsoni* has eight-jointed palpi, instead of the usual nine for the genus. From table 3, giving ratios and comparison of anatomical characters, it can be seen that *C. wilsoni* agrees more closely with *D. antarctica* than with *D. australis* except in the leg-trunk ratio, in which respect it agrees with the specimen of *Decolopoda* from Heard Island measured by Gordon (1944). It is of interest to note that this Heard Island specimen, which is the nearest record for *Decolopoda* to the type and only known locality for *Dodecolopoda*, shows more similarities to *Dodecolopoda* than to these species of *Decolopoda* from the American quadrant of the Antarctic. The intermediate character of the ratios of *Colossendeis wilsoni*, as contrasted with those of *Decolopoda antarctica* from the Antarctic archipelago and *D. sp.* from Heard Island, is of

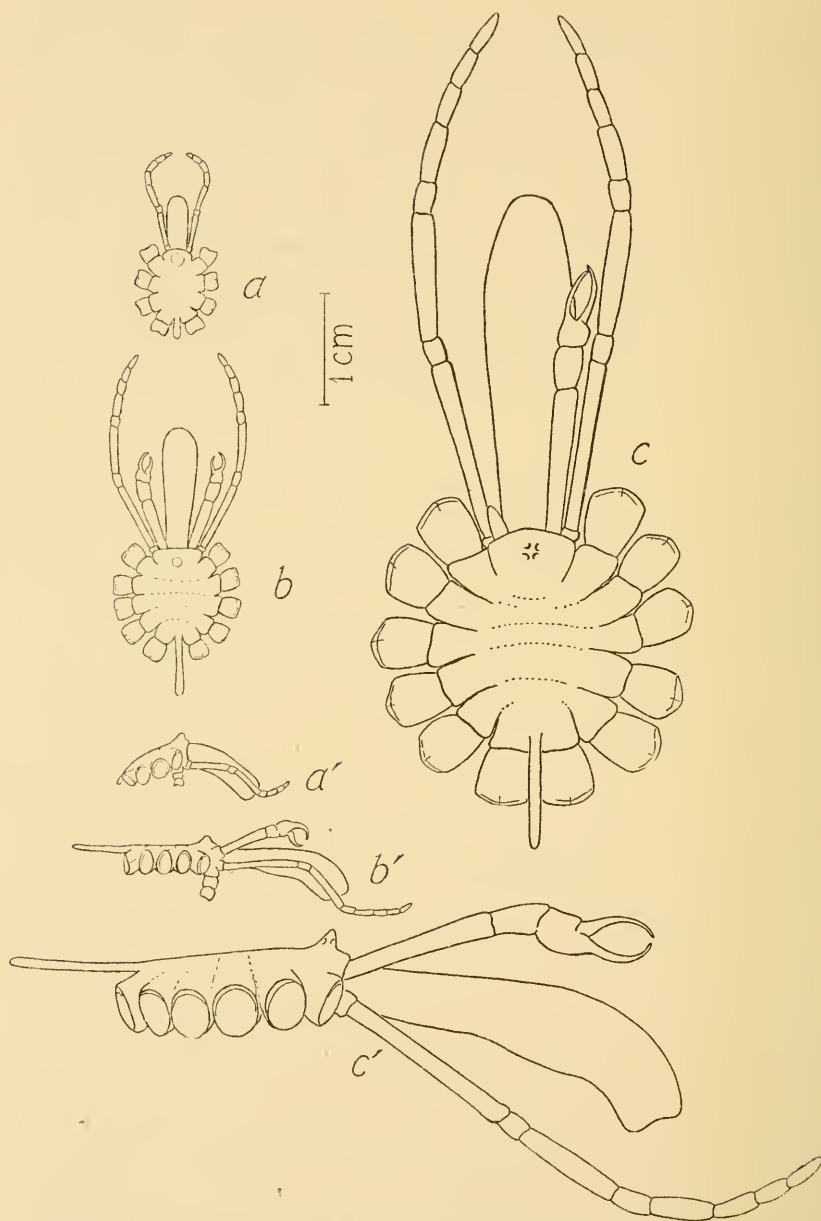


FIG. 8.—a, *Colossendeis wilsoni* (after Calman, 1915); b, *Decolopoda australis*; c, *Dodecolopoda marwsoni* (after Calman and Gordon, 1932). Dorsal and lateral views of trunk. All drawings to the same scale.

further interest in view of the occurrence of *C. wilsoni* at Cape Adare, about midway between those localities.

As Calman and Gordon (1932, p. 110) pointed out, the occurrence of a pycnogonid with six trunk somites "does not really involve any important modification of the problem presented by the ten-legged species." As table 3 shows, the widest divergence between *Dodeco-*

TABLE 3.—*Anatomical characters and measurements, Colossendeis, Decolopoda and Dodecolopoda*  
(Compiled principally from Gordon, 1932 and 1944.)

|  | <i>Colossendeis wilsoni</i>           | <i>Decolopoda antarctica</i>          | <i>Decolopoda australis</i>           | <i>Decolopoda</i> sp. (Heard Island)  | <i>Dodecolopoda mawsoni</i>           |
|--|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|
| Trunk:   |                                       |                                       |                                       |                                       |                                       |
| length, mm.....                                  | 5.28                                  | .....                                 | 9-10*                                 | .....                                 | 18                                    |
| area.....  | 28                                    | .....                                 | 55                                    | .....                                 | 148                                   |
| $\sqrt[3]{\text{area}}$ .....                    | 3.03                                  | .....                                 | 3.8                                   | .....                                 | 5.28                                  |
| $\frac{\text{width, 2d lat. proc.}}{\text{leg}}$ | .94                                   | .96-1.00                              | .85-.92                               | .97                                   | 1.00                                  |
| Palpus, No. of jts..                             | 8                                     | 8-10                                  | 9                                     | 9                                     | 9                                     |
| Chelifore:                                       |                                       |                                       |                                       |                                       |                                       |
| length, 1st jt. ....                             | ×                                     | .66-.75                               | .5-.65                                | .46                                   | .75                                   |
| length of trunk ...                              | ×                                     | 6.00-8.00                             | 4.0-5.3                               | 3.0                                   | 5.4                                   |
| width 1st jt. ....                               | ×                                     | palm long, fingers slightly arched    | palm short, fingers strongly arched   | palm short, fingers strongly arched   | palm short, fingers strongly arched   |
| chela.....                                       | ×                                     | more than half width of cephalic seg. | less than half width of cephalic seg. | less than half width of cephalic seg. | less than half width of cephalic seg. |
| Eye tubercle.....                                | more than half width of cephalic seg. | more than half width of cephalic seg. | less than half width of cephalic seg. | less than half width of cephalic seg. | less than half width of cephalic seg. |
| Leg:   |                                       |                                       |                                       |                                       |                                       |
| length, mm.....                                  | 34.39                                 | .....                                 | 90-100*                               | .....                                 | 240.3                                 |
| tibia 1.....                                     | 1.06                                  | 1.05-1.08                             | 1.00-1.04                             | 1.12                                  | 1.19                                  |
| femur tibia 2.....                               | 1.25                                  | 1.22-1.33                             | 1.04-1.13                             | 1.24                                  | 1.20                                  |
| femur leg.....                                   | 6.5                                   | 10.-11.                               | 10.-11.                               | 5.40                                  | 13.4                                  |
| trunk.....                                       |                                       |                                       |                                       |                                       |                                       |

\* Estimated from photograph of neoholotype.

*lopoda* and *Decolopoda* is the leg-trunk ratio. Unlike the decapodous nymphons, in which the body length is materially increased by the addition of a fifth somite, *Decolopoda* and *Dodecolopoda* appear to incur no noticeable increase in body length with the addition of somites over the ratio for the closely related *C. wilsoni*. Recognizing that their species might just as easily be called a *Decolopoda*, Calman proposed a new generic name for it simply as a taxonomic conveni-

ence, and it is certain that *Dodecolopoda* represents one more step in the pattern of variation beyond *Decolopoda*. Its cognate decapodous form is probably *Decolopoda australis*. Unlike the decapodous forms of the other genera, these polymerous colossendeids are much larger than the related octopodous form.

This larger size, however, is not disproportionate, but appears to represent an arithmetic progression between *Colossendeis wilsoni*, *Decolopoda australis* and *Dodecolopoda mawsoni*. Furthermore, when the ratio of trunk length to leg length is plotted against the

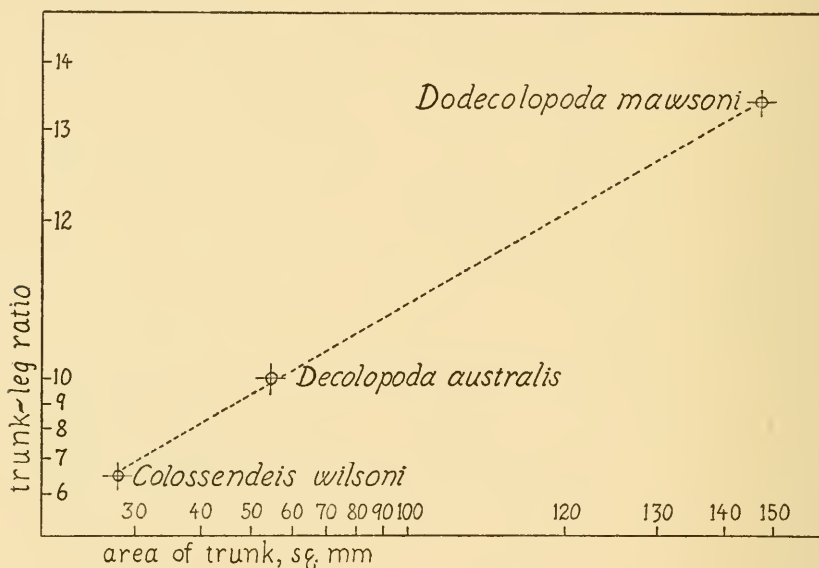


FIG. 9.—Logarithmic graph of trunk-leg ratio as compared to trunk area of polymerous colossendeids.

area of the trunk (as determined by projecting the trunk on squared paper), the relationship between the three forms is very similar to the curves for differential growth of a part as compared to the whole of the different stages of the same organism (fig. 9). Many such graphs of heterogonic growth are presented by Huxley in his work on relative growth.<sup>7</sup> Admittedly, the available data is inadequate, but it appears to be consistent. Plotting the trunk and leg lengths (fig. 10), for example, gives virtually the same curve as the trunk-leg ratio to trunk area graph. There is the same angle of  $30^\circ$  and the location of *Decolopoda australis* at about one-fourth the distance (or 1:3) be-

<sup>7</sup> Huxley, Julian S., Problems of relative growth. 276 pp. New York, 1932.



tween *C. wilsoni* and *D. mawsoni*. A further coincidence is the indication that the curve for leg-trunk ratio of the *Nymphon*-*Pentanympion* group is also at an angle of  $30^\circ$ , although it has a downward rather than an upward trend.

More precise and extensive data might reveal some interesting facts about ratios and growth rates, especially if a growth series could be assembled. It would be particularly interesting to verify the *Nymphon*-*Pentanympion* curve, and confirm the apparent trend of

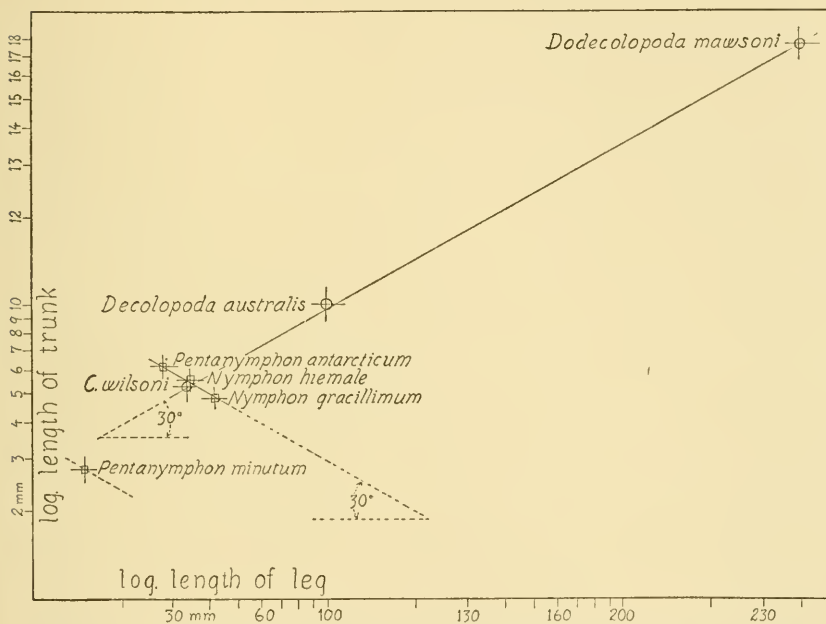


FIG. 10.—Combined logarithmic graph of trunk-leg ratios of *Nymphon*, *Pentanympion*, *Colossendeis*, *Decolopoda*, and *Dodecolopoda*.

$30^\circ$  for the polymerous forms in both families. It is not certain that much can be proved by such analysis, other than to demonstrate a common set of numerical values for the different types of polymerous forms. One should be wary of inferring too much from the trends revealed by logarithmic plotting, for they are inherent in the method itself. It is easy to become bemused by these pretty graphs, and they have fascinated several biologists to the extent that their contributions on the subject might be termed a logarithmic analysis of the λόγος.

Although *Pentacolossendeis reticulata* is not a rare species, and may presumably be collected almost at will along the hundred-fathom line south of the Florida Keys, no closely related *Colossendeis* from



the same region has come to light. It is of particular importance, however, in demonstrating that the occurrence of 10-legged pycnogonids in the tropical American region is not an isolated phenomenon, confined to a single species. It is also of further interest in that in two of the five known specimens the second trunk somites are smaller, and the second pair of legs arising from this somite are slightly shorter than the remaining legs. Since this difference occurs not once, but twice, it would seem that this is not an individual variation, but is in some way correlated with the decapodous condition.

It is difficult to ascribe any external environmental cause to the origin of the decapodous (and dodecapodous) forms, for two more diverse sets of conditions than those prevailing in the Antarctic and the American subtropical or Caribbean regions could not be imagined. These regions are widely divergent in both salinity and temperature. For example, the salinity of the Antarctic region of the South Atlantic ranges from 33 to 35 parts per thousand, whereas that of the tropical American region has a range of 36 to 38 parts per thousand. Indeed, the only physical condition these areas appear to have in common is that both overlie tectonic arcs, areas of stress in the earth's crust where negative anomalies in gravity may occur.<sup>8</sup> However, this geophysical condition shows little correlation with the occurrence of decapodous pycnogonids, since they are unknown from the East Indies, Japan, and other island arc regions. If future collections do bring more decapodous pycnogonids to light, however, it is safe to suggest that the most likely area in which they will be found is the East Indies.

It may be significant, for reasons still not apparent, that decapodous pycnogonids are most numerous, both in species and numbers, along the Antarctic arc from the Palmer Peninsula to South Georgia. Furthermore, within this critical area the decapodous forms and their corresponding octopodous forms occur only south of the zone of Antarctic-South Atlantic convergence. Although the available data are not extensive, there seems to be a further limitation of decapodous forms to the colder waters of the Antarctic, whereas the corresponding octopodous forms, at least in the genus *Nymphon*, occur in higher temperatures. This becomes evident when the distribution of the *Nymphon*-complex is mapped against the temperature distribution (fig. 11). Of course it is also true that a similar correlation can be assumed for salinity, but in this case the range does not seem

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<sup>8</sup> Measurements of isostasy have not yet been made in the Antarctic, but Hess (Proc. Amer. Philos. Soc., vol. 79, No. 1, p. 73, 1938) suggests that a negative anomaly strip "will almost be certainly present around the Cape Horn, South Georgia-Antarctica island arc."

to be great enough to justify any generalization, inasmuch as it is in the magnitude of 00.3 parts per thousand.

Because of the virtually identical distribution of the two species of *Decolopoda*, no generalizations as to their distribution can be inferred. As for *Pentapycnon charcoti* and *Pycnogonum gaini*, it would seem, in this case, that the decapodous form is the more northern one, for it was found in the South Shetlands, north of the Palmer Peninsula, whereas *Pycnogonum gaini* occurs near the base of the peninsula, in the Ross Sea, and along the edge of the Antarctica south of New Zealand and Australia. This distribution pattern is tentative, inas-

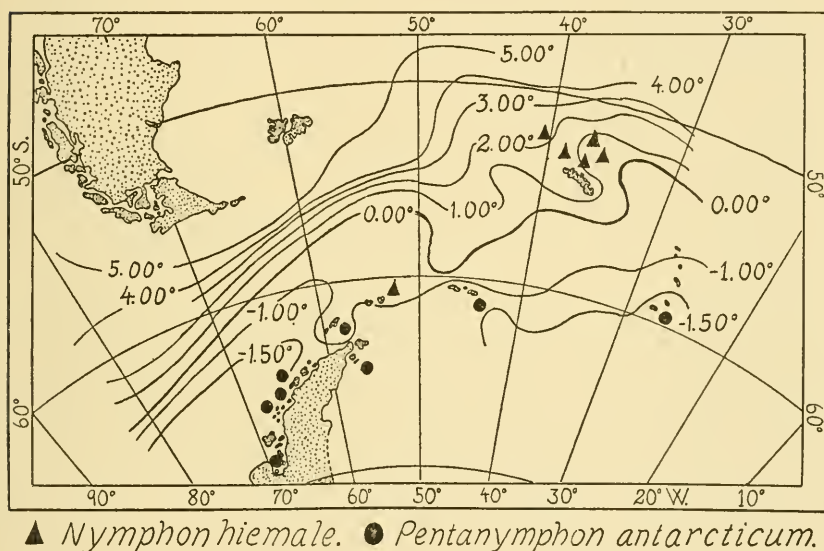


FIG. 11.—Distribution of *Nymphon-Pentanymphon* compared with temperature of 100-meter surface layer. (Isotherms from Deacon, A general account of the hydrology of the South Atlantic Ocean, *Discovery Rep.*, vol. 7, fig. 12, 1933.)

much as *Pentapycnon charcoti* is so far known from a single collection.

The distribution of the warm-water forms in the American subtropical region is inadequately known, despite the greater accessibility of the area to collectors, and a comprehensive hydrography of the region is yet to be worked out. Hence little can be said about distribution in this area that cannot be inferred from an inspection of the map (fig. 4, A) which indicates all the known localities for decapodous forms, as well as for the closely related *Pycnogonum* sp.

Once the existence of 10-legged forms had been established, the inevitable discussion as to their phylogenetic significance got under

way. Those who participated in the argument immediately divided themselves into opposing camps: the proponents of the theory that the 10-legged condition represented the original, primitive state of the Pycnogonida, and those who believed it to be a secondary phenomenon arising out of the octopodous condition. The first to suggest the primitive nature of the decapodous condition was Cole (1905), who argued that *Decolopoda* represented the progenitor of two diverging series of phylogenetic lines, leading to *Pycnogonum* on one hand and to *Colossendeis* on the other. The most persistent advocate of this position was Bouvier, who maintained his belief in the primitive origin of the decapodous type in his last paper on Pycnogonida (1937), in spite of the discovery of *Dodecolopoda*, for he considered the five ventral ganglia of the octopodous pycnogonid an indication of the original number of trunk somites. If that were the case, we might expect a radical change in the anterior ganglia of decapodous forms, but such is not the fact. In *Decolopoda* there is simply one more ventral ganglion added to the end of the chain, and the enervation of the cephalic region remains unchanged. (See Gordon, 1932, pp. 128-130, fig. 73.)

Bouvier placed particular emphasis upon a larva described by Dogiel (1911) from the Murman Station in the Arctic as evidence in favor of the primitive character of the decapodous condition. This larva (see fig. 12, c) of *Nymphon spinosum* was fairly well advanced, and possessed a fifth pair of rudimentary legs on the posterior segment. Dogiel believed this to be an atavistic deformity, but it seems more likely that it was simply an isolated example of faulty development. If it were actually a throw-back, we should expect it to have an indication of the fifth segment, which it does not have, in the illustration at least, and we might also expect it to be a more common occurrence. Dogiel's example is the only one recorded in the literature. For that matter, anomalies and deformities seem to be rare among the Pycnogonida, aside from those caused by the regeneration of lost parts. The most conspicuous one I have encountered is a specimen of *Achelia borealis* from the North Pacific, which has but three legs on the right side. (Fig. 13, b.) There is no evidence of traumatic injury in this specimen and it appears to be a congenital deformity. What is apparently the result of regeneration is described by Schimkewitsch and Dogiel (1913) in a specimen of *Anoplodactylus petiolatus* from Millport, Scotland (fig. 13, c). Bouvier (1914) examined a collection of 3,268 specimens of *Pycnogonum littorale* from Plymouth, England, and found only one abnormal specimen, a female with seven legs, the last pair being replaced by a median one. Bouvier

considered this deformity to be the result of an injury at a fairly early stage.

Two indubitable examples of congenital abnormalities have recently

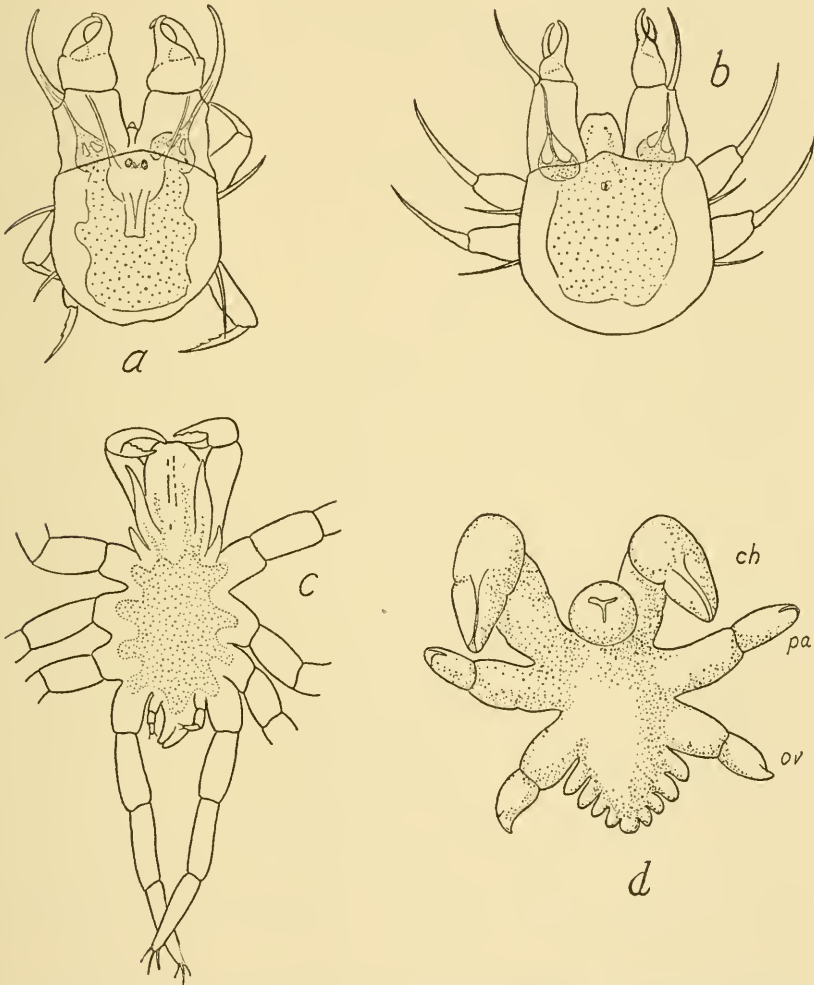


FIG. 12.—a, Protonymphon larva of *Achelia echinata* (after Dohrn, 1881); b, protonymphon larva of *Pentanymphon antarcticum*; c, larva of *Nymphon spinosum* (after Dogiel, 1911); d, larva of *Nymphonella tapetis* (after Ohshima, 1942b).

been described by Ohshima (1942a, b). The first of these is a specimen of *Callipallene brevirostris* from Sasebo, in which there are but three pairs of walking legs. Otherwise the specimen is a perfectly formed male, bearing eggs. There are four pairs of trunk ganglia,

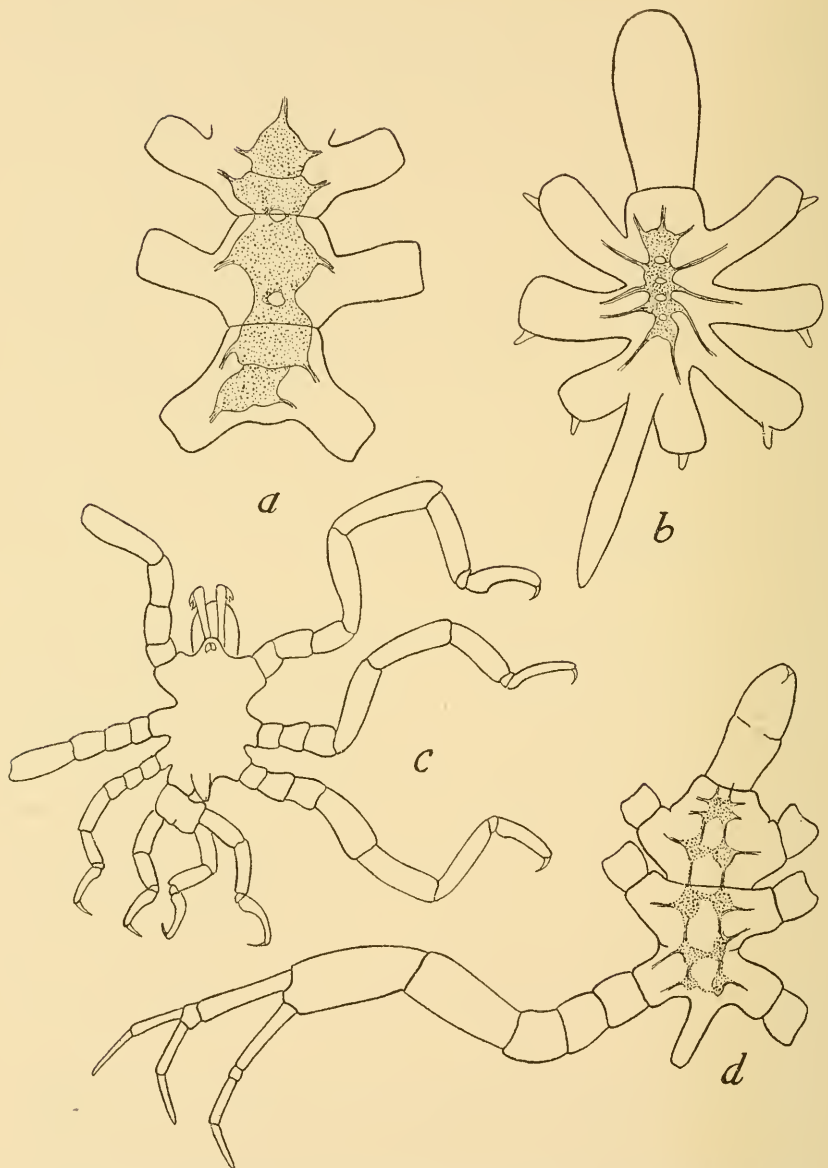


FIG. 13.—Ventral view of trunk of six-legged specimen of *Callipallene brevirostris* (after Ohshima, 1942a) ; b, ventral view of trunk of seven-legged specimen of *Achelia borealis* (from Albatross station 5037, 1906) ; c, six-legged *Anoplodactylus petiolatus* with trifold last leg (after Helfer and Schlottke, fig. 142) ; d, six-legged *Nymphonella tapetis* with trifold leg (after Ohshima, 1942b).



the fourth also serving the third pair of legs so that this pair receives a double set of nerves (fig. 13, a). Obviously the fourth pair of legs is missing here. It is interesting to note that the angle of the third pair of lateral processes in this specimen is approximately the mean value of the angles of the third and fourth processes of a normal individual. The second abnormality described by Ohshima is more complicated. In this case it is a six-legged advanced larva of *Nymphonella tapetis*, a form in which the legs arise by simultaneous budding rather than by addition from the anterior region in successive molts, as in most other pycnogonids in which the larval stages have been observed. On the left side, the second leg receives nerves from the second and third trunk ganglia, whereas on the right side the third and fourth trunk ganglia serve the third leg, which is trifurcate distally (fig. 13, d). This abnormal distal branching of appendages is not rare among arthropods, and there are several reported examples of its occurrence in pycnogonids independent of abnormalities in segmentation. (See Gordon, 1932, pp. 130-131.) It appears to have no relation to the problem of polymerism, although the duplication of nerve supply may have induced it in the examples described by Schimkewitsch and Dogiel, and Ohshima.

In the seven-legged specimen of *Achelia borealis*, the odd leg on the right side receives the nerves from the ganglia which serve the second and third legs on the other side (fig. 13, b). This median leg is so located that it balances the second and third legs of the normal side. Like Ohshima's six-legged specimen of *Callipallene brevirostris*, this anomalous specimen is an ovigerous male. Ohshima (1942b) suggested that the aberrant specimen of *Nymphonella tapetis* may have been formed by the failure of the limb buds to divide, but as he anticipated, this would not account for a similar abnormality in a form in which the legs were not formed in this manner. Probably the difference in larval development between *Nymphonella* and other pycnogonids is actually not as great as he seems to believe.

From these anomalies it is apparent that the occurrence of four trunk ganglia is very stable. They would also seem to indicate that the loss of ganglia is a rare occurrence, in contradiction to Bouvier's suggestion that the octopodous forms have lost a trunk ganglion. It seems more likely that it is easier for a pycnogonid to add ganglia than to discard them, although several forms have post-trunk ganglia in the larvae which are coalesced with the last trunk ganglia in the adult forms, and there is a tendency toward fusion of the anterior trunk ganglia and cephalic ganglia in the compact, disciform types.

As early as 1905, G. H. Carpenter expressed the opinion that the

decapodous condition was a secondary modification, and he was promptly seconded by Calman in 1909, who reaffirmed his position in his *Terra Nova* report (1915) as a rebuttal of Bouvier's contentions in behalf of the primitive character of the decapodous condition. Calman also denied Bouvier's suggestion that the phenomenon could be localized; it was Bouvier's belief that the octopodous forms had lost the fourth trunk somite. Although Calman did not believe that the extra segment could be so precisely localized, his suggestion (Calman and Gordon, 1932, p. 111) that "the metameric instability which we believe to have affected the trunk somites may possibly have influenced the segmentation of [the palpus of *Decolopoda antarctica*]," contains a hint that the instability may be primarily effective in the anterior region. This possibility cannot be ignored, although Dr. Calman has assured me, in litteris, that he does not believe it can be so localized. Moreover, the fact remains that the major differences among the families and genera involve the varying combinations of anterior appendages. This is further suggested by *Nymphonella*, in which the essential difference between it and the closely related *Ascorhynchus* is the secondary segmentation of the palpus and first pair of legs. Also, the smaller second trunk somites of *Pentacolossendeis reticulata* would seem to indicate that the extra somite, in this decapodous form at least, arose in the anterior region. On the other hand, instability in the last trunk segment is suggested by Ohshima's six-legged specimen, and he (1942a, p. 260) is of the opinion that the pentamerous forms arose through such instability: "Thus either the increase or decrease in the number of body segments, and consequently in appendages, takes place at the junction of the trunk and the tail (abdomen), but not as hypertrophy or abortion occurring at the morphological posterior end of body."

The possible localization of this phenomenon in a particular region is not the major problem, however. Even if that could be satisfactorily answered, the question still remains: what, exactly, is the nature, the cause, and significance of the decapodous condition in the Pycnogonida? It is a phenomenon without counterpart in any other known group of animals, and the various attempts to compare it with the supernumerary pregenital somites of *Polyartemia* (Calman, 1915) and the additional gill arches of the shark *Pliotrema* are of little more than academic interest.

The uniqueness of the phenomenon can be appreciated when it is remembered that it occurs in three widely divergent family types, yet is at the same time closely correlated with particular species or species complexes. Furthermore, it is apparently correlated with the evolu-



tionary force which governs variation within the group as a whole, since it occurs in those groups in which variation is confined to the specific rather than to the generic rank. As a corollary to this, it is interesting to note that the only established example of supernumerary segmentation in other branches occurs in the Ammotheidae (in which, incidentally, the number of joints of the palpus varies, often within the genus), namely, the reduplicated segmentation of the palpus and first pair of legs of *Nymphonella*.<sup>9</sup>

It should also be pointed out that this phenomenon of reduplicated segmentation, or polymerism, occurs in those branches of the Pycnogonida which may be considered, because of their large numbers of narrowly separated and numerically abundant species, as the most successful from the evolutionary standpoint. In other words, the

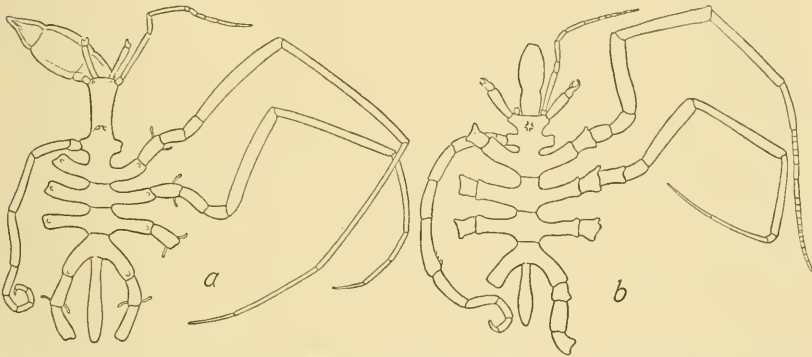


FIG. 14.—*Ascorhynchus ramipes* (after Lou, 1936); b, *Nymphonella tapetis* (after Ohshima, 1935b).

maintenance of generic form throughout a large series of species in certain branches or families is a possible symptom of dynamic tension—*δύναμις*, as Aristotle would have called it—and when the tension is high, extra-legged forms are the result.<sup>10</sup> Conversely, in those groups where the wide divergence of generic pattern and a correspondingly low ratio of species to genus may indicate a low dynamic potential, the basic metameric stability is not upset. It is of further interest to note that, among the Antarctic species at least, the 10-legged forms

<sup>9</sup> Bouvier (1910) reported a specimen of *Eurycyde* with 17 joints in the palpus, but this appears to have been an individual anomaly. This genus is closely related to *Ascorhynchus*.

<sup>10</sup> For a discussion of the dynamics of evolution, see Lotka, Alfred J., *Elements of physical biology* (Williams & Wilkins, Baltimore, 1925), chaps. 2-4. Lotka defines evolution as "the history of a system undergoing irreversible changes." (P. 24.)

are more abundant and more widely distributed than the corresponding 8-legged forms. Incidentally, the relatively greater success of the decapodous forms should be another point against the theory of primitive origin, for evolution does not go backward (although it may sometimes stand still) and there would be no conceivable advantage in reverting to a primitive type once the octopodous type had proved so successful.

The characters of the decapodous pycnogonids, their close resemblance to particular species, greater success as organisms (as indicated by their wider distribution and abundance vis-à-vis the cognate octopodous forms), and overlapping but not precisely identical distribution, suggest that they are polymorphic forms of the octopodous species.<sup>11</sup> This cannot be proved until studies of the chromosomes are available, but it seems the most plausible explanation in this day and age when chromosomes are quite the fashion. Certainly it is tempting to suggest that decapodous forms are the immediate result of doubled chromosomes and that the dodecapodous form is a possible tetraploid type. There is some support for the suggestion that this is a polyploid condition in the fact that the 10-legged forms occur in what are probably the maximum and minimum temperature ranges for pycnogonids. Temperature extremes appear to induce polyploidy, particularly in plants (cf. Huxley, *op. cit.*, p. 337).

Unfortunately, live material of the species involved is inaccessible to laboratory workers, and, for that matter, the normal chromosome number of any pycnogonid is yet to be determined. Furthermore, polymorphism is not necessarily a result of polyploidy, complete or partial, and can only be finally determined by the discovery of both 8- and 10-legged forms in a single brood or from successive or alternating broods of a single female. Hence, before this problem can be adequately investigated, it will be necessary to determine the chromosome number of common species as well as of those involved in the 10-legged problem, and to develop laboratory culture of living material.<sup>12</sup>

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<sup>11</sup> For an extended discussion of polymorphism, see Ford, E.B., *Polymorphism and taxonomy*, in *The New Systematics*, pp. 493-513, and Huxley, Julian, *Evolution: The modern synthesis*, especially p. 96 et. seq.

<sup>12</sup> Of course, as Goldschmidt maintains, it is possible that chromosome differences may or may not indicate anything, and that the chromosome pattern may change without visible effect on the genotype, but Goldschmidt's heresies are not well received in the strongholds of the chromosome cartographers. (See Goldschmidt, Richard, *The material basis of evolution*, Yale University Press, 1940, especially pp. 186 and 191.) As for laboratory culture, it is probable that it will prove to be relatively easy. Dohrn (1881) kept an amputated specimen

Such laboratory investigations may demonstrate that metameric reduplication among the Pycnogonida is a completely different type of variation than heretofore known, but whatever its mechanism, the fact remains that it is too intimately bound up with particular species to be a random coincidence or genetic accident. It may be discovered that the basic chromosome pattern of the three families in which it occurs is identical and possibly different from that of the other families. The success of this variation, as indicated by its relative abundance, indicates that it is in some way advantageous, although we may not be able to perceive wherein the advantage lies. The late Dr. C. Tate Regan, participating in a discussion of this problem at a meeting of the Linnean Society, remarked that *Dodecolopoda* and the decapodous forms appeared to be an example of "evolution by accident, a phenomenon difficult to understand."<sup>13</sup> Possibly he had in mind the same difficulty which led Aristotle to deny that variation could be accidental (and hence infinite): "Nature, however, avoids what is infinite, because the infinite lacks completion and finality, whereas that is what nature always seeks."<sup>14</sup>

Undoubtedly William Morton Wheeler would have considered the polymerous Pycnogonida an example of emergence, which he was careful to restrict to its "epigenetic" meaning, as distinct from the all-inclusive sense (with its overtones of spiritual emergence, creative evolution, *elan vital* and the rest of it) of less realistic biologists and philosophers. Emergence would indeed be a handy name for this phenomenon, but it is little more than a name, and with all deference to the late Dr. Wheeler, a rather dangerous name, because of its philosophical aura. As a concept, emergence now has little sanction, either in biology or philosophy.<sup>15</sup>

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alive for 4 weeks while observing regeneration, and Arita (1937) kept a colony alive in flowing sea-water for 10 weeks. Specimens of pycnogonids collected on the shore often live in small jars for a day or more without a change of water. Temperature control, especially for cold water species, may be as important as salinity and oxygen conditions.

<sup>13</sup> Cf. Proc. Linn. Soc. London, Sess. 145, 1932-33, pt. 2, pp. 91-93.

<sup>14</sup> Gen. Anim. I, 1. (715 b, 15-16), Loeb Classics ed., pp. 6-7:

ἡ δὲ φύσις φεύγει τὸ ἄπειρον· τὸ μὲν γὰρ ἄπειρον ἀτελές, ἡ δὲ φύσις αἰεὶ ζητεῖ τέλος.

<sup>15</sup> For a statement of Wheeler's position, see Emergent evolution and the development of societies, in *Essays in Philosophical Biology*, pp. 143-169 (Harvard Univ. Press, 1939). Julian Huxley, in his *Evolution: The modern synthesis*, does not even mention emergence, and denies the need for postulating an "*elan vital*" (p. 568). For the present philosophical status of the concept, see Irwin Edman's introduction to the Modern Library edition of Bergson's *Creative evolution*.

Nevertheless, this inferentially invites the ghosts of teleology into the discussion, but they implicitly haunt all speculations in theoretical biology, and no one, including the late Dr. Wheeler, despite his unkind remarks about the neo-Thomists, has yet discovered an efficacious formula of exorcism. The whole range of form and variation within the Pycnogonida is a compact, integrated pattern, and patterns are not aimless accidents induced by genes behaving like Mexican jumping beans on a warm day. No one has done more to show that growth and form are achieved in conformity with physical laws than that enthusiastic student of Aristotle, D'Arcy Wentworth Thompson, and if any inference can be drawn from his classic monograph, "On Growth and Form," it is that teleology is far from being a dead concept and that at least one purpose of an organism or group of organisms is adaptation to and exploitation of its environment to the limit of its capacity to utilize physical laws.<sup>16</sup> True, this can be construed simply as a description of the evolutionary process without invoking the Aristotelean *τέλος*, but so clear a process as evolutionary adaptation implies a Cause. Dr. Julian Huxley suggests that the purpose, or Cause, of evolution is Progress, and perhaps this is as good a guess as any, although some will protest that it still leaves us within the philosophical circle without a clear way out.<sup>17</sup>

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<sup>16</sup> On growth and form (Macmillan Co., New York, new ed., 1942). "Still, all the while, like warp and woof, mechanism and teleology are interwoven together, and we must not cleave to the one nor despise the other, for their union is rooted in the very nature of totality." (P. 7.) See also Lotka, *op. cit.*, chap. 9.

<sup>17</sup> Huxley, *op. cit.*, chap. 10. It seems to me that "progress" is an unfortunate term for Dr. Huxley's conception of evolutionary development. Furthermore, while remaining a staunch mechanist up to his last chapter, he inevitably commits that anthropomorphic and logical error of the mechanists, i.e., granted that man is the inevitable result of evolutionary progress, he has now attained the power to interfere with that mechanistic process of evolution which produced him and direct its course so as to alter his own evolutionary future. "The future of man, if it is to be progress and not merely a standstill or a degeneration, must be guided by a deliberate purpose." (P. 577.) This is tantamount to endowing man with the attributes of divinity, of being a First Cause within himself, and while this is not to deny that man is without the power to improve his racial stock by selective breeding, the full implications of this notion would tempt even a liberal clergyman in a university town to resort to St. Thomas Aquinas: "It is possible for an effect to happen outside the order of some particular cause, but not outside the order of the universal cause." (*Summa Theol.* I, Q. 103, Art. 7.) Of course, man cannot expect too much from St. Thomas, who denies such power to the angels (*ibid.*, Q. 52, Art. 2), and says also: "For an individual man cannot be the cause of human nature absolutely, because he would then be the cause of himself; but he is the cause that human nature exists in the man begotten." (*Ibid.*, Q. 45, Art. 5.) As an exercise in logic, it would be



But biologists are not alone in this philosophical dilemma: physicists, having pursued matter down to apparently anarchistic particles they call quanta, now find themselves again obliged to become philosophers and speculate upon First Causes, after what had seemed for a time a blessed emancipation from philosophy.<sup>18</sup> As long as we search for an explanation for the nature of things as we find them in the natural world, so long will we be haunted by teleology, and that will doubtless be as long as man is on earth. Of course, it is dangerous to argue by analogy from the human mind, but the basic urge of all great intellects, be they scientists or philosophers, theologians or poets, to achieve unity out of the multiplicity of things known and perceived, suggests that Nature is up to the same thing in her endless adaptations of diverse yet basically similar forms to the exigencies of the external environment.<sup>19</sup>

### III. CONCERNING DISTRIBUTION AND DISPERSAL

Although the observation of Marcus (1940a, p. 197) that "the active and passive means of distribution of the Pycnogonida seem to be less than those in all other marine arthropods" is essentially true for littoral species, there are several noteworthy examples of widespread distribution which are difficult to explain, and future collections, especially of the smaller forms, may prove many apparently local species to be widely distributed. This, however, would not vitiate

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interesting to know on what grounds Dr. Huxley assumes that the future trend of human evolution is going to be static or even downhill, since he has assumed that it has been "progressive" up to now. One might also infer that Dr. Huxley, like the late Dr. Wheeler, is more of a Lamarckian than he cares to admit in public, although the Chevalier's august name is mentioned in his book. As for progress, I will have more to say in *Bios*, March 1947, under the title "The Philosophic Jellyfish."

<sup>18</sup> Cf. Jeans, Sir James, *Physics and philosophy* (Macmillan Co., New York, 1943). D'arcy Thompson is, naturally, fully aware of this difficulty: "Moreover, the naturalist and the physicist will continue to speak of 'causes,' just as of old, though it may be with some mental reservations: for, as a French philosopher said in a kindred difficulty: 'ce sont là des manières de s'exprimer, et si elles sont interdites il faut renoncer à parler de ces choses.'" (Op. cit., p. 9.)

<sup>19</sup> Perhaps I do not sidestep "the vitalists, teleologists, *et hoc genus omne*" as adroitly as my former professor Dr. S. J. Holmes does in his paper, *The problem of organic form* (*Sci. Month.*, vol. 59, pp. 226-232, 253-260, 379-383, 1944). Dr. Holmes discusses form as a result of chemical and physical equilibria and interactions within the organism. His suggestion that life is "a ceaseless striving for a peaceful heterogeneous equilibrium, the attainment of which would result only in death" is not much different, philosophically, from my own statement, although I am limited by my material to external morphology.

Marcus' suggestion (*idem*) that the comparatively slight mobility of the Pycnogonida "may in some cases have favoured the development of the great number of minutely separated species," for the majority of littoral species are probably limited to comparatively small areas.

The most puzzling distribution is that of *Ammothella bi-unguiculata*, originally described from the Bay of Naples. This littoral species is easily identifiable by the absence of the terminal claws of the legs, and all workers who have identified it from widely scattered parts of the world have been obliging enough to supply adequate figures, hence there can be little doubt that all the records, as widely scattered as they are, represent the same species. Although most of

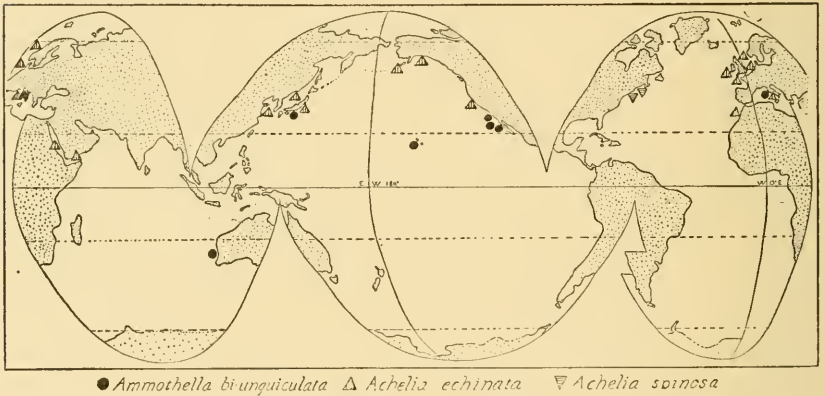


FIG. 15.—Distribution of *Ammothella bi-unguiculata*, *Achelia echinata* and *A. spinosa*. (Based on Goode Base Map No. 205, by permission of the University of Chicago Press.)

these records have been described as geographical varieties, there do not seem to be enough anatomical differences among the various specimens to merit subspecific names. This species has been found along the shore of southern California, in Japan, Hawaii, and at Rottnest Island near Perth, Western Australia, in addition to the Bay of Naples.

Another widely distributed littoral species is *Achelia echinata*, which has been identified from northern Europe, the Bay of Naples, the Atlantic coast of Morocco, San Francisco, southern Alaska and the Aleutians, Japan, the Siberian coast near Vladivostok, and Kiaochow, China. There is also a closely related species from northeastern America, *Achelia spinosa*, which some taxonomists have considered a synonym of *A. echinata*, although it seems to me to be distinct enough to merit specific rank. Nevertheless, it is probably a member of

the same species complex. The range of variation in *A. echinata* is apparently large enough to justify a number of geographic varieties, and such a range of variation suggests that it is an older species than *Ammothella bi-unguiculata*. The distribution of *Achelia echinata* is that of a typical Boreal species, and may represent a dispersal from higher latitudes as a result of the ice age.

On the other hand, *Ammothella bi-unguiculata* is a warm-water form whose distribution cannot be explained on such geological grounds. Furthermore, the uniform character of the specimens from various localities suggests that it is a young species. Unfortunately, we cannot tell whether or not this distribution antedated the sailing ship with its bottom growth of hydroids and crannies in the hull in which such slow-moving organisms as pycnogonids might find refuge, but its pattern of dispersal suggests that sailing vessels had little to do with the distribution of this species.<sup>20</sup>

Sporadic distribution, such as that of *Ammothella bi-unguiculata*, is not a rare occurrence among marine invertebrates, including those forms with limited locomotive powers. The most conspicuous example to come to recent notice is that of a nemertean, *Gorgornorhynchus*, which is represented by closely allied species recently discovered in Bermuda and New South Wales. J. F. G. Wheeler, in an extended paper on this form, which differs from all other nemerteans in the possession of a branched proboscis, advanced the suggestion that the Australian and Bermudian forms arose simultaneously within the last few years, possibly by mutation, and that here was an example of evolution caught in the act. This rather extreme hypothesis overlooks, as Zimmerman pointed out, the accidents of distribution and collecting, and the possibility of fluctuating populations (at a low cycle of abundance in the past it might easily have been overlooked).<sup>21</sup>

<sup>20</sup> Concerning the possibility of dispersal on vessel bottoms, this comment (in litteris) by Dr. J. E. Benedict, Government Naturalist for the Falkland Islands, is interesting: "I have taken Caprella in a tow net in, roughly speaking, the middle of the Atlantic. They were dead and could only have come from the fine bottom growth the ship had acquired in harbour in England." Shipworms are often dispersed on wooden vessel bottoms. See, for example, Edmondson, C. H., Dispersal of shipworms among central Pacific islands, with descriptions of new species, Occ. Pap. Bishop Mus., vol. 18, No. 15, pp. 211-224, 1946.

<sup>21</sup> Wheeler, J. F. G., The discovery of the nemertean *Gorgornorhynchus* and its bearing on evolutionary theory (Amer. Nat., vol. 76, pp. 470-493), and Zimmerman, E. C., On Wheeler's paper concerning evolution and the nemertean *Gorgornorhynchus* (ibid., vol. 77, pp. 373-376). Coe, the nemertean authority, considers Wheeler's idea a "naive assumption." Cf. Coe, Wesley R., The nemertean *Gorgornorhynchus* and the fluctuation of populations (ibid., vol. 78, pp. 94-96).



However, the character of this variation, namely the longitudinal division of the proboscis, suggests that it may be analogous to the decapodous condition in pycnogonids, itself a variation whose distribution is curiously dispersed. When Wheeler suggests that *Gorgornorhynchus* is a simultaneous mutation in two widely separated parts of the world, caused perhaps by "an internal inevitable disruption of some sort," he takes two long steps ahead of his data and a hesitant sidestep toward Lamarckianism. However, it is certain that there are conditions prevailing in some areas (such as the American Tropics and the Antarctic insofar as pycnogonids are concerned) which induce speciation, or at least give a kind reception to variations. It follows that there must be a tendency within the organism to enable it to respond to those external conditions. If this be Lamarckianism, so be it. One suspects that many biologists have been browbeaten out of their sympathies toward Lamarckianism, for what is paleontology but a long record of organisms which were capable or incapable of responding to changes in their environment, through the inheritance of acquired or induced adaptations?

Whatever the explanation for the distribution of *Ammothella biunguiculata* may be (future collections may prove it to be a circum-tropical species), the distribution of many small species in the North and South Atlantic can be explained on the assumption that the *Sargassum* provides a medium for their dispersal. At least nine small species are found on both sides of the Atlantic, and on the American side six of these are found at Tortugas in the Florida Keys. On the European side of the ocean these species are scattered from Norway to Cape Verde, and the general pattern of distribution suggests a dispersal from the American side of the Atlantic. At least two of these species, *Anoplodactylus petiolatus* and *Endeis spinosa*, are permanent members of the sargassum fauna in mid-Atlantic, and I have found *Tanystylum orbiculare*, a species known from Brazil and the United States, on *Sargassum* along the coast of Texas.<sup>22</sup> The suggestion that the West Indian region may be a center of dispersal for these various species gains some support from the occurrence of identical and similar species on both sides of the Isthmus of Panama. Perhaps more significant than the

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<sup>22</sup> Another method of dispersal is suggested by Lebour's (1916) discovery of larvae of *Anoplodactylus petiolatus* in the medusa stage of hydroids, at Plymouth, England. An excellent summary of the sargassum fauna will be found in the paper by G. Timmermann, Biogeographische Untersuchungen über die Lebensgemeinschaft des treibenden Golfkrautes, Zeitschr. Morphol. and Oekol. Tiere, vol. 25, pp. 288-335, 1932.

identical species, from the standpoint of the distribution pattern, are the pairs of closely related species, for three of the five Atlantic species with closely related Pacific species occur on both sides of the Atlantic. This may indicate that their occurrence in the western Atlantic antedates their distribution to the eastern shores of the ocean. This relationship is best illustrated in tabular form:

| CARIBBEAN REGION                            | PANAMIC REGION (chiefly)                    |
|---|---|
|   | <i>Callipallene</i>                         |
| <i>emaciata</i> * (Tortugas)                | <i>californiensis</i> (Southern California) |
|   | <i>Ammothella</i>                           |
| <i>rugulosa</i> (Brazil, Bermuda, Tortugas) | <i>heterosetosa</i> (Galapagos)             |
|   | <i>Ascorhynchus</i>                         |
| <i>armatus</i> * (Hatteras to Cuba)         | <i>agassizi</i> † (Gulf of California)      |
|   | <i>Eurycyde</i>                             |
| <i>raphiaster</i> * (Tortugas)              | <i>longisetosa</i> (Colombia)               |
|   | <i>Tauzystylum</i>                          |
| <i>orbiculare</i> (Brazil to Massachusetts) | <i>duospinum</i> (Central California)       |

\* On both sides of Atlantic.

† Possibly synonymous with *armatus*.

A curious aspect of the distribution of pycnogonids in the Atlantic is the occurrence of several species in Brazilian and European waters and their absence from northeast America and the West Indies. It is possible that this may be more apparent than real, for collections from the northern shore of South America and the West Indies are very inadequate, and several species described from Brazil have turned up in collections from the West Indies.<sup>23</sup>

According to Ekman, the littoral fauna of the North Pacific is six to eight times as rich as that of the North Atlantic.<sup>24</sup> While it does not seem that this is altogether true for pycnogonids, this element of the fauna is more diversified in the North Pacific than it is in the North Atlantic. There is but one endemic genus in the North Atlantic, *Paranymphon*, and that is a deep-water, not a littoral

<sup>23</sup> See Hedgpeth, 1943b. A more exhaustive discussion of western Atlantic and Caribbean species is now in press.

<sup>24</sup> Ekman, Sven, Tiergeographie des Meeres, p. 231, Leipzig, 1935. An English version of this work is now in preparation, under the direction of Karl P. Schmidt, of the Chicago Natural History Museum.

form. Another genus, *Pigrogromitus*, is known by a single species; certainly it cannot be called an Atlantic form. There are at least three genera, *Lecythorhynchus*, *Nymphonella*, and *Decachela*, so far known only from the North Pacific. The most striking difference between the pycnogonid faunas of the two oceans is the relatively few species widely distributed along both shores of the Pacific, in contradistinction to the considerable number of littoral species (including Boreal-Arctic forms), found on both sides of the Atlantic. As for the Boreal-Arctic species, it should be mentioned that relatively few of them are found in the North Pacific: *Nymphon grossipes*, *N. longitarse*, and *Phoxichilidium femoratum* are those most

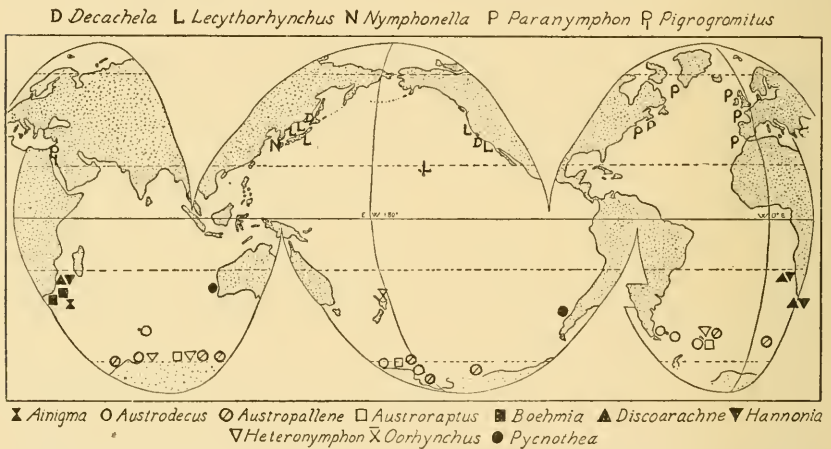


FIG. 16.—Distribution of endemic genera of the Northern and Southern Hemispheres. (Because of dubious Northern Hemisphere records, *Ammonothea*, the most abundant and widely distributed endemic genus of the Antarctic, has been omitted.) (Based on Goode Base Map No. 205, by permission of the University of Chicago Press.)

certainly present. Oddly enough, species of two of the endemic genera are found on both sides of the Pacific: *Lecythorhynchus marginatus* and *Decachela discata*. *Pycnosoma* may also be endemic to the North Pacific, for Helder's (1938) reference of a species from Chile to this genus is open to question (cf. Marcus, 1940b, p. 48). The California coast is especially rich in small littoral forms, there being perhaps 30 species in all identified from the coast between Marin County (north of San Francisco) and San Diego.

Although the littoral fauna of Japan is still incompletely known it is evidently a rich one.<sup>25</sup> In addition to a large number of endemic

<sup>25</sup> In the collections made by the *Albatross* in 1900 and 1906, there are 18 undescribed species, 6 of which were taken in shallow water. A systematic report on these collections is now awaiting publication.

forms, it includes a strong element from the East Indies, which is not found north of  $35^{\circ}$  N. lat., and a somewhat weaker representation of the Pacific Boreal fauna north of  $35^{\circ}$ . The facies of the combined littoral and shallow-water (less than 100 fathoms) fauna is markedly different from that of the eastern part of the Pacific. One of the most conspicuous differences is the absence of *Tanystylum* from Japan and the northwestern Pacific as a whole, although there are several species along the California coast. This divergence between the fauna of the western and eastern shores of the Pacific can be explained in part by the lack of a convenient bridge of floating sargassum such as exists in the North Pacific. The intrusion of large masses of Arctic water south of the Aleutian chain is probably also an inhibiting factor, and in this connection it is interesting to note that the species found both in Japan and California appear to be cold-water forms, with the exception of *Ammothella bi-unguiculata*.<sup>26</sup>

With the exception of the Antarctic, South Africa, and parts of South America, the pycnogonids of the Southern Hemisphere are known only from sporadic records, and much collecting remains to be done before generalizations can be safely drawn. However, enough is known to confirm again that bipolarity, in the sense of identical species occurring in Arctic and Antarctic regions, does not exist except in the case of ubiquitous or cosmopolitan species (particularly the genus *Colossendeis*) which are found in deep water in all oceans. Fifty or sixty years ago the bipolar hypothesis received much attention, but D'Arcy Thompson gave it a rough handling, pointing out that the theory had been built upon a foundation of inadequate systematics.<sup>27</sup> Now the bipolar hypothesis, insofar as Arctic and Antarctic faunas is concerned, is no longer accepted, but the name lingers on and has been applied in a different sense than its originators intended. In the words of Sverdrup, Johnson, and Fleming, "bipolar animals need not necessarily be bipolar."<sup>28</sup>

<sup>26</sup> For a comprehensive comparison between the Japanese and California coasts, see Gislén, T., *Physiographical and ecological investigations concerning the littoral of the northern Pacific*. Section I, A comparison between the life conditions in the littoral of central Japan and California, Univ. Årsskr. Lund, (2), vol. 39, No. 5, 63 pp., 1943, and Sections II-IV, Regional conditions of the Pacific coast of America and their significance for the development of marine life, *ibid.*, vol. 40, No. 8, 91 pp., 1944.

<sup>27</sup> On a supposed resemblance between the marine faunas of the Arctic and the Antarctic regions. (*Proc. Roy. Soc. Edinburgh*, vol. 22, pp. 311-349, [1898].)

<sup>28</sup> Sverdrup, H. U., Johnson, Martin W., and Fleming, Richard H., *The oceans: Their physics, chemistry and general biology*, p. 849, New York, 1942.



To be sure, there are an extraordinarily large number of species of *Nymphon* in both Arctic and Antarctic waters, but the genus is far from rare in tropical waters, and all that can be certainly said of this distribution is that this genus flourishes best in the cold waters of the higher latitudes. With one dubious exception (*Nymphon longitarse* var. *antarcticum*), there is no bipolar species of *Nymphon*. Another significant fact is the absence of 10-legged forms from the Arctic, which gives a radically different facies to the Antarctic fauna.

There are, however, some examples of distribution which may be construed as support of the revised bipolar—or abipolar—pattern of distribution. The most conspicuous example is that of the genus *Rhynchothorax*, one species of which is known from the Isle of Capri in the Mediterranean, while the other appears to be a circumpolar Antarctic and Magellanic species. No intervening records are yet known. Several genera, such as *Achelia*, *Tanystylum*, and *Pallenopsis*, prefer the temperate latitudes of both Northern and Southern Hemispheres and are poorly represented in the Tropics. The case of the bathypelagic *Pallenopsis calcanea* is not so clear. This species has been taken at moderately great depths (600 to 800 fathoms) in Davis Strait and the Indian Ocean off South Africa. There is a third record of this species from the vicinity of Bermuda, and it is possible that this may be a widely distributed species which has not often been collected because of its bathypelagic habit.

The Antarctic genus *Austropallene* is apparently the southern counterpart of the Northern Hemisphere *Cordylochele*, but a South African species described by Flynn (1928) as *Pseudopallene gilchristi* differs from *Cordylochele* solely in the possession of a setose fringe around the mouth, and it is probably actually a *Cordylochele*.<sup>29</sup> This would deprive *Cordylochele* of its status as a northern genus and weaken the “bipolar” relationship between *Cordylochele* and *Austropallene*.

Exclusive of extra-legged forms, and of tropical genera which are found on both sides of the Equator, there are perhaps 10 genera endemic to the Southern Hemisphere.<sup>30</sup> Of these, four are restricted

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It is unfortunate that the archaic class designation Arachnoida, comprising sea mites, pycnogonids, and *Limulus*, is sanctioned in this comprehensive treatise.

<sup>29</sup> The presence or absence of a setose fringe may be a specific character in this genus as it appears to be in *Pallenopsis*. Cf. *Pallenopsis denticulata* Hedg-peth (1944).

<sup>30</sup> *Ammothea* s. str. may be a southern genus, but there are several dubious Northern Hemisphere records which are not yet confirmed. The taxonomic status of other genera is uncertain.

to the Antarctic (*Austropallene*, *Austrodecus*, *Austroraptus*, and *Heteronymphon*), and two are known only from the Cape region of South Africa (*Boehmia*, *Ainigma*). There are also two other genera which are characteristic members of the Cape fauna (*Discoarachne* and *Hannonia*), but both of these have been identified from Port Natal. *Pycnothea* is so far known from one species at Juan Fernandez and another at Rottneest Island. The genus *Oorhynchus* is known only from a deep-water species taken north of New Zealand by the *Challenger*. It will be noted that four of the Southern Hemisphere genera occur along the South African coast. This concentration is not surprising in view of Ekman's (op. cit., p. 275) summary of endemic forms from this region.

Although there are many small genera in scattered parts of the Tropics, there is only one large genus, *Anoplodactylus*, which might be considered typically tropical. While it is represented by several species in temperate latitudes, it attains its greatest speciation in the Tropics, especially in the West Indies. There is also but one littoral genus which might be said to be cosmopolitan in the sense that its species occur in about the same proportions (usually two or three well-differentiated species in any given region) throughout the oceans. This is *Pycnogonum*, and its large number of endemic species is possibly due to the heavy body form and sluggish movements which are characteristic of the genus.

In general, it appears that the endemic genera of the Southern Hemisphere are more widely distributed than those of the Northern, which is not surprising in view of the more open character of the southern oceans. Each successive Antarctic expedition establishes the circumpolar distribution of more Antarctic species, and littoral collections in the South Sea islands will doubtless bring to light many species described from the East Indies and the Indian Ocean. A close relationship between the fauna of South Africa and the East Indies has already been noted by Flynn (1928, p. 3) who suggests that "the great equatorial current is responsible for such phenomena."

#### SUMMARY

1. The characters and ontogeny of the Pycnogonida entitle them to the stature of a class or subphylum of the Arthropoda, although their relationship to other groups of arthropods still remains uncertain.
2. The Pycnogonida constitute a compact self-contained group of families without ordinal distinctions.
3. The pattern of variation within the Pycnogonida is correlated



with extra-legged or polymerous forms. In families where variation is most active at the generic rank, polymerous forms do not occur, whereas in families composed of a large number of species in one or two genera, several 10-, and in one case, 12-legged forms are present. The great majority of species, however, are octopodous.

4. Extra-legged forms are closely similar to "normal" octopodous species, and may be polymorphic forms of these species. Certainly the 10-legged forms and their cognate 8-legged species are representatives of the same racial stocks. The occurrence of this polymerous condition in the Antarctic and tropical America, at the temperature extremes of the marine environment, is suggestive of polyploidy as it occurs in many plants. These polymerous forms appear to be more numerous and widely distributed than their cognate octopodous forms, suggesting that they are more successful from the evolutionary standpoint.

5. The *Sargassum* of the North Atlantic is an active agent in the distribution of small, relatively immobile species in that ocean. In the North Pacific such small species tend to remain endemic. There is no evidence in the distribution of the Pycnogonida to support the outworn concept of bipolarity. There are at least twice as many endemic genera in the Southern Hemisphere, as contrasted with northern waters, and most of these are widely distributed, whereas all the endemic genera (except an Atlantic deep-water form and an anomalous genus from Suez Canal) of the Northern Hemisphere are restricted to the Pacific, exclusive of tropical forms.

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## APPENDIX

Table of locality records for *extra-legged pycnogonids*

(For descriptions of the Antarctic localities, see U. S. Hydrographic Office Publ. No. 138, 1943, "Sailing Directions for Antarctica." An excellent map, No. 2562, accompanies this volume.)

| Station number | Date           | Locality   | Depth       | Temp. | Type of bottom     | No. of specimens       | Remarks  |  |
|----------------|----------------|--|-------------|-------|--------------------|------------------------|--|--|
|                |                | <b>Decolopoda australis</b> Eights   |             |       |                    |                        |  |  |
|                |                | <i>James Eights, collector—"Annawan" (Eights, 1835)</i>                          |             |       |                    |                        |  |  |
| 1829           |                | South Shetlands  |             |       |                    | Several                | One specimen now in M. C. Z., No. 12271                |  |
|                |                | <i>Swedish Antarctic Expedition—"Antarctic" (Loman, 1923)</i>                    |             |       |                    |                        |  |  |
| 1902<br>VI-5   |                | 54° 11' S, 36° 18' W.<br>Seymour Island  | 252-310 m.  | 1.45° | gy. cl., fine. st. | 2 ♂♂<br>1 juv.<br>2 ♀♀ | (Not reported until 1923)<br>Found dead on shore       |  |
|                |                | <i>Scottish National Antarctic Expedition—"Scotia" (Hodgson, 1905, 1907)</i>     |             |       |                    |                        |  |  |
| 1903<br>VI     |                | Scotia Bay, South Orkneys  | 9-10 faths. |       |                    | Several                | Second reported collection;<br>re-described with figs. |  |
|                |                | <i>Deuxième expédition antarctique française—"Pourquoi Pas?" (Bouvier, 1913)</i> |             |       |                    |                        |  |  |
| 1909<br>XII-27 |                | Admiralty Bay, South Shet-lands  | 75 m.       | 0.2°  | gy. m., p.         | 1 ♀                    |  |  |
| XVIII ..       | ?              | South Orkneys  |             |       |                    | 1 ♂                    | Collected by M. Lahille                                |  |
|                |                | <i>"Discovery" Committee (various vessels) (Gordon, 1932)</i>                    |             |       |                    |                        |  |  |
| MS 68 ..       | 1925<br>III-2  | East Cumberland Bay,<br>South Georgia  | 220-247 m.  |       |                    | 1 ♂                    | Legs bright orange; trunk,<br>etc., brownish-red       |  |
|                |                | <i>"Discovery II"</i>  |             |       |                    |                        |  |  |
| 39 .....       | 1926<br>III-25 | East Cumberland Bay,<br>South Georgia  | 179-235 m.  |       | gy. m.             | 1 ♂                    | Brachiopod attached                                    |  |
| 123 .....      | XII-15         | Off Cumberland Bay,<br>South Georgia   | 230-250 m.  |       | gy. m              | 2 ♂♂                   | With <i>D. antarctica</i>                              |  |
| 142 .....      | XII-30         | East Cumberland Bay,<br>South Georgia  | 88-273 m.   |       |                    | 2 ♀♀                   |  |  |

## APPENDIX—CONTINUED

| Station number                       | Date           | Locality   | Depth                                  | Temp. | Type of bottom | No. of specimens | Remarks  |
|--------------------------------------|----------------|--|--|-------|----------------|------------------|--|
| 148.....                             | 1927<br>I-9    | Off Cape Saunders,<br>South Georgia                | "Discovery II"—Continued<br>132-148 m. | ..... | gy.m., st.     | 1 ♂              |  |
| 149.....                             | I-10           | Mouth of East Cumberland<br>Bay, South Georgia     | 200-234 m.                             | ..... | .....          | 1 ♀              | With <i>D. antarctica</i>  |
| 154.....                             | I-18           | Jason Harbor, Larsen Point,<br>South Georgia       | 60-160 m.                              | ..... | .....          | 2 ♀ ♀            |  |
| 195.....                             | III-30         | Admiralty Bay, South Shet-<br>lands                | 391 m.                                 | ..... | m., st.        | 1 ♀              | Spiny legs   |
| <b>Decolopoda antarctica</b> Bouvier |                |  |  |       |                |                  |  |
| 254.....                             | 1904<br>IV-4   | Port Charcot, Wandel<br>Island                     | 40 m.                                  | ..... | .....          | 1 ♀              | <i>Expedition antarctique française</i> —"Française" (Bonnevier, 1906)                   |
|                                      | 1919?<br>?     | Scotia Bay, South Orkneys                          |  | ..... | .....          | 1 ♀              | <i>A. G. Bennett, collector</i> (Calman, 1920)   |
| 39.....                              | 1926<br>III-25 | East Cumberland Bay,<br>South Georgia              | 179-235 m.                             | ..... | gy.m.          | 1 ♂              | "Shallow water"<br>Large brachiopod and<br>Bryozoa attached; with<br><i>D. australis</i> |
| 42.....                              | IV-1           | Off Cumberland Bay, South<br>Georgia               | 120-204 m.                             | ..... | .....          | 1 ♀              |  |
| 123.....                             | XII-15         | Off Cumberland Bay, South<br>Georgia               | 230-250 m.                             | ..... | gy.m.          | 1 ♂              | Ventral surface covered<br>with large sponge; with<br><i>D. australis</i>                |
| 140.....                             | XII-23         | Stromness Harbor to Larsen<br>Point, South Georgia | 122-136 m.                             | ..... | gn.m., st.     | 1 ♀              |  |

## APPENDIX—CONTINUED

| Station number | Date          | Locality   | Depth                                   | Temp.  | Type of bottom | No. of specimens | Remarks   |
|----------------|---------------|--|---|--------|----------------|------------------|---|
| 149.....       | 1927<br>1-10  | "Discovery" <i>Commlitee (various vessels)</i> —"Discovery II" (Gordon, 1932)—Continued<br>Mouth East Cumberland Bay, South Georgia                                  | 200-234 m.                              | .....  | .....          | 1 ♂, 1 ♀         | With <i>D. australis</i>                        |
| 164.....       | 11-18         | Normann Strait, South Orkneys  | 24-36 m.                                | .....  | .....          | 1 ♂              |   |
| 19.....        | 1929<br>XI-8  | <b>Decolopoda sp.</b> (Gordon, 1944)<br><i>B. A. N. Z. A. R. Expedition</i> —"Discovery II" (Gordon, 1944)<br>Atlas Cove, Heard Island                               | Shore                                   | .....  | .....          | 1 ♀?             |   |
| 107.....       | 1931<br>11-16 | <b>Dodecalopoda mawsoni</b> Calman and Gordon<br><i>B. A. N. Z. A. R. Expedition</i> —"Discovery II" (Calman and Gordon, 1932; Gordon, 1944)<br>66°45' S., 62°03' E. | 219 m.                                  | -1.19° | .....          | 1 ♂              | Some encrusting Bryozoa                         |
| 1872<br>IV-13  | 1872<br>IV-13 | <b>Pentacalossendeis reticulata</b> Hedgpeth<br><i>U. S. Coast and Geodetic Survey</i> —"Bache" (Hedgpeth, 1943b)<br>Off Sand Key, Florida                           | 104 faths.                              | .....  | .....          | 1 ♀              | Diagnosis published                             |
| 1893<br>VI-29  | 1893<br>VI-29 | <i>State University of Iowa Expedition</i><br>Near American Shoal Light, Pourtales Plateau   | 110 faths.                              | .....  | .....          | 1 ♀              | First published record                          |
| 7279.....      | 1902<br>11-14 | <i>U. S. Fish Commission</i> —"Fish Hawk"  | 24°21'55" N., 81°58'25" W.<br>98 faths. | .....  | .....          | 3                | First published record; full description in MS. |

| Station number                          | Date           | Locality   | Depth         | Temp. | Type of bottom | No. of specimens | Remarks                               |
|---|----------------|--|---------------|-------|----------------|------------------|---------------------------------------|
| <b>Pentamymphon antarcticum</b> Hodgson |                |  |               |       |                |                  |                                       |
|   | 1902-04        | <i>National Antarctic Expedition—"Discovery" (Hodgson, 1907)</i>                 |               |       |                |                  |                                       |
|   |                | Winter Quarters<br>(near 77°51' S., 166°40' E.)                                  | 12-125 faths. |       |                | About 30         | Type locality; with <i>N. hiemale</i> |
|   | 1902-03        | <i>Deutsche Sud-polar Expedition—"Gauss" (Hodgson, 1927)</i>                     |               |       |                |                  |                                       |
|   |                | Winter Quarters<br>(near 67° S., 90° E.)   | 350-385 m.    |       |                | 11               |                                       |
|   | 1901           | <i>Swedish Antarctic Expedition—"Antarctica" (Loman, 1923)</i>                   |               |       |                |                  |                                       |
| 6                                       | 1-20           | 64°36' S., 57°42' W.   | 125 m.        |       | st., gr.       | 2                |                                       |
|   | 1904           | <i>Expedition antarctique française—"Française" (Bouvier, 1906)</i>              |               |       |                |                  |                                       |
| 115                                     | III-15         | Booth-Wandel Island  | 20 m.         |       |                | 1                |                                       |
| 116                                     | III-15         | Booth-Wandel Island  | 20 m.         |       |                | 1                |                                       |
| 669                                     | XI-8           | Booth-Wandel Island  |               |       |                | 1                |                                       |
|   | 1908           | <i>Deuxième expedition antarctique française—"Pourquoi Pas?" (Bouvier, 1913)</i> |               |       |                |                  |                                       |
| III                                     | XII-26         | 64°48' S., 65°51' W. (Paris)   | 129 m.        | 0.55° | r., m., p.     | 3                |                                       |
| V                                       | XII-29         | Goetschy and Doumer Islands  | 92 m.         | 0.1°  | gy.m.          | 3                |                                       |
|   | 1909           |  |               |       |                |                  |                                       |
| VII                                     | I-16           | 68°54' S., 72°05' W. (Paris)   | 250 m.        | 1.6°  | r.             | 2♂♂              |                                       |
| XV                                      | XI-26          | 64°49' S., 65°49' W. (Paris)   | 70 m.         |       | m., p.         | 3♀♀, 2♂♂         |                                       |
|   | 1911           | <i>British Antarctic Expedition—"Terra Nova" (Culman, 1915)</i>                  |               |       |                |                  |                                       |
| 318                                     | VI-13 to IX-16 | Between Cape Evans and Inaccessible Island                                       | 130-180 m.    |       |                | 1                |                                       |
|   | 1912           |  |               |       |                |                  |                                       |
| 220                                     | I-3            | Off Cape Adare   | 45-50 faths.  |       |                | 1                |                                       |
| 331                                     | I-14           | Off Cape Bird Peninsula entrance McMurdo Sound                                   | 250 faths.    |       |                | 1                |                                       |
| 338                                     | I-23           | 77°13' S., 164°18' E.  | 207 faths.    |       |                | 12               |                                       |
| 340                                     | I-25           | 76°56' S., 164°12' E.  | 160 faths.    |       |                | 3                | With <i>N. hiemale</i>                |

## APPENDIX—CONTINUED

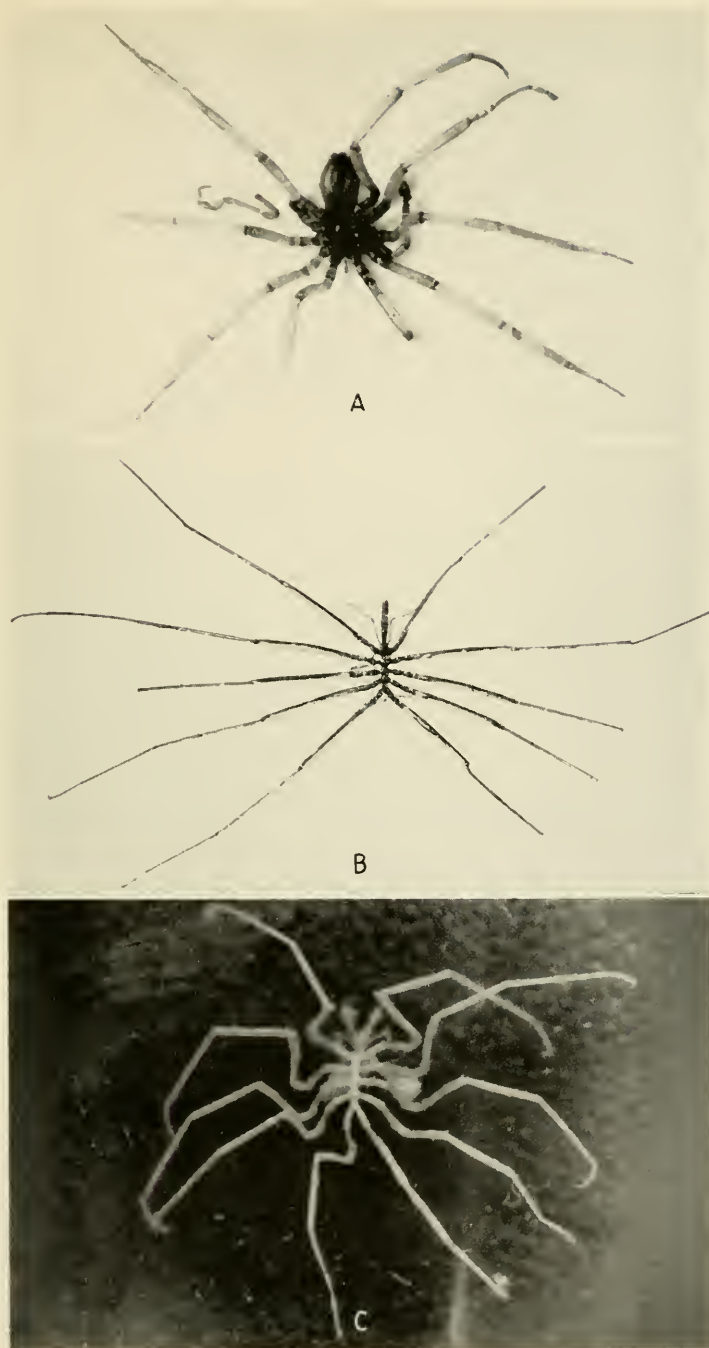
| Station number | Date           | Locality   | Depth                          | Temp.  | Type of bottom | No. of specimens                | Remarks                          |
|----------------|----------------|--|--------------------------------|--------|----------------|---------------------------------|----------------------------------|
| 355.....       | 1913<br>I-20   | British Antarctic Expedition—"Terra Nova" (Calman, 1915)—Continued<br>Off Granite Harbor, entrance McMurdo Sound | 300 faths.                     |        |                | 1                               |                                  |
| 356.....       | 1-22           |  | 50 faths.                      |        |                | 18                              |                                  |
| 7.....         | 1912<br>IX-3/4 | Australasian Antarctic Expedition—"Aurora" (Gordon, 1938)  | 25 faths.                      |        |                | 1 ♂                             |                                  |
|                | 1914           |  | 60 faths.                      |        |                | 1 ♀, 1 ♂                        |                                  |
|                | 1-27           |  | Scotia Bay, South Orkneys      |        |                |                                 | 2                                |
| 181.....       | 1927<br>III-12 | "Discovery" Committee—"Discovery II" (Gordon, 1932)  | 160-335 m.                     |        |                | 1 ♂                             |                                  |
| 195.....       | III-30         |  | Admiralty Bay, South Shetlands | 391 m. |                | m, st.                          | 5                                |
| 366.....       | 1930<br>III-6  | South of Cook Island, South Sandwich Island  | 77-152 m.                      |        |                | 4                               |                                  |
| 39.....        | 1930<br>I-17   | B. A. N. Z. A. R. Expedition—"Discovery II" (Gordon, 1944)   | 300 m.                         |        |                | 1 ♂ -ov.,<br>1 imm.             |                                  |
| 40.....        | I-17           |  | 66°10' S., 49°41' E.           |        |                |                                 |                                  |
| 41.....        | 1-24           | 66°12' S., 49°37' E.<br>65°48' S., 53°16' E.   | 180-209 m.                     | -1.77° |                | 1 ♀, 1 juv.<br>3 juv.<br>4 juv. |                                  |
| 42.....        | I-26           | 65°50' S., 54°23' E.   | 220 m.                         |        |                |                                 |                                  |
| 90.....        | 1931<br>I-7    | 66°21' S., 138°28' E.<br>67°03' S., 74°29' E.<br>67°46' S., 67°03' E.  | 640 m.                         |        |                | 1 ♂                             | Very small                       |
| 103.....       | II-10          |  | 437 m.                         |        |                | 1                               | 2 ov.                            |
| 105.....       | II-13          |  | 163 m.                         |        |                | 4 ♂♂,<br>2 ♀♀, 3 juv.           | With <i>Dodecolopoda maasoni</i> |
| 107.....       | II-16          | 66°45' S., 62°03' E.   | 219 m.                         | -1.19° |                | 4 ♂♂, 3 ♀♀,<br>9 juv.           |                                  |

## APPENDIX—CONTINUED

| Station number | Date           | Locality   | Depth      | Temp.  | Type of bottom | No. of specimens        | Remarks                                       |
|----------------|----------------|--|------------|--------|----------------|-------------------------|---|
| 170.....       | 1940<br>III-20 | U. S. Antarctic Service Expedition—"Bear" (Schmitt, 1945)<br>Neny Fjord, Palmer Land                                   | 15 faths.  |        |                | 4                       | Including 1 ♂ with <i>Protolymnion</i> larvae |
|                |                | <b>Pentanympion minutum</b> Gordon   |            |        |                |                         |   |
| 170.....       | 1927<br>II-23  | "Discovery" Committee—"Discovery II" (Gordon, 1932)<br>61°25'30" S., 53°46'00" W.                                      | 342 m.     |        | r.             | 1 ♂                     | With <i>N. litense</i>                        |
| 41.....        | 1930<br>I-24   | B. A. N. Z. A. R. Expedition—"Discovery II" (Gordon, 1944)<br>65°48' S., 53°16' E.                                     | 180-209 m. | -1.77° |                | 6 ♂ ♂,<br>2 ♀ ♀, 2 juv. | With <i>P. antarcticum</i>                    |
| 105.....       | 1931<br>II-13  | 67°46' S., 67°03' E.   | 163 m.     |        |                | 1 ♂                     |   |
|                |                | <b>Pentapycnon charcoti</b> Bouvier  |            |        |                |                         |   |
| XVII.....      | 1908-09        | <i>Deuxième expedition antarctique française—"Pourquoi Pas?"</i> (Bouvier, 1913)<br>St. George Island, South Shetlands | 420 m.     | 0.5°   | m, p.          | 1 ♂, 2 juv.             |   |
|                |                | <b>Pentapycnon geayi</b> Bouvier   |            |        |                |                         |   |
| 16.....        | 1910 or '11?   | Mahury Bay,<br>SW. of Cayenne  |            |        |                | Several                 | From hydroids                                 |
|                | 1933<br>II-3   | <i>Johnson-Smithsonian Expedition—"Caroline"</i><br>18°31' N., 66°10'15" W.<br>(N. of Puerto Rico)                     | 38 faths.  |        |                | 1 ♀                     | Incomplete specimen; several legs lost        |







## PYCNOGONIDA

A, Neoholotype, *Decolopoda australis* Eights; B, *Pentacolossendeis reticulata* Hedgpeth; C, *Pentanympion antarcticum* Hodgson. (A, about  $\frac{1}{2} \times$ ; B, nearly natural size; C, slightly enlarged.)