PYCNOGONIDA

BY JOEL W. HEDGPETH

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MORPHOLOGICAL FEATURES

The pycnogonids are exclusively marine arthropods, superficially resembling the Chelicerata in having the 1st pair of appendages chelate, but otherwise distinct from that subphylum, since they lack the well-developed abdomen of chelicerates, which houses the gonads and bears the **gonopores** on its 2nd segment. The 2nd pair of appendages is palpiform, but the 3rd is a highly modified pair of legs, the **ovigers** (Figs. 117; 120,*3*), adapted in the male to carrying the eggs during incubation. Generally there are 4 pairs of **walking legs** and 4 corresponding **trunk somites;** a few species have an extra trunk somite and pair of legs, and one 12-legged form is known (Fig. 120, *1b*). All appendages are uniramous. No well-formed body or prosoma occurs, the so-called trunk being merely a series of cylindrical somites bearing lateral outgrowths (**lateral processes**) from which the legs originate. In many species the trunk has been coalesced into a compact disc. The 1st segment of the trunk which bears the 3 pairs of anterior appendages is termed cephalic; a dorsal tubercle on this segment carries the eyes, although eyes are lacking in many deep-sea forms. The **abdomen** is a small papilliform or elongate tubercle (Figs. 117, 119-122). The most conspicuous external feature of a pycnogonid is the so-called **proboscis,** a large structure composed of a dorsal and 2 lateroventral antimeres, housing the specialized stomodeum. The integument is thin and fragile, unfavorable for fossilization.

The nervous system is of the basic arthropod type, consisting of paired ventral ganglia, a circumesophageal ring and a dorsal "brain." There is a simple dorsal heart with 2 or 3 pairs of lateral ostia, but no respiratory system. The digestive system is a simple tube without specialized glands (digestion being intracellular), with branches into the legs and 1st pair of appendages (**chelifores**). The reproductive system also has lateral diverticula extending into the legs, and eggs ripen in the swollen femurs of the female. The gonopores are typically on the ventral surface of the 2nd coxae of the last 2 pairs of legs in the males and they occur on all pairs in the females in some genera, thus placing them from the 4th to 7th pair of appendages. The males of many species have femoral glands which secrete a substance that aids in binding eggs together in a compact ball. The sexes are separate (although one hermaphroditic form is known); the male carries the eggs until they hatch.

The larval stage, termed **protonymphon**

(Fig. 118), has a proboscis, 2 simple eyes and 3 pairs of appendages, the first chelate. While this superficially resembles the nauplius, it does not have biramous appendages and resemblance is more apparent than real. It is not free-living.

MODE OF LIFE

Pycnogonida are stenohaline, benthic succivorous predators, although a few ascend to the surface to spawn and one is bathypelagic. They occur from the intertidal zone to a depth of nearly 7,000 m. and are especially abundant in arctic and antarctic waters, although a large variety of species occurs in tropical seas. They range in size from a few mm. in some intertidal species to a span of more than 40 cm. in the deep-sea *Colossendeis* (Fig. 120,*1*). The young are characteristically parasitic; many species encyst in hydroids soon after hatching, some form galls on hydroids or octocorals, others live in or on mollusks and some have been found in hydromedusae. In some species, the young stay with their fathers until able to shift for themselves. The adults feed

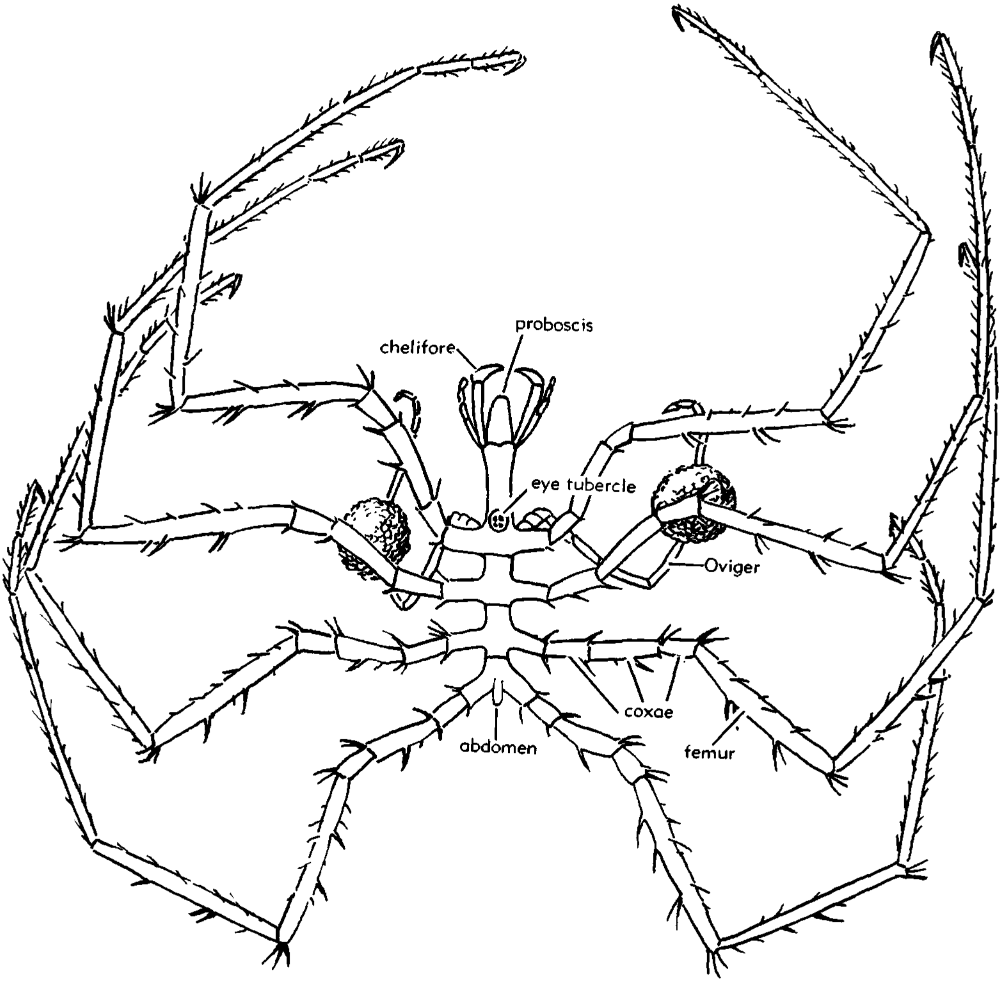

FIG. 117. Dorsal side of a typical living pycnogonid, *Nymphon rubrum* HODGE, ×7.5 (13, slightly modified). The illustrated specimen is a male which is carrying a ball of eggs attached to each of its ovigers (3rd pair of appendages from front); the small chelifores (1st pair), palpi (2nd pair) and proboscis are borne by the anterior prolongation of the 1st body somite (cephalic segment). This genus has 4 pairs of walking legs joined to lateral processes of the body somites. At the rear end is the diminutive tail-like abdomen.

usually on coelenterates, nudibranchs, and similar soft-bodied organisms.

CLASSIFICATION

About 500 species of pycnogonids are known, living forms being divided into 8 families which contain approximately 70 genera; more than 100 of the known species belong to the genus *Nymphon.* The wealth of transitional forms makes it impossible to recognize different suprafamilial groups even though some authors (Bouvier, 1913; Fage, 1949, ref. 3) have distinguished orders named Colossendeomorpha Cole (1903), Nymphonomorpha Pocock (1904), Pycnogonomorpha Pocock (1904) and Ascorhynchomorpha Pocock (1909). All living species are assigned here to a single order, Pantopoda. The Palaeopantopoda of Broili (1929) may be recognized provisionally as another order which includes the fossil *Palaeopantopus,* of Devonian age (Fig. 122). Only the lack of a proboscis and presence of a 2-segmented abdomen, instead of a nonsegmented abdominal tubercle at the rear end of the body, distinguish *Palaeopantopus* from Recent forms; the extra leg segments seen in *Palaeopantopus* may be a secondary development. All other anatomical characters, insofar as discerned, are not of a nature to prevent inclusion of this Devonian form with Recent species; hence, the classification adopted here is based more on absence of definite differing characters than on presence of clear-cut features indicating relationship with living forms.

In the past, the Pyconogonida have been classified most commonly with the Arachnida, or they have been treated somewhat vaguely as an appendix to this class. Some zoologists refer them to a meaningless assemblage called Arachnoidea. In recent years, the pycnogonids have been considered to be of chelicerate stock, constituting an aberrant group assignable to a separate class having rank equal to that of the Merostomata and Arachnida. Actually, the Pycnogonida differ from chelicerates in having the 3rd pair of appendages modified as ovigers, the anterior part of the body being produced as a proboscis and the abdomen reduced to almost vestigial proportions; in addition, the pycnogonids possess multiple genital openings (gonopores) located on preabdominal (body) somites and the legs have 3 coxal segments (Fig. 119). The development of intratarsal muscles in terminal segments of the ovigers is a feature found in no other arthropods. Effort to fit the Pycnogonida in a classificatory scheme that associates them closely with arachnids and other chelicerates should be abandoned. The group is recognized here as an independent subphylum.

Fig. 118. Protonymphon larva of a pycnogonid, enlarged (12).

SYSTEMATIC DESCRIPTIONS

Subphylum PYCNOGONIDA Latreille, 1810

[*nom. transl.* Hedgpeth, herein (*ex* Pycnogonida Latreille, 1810, distinguished as an assemblage without explicitly designated taxonomic rank)]

Arthropoda superficially resembling Chelicerata in having 1st pair of appendages chelate, but differing from them in presence of gonopores on preabdominal or body somites and in lacking well-developed abdomen; 3rd pair of appendages modified as ovigers, which occur commonly in both

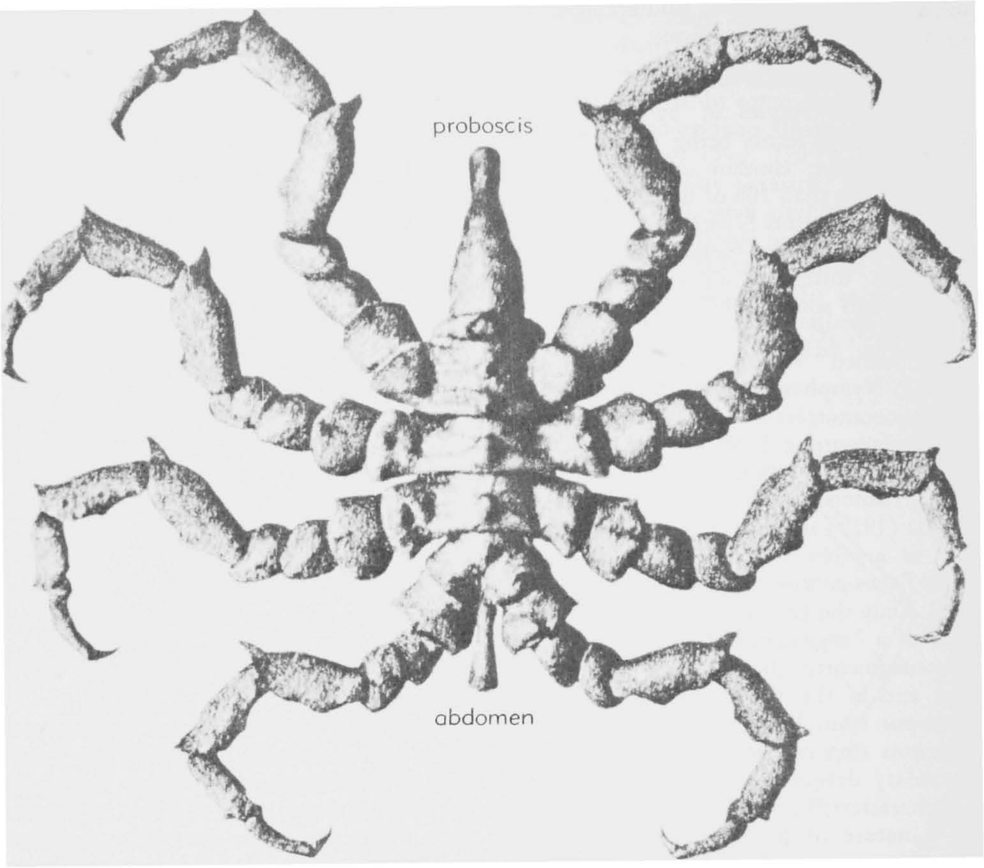

FIG. 119. *Pycnogonum littorale* (STRÖM), a modern pycnogonid, of the North Atlantic littoral zone, ×3 (14).

sexes but serve functionally only in males for carrying eggs; anterior part of body produced as a prominent proboscis. Trunk with 4 to 6 somites and legs with 3 coxal segments. Digestive system consisting of a simple tube with diverticles extending into legs but lacking specialized glands; respiratory system absent. Sexes typically separate but hermaphrodite forms may occur. Exclusively marine. *L.Dev.-Rec.*

Order PANTOPODA Gerstaecker, 1863

Proboscis well developed; chelifores, palpi, and ovigers present; postcoxal part of legs composed of 6 segments (from body outward, femur, 1st tibia, 2nd tibia, basitarsus, tarsus, dactyl); abdomen reduced to a tubercle. *Rec.*

Families of the Pantopoda are defined primarily by the presence of 3 pairs of appendages (chelifores, palpi, and ovigers) in front of the walking legs and the nature of these appendages, or alternatively, by absence of these appendages. Under each briefly diagnosed family, a few representative genera are cited but records of type species are omitted.

Family NYMPHONIDAE Wilson, 1878

Ovigers 10-segmented, in both sexes; chelifores 2-segmented, chelate; palpi 5-segmented. Includes a single decapodous genus. *Rec.*

Nymphon FABRICIUS, 1794.—FIG. 117. *N. rubrum* HODGE, ×7.5 (8).—FIG. 120,*2,3*. **N. grossipes* (FABRICIUS), ×6 (7). **Pentanymphon** HODGSON, 1904. **Heteronymphon** GORDON, 1932.

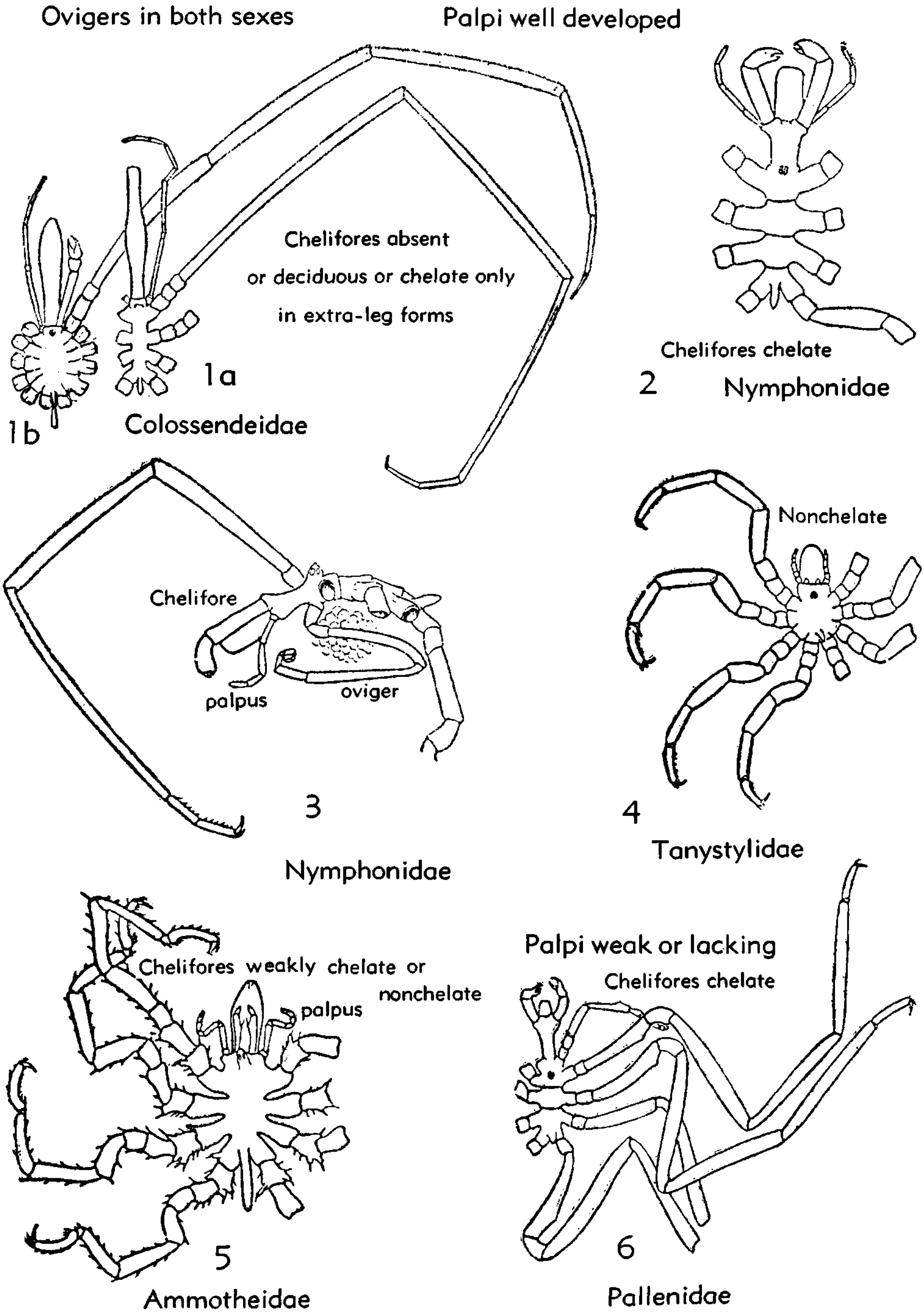

FIG. 120. Representative Pantopoda having ovigers in both sexes (p. P166-P168).

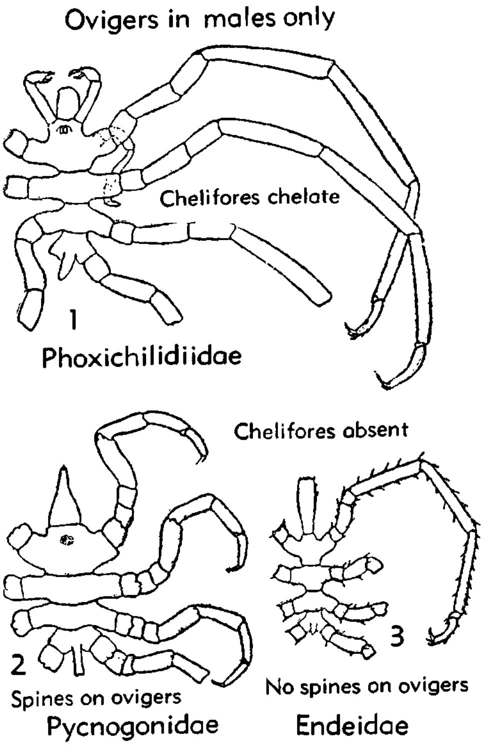

FIG. 121. Representative Pantopoda in which ovigers are carried by males only (p. P168).

Family PALLENIDAE Wilson, 1878

Ovigers 10-segmented, with or without terminal claw, in both sexes; chelifores usually chelate, proximal part (scape) with 1 or 2 segments; palpi represented by rudimentary knobs or lacking. *Rec.*

Callipallene FLYNN, 1929.—FIG. 120,*6*. **C. brevirostris* JOHNSTON, ×12 (7). **Pseudopallene** WILSON, 1878. **Pallenopsis** WILSON, 1881. **Hannonia** HOEK, 1881. **Propallene** SHIMKEVICH, 1909. **Austropallene** HODGSON, 1914. **Pycnothea** LOMAN, 1920. **Pigrogromitus** CALMAN, 1927. **Oropallene** SHIMKEVICH, 1930.

Family COLOSSENDEIDAE Hoek, 1881

Ovigers 10-segmented, with terminal claw, present in both sexes; chelifores generally lacking in adults but chelate when present; palpi 9- or 10-segmented. Trunk with 4 to 6 leg-bearing somites. *Rec.*

Colossendeis JARZYNSKY, 1870.—FIG. 120,*1a*, *C. colossea* WILSON, ×0.5 (6). **Dodecolopoda** CALMAN & GORDON, 1933.—FIG. 120,*1b*. **D. mawsoni* CALMAN & GORDON, ×0.5 (6). **Decolopoda** EIGHTS, 1837. **Rhopalorhynchus** WOOD-MASON, 1873. **Pentacolossendeis** HEDGPETH, 1943.

Family AMMOTHEIDAE Dohrn, 1881

Ovigers 9- or 10-segmented, present in both sexes; chelifores 2-segmented, usually subchelate; palpi 6- to 10-segmented but generally 8- or 9-segmented. *Rec.*

Achelia HODGE, 1864.—FIG. 120,*5*. *A. spinosa* (STIMPSON), ×12 (6). **Ammothea** LEACH, 1814. **Eurycyde** SCHIÖDTE, 1857. **Ascorhynchus** SARS, 1877. **Lecythorhynchus** BÖHM, 1879. **Boehmia** HOEK, 1881. **Nymphopsis** HASWELL, 1884. **Paranymphon** CAULLERY, 1896. **Ammothella** VERRILL, 1900. **Austroraptus** HODGSON, 1907. **Cilunculus** LOMAN, 1908. **Nymphonella** OHSHIMA, 1927. **Ephyrogymna** HEDGPETH, 1943. **Pycnofragilia** HEDGPETH, 1943. **Heterofragilia** HEDGPETH, 1943. **Calypsopycnon** HEDGPETH, 1948.

Family TANYSTYLIDAE Shimkevich, 1913

Ovigers 10-segmented, present in both sexes; chelifores 1- or 2-segmented, very small; palpi 4- to 6-segmented. *Rec.*

Tanystylum MIERS, 1879.—FIG. 120,*4*. *T. orbiculare* WILSON, ×12 (6). **Rhynchothorax** COSTA, 1861. **Discoarachne** HOEK, 1881. **Oorhynchus** HOEK, 1881. **Trygaeus** DOHRN, 1881. **Austrodecus** HODGSON, 1907. **Scipiolus** LOMAN, 1908.

Family PHOXICHILIDIIDAE Sars, 1891

Ovigers 5- or 6-segmented, present in males only; chelifores 2-segmented, chelate; palpi lacking. *Rec.*

Phoxichilidium EDW., 1840.—FIG. 121,*1*. **P. femoratum* (RATHKE), ×12 (6). **Anoplodactylus** WILSON, 1878. **Halosoma** COLE, 1904. **Hodgsonia** SHIMKEVICH, 1929.

Family ENDEIDAE Norman, 1908

Ovigers 7-segmented, present in males only; chelifores and palpi absent. *Rec.*

Endeis PHILIPPI, 1843.—FIG. 121,*3*. **E. spinosa* (MONTAGU), ×5 (6).

Family PYCNOGONIDAE Wilson, 1878

Ovigers 6- to 9-segmented, present in males only; chelifores and palpi absent. *Rec.*

Pycnogonum BRÜNNICH, 1764.—FIGS. 121,*2*; 119. **P. littorale* (STRÖM) ×9, ×25 (6). **Pentapycnon** BOUVIER, 1910. ?**Queubus** BERNARD, 1946 (females unknown).

Order PALAEOPANTOPODA Broili, 1930

Trunk with 4 somites, proboscis not evident, possibly absent; chelifores lacking; palpi (?ovigers) present; abdomen with 2 or 3 segments, with lateral processes that bear annular markings or swellings; legs with 3 coxal segments, ?5 longer segments, and several (?5) short terminal segments; gonopores doubtful. *L.Dev.*

This order is represented by a single known species described from 2 specimens discovered in the Hunsrück shale (L. Dev.) of western Germany (1, 2). The fossils do not resemble very closely any other arthropods, living or extinct, although they are enough like the Pantopoda to suggest the name chosen by Broili (*Palaeopantopus*) who classed them without question as members of the Pycnogonida (Fig. 122). Such classification has been accepted with reservation by some students of modern pycnogonids (Calman & Gordon, 1933; Hedgpeth, 1947, ref. 4; Fage, 1949, ref. 3), somewhat less skeptically by others (Marcus, 1940, ref. 6), and unreservedly by still others (Størmer, 1944; Petrunkevitch, 1952, ref. 8).

Valid evidence for excluding *Palaeopantopus* from the arthropod assemblage which contains living pycnogonids cannot be cited, even though certain characteristic features of Pycnogonida are very obscure, to say the least, or are lacking. Neither of the described specimens shows any sign of a proboscis, but since only the dorsal surface is known, the possible existence of some sort of recurved, ventrally borne proboscideal structure must be allowed. The absence of eyes

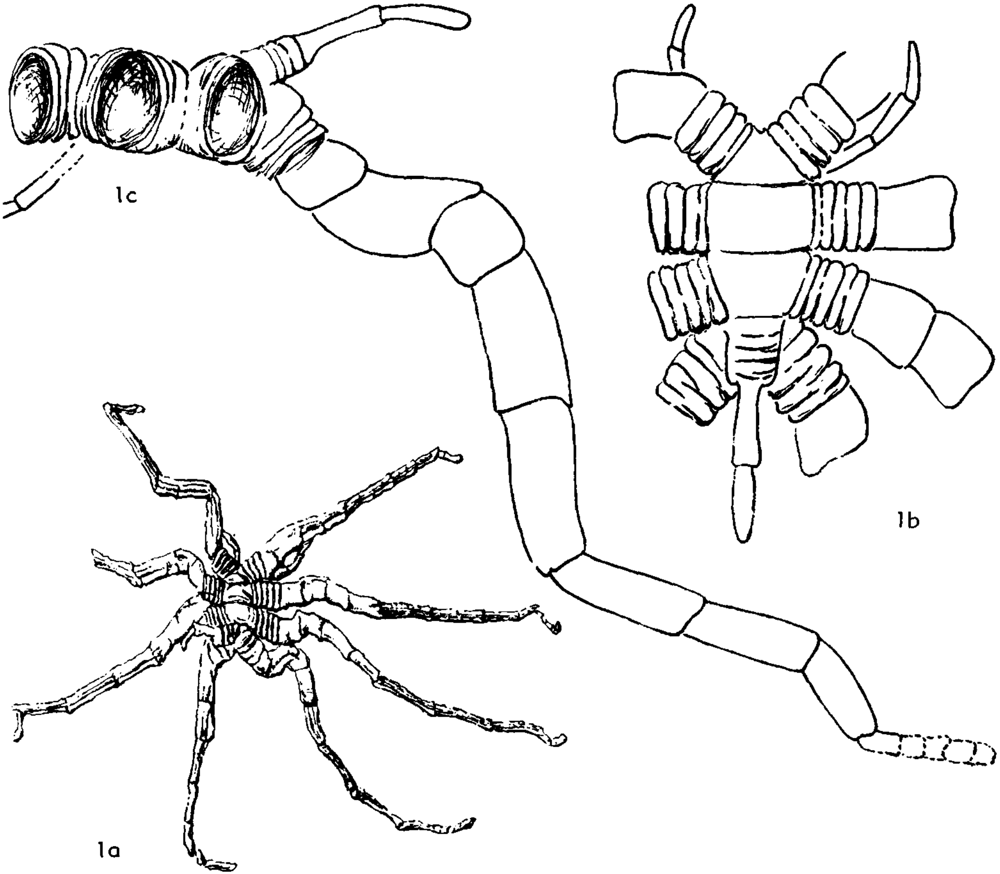

Fig. 122. Palaeopantopoda (p. P170).

and of various anterior appendages lacks significance because many living pycnogonids also are deficient similarly, and the numerous small distal leg joints suggest the condition in *Nymphonella.* The occurrence of 2 or 3 segments in the abdomen of *Palaeopantopus* is compatible with the range of variation observed in existing pycnogonids, for some of these possess 2 pairs of abdominal ganglia. The segmented abdomen might be cited as evidence of migration of the gonads into the prosoma during early history of the group along with gradual reduction of the abdomen from the most posterior somites, narrowed to little more than a jointed tube. PETRUNKEVITCH (1949, ref. 7) has demonstrated the evolutionary tendency of arachnids to lose segmentation of the abdomen and has presented evidence that the major chelicerate groups completed their differentiation by Devonian time. Accordingly, differentiation of a pycnogonid-like animal early in the Devonian, already well separated from any chelicerate stock, may be accepted with equanimity.

A logical disposition of *Palaeopantopus* is to recognize it as representative of an order (Palaeopantopoda) distinct from that (Pantopoda) containing the modern pycnogonids and to assign both to the Pycnogonida, designated as a subphylum. Definition of a class having scope identical to that of the subphylum seems to be unnecessary. By accepting *Palaeopantopus* as a pycnogonid, we are forced to conclude that within this peculiar group the trend toward reduction of the arthropod abdomen had been completed largely before mid-Devonian time. This signifies that instead of being a relatively new group of arthropods, as was my view at earlier date (4), the living Pycnogonida may be survivors of one of the oldest arthropod groups.

Family PALAEOPANTOPODIDAE Hedgpeth, nov.

Characters of the order. *L.Dev.*

Palaeopantopus BROILI, 1929 [**P. maucheri*]. *L. Dev.(Hunsrück.),* Ger.—FIG. 122,*1*. **P. maucheri; 1a,* dorsal side of nearly complete specimen, ×0.7 (6); *1b,* dorsal side of body and proximal part of appendages (reconstr.), enlarged (7); *1c,* side view of body showing walking leg attached (reconstr.), enlarged (7).

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SOURCES OF ILLUSTRATIONS

(11) **Broili, F.**
(12) **Hedgpeth, J. W.**
(13) **Sars, G. O.**
(14) **Shimkevich, V. M.**

PALAEOISOPUS

By Joel W. Hedgpeth

INTRODUCTION

The large, dorsoventrally flattened arthropod named *Palaeoisopus problematicus,* from the Hunsrück shale (L.Dev.) of western Germany, when first discovered was attributed by Broili (1) to the Isopoda. Subsequently, when specimens of the form called *Palaeopantopus maucheri* were obtained from the same strata and region, their resemblance to pycnogonids (order Pantopoda) and to *Palaeoisopus* led Broili to classify both genera as fossil representatives of the Pycnogonida (2, 3). Despite obvious dissimilarities of *Palaeopantopus* and *Palaeoisopus,* both have been accepted as somewhat aberrant ancient pycnogonids by Størmer (8) and Moore *et al.* (5). As one who has made extensive studies of modern pycnogonids, it is obvious to me that whatever affinities the creature known as *Palaeoisopus* has with other arthropod groups, they are surely insufficient to warrant classification of this fossil with the Pycnogonida.

DESCRIPTION

Palaeoisopus is known from 4 specimens which have been described by Broili (1-3), who finally prepared a reconstruction (Fig. 123) showing the animal with outspread appendages as it might appear swimming gracefully amid a group of crinoids in the moderately deep quiet waters of the Hunsrück sea.

This arthropod was a relatively large creature, having a span of approximately 20 cm. across the last pair of legs. It possessed 4 pairs of appendages, the rearmost pair being largest and paddle-shaped, which suggests a swimming habit. In front of the body, composed of 4 somites bearing lateral processes, was an elongate proboscis which was apparently formed by at least 5 distinct segments. The bulbous abdomen was short and segmented; relatively it much exceeded the abdomen of any pycnogonid, differing both in shape and size also from the segmented abdomen of *Palaeopantopus.* The 1st 3 pairs of appendages were apparently 8-jointed, the last 7-jointed; all the legs terminated in hooklike claws. There was no well developed body, thus suggesting the usual form of a pycnogonid, and the cephalic segment seems to have been the smallest. A most curious feature, which *Palaeoisopus* shares with *Palaeopantopus,* is the formation of ringlike markings or structures on the lateral extensions of the body somites. These markings are apparent in only one leg of another nearly complete fossil (3). They are, however, very conspicuous in *Palaeopantopus.* At any rate, this ringlike structure is actually the only external feature, aside from the general reduction of the body to a pycnogonid-like aspect, that these 2 fossils share in common.

This arthropod *Palaeoisopus* is a strange and fascinating object, with its jointed anterior process and bulbous posterior. Broili discerned no less than 5 segments in this proboscis, behind which he counted the 1st trunk segment (Fig. 117). If we accept this interpretation, the last pair of legs falls to the 9th somite (counting from the anterior extremity of the proboscis). This, of course, proves nothing, and confronts us with the difficulty of homologizing several apparently cylindrical somites with those bearing the chelifores, palpi, and ovigers in living pycnogonids. If we are to take this at face value, the anterior nozzle-like structure of *Palaeoisopus* represents a high degree of specialization. The posterior end of the fossil poses some additional difficulties. As Petrunkevitch (7) has pointed out, the loss of abdominal segments is one of the most important evolutionary trends in the Arthropoda. In the living Pycnogonida this reduction has reached an end point, the abdomen being no more than a tubercle with a distal anus, although in a few species it may be rather long and spinose. The large abdomen of *Palaeoisopus* is evidently connected to the trunk by a constriction, suggesting a specialized condition, which if the animal belongs to chelicerate stock at all, seems to set it off on a divergent line from the basic arachnid type. A large abdomen suggests retention of the gonads in the structure, so we cannot say that the Pycnogonida are derived from *Palaeoisopus* by simply pinching off the abdomen at the constriction without somehow getting the gonads through it into the thorax or prosoma, which seems unlikely. In *Limulus,* in which the gonads have anterior branches into the prosoma, the abdomen is broadly joined to the prosoma; if the Pycnogonida have stemmed from some chelicerate stock, it is more reasonable to suppose that the gonads have attained their present anterior position by migrating through a similarly broad connection between the abdomen and the prosoma.

In those chelicerates which have been studied in detail, the germ primordia appear very early in development, although the position of the genital openings is remarkably constant (on the 2nd abdominal segment). It is difficult to see how new genital openings could be developed on all body somites in response to a forward migration of the gonad from the abdomen. However, the possibility of early development of the gonads in the Pycnogonida might have been associated with an inhibition of the original posterior migration. That is, the gonads might have matured before their migration into the posterior part of the body could take place.

It is possible that the ventral groove suggested in the abdomen by Broili in his reconstructed *Palaeoisopus* is the genital orifice (Fig. 123); if so, it seems to be well back of the 2nd abdominal somite, which Petrunkevitch (6) considers one of the few good reference points in the anatomy of fossil arachnids. On the basis of the available evidence, therefore, we cannot even place *Palaeoisopus* near the Chelicerata, and if anything is plain about this fossil, it is that it lacks 2 pairs of antennae and biramous appendages, so it cannot be a crustacean. Possibly it constitutes a larval form of some sort of marine arachnid, although larval forms usually possess anterior ap-

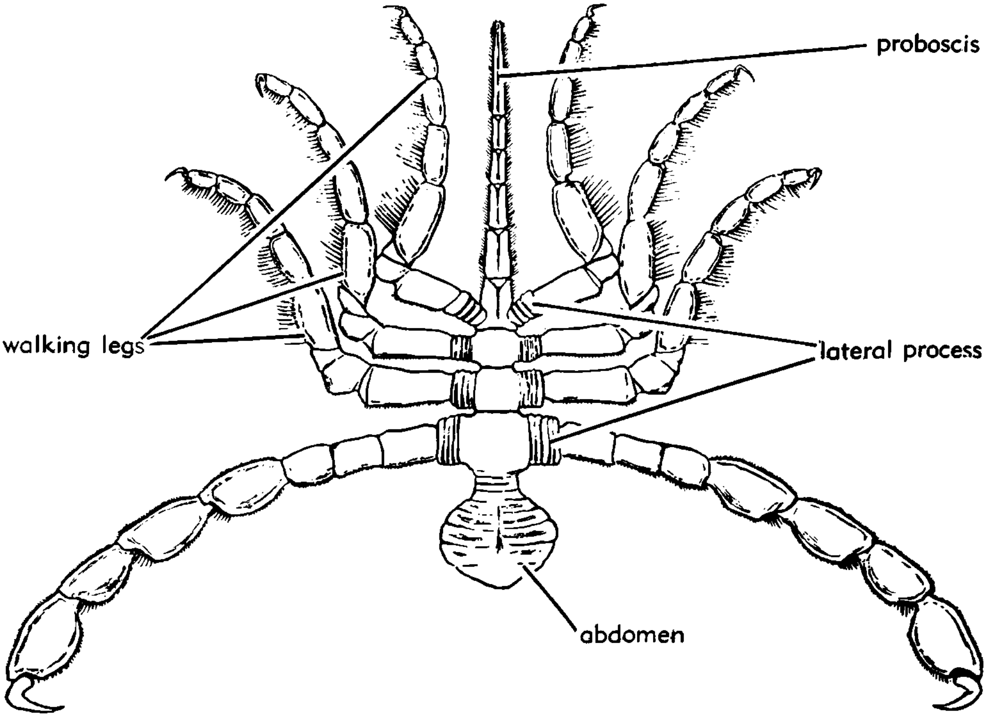

Fig. 123. *Palaeoisopus problematicus* Broili, ventral view (reconstr.), ×0.7 (after Broili)

pendages; the well-developed abdomen suggests maturity and it seems very unlikely that 4 larval specimens of similar form would be found without associated remains of adults. *Palaeoisopus* may be a neotenic form. If it is sexually mature, it seems reasonable to assume that, as in Recent arachnids, a large part of the abdomen was occupied by gonads. In the Pantopoda, the gonads open on the 1st to 4th pairs of legs (4th and succeeding pairs of appendages), a characteristic that distinguishes them from all living Chelicerata (4). No gonopores are discernible on the legs of *Palaeoisopus.*

In summary, all we can say of *Palaeoisopus* is that it belongs among the arthropods. It is classified here as Arthropoda *incertae sedis.*

Palaeoisopus Broili, 1928 [**P. problematicus*]. Trunk reduced, with 4 segments, as in Recent Pantopoda; proboscis jointed, with 5 separate segments; 4 pairs of legs, the last pair pleopod-like, adapted for swimming; abdomen large, oval-shaped, with at least 5 segments. There are no indications of other appendages or of eyes. *L.Dev.*, Ger.—Fig. 123. **P. problematicus;* ventral side (reconstr.), ×0.7 (after Broili).

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