

Host utilization during ontogeny by two pycnogonid species (*Tanystylum duospinum* and *Ammothea hilgendorfi*) parasitic on the hydroid *Eucopella everta* (Coelenterata: Campanulariidae)

David J. Russel¹; postscript: Joel W. Hedgpeth²

¹1629 Notre Dame Drive, Mountain View, CA 94040, USA; ²5660 Montecito Ave., Santa Rosa, CA 95404, USA

Keywords: Pycnogonids, host, hydroids, ontogeny, Monterey Bay

Abstract

The calyptoblast hydroids *Aglaophenia struthionides* (Murray, 1860), *Eucopella* (= *Campanularia*) *everta* (Clark, 1896), and *Abietinaria* spp. in the low intertidal zone at Mussel Point, Pacific Grove, Monterey Bay, California, often bear the adult pycnogonids *Tanystylum duospinum* Hilton, 1939 and *Ammothea hilgendorfi* (Böhm, 1879). Larval stages of these pycnogonids were found living and feeding on *Eucopella everta*. The larvae of *Tanystylum duospinum* are ectoparasitic. Those of *Ammothea hilgendorfi* are endoparasitic in the gastrovascular cavities of hydranths. Larvae of both species feed on the gut contents of *Eucopella everta*, often on the same hydroid colony.

Résumé

Les Hydroïdes calyptoblastes *Aglaophenia struthionides* (Murray, 1860), *Eucopella* (= *Campanularia*) *everta* (Clark, 1896) et *Abietinaria* spp., sont souvent parasités par les Pycnogonides adultes *Tanystylum duospinum* (Hilton, 1939) et *Ammothea hilgendorfi* (Böhm, 1879) dans la zone intertidale inférieure à Mussel Point, Pacific Grove, Monterey Bay, Californie. Les stades larvaires de ces Pycnogonides ont été trouvés vivant et se nourrissant sur *Eucopella everta*. Les larves de *Tanystylum duospinum* sont ectoparasites. Les larves d'*Ammothea hilgendorfi* sont endoparasites dans les cavités gastrovasculaires des hydrants. Les larves des deux espèces se nourrissent du contenu digestif d'*Eucopella everta*, souvent sur la même colonie d'Hydroïdes.

Introduction

Several species of pycnogonids are found associated with hydroid colonies in the low intertidal zone

along the rocky California coast. Of such hydroids the Ostrich plume hydroid *Aglaophenia struthionides* (Murray, 1860) attracts several species including *Pycnogonum stearnsi* Ives, 1892, *Tanystylum* spp., *Achelia* spp., *Nymphopsis spinosissima* (Hall, 1912), and *Ammothea hilgendorfi* (Böhm, 1879). At Mussel Point, Pacific Grove, adults of the sea spider *Tanystylum duospinum* Hilton, 1939 are frequently found on the hydroid *Aglaophenia struthionides*, and less often on other hydroids, bryozoans, and tunicates. Adults of the pycnogonid *Ammothea hilgendorfi*, less abundant at Mussel Point during this study, were found on the hydroids *Eucopella everta* (Clark, 1896), *Aglaophenia struthionides*, and *Abietinaria* spp.. Larval stages of both pycnogonid species were found only on *Eucopella everta*, often on the same colonies.

The occurrence of two similar forms undergoing larval development on the same substrate provided an opportunity to make comparisons of the mode of parasitism and to examine the possibilities of resource partitioning.

Materials and methods

All material was collected from low intertidal areas at Mussel Point, Pacific Grove, Monterey Bay, California, between 18 April and 30 May, 1980. Hydroid colonies were generally collected from red algae (*Prionitis*, *Gastroclonium*, and *Gigartina* spp.), but occasionally from rocks. Both homo-

geneous hydroid clusters (colonies consisting of a single species) and heterogeneous clusters (consisting of two or more species growing closely together) were kept separate both during collecting and later in the laboratory. Samples brought back to the laboratory were observed while fresh. Some colonies were kept for up to one week without feeding, in aquaria and finger bowls with constantly running seawater at approximately 14°C, during which time additional observations were made.

Identification of larval *Tanystylum duospinum* was made by arranging the stages found into a continuous developmental series, and then working backwards from the adult. The earliest larval form observed possessed three pairs of larval appendages and lacked any adult walking legs.

Results

Tanystylum duospinum Hilton, 1939

Tanystylum duospinum is a small, inadequately known species found mostly on hydroids. It is similar in habit to *T. californicum* Hilton, 1939, a more conspicuous species because of its heavier pigmentation. It is so far known from the central California coast. Adult *Tanystylum duospinum* were found most abundantly on fronds of *Aglaophenia struthionides*, but were collected from a variety of substrates including the hydroids *Abietinaria* and *Sertularella*, a tunicate *Archidistoma* sp., and an arborescent bryozoan. Females with developed eggs in their legs and males carrying egg masses were occasionally found. No males carrying protonymphon larvae were seen.

Protonymphon larvae with clear exoskeletons were found, firmly attached by the grip of the two chelifores, on the stolons, stalks, and hydrothecae of *Eucopella everta*. When larvae were gently pulled from the substrate, breaking the grip of the chelifores, they retained a connection with the hydroid via a thread formed by secretion of the cement gland. The thread, which may be at least twice the length of the larva, acts as a safety line, preventing the animal from being swept from the substrate if the chelifores lose their grip. In still water a larva was observed to slowly ascend the line, until it

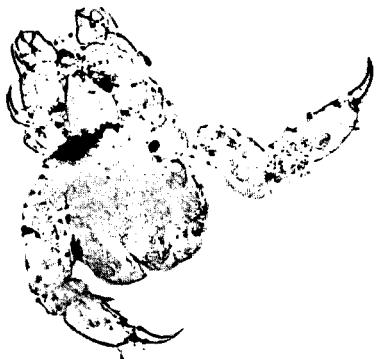
regained the substrate. A larva dislodged in a current was swung in an arc, and rapidly regained a foothold on the substrate.

Undisturbed protonymphon larvae found attached to *Eu. everta* as noted above, were often observed to have the proboscis inserted through the perisarc and body wall into the hydroid coelenteron. In one such individual, observed over a ten minute period, feeding was seen to be suctorial. Expansion of the pycnogonid's gut from anterior to posterior caused fluid to be drawn from the hydroid's coelenteron into the pycnogonid. After a variable length of time a contraction of the pycnogonid gut, starting at the posterior and moving anteriorly, forced much of the ingested material back into the hydroid coelenteron. The process was repeated at irregular intervals. More advanced larvae (stages V and VI of Dogiel, 1913) possessing their first and second pairs of walking appendages and an unpigmented exoskeleton (Figs. 1 & 2) were found attached to the host hydroid in the same sorts of places and appeared to feed in the same manner. *T. duospinum* with three and four pairs of walking legs and a clear exoskeleton was not observed feeding, nor was an attachment thread seen in these stages.

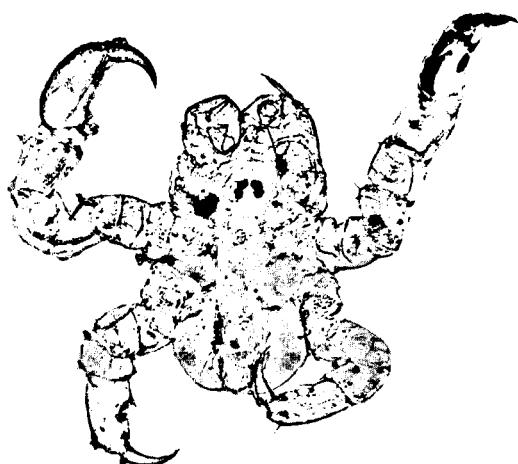
The most advanced stage of *T. duospinum* found on *Eu. everta* had a maximum leg span of only 4 mm, still possessed functional chelifores and a clear exoskeleton, and had an incompletely developed fourth pair of walking legs. This corresponds closely with the earliest stage of *T. duospinum* found on *Aglaophenia struthionides*. Larger *T. duospinum* with four fully developed pairs of walking legs and a leg span of up to 10 mm were found on *A. struthionides*, *Abietinaria*, and *Sertularella* but were not found on *Eu. everta*. The small eight-legged individuals were light straw in color, while the larger specimens were a darker golden brown and were occasionally fouled by epiphytes.

Ammothea hilgendorfi (Böhm, 1879)

This species, formerly known along the California coast as *Lecythorhynchus marginatus* Cole, 1904 (or *hilgendorfi*) occurs along the north Pacific shores from China and Japan, southern Alaska and Washington, and along the California coast as far



1



2



3



4

Fig. 1. *Tanystylum duospinum*, larva (stage V, Dogiel 1913), ventral view.

Fig. 2. *Tanystylum duospinum*, larva (stage VI, Dogiel 1913), dorsal view.

Fig. 3. *Ammothea hilgendorfi*, larva (stage IV, Dogiel 1913) encysted in hydranth of *Eucopella everta*.

Fig. 4. *Ammothea hilgendorfi*, larva (stage V, Dogiel 1913), encysted in *Eucopella everta*.

south as Baja California, but not in the Gulf of California (Child, 1979). It is the largest intertidal species on the California coast and is considered by Hedgpeth (1975) to be "one of the characteristic

species of the California intertidal zone as well as Japanese shores". It is most often found associated with various hydroids, but also occurs in crevices, under stones, and in algal holdfasts. In Japan *A.*

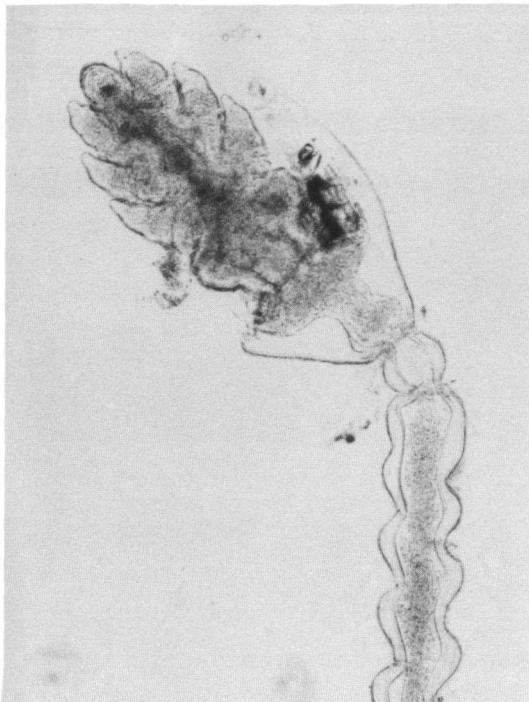


Fig. 5. *A. hilgendorfi*, larva (stage uncertain) attached to deteriorating hydranth of *Eucopella everta*. Legs consisting of three pairs of stubs without extensions of the gut.

hilgendorfi has also been implicated as a possible ectoparasite of a holothurian (Ohshima, 1927).*

The earliest developmental stage of *A. hilgendorfi* was observed in large galls derived from hydranths of *Eucopella everta*. Both hydranth and parasite were encased in a capsule attached within the original hydrotheca, but extending outward considerably beyond the hydrothecal margin (Fig. 3). Each hydranth contained a small pycnogonid (stage IV, Dogiel, 1913) with a proboscis, chelicerae, a small pair of appendages, and three pairs of short walking legs. The gut was clearly branched. Within the hydranth the pycnogonid proboscis was inserted into the coelenteron of the hydroid stalk,

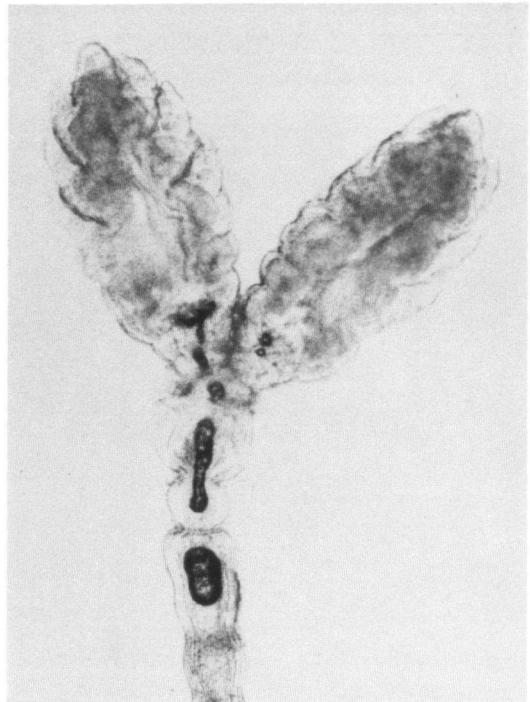


Fig. 6. *A. hilgendorfi*, larvae (same as Fig. 9), double infestation of a single *Eucopella everta* hydranth.

the chelifores, directed forward, held the pycnogonid in place. Slightly larger pycnogonids with longer legs (stage V of Dogiel, 1913) were also found in an identical orientation (Figs. 4, 5).

At the next observed stage the capsule, and often most or all of the hydrotheca and hydranth of the infected hydroid were absent (Fig. 9). The three pairs of walking legs of the now exposed pycnogonid were present as stubs which no longer contained the branches of the gut seen in the two preceding stages. Occasionally two pycnogonids at this stage were found at the end of a single hydroid stalk (Fig. 6).

In the next developmental stage the pycnogonid's walking legs were well developed (Fig. 7). These legs still lacked extensions of the gut; they waved slowly in walking motions similar to those of a normal adult pycnogonid. Pycnogonids at this stage were also found in double infections, occasionally sharing a stalk with a pycnogonid at the previously described stage.

The last pre-adult stage seen was found detached from the stalk, and walking slowly over the stolons,

* A few years ago Stock (1979) described a species of *Anoplodactylus* from an ophiuroid from Aldabra collected by Sloan (1979), and a few years later he described a species of *Pycnosomia* from an asteroid in the Philippines (Stock, 1981). Thus Jan Stock has contributed to our knowledge of pycnogonid infestation in two of the five major classes of echinoderms; the recently discovered deep sea class Concentricycloidea seem unlikely sustenance for pycnogonids, but they will probably show up on crinoids. [J.W.H.]

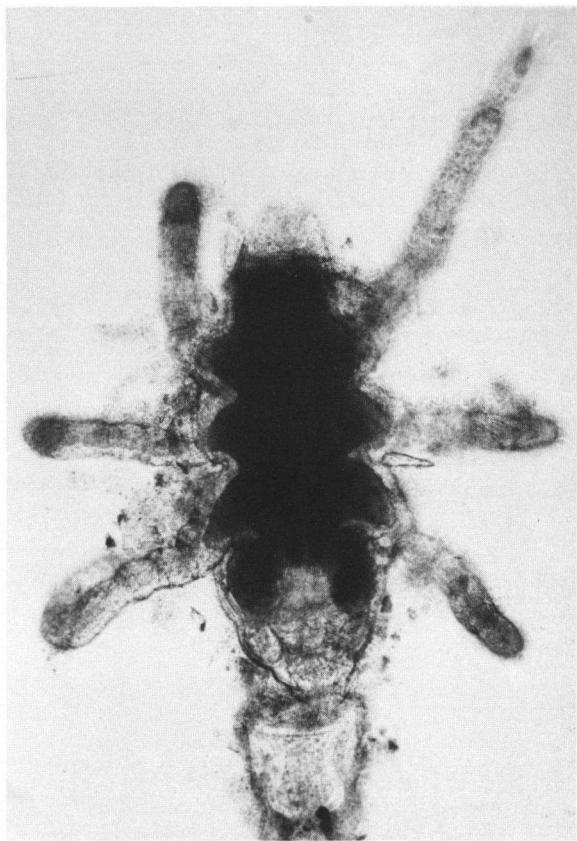


Fig. 7. *A. hilgendorfi*, larva (stage VII, Dogiel 1913), attached to remnant of *Eucopella everta* hydranth by chelipores; distended gut extending into the chelipores but not into the three pairs of walking legs.

stalks, and hydrothecae of the *Eu. everta* colony. The three pairs of walking legs still lacked extensions of the gut, and the chelipores were now achelate.

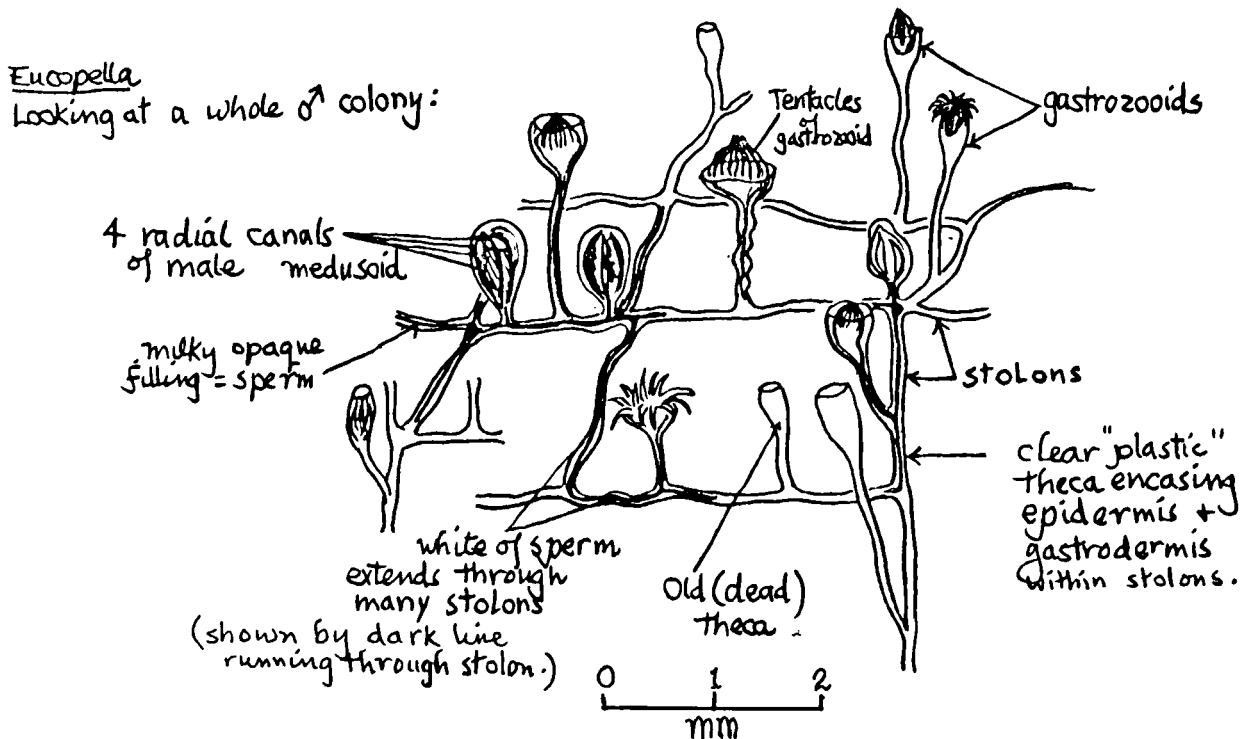
Active feeding of the encysted pycnogonid on the hydroid was not observed. However, a direct connection between the pycnogonid and hydroid gut was demonstrated in live whole-mount preparations. Pressure on the pycnogonid forced a flow of fluid from the gut directly into the coelenteron of the hydroid stalk. Pressure on the stalk caused fluid to flow back into the pycnogonid gut. In neither case was there any leakage of fluid at the junction of host and parasite.

Discussion

It has long been known that pycnogonids prey upon hydroids, and that some species invade hydranths as larvae and encyst during their early developmental stages, forming a sac or gall in the process. Often several species of pycnogonids have been recorded from the same species of hydroid (not necessarily at the same time), and some pycnogonids are associated with several species of hydroids (see tabular summary of Helfer & Schlottke, 1935: 198–199). Dogiel (1913: 617, 685) thought he observed two species of pycnogonids forming similar galls on the same hydroid colony at the same time, but this was doubted by Lebour (1916). Most of the observations of hydroid galls and other varieties of pycnogonid infestation of coelenterates have been incidental to studies of pycnogonid development, with little attention paid to the hydroids, other than as fortuitous culture media for embryological studies.

Despite the early observations of the phenomenon by Van Beneden (1844), Allman (1859), Hodge (1862), Semper (1874), Dohrn (1869), and the more detailed observations of Hallez (1905) and Dogiel (1913), there is very little information about the exact nature of the modifications of the hydranths caused by infestation ("parasitism") of larval pycnogonids (although Hallez suggested that the process is analogous to gall formation in plants), and no consideration has been given to the different impact of potentially competing species on the same species of hydroids. Unpublished notes and drawings by Martin D. Burkenroad (communicated by J.W. Hedgpeth) made in Bermuda in 1942 of gall formation by *Anoplodactylus petiolatus* (Krøyer, 1845) in *Clytia* sp. indicate that the gall tends to resemble a gonangium.

The infestation of coelenterates by larval pycnogonids has not been observed, or at least noticed, very frequently in North Pacific waters. Hilton (1916) observed the infestation of early stages of *Anoplodactylus erectus* Cole, 1904 in *Tubularia crocea* (L. Agassiz, 1862) and remarks that the larvae "were very abundant in the digestive cavities of nearly every polyp. In some cases three or four might be found in one place." The manner of in-



This is a male colony growing on the blade of a red alga. Caprellids are clambering all over it. Several parasitic pycnogonids are present in or around thecae

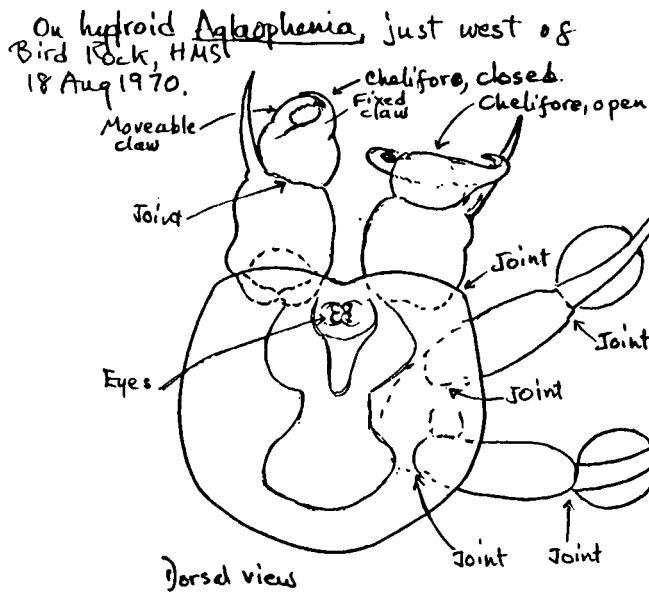
Fig. 8. Colony of *Eucopella*. Drawing by G.H. Hilgard, from Abbott (1987).

festation was not observed in adequate detail. In a later paper Hilton (1934) remarks casually that "Specimens of the hydroid *Syncoryne* from Washington near Friday Harbor show immature specimens of some species within the coelenteric cavity." These observations do not appear to have been repeated. The most remarkable infestation is that of the anthomedusan *Polyorchis penicillatus* (Eschscholtz, 1829) by larvae of *Achelia alaskensis* (Cole, 1904) in Japan (Okuda, 1940). In this case the pycnogonids are apparently ectoparasitic as larvae, adhering to the outer surface of the manubrium. This association is especially remarkable because the polyp stage of *Polyorchis* is as yet unknown, and the manner in which a benthic organism like a pycnogonid can infest a free swimming medusa can only be surmised. *Polyorchis* is common in the Monterey Bay area. Child & Harbi-

son (1986) have indeed surmised that infestation may occur when medusae are resting or spawning on the bottom, and that benthic pycnogonids may then be able to attach to jellyfish. This suggestion was made to account for infestation of bathypelagic scyphozoans, but seems even more plausible for such neritic forms as *Polyorchis*.

Only 13 of the approximately 700 species of pycnogonids have previously been observed feeding while on a host organism (King, 1973). The host itself may be the food source, being parasitized (Allman, 1862; Dogiel, 1913; King, 1973) or preyed on (King, 1973), or the host may simply provide a surface from which food such as small attached plants, animals, microorganisms, or detritus is obtained.

The present study shows that the early developmental stages of *Tanystylum duospinum* and



Protonymphon
Larva of pycnogonid
Tanystylum duospinum
(typically on Aglaophenia,
Marin Co., & Pacific Grove –
Hedgpeth, in high tides Hamer)

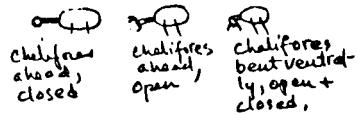
animal very active
last 2 pr appendages
alternately extend
laterally + fold in-
ward below body,
Also, both lateral ap-
pendages perform
broad A \Rightarrow P
swinging move-
ments.

Found crawling on surface of
egg mass carried on ovigerous
legs of ♂ adult. ♂ was holding
4 clusters of ♀ eggs:

- 1 cluster - hatching, w/many free young crawling about
- 2 clusters - well along in devev.,
eyes visible as dark spot.
- 1 cluster eggs white, cleaving,
but much younger than all other
clusters.

Each cluster appears bounded by
an enclosing membrane.

chelipores alternately ex-
tended forward (claws closed)
or bent downward (↑ opened)



Whole behavior is one
of clutching, grasping,
+ clinging.

PYCGNOGONIDA

Tanystylum duospinum

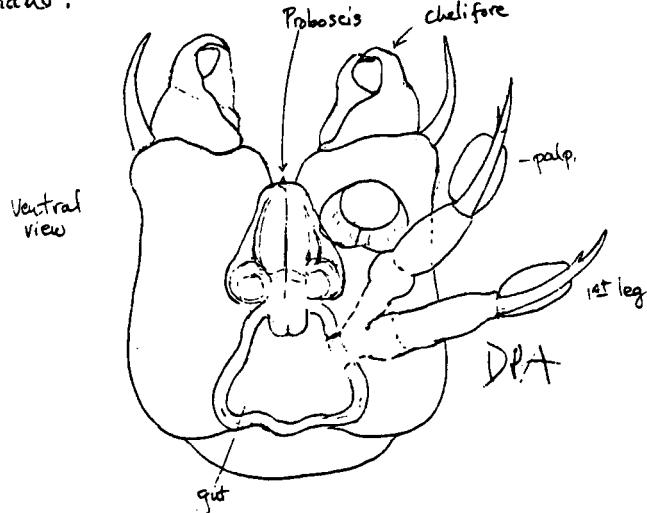


Fig. 9. Study notes of protonymphon stage of *Tanystylum duospinum* by Donald P. Abbott, from Abbott (1987: 365, 367, rearranged).

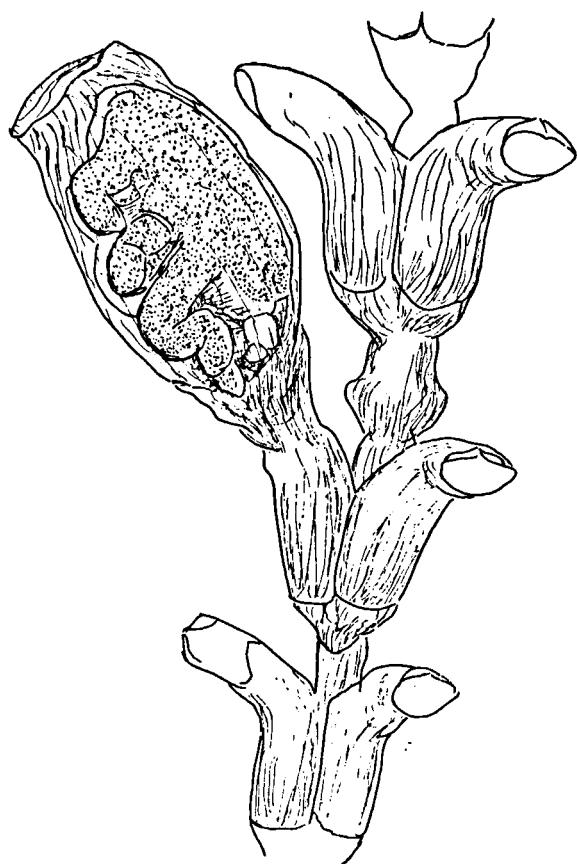


Fig. 10. Infestation of *Anoplodactylus* sp. of a species of *Sertularia*, Bermuda, 1936. After a drawing by Martin D. Burkenroad.

Ammothea hilgendorfi feed directly from the gut contents of the hydroid *Eucopella everta*. Both species of pycnogonid often occur on the same hydroid colony. The early developmental stages of *T. duospinum* are ectoparasitic, while those of *A. hilgendorfi* are endoparasitic. While adults of neither species were seen to feed, adults of *T. duospinum* were found in abundance on only one substrate, *Aglaophenia struthionides*, a hydroid whose color is matched by the color of the adult pycnogonid.

By adopting different strategies (ecto-, and endoparasitism) while employing basically similar suctorial feeding methods *T. duospinum* and *A. hilgendorfi* effectively divide a given hydroid colony into two non-overlapping resources for food and space, and thus avoid competition.

Acknowledgements

I am indebted to Stanford University for making such a course as Biology 176H possible, and to my fellow students in the course who contributed much to making it a pleasant and memorable learning experience. I wish to thank Dr. Joel W. Hedgpeth for advice and help in preparing this paper and with the literature. My greatest debt is to the late Professor Donald P. Abbott, who followed this study with energy and interest and recommended publication, and I dedicate this paper to his memory.

David J. Russel

I thank Galen Howard Hilgard for permission to use her drawing of the *Eucopella* colony, and to the Stanford University Press for permission to use this and other material from Don Abbott's "Observing marine invertebrates." I also thank Dr. Edmund H. Smith for assistance with photography. I am pleased that it has been possible to include this evidence of the interaction between student and professor to honor Jan Stock, who in a distant land has also labored valiantly in the cause of classical zoology.

Joel W. Hedgpeth

Postscript

This paper by David Russel was developed from his project during the Spring Quarter of 1980 when he was enrolled in Donald P. Abbott's (1920–1986) famous course in invertebrate zoology that emphasized the functional morphology of the animals living in the Monterey (California) tidal zone. Classes lasted all day, often starting with an early morning low tide trip, and the rest of the time in the laboratory observing the animals, alive if possible. Don stayed with his students, often in the back of the room, working with the same animals brought in by the students, and lecturing as the occasion demanded. It was invertebrate zoology as seldom taught these days, and it can never be done just that way again, with its emphasis on "asking the animals", and his warning to "cultivate a suspicious attitude toward people who do phylogeny."

A selection of Don's informal, annotated drawings made during the class sessions, together with a few by his students were gathered together during his last days and published in commemoration of his course and his way of teaching (Abbott, 1987). The sketch of *Eucopella*, illustrating the nature of this small, dainty hydroid (Fig. 8) is by his student, later his assistant, Galen Howard Hilgard. It is odd that these dainty, minute colonies, located on such ephemeral substrates as the thalli of seaweeds should be hosts to two different pycnogonids, one infesting the hydranths to form galls, the other attacking from the outside, but both living as adults in very different situations in the tidal zone.

Abbott's drawings of the protonymphon larva of the ectoparasitic *Tanystylum duospinum* reveal a structure not observed before in this larval stage of other species: the flat, paddle-like surfaces on the ventral distal part of the legs (see Fig. 9). It has long been known that the protonymphon varies in different species; some have long thread-like whips at the ends of the two

pairs of larval legs and in others the filament extends from the large spine at the base of the chelifores, or there is no such structure at all (see Arnaud & Bamber, 1987: 41, fig. 20). It has been considered that the protonymphon larva is not very motile, but clings to the egg mass at birth and somehow gets to its host, and I have been guilty of conveying this idea as fact in Hedgpeth & Haderlie (1980). This has been picked up and made even more dogmatic by Salazar-Vallego & Stock (1987). Abbott did not label this structure; it was not his habit to label structures when he did know what they were rather than provoke misunderstanding. He also did not label the unique gland peculiar to the protonymphon that supplies the duct in the spine at the base of the chelifore; if there was a duct he did not see it, but it is possible it may have been replaced by a porous ventral surface which would have made the paddle-like structures possible. In any event he did comment on the active movement of the larval appendages both forward and backwards, in "broad sweeping movements" that suggest swimming ability. Attachment threads may be developed after the larva finds its host [for an obituary of Donald P. Abbott, see Newberry & Hadfield, 1987].

Another promising location for studies may be Bermuda. In May of 1936 Martin D. Burkenroad made some preliminary studies of pycnogonid infestation of hydroids (mostly on floating *Sargassum*). He made many drawings and drafted some text, mostly speculation on the nature of the parasitism involved. Unfortunately his papers had at some time got very damp, and paper clips had rusted and stained the pages and the drawings were damaged. His observations had stimulated him to some preliminary speculations that parasitism by pycnogonids caused galls in calyptoblast hosts to resemble the gonangium of gymnoblast hydroids, and that the formation of such galls required deep invasion to regions of active growth by the pycnogonid larvae. Unfortunately little more than what Russel has stated can be made of this material. There is, however, a retrievable drawing of an infestation in a species of *Sertularia*, which is not one of the hosts usually encountered in these studies (Fig. 10). Morris & Mogelberg (1973) list ten species of *Sertularia* associated with *Sargassum* in Bermuda, but Burkenroad (1939) mentioned only two. The species illustrated here from his drawing seems to be *Sertularia inflata* (Versluyss, 1899) [for an obituary of Burkenroad, see Schram, 1986].

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Received: 20 November 1989