Metamorphosis of a Pycnogonid parasitic in a Hydromedusa[1)]

By

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(*With 10 Text-figures*)

Although it is rather common that pycnogonids in their early larval stages feed on hydroid polyps, so far as I am aware, only a few cases are recorded where the young or the adult are found parasitic in medusa. H. Prell (1909) found a species of *Nymphon* eating the tentacles of *Lucernaria*. M. Lebour (1916) discovered at Plymouth many pycnogonids, which she named *Anaphia petiolata* (Kröyer), attached to the manubrium and at the junction of manubrium and stomach of various medusae. The medusae noticed by her to contain pycnogonids were *Obelia* sp., *Cosmetira pilosella, Turris pileata, Stomotoca dinema* and *Phialidium hemisphericum*. T. Uchida (1927) mentioned in his "Studies on Japanese Hydromedusae" that one specimen of *Polyorchis karafutoensis,* which is commonly found along the southern coasts of Sakhalin and the eastern parts of Hokkaido, was parasitised by several pycnogonid larvae of the genus *Ammothea* clinging with their pincers to the tentacles and the subumbrella.

During my short stay at the Akkeshi Marine Biological Station in July, 1934, I could find a great number of young parasitic pycnogonids among the lot of the Anthomedusa, *Polyorchis karafutoensis,* collected by dredging from the muddy bottom. On examination they were determined to be larval stages of *Ammothea alaskensis* Cole, a pycnogonid distributed in the boreal regions such as Alaska, Sakhalin, Kamchatka and the North Kuriles. The immature form of the species corresponding to Stage VII in this paper

1) Contribution from the Akkeshi Marine Biological Station, No. 28.

has been formerly described by H. Ohshima (1933) from Japan from the North Kuriles. At Akkeshi the adult pycnogonids are rather commonly found crawling over the seaweeds and the sedentary animals. Although it is not possible, at present, to give accurate information as to the percentages and season of infection, the largest number of parasites in one host examined was found to be about 30. The young pycnogonids may be found under the exumbrella and on the wall of the manubrium, with their proboscis bent perpendicularly to, and piercing into, the soft tissue of the host. Considering the absence of the adult pycnogonids in the medusae, it seems probable the young larvae are hatched out outside the host, but it remains still unknown how these larvae reach the jelly-fish.

This work has been carried out under the supervision of Prof. H. Ohshima of the Kyūsyū Imperial University, to whom I am greatly obliged.

Metamorphosis of the larvae inside the medusae

Stage I: The larva of the earliest stage that could be found attached to the manubrium is somewhat oval in its shape measuring 0.26 mm in length exclusive of proboscis (Fig. 1). The first pair of appendages, the chelifors, are much longer than the proboscis and is three-jointed ending with a sharp chela. The basal joint bears a single, stout spine situated laterally and a short small one dorsally.

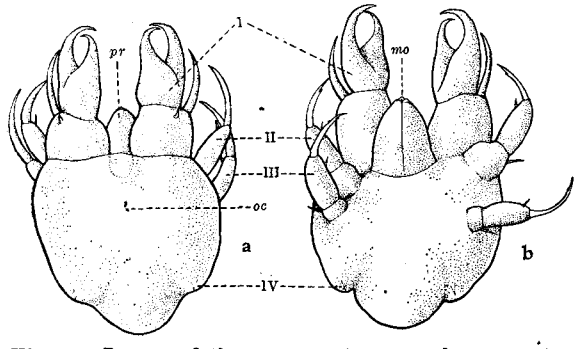

Fig. 1.—Larva of the youngest stage that can be found parasitic in *Polyorchis*. a, Dorsal view. b, Ventral view. × 90. mo, mouth; oc, eyes; pr, proboscis; I, chelifor; II-III, larval appendages; IV, rudiment of the first walking leg.

The following two pairs of larval appendages are each two-jointed. Each basal segment of these appendages bears a small spine projecting from its distal portion. The proboscis situated between the chelifors is robust. The eyes are represented by two small black pigmented spots arranged one after another. The postero-lateral protuberances of the posterior body indicate the external boundaries of the fourth appendages. The terminal claw of the rudiment of the fourth appendage can only be observed beneath the hypoderm. The larva is quite opaque, and nothing of the internal organs such as the ventral ganglia and mid-gut could be made out as yet from the surface.

Stage II: In the next stage, the body posterior to the third pair of appendages is greatly enlarged (Fig. 2). The sausage-like

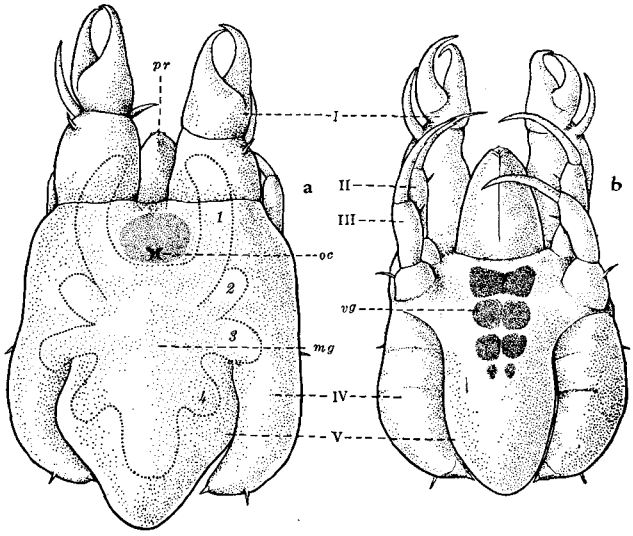

Fig. 2.—Stage II. a, Dorsal view. b, Ventral view. × 90. mg, mid-gut; oc, eyes; pr, proboscis; vg, ventral ganglia; I, chelifor; II-III, larval appendages; IV, the first walking leg; V, rudiment of the second walking leg; 1-4, diverticula of mid-gut.

lateral pouches indicate the rudiments of the fourth appendages. They are closely attached to the body and each bears a single terminal and two small spines. These appendages as well as the trunk show no external segmentation as yet. A pair of crescent-shaped eyes arranged side by side is located on the thickened ocular tubercle on

the anterior dorsal surface. The first three pairs of appendages are similar in their essential forms to those of the former stage. The mid-gut gives rise to four pairs of diverticula on both lateral sides; the first pair project into the chelifors, nearly reaching the terminal portion beyond the half length of the basal segment; the second pair extend to the base of the third appendage, and the third pair towards the fourth appendage; lastly the short fourth pair pass into the lateral bulging portion of the posterior body which corresponds to the rudiment of the fifth appendage. Four pairs of ventral ganglia are seen externally, of which the last pair are small and rudimentary.

In the further development, the fourth appendage is separated from the body and increases in length. The fifth pair of appendages are clearly made out as lateral swellings of the middle body lobe. The internal change is obscure on account of the thick coating of cuticle. This stage seems to be the one just preceding the next moulting.

Stage III: The whole larva (Fig. 3) shows a considerable increase in size. The most marked external change lies in great elongation and modification of the fourth pair of appendages. The fourth appendage, i.e. the first walking leg is well developed, with

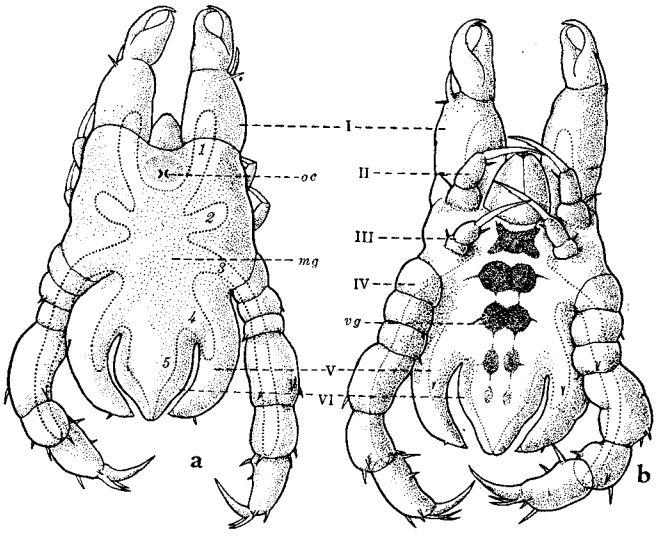

Fig. 3.—Stage III. a, Dorsal view. b, Ventral view. × 50. mg, mid-gut; oc, eyes; I, chelifor; II-III, larval appendages, IV-V, walking legs; VI, rudiment of the third walking leg; 1-5, diverticula of mid-gut.

six segments. A stout terminal claw is accompanied by two smaller accessory spines protruding one on each side. The fifth pair of appendages not yet fully developed have faint terminal claws and are now distinct from the median body lobe. The rudiments of the sixth pair of appendages are represented by the swellings of posterior body. The diverticula of the mid-gut are well developed, of which the first two pairs are not different from the previous stage. The third pair of diverticula are greatly elongated, reaching as far as the end of the fifth segment of the first walking leg. The fourth pair stretch into the second rudimentary walking leg, and lastly the fifth pair remain as lateral protuberances. There are found five pairs of ventral ganglia. The ganglia of the first pair are fused with each other to form a large compact mass, and the last pair are all but rudimentary. Eyes in a pair situated on the anterior dorsal surface are perfectly separated from each other. Excepting the reduction in size of the lateral spine on the basal segment of chelifor the first three pairs of appendages are not different from those of the preceding larva.

As the larvae develop the fourth appendage grows longer and acquires seven segments. The rudiment of the fifth appendage is more protruded laterally, with a visible terminal claw under the hypoderm. The fifth pair of diverticula of the mid-gut are now marked off as two lateral cylindrical pouches.

Stage IV: The stage is represented by Fig. 4. The most remarkable change in this stage is the formation of the two pairs of eyes. The first pair are larger and set more closely to each other than are the posterior ones. In this stage the pair of second walking legs are provided with six segments. The first walking leg has now acquired the adult number of segments, i.e. eight. Each chela of the chelifors has three minute teeth along the inner border. The lateral spines on the basal segment of the chelifors are much decreased in size. Both the fourth and fifth appendages have each a well developed terminal claw bent inwards. The rudiment of the sixth appendage is formed on both lateral sides of the posterior body. Five pairs of ventral ganglia are seen, of which the first four pairs are fused together. The diverticula of the mid-gut enter the first, fourth, fifth and sixth appendages.

Fig. 5 shows a little advanced stage. The fifth pair of appendages have seven segments. The five pairs of ventral ganglia are distinctly formed.

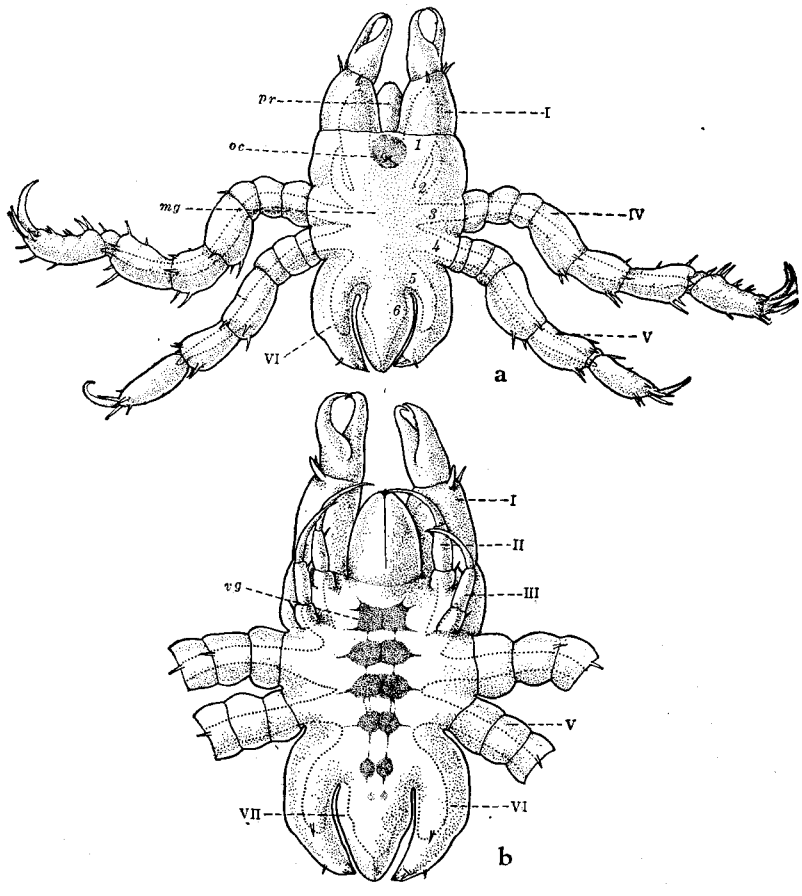

Fig. 4.—Stage IV. a, Dorsal view. × 50. b, Ventral view. × 90. mg, mid-gut; oc, eyes; pr, proboscis; vg, ventral ganglia; I, chelifor; II-III, larval appendages; IV-VI, walking legs; VII, rudiment of the last walking leg; 1-6, diverticula of mid-gut.

Stage V: In this stage (Fig. 6) the most important change lies in the remarkable reduction of the third pair of appendages, which now remain as finger-shaped processes each with a terminal claw. The body measures about 0.6 mm in length exclusive of proboscis. The first and second pairs of appendages remain unchanged in structure.

On the dorsal surface are seen the two pairs of eyes symmetrically arranged. The third walking leg (the sixth appendage) has acquired seven segments. The first and second pairs of walking legs have the adult number of segments. The rudiment of the last walking leg is divided internally into three segments under the cuticle, having

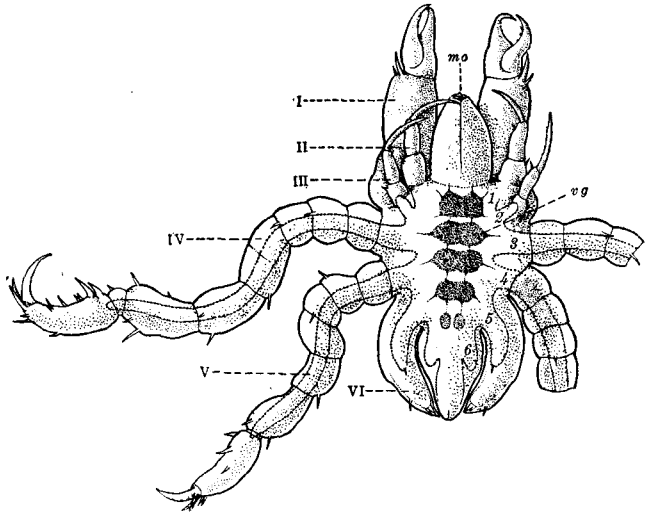

Fig. 5.—A further advanced stage than the one shown in fig. 4. × 50. mo, mouth; vg, ventral ganglia; I, chelifor; II-III, larval appendages; IV-VI, walking legs; 1-6, diverticula of mid-gut.

two spines on the terminal segment. The abdomen is indicated by an unpaired median rod directed posteriorly. These are five compound ventral ganglia and a faint sixth paired ones. At the antero-lateral corner of the trunk there are a pair of thick oval protuberances of cuticle armed with a few small spines.

Stage VI: The most marked external change has taken place in the second and third pairs of appendages (Fig. 7). The second pair of appendages, 0.45 mm in length, lose their early larval structure and take the rudimentary form of a palp. They are three-jointed, having lost the long terminal spine, and bear many short spines. The third pair of appendages measuring 0.15 mm long are fully atrophied and are only indicated by a renewed pair of peach-shaped masses. The proboscis measures 0.5 mm and the trunk

0.8 mm in length. The chelifors decrease gradually in size. Four simple round eyes are arranged about an equal distance from each other on a raised ocular tubercle. All the walking legs have segments of the adult number. The abdomen, slightly shorter than the proboscis, is cylindrical with several spines near the end. Five

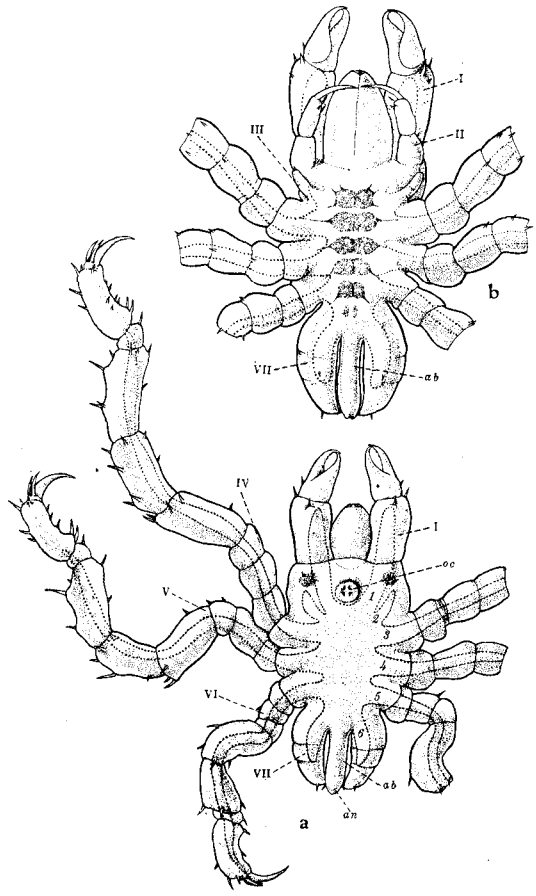

Fig. 6.—Stage V. a, Dorsal view. × 30. b, Ventral view. × 40. Showing reduction of third pair of appendages. ab, abdomen; an, anus; oc, eyes; I, chelifor; II-III, larval appendages; IV-VII, walking legs; 1-6, diverticula of mid-gut.

pairs of compact ventral ganglia can be clearly detected, and the sixth pair, which were rudimentary in the previous stage, cannot be made out externally. The mid-gut sends out diverticula to the first, fourth, sixth and seventh pairs of appendages and to the base of the rudimentary third pair of appendages.

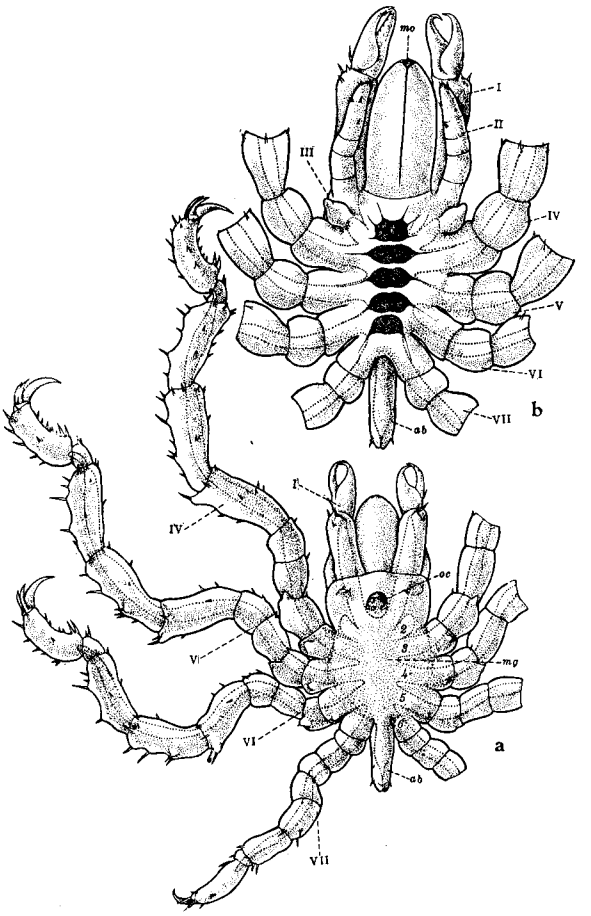

Fig. 7.—Stage VI. In this stage the larval appendages are metamorphosed. a, Dorsal view, × 30, b, Ventral view. × 40. ab, abdomen; mg, midgut; mo, mouth; I, chelifor; II, palp; III, rudiment of oviger; IV-VII, walking legs; 1-6, diverticula of mid-gut.

As development proceeds (Fig. 8) the palp greatly increases in length with the complete adult number of segments, i.e. eight. The

lengths of chelifors and palpi are almost equal to that of proboscis. The oviger is now three-jointed.

Stage VII: The larva (Fig. 9) approaches nearer to the adult structure. The proboscis is directed obliquely ventrad, cylindrical in shape. It measures 0.82 mm in length. The trunk is about 1 mm in length. The chelifor is still well developed measuring 0.9 mm long and is armed with a triangular projection distally on the dorsal side of the first segment. The palp (Fig. 9,e) is longer than the proboscis and consists of eight segments: the first segment is short and rounded; the second segment is much longer with a distal spine while the third segment is again short and small; the fourth segment is longest; the fifth to the eighth segments are short being furnished with a row of strong spines on their ventral distal sides. The oviger measures 0.8 mm in length and has six segments, of which the terminal three segments are strongly incurved. The third segment is the longest. On account of undeveloped condition of the oviger (in the adult it has ten segments) sexual difference cannot be observed. The denticulate spine on the terminal segment is not found as yet. The ocular tubercle is oblong with four subequal round eyes. Each of the leg-bearing lateral processes of the trunk has near its distal end two obtuse cone-shaped tubercles, of which the lower one is stouter and well developed. The first coxa bears a long protuberance. All of the three coxae are short, being almost equal in length to each other. The femur, the first and the second tibiae are the longest, being nearly of equal length to the coxal region. The femur has a conical protuberance with a short spine at its dorsal corner. The first tarsus is the shortest, while the second tarsus is well developed with a strong terminal and two auxiliary claws. No genital opening is formed as yet. The abdomen measures 0.55 mm

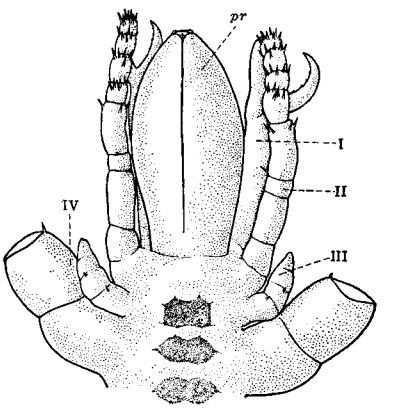

Fig. 8.—A little advanced stage showing the further development of palp and oviger. × 35. pr, proboscis; I, chelifor; II, palp; III, oviger; IV, first walking leg.

in length. It is cylindrical in shape and has a thickened area with short spines near the end.

Fig. 10 shows a young little further advanced than the former stage. This young represents the last stage found among the lot now

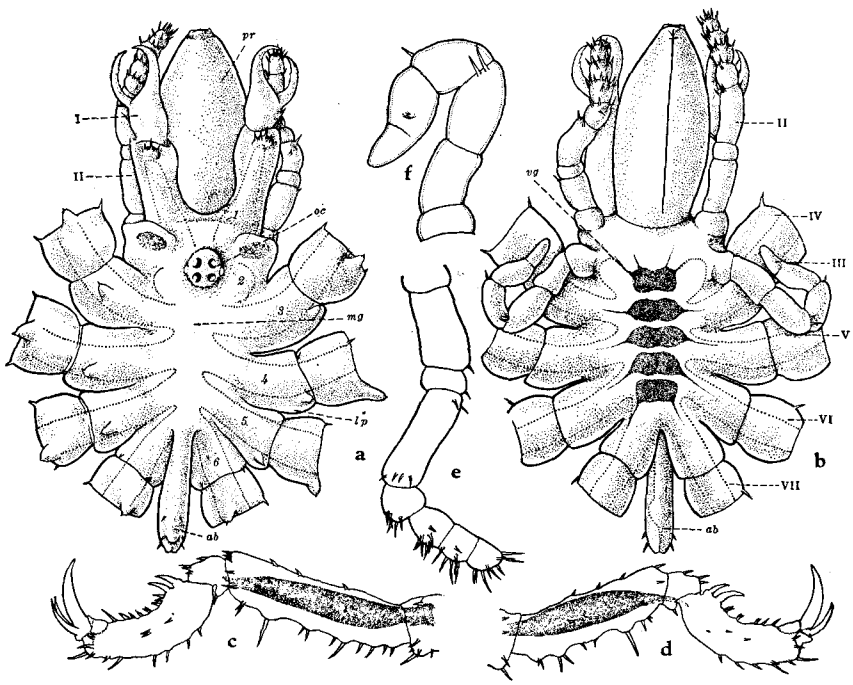

Fig. 9.—Stage VII. a, Dorsal view. b, Ventral view. × 30. c, Terminal portion of the second walking leg. d, The same of the fourth walking leg. × 35. e, Palp. × 40. f, Oviger. × 40. ab, abdomen; mg, mid-gut; oc, eyes; pr, proboscis; vg, ventral ganglia; I, chelifor; II, palp; III, oviger; IV-VII, walking legs; 1-6, diverticula of mid-gut.

at hand. It has many features which seem to characterize the adult animal. A pair of rounded tubercles with small spines on the lateral corner of the eye-bearing segment as are shown in Stage VI are now degenerated. The ocular tubercle is obtuse cone-shaped. The chelifor decreases further in length. The oviger is still in an undeveloped condition with seven segments, of which the terminal segment bears a denticulate spine (Fig. 10,c). The fourth segment is armed with a row of short spines at the distal portion. The trunk is oval in outline measuring 1.2 mm in length. All of the walking legs have

increased greatly in length, and each contains a long diverticulum from the mid-gut. Five pairs of ventral ganglia are seen, and all of them are completely fused up. As to the other characteristics there are no noticeable changes compared with the foregoing stage. This larva may further undergo several moults and then leave the body of the host. Excepting the small body size the last stage treated

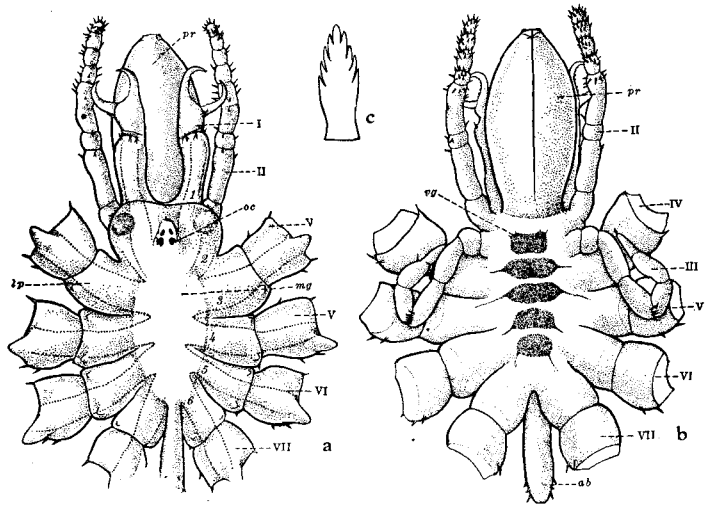

Fig. 10.—A further advanced stage. a, Dorsal view. b, Ventral view. × 30. c, Denticulate spine of oviger. × 320. lp, leg-bearing lateral process; mg, mid-gut; oc, eyes; pr, proboscis: vg, ventral ganglia; I, chelifor; II, palp: III, oviger; IV-VII, walking legs; 1-6, diverticula of mid-gut.

here is different mainly from the adult in having the rather large chelifor and the undeveloped oviger showing as yet no sexual differentiations. As already mentioned by H. Ohshima (1933) the leg-bearing lateral process has always two cone-shaped protuberances instead of one as described by former authors.

Remarks

Very little is known about the development of *Ammothea*. The earliest record of young stages is that of Dohrn who in 1869 treated partially the metamorphosis of *Ammothea laevis*. In 1902 Meisen-

heimer gave an account of the early development from the egg to the six-legged larva of *Ammothea echinata*. Dogiel (1913) described and figured the post-embryonal development of *Ammothea laevis* from the protonymphon stage to the late stage just prior to the metamorphosis of the third appendage. Recently Ohshima (1933) has described larval stages of two species of *Ammothea* sp. found parasitic on Nudibranchs. Both these young of *Ammothea* sp. described by Ohshima are quite different from the present form. In general the process of the post-embryonal development of our young has much in common with that of *Ammothea laevis* described by Dogiel and especially with that of *Tanystylum orbiculare* studied by Morgan (1891). As to the method of increase of appendages and their order of development the present species agrees well with Morgan's *T. orbiculare*. Excepting the earlier appearance of two pairs of eyes in *Tanystylum* the development from the six-legged protonymphon stage to Stage V takes place in a similar way in the two. In Stage VII *Ammothea* bears a segmented palp newly formed, while in the corresponding stage of *Tanystylum* the larval palp is not as yet metamorphosed. The most marked difference between these two species lies in the fate of the first pair of appendages, i.e. the pair of chelifors. In *Tanystylum* the chelifors are lost almost totally in Stage VII, while in the present species they remain in a well-developed condition.

Literature

COLE, L. J. 1904 Pycnogonida of the west coast of North America. Harriman Alaska Expedition. New York.

DOGIEL, V. 1913 Embryologische Studien an Pantopoden. Zeit. f. Wiss. Zool., Bd. 107, Heft 4.

DOHRN, A. 1869 Über Entwicklung und Bau der Pycnogoniden. Jena. Zeitschr. Naturw., Bd. 5.

LEBOUR, M. 1916 Notes on the life history of *Anaphia petiolata*. Jour. Mar. Biol. Assoc., vol. 11, no. 1.

MEISENHEIMER, J. 1902 Beiträge zur Entwicklungsgeschichte der Pantopoden. Zeit. f. wiss. Zool., Bd. 72.

MORGEN, T. H. 1891 A contribution to the embryology and phylogeny of the pycnogonids. Studies from Biol. Labor. Johns Hopkins Univ., vol. 5, no. 1.

OHSHIMA, H. 1933 Young pycnogonids found parasitic on Nudibranchs. Annot. Zool. Japon, vol. 14, no. 1.

OHSHIMA, H. 1933 Pycnogonids of the North Kuriles. Bull. Biogeogr. Soc. Japan, vol. 4, no. 2.

PRELL, H. 1909. Beiträge zur Kenntnis der Lebensweise einiger Pantopoden. Bergens Museum Aarbok, Nr. 10.

SEMPER, C. 1874 Über Pycnogoniden und ihre in Hydroiden schmarotzenden Larvenformen. Verh. d. Würzburger Phy. Med. Ges., Bd. 7.

UCHIDA, T. 1927 Studies on Japanese Hydromedusae. Jour. Fac. Sci. Imp. Univ. Tokyo, vol. 1, part 3.