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The Biology of a Harpacticoid Copepod, *Tigriopus japonicus* Mori¹⁾²⁾

By

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(With 12 Text-figures, 1 Table and 2 Plates)

Several species of the genus *Tigriopus*, harpacticoid copepods, have been used by many workers as good materials for experiments of their physiology, genetics, ecology, etc.: Fraser (1936 a, b), Takeda (1939–1954), Ranade (1957), Bozic (1953–1960) and many others. Their frequent use as materials is due to the following reasons. Population of the species is easily maintained in the laboratory, because the animals well tolerate various environmental changes and have higher ability of reproduction in artificial conditions as well as in natural one than that of the other so far known harpacticoids. And the peculiar life manner, which is closely related to the characteristics in the habitat, is so interest as to attract various attentions of many investigators. Only one species of the genus known from Japan, *Tigriopus japonicus*, was described by Mori (1938) from Shimoda on the Pacific coast of the middle part of Honshû. Since that time, many informations on its physiology, genetics and ecology, have been successively published in nearly twenty papers by the following workers: Takeda (1939–1954), Tokioka & Suzuki (1939), Igarashi (1959–1964), Egami (1950) and Matsutani (1959–1961). On the other hand, some biological knowledge still remains very poor especially in anatomical, developmental and ethological points of view. In this first report of serial work, observations with some new findings on this species are reported and discussed based upon above mentioned points. The internal structure will be treated in the further paper.

Most materials were collected from Oshoro and Kutsugata (Rishiri Isl.), both on and off Japan Sea Coast of Hokkaido. Some of the materials were cultured in the laboratory. All slide preparations were mounted in Neo-Shigalar medium. Details of materials and methods are proposed in the following text.

Before going further, the author wishes to express his cordial thanks to Prof. Mayumi Yamada, Zoological Institute, Hokkaido University, for his kind guidance to the present study.

1) Contribution No. 878 from Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

2) Studies on the biology of *Tigriopus japonicus*, I.
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Ethology

1. Feeding behaviour and food materials.

Fahrenbach (1962) observed the feeding mechanism in detail in both naupliar and copepodid stages of *Diarthrodes cystoecus* Fahrenbach, and described the function of each oral appendage together with the certain structures.

In the present investigation, the author was unable to examine so minutely as the work carried by Fahrenbach, and only some gross observations are described.

In the case of feeding of a small solid material, for example a grain of shrimp meal or a piece of alga, they handle their antennae dexterously to hold the food material underneath the mouth. They push powerfully the distal edge of their labrum on the food material and move hurriedly their mandibles to graze it. It is occasionally observed that their maxillipedes and leg 1 are used for subsidiary holding of such food material. The antennules in both sexes, however, are never used for feeding, although those of the male are an important grasping organ in mating behaviour. The well-developed spines on the distal edge of the antenna are very functional in the food-holding behaviour as they act like the fingers of human hand, but the spines on the exopodite as well as on the endopodite of leg 1 are not.

Occasionally it was observed that the feeding was done keeping their back down or swimming in mating couple in both smaller copepodid and adult male handling their antennae.

The present species is apparently euriphagous and takes as food several kinds of materials given experimentally, for example a green alga *Enteromorpha prolifera*, small grains of dried bonito and dried shrimp meal.

Many transparent shells of diatoms, one of them is probably *Pleurosigma* sp., were recognized in the mid gut in some sections of a specimen from Rishiri.

Egami (1951) used small pieces of mulberry leaves as the nutrition in his experimental study. Further, other various kinds of materials, protozoans, bacteria and other organic particles, may be also utilized.

2. Mating behaviour and breeding.

Mating behaviour consists of two successive and different behaviours, pairing and copulation. The pairing is able to observe without difficulty in natural habitat as well as in laboratory. In the pairing, the adult male grasps with his antennules both lateral hind edges of the cephalothoracic carapace of his partner (Pl. VII, Fig. 5).

Whereas one of the pairing couple, at least the posterior one, is always the fully grown adult male, his partner is not always a certain stage of female. Fraser (1936 a) referred to the mating in *T. fulvus*, "the mating female is usually much smaller (about 800 μ) and at the fifth copepodid stage although fully grown females can often be seen mating", and further, "females at this fourth stage can be seen

swimming about with males attached, although copulation either does not take place or is ineffective", and he proposed a figure of a mating couple of the species in another paper (Fraser, 1936 b). Contrary to this, Igarashi (1960) described of *T. japonicus*, "copulation is successful between the adult male of the sixth copepodid stage and females of the fourth copepodid or later stages."

These different opinions of two species of the genus apparently differ from each other. It does not seem to the present author, however, that the difference may be caused only by a species specificity. It is certain that Fraser treated the mating behaviour in distinguishing the actual copulation from the mating (=pairing), but uncertain whether Igarashi treated so or not. The present author has some hesitation to accept the opinion of Igarashi. It is not always certain that the partner of the adult male was the fourth, fifth copepodid or fully grown adult females. In some cases, the partner was the first, second and third copepodid stages, in each of which sex was unknown.

Although the present author observed many couples in pairing ever so often for about three years, he so far chanced to observe only two cases in the actual copulation. According to his experience, it is very difficult and a rare chance to observe such actual copulation, because their copulation completes for very short time within only a few minutes, though the pairing is maintained for several days. In the present, three examples including an observation of actual copulation, are proposed as follows.

The first example. An adult female collected from Oshoro (10-IX-'68) produced many nauplii (15th, Sept.). The nauplii grew into some copepodids, and a couple of them copulated (probably 25th, Sept.) and the female, the second generation, produced some nauplii (13th, Oct.) as the third generation. A female of the fourth copepodid stage of the third generation mated with her father, the male of the second generation.

24th, Oct. The fourth copepodid female paired with her father.

25th, Oct. The couple in pairing. There was a castoff carapace of the fourth copepodid stage. The female became into the fifth copepodid stage.

26th and 27th, Oct. The couple in pairing.

28th, Oct. The pairing was already over, and they separated from each other. There was a castoff carapace of the fifth copepodid stage. The female became into the last copepodid stage. The female cultured alone.

29th-31st, Oct. No marked changes in her behaviour were observed.

1st, Nov. The female produced a white egg sac.

The second example. A fourth copepodid female mated with her father, both originated from a female collected from Oshoro.

28th, Oct. The couple in pairing.

29th, Oct. The couple in pairing. There was a castoff carapace of the fourth copepodid. The female became into the fifth copepodid stage.

30th, Oct. The couple in pairing.

31st, Oct. The pairing was already over. There was a castoff carapace of the

fifth copepodid. The female became into the sixth copepodid.

4th, Nov. The female produced a white ovisac.

The third example. A virgin of the fifth copepodid stage from Oshoro was mated experimentally with an adult male collected from Aburatsubo (22-X-'68).

26th and 27th, Nov. The couple in pairing.

28th, Nov. They were copulating under the author's observation for a few minutes. There was a castoff carapace of the fifth copepodid stage. The female already became into the sixth copepodid stage. Unfortunately the author was unable to recognize the actual day of her oviposition, but two weeks later he observed many copepodids swimming in culture vessel.

These three examples are only a little part of the author's observations. According to these examples as well as all his other observations, it is still unknown whether the pairing is maintained continuously for all period including her several moltings or not. And further, it remains probabilities that their copulation was occurred in unobserved period in all cases. The author, however, persists his view, which is almost like to that of Fraser, that the pairing is only an engagement between them and their actual copulation is occurred to the fresh sixth copepodid female just after the final molting.

On the other hand, the behaviour in the male to the female or others are not always completely analyzed. In the present, two examples of curious behaviour in the male are proposed.

The author found the pairing of two adult males within some individuals which were collected a day before from Oshoro (7-VIII-'68) and preserved in a refrigerator until just before his observation. They acted violently and soon after while, further, more one adult male joined into the pairing. The pairing with three adult males was under his observation for several minutes and, unfortunately, they separated from each other when he transferred into an other vessel with a pipet to attempt taking a photograph.

Another example was found within some individuals, which were preserved in a refrigerator as in the above, collected from Oshoro (18-XII-'69). One adult male suddenly made a clutch at an another adult male and grasped with his antennules any part of the body of passive one who acted violently as if he wanted to tear himself away from his unexpected partner. Several minutes later, the positive one succeeded to grasp firmly the base of the furcal setae of the other one, and he repeatedly tried to attach his abdomen to that of the other one as in the manner of copulation illustrated by Donner (Lang, 1948. p. 1512). The appearance of their entwinings is shown in two pictures (Pl. VIII, Figs. 1 and 2).

According to these two observations, the ability of the male to recognize in the female as his partner is not always certain or rather questionable. The behaviours in these two observations, however, might be unusual ones, because all individuals in both cases were preserved in a refrigerator at once, and some unknown factors, for example rapid increase of the temperature from low one in the refrigerator to

relatively high room temperature especially caused by a lamp, might give some effects on their behaviour. If such probability is accepted, the supposition described is also supported with the facts that the adult male occasionally behaves himself as in the mating, particularly as in the pairing, to younger copepodid stages and ovigerous females too. The adult male is probably able to recognize the young female as his expected partner with the aid of several sensibilities in a combination of tactile, smell or visual ones together with the behaviour of his partner as a response to the attaching with his antennules. And the adult male is able to mate with his expected partner, rather by chance or through his several trials and errors.

It seems that their breeding takes place during all seasons except for the winter from December to May in Oshoro. During the long winter they are exposed to very critical condition covering with snow or ice in the habitat (Pl. VII, Fig. 2) and no pairing couples or ovigerous females are observed. The female, however, has always an ability to produce the egg sac, inhibited by lower temperature, during the winter.

3. *Longevity.*

A male lived for 67 days in the laboratory, and the other male for 66 days, both were the first copepodid stage at the beginning of culture (9-IX-'68). On the assumption that the nauplius stage lasts for five days, the longevity in each individual described is estimated at 72 days and 71 days respectively, after their hatching.

Both individuals collected from Oshoro were cultured in a small glass vessel containing with 50c.c. of filtrated sea water in room temperature, and given a small amount of grains of dried shrimp meal as the nutrition.

In the natural habitat, the longevity is estimated at four months at least in the winter in Oshoro, supposing from the fact that the individuals hibernated with no reproduction in the severe condition covered with snow and ice in the winter, from December to May.

4. *The velocity of growth.*

In the case of the fastest growth, it took only nine days after hatching to grow into the adult in the room temperature ranging from 15°C to 25°C. It is well known that such velocity depends on the temperature. Further, Igarashi (1960) showed that the velocity was easily effected by salinity. Since an investigation concerning with such problem is now on progress in the present author, the result will be proposed in a further paper.

Ecology

The seasonal population dynamics in the present species has been already studied and reported by Tokioka & Suzuki (1939). The study, which was

carried out in Shirahama from 1937 to 1938, is worthy of note as he studied in ecological point of view in contrast with that many other investigators who were probably more or less interested in the peculiar life of the species studied rather physiologically. In the following, some results in Shirahama are proposed.

The water temperature varied extremely between 4°C in winter and 40°C in summer. The salinity was 0.25‰ as the lowest value and 49.59‰ as the highest. The salinity fluctuated not always depending on the season but rather on the tidal change, wave, evaporation and rain, etc. The higher value more than 30‰, however, was concentrically gained in summer between July and September. This phenomenon is explained by the evaporation under stronger solar irradiation in summer. In such condition, several pools were dried up completely. He, further,

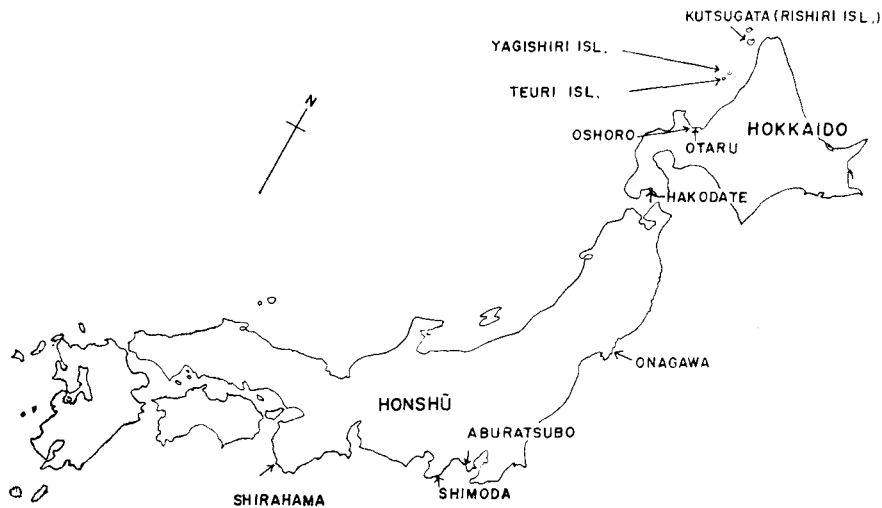


Fig. 1. The localities of *Tigriopus japonicus* so far recorded.

referred to his observation concerning with the temporary desiccation in some pools, and just after rainfall a little swimming animals of the species were appeared again in such pools except for several ones, in which the appearance of the animals was recognized about more two weeks later. In the latter case, it is very important fact that the animals appeared consist of many younger stages. Because it seems that one of the influential evidences to interpret such later appearance of younger animals is not derived from the adults or youngs endured the desiccation but rather from the eggs which are covered with an egg sac membrane in each brood and probably able to tide over such critical condition in resting state.

The population indicated the highest density at May in 1937 and the lowest at January in 1938. At present, it is not certain whether the highest density

always appears at May, early summer, or not rather than at mid summer. Such investigation of population ecology is very interesting with relation to the many physiological data as studied by some authors, namely, Takeda, Igarashi, Matsutani, etc.

The present author has also attempted to study the population ecology more minutely and searched for adequate pools in the suburban district around Sapporo where his laboratory is present. But the populations of Oshoro and all other districts investigated were very poor and not sufficient to collect the animals frequently for the quantitative study. Only the population of Rishiri Island was available to such study but the field was extremely out of traffic facilities. Accordingly, the author resigned the primary attempt and was obliged to make alteration. The author, at present, is able to propose only some data of the environmental condition.

Some new habitats of the species were found during his searching described in addition to the localities already reported (Itô, 1969): Teuri Island, Yagishiri Isl., Tachimachimisaki (Hakodate) and Otaru, as shown in the figure (Fig. 1).

1. *Environmental condition.*

It is generally accepted that the environmental condition of the species especially in the physiological factors is extremely changing at all times. The actual data or informations denoting the degree particularly concerning with the dynamic change, however, are not so much.

1.1. *Seasonal change.* The present author began to record the environmental condition of the habitat in Oshoro in 1968, and still now it is on progress not periodically.

Some pools were chosen for the purpose, but only one of the pools, namely P-1, was fully recorded in his all visitings. All recordings were carried out between 1:00 p.m. and 3:00 p.m. The datum at July in 1969 was cited from the one for the study of diurnal change which is described below.

The water temperature of P-1 (Fig. 2-1) was fluctuated between 31.4°C in the mid summer in 1969 and -2.0°C in the mid winter in 1968. The annual fluctuation of the water temperature between the highest value and the lowest one will be increased to 40°C even at the lowest estimate, in more minute study.

The salinity was measured with the Akanuma's Hydrometer (Rigosha, N. 2504-AA) for the specific gravity.

Remarkable increase of salinity was recorded in the mid winter ($\sigma_{15}=2.0071$, -1.0°C, 18-XII-'69). At that time, the pool was entirely covered with thick ice and snow. Such phenomenon in the condition described is well explainable by the fact that the dissolved salts are concentrated in the freezing. In this respect, the environmental condition in Oshoro differs from that in Shirahama, and is recognizable as a distinctiveness in winter.

1.2. *Diurnal change.* The diurnal change of environmental condition (Fig. 2-2) was investigated at the same pool in Oshoro (24 and 25-VII-'69).

The water temperature was measured in every hour and salinity as specific gravity in every three hours.

In the P-1, the water temperature was 31.4°C as the highest value at 3:00 p.m. and 23.1°C as the lowest one at 5:00 a.m. The mean was 26.3°C. The salinity in the same pool was about a fifth at the beginning of the study and gradually increased, finally reached a quarter, regarding the salinity of the sea water below the rock as a standard. The lower value compared with that of the sea water may be effected by the rain fall in the previous day.

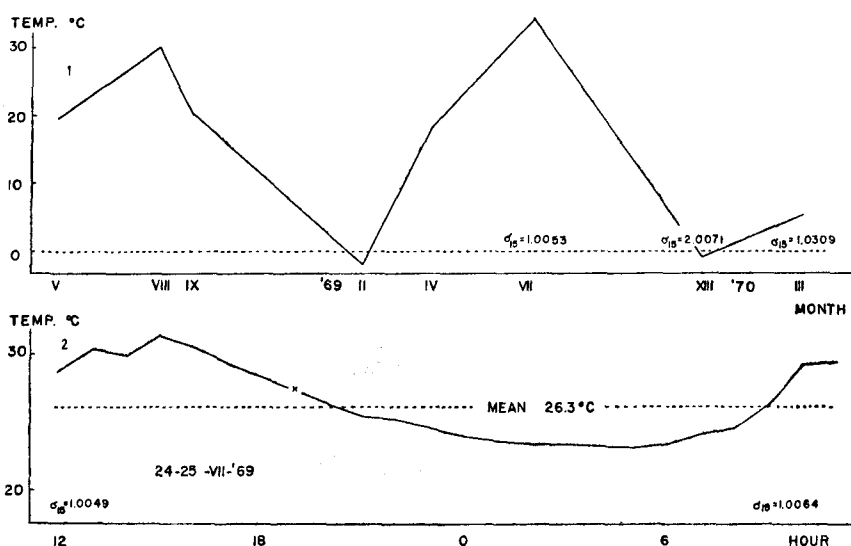


Fig. 2. Annual (1) and diurnal (2) fluctuation in water temperature taken at P-1, Oshoro. σ_{15} is specific gravity converting at 15°C.

External morphology

The external structure of the adult was described originally by Mori (1935) and further, more minutely redescribed by Itô (1969). In the present, some additional structures which were overlooked in the two papers will be described particularly concerning with sexual dimorphic characters.

Measurement of the body length was carried out based upon figures in lateral view. The length of the cephalothorax was measured as a standard straight line linked the base of rostrum to the dorsal hind edge of cephalothorax. The roundness was taken no account also in all other segments. The length of furcal seta means only that of the principal terminal seta. The height of the cephalothorax was represented by the greatest height on the standard straight line of the segment described,

1. *The adult.*

Body is a little shorter in the male than in the female and further, the cephalothorax of the male has a slighter appearance in lateral view as indicated by the value of the height (Tab. 1).

Table 1. Mean length, in millimeter, of three parts in adult specimens, six males and six ovigerous females, from Hakodate (14-IX-'69) preserved in 70% alcohol solution. Each number in the parenthesis is maximum value in the former and minimum in the latter.

	Body	Furcal seta	Height of ceph.
Female	1.03 (1.04, 1.00)	0.63 (0.69, 0.58)	0.073
Male	0.92 (1.00, 0.83)	0.73 (0.79, 0.70)	0.053

Rostrum in the female (Pl. VIII, Fig. 3) is not furnished with a pair of sensory hairs but two pairs of ones, and in the male (Pl. VIII, Fig. 4) relatively smaller rostrum with only a pair of such hairs. The terminal segment of antennule in the female has a trifurcate seta, one of the furcations is aesthetasc-like, on the distal end (Pl. VIII, Fig. 5). The principal terminal seta of furcal ramus in both sexes is furnished with many spinules and hairs almost reciprocally (Pl. VIII, Fig. 6) and outer terminal seta with very minute hairs. The length of furcal seta in the male is apparently longer, than in the female (Tab. 1). Such difference between both sexes is also able to be recognized in the figures of *T. fulvus* by Sars (1904). Some minute hairs on the body surface were observed in some total specimens and fragments of the carapace dissected. The estimation of actual numbers and the situation of the hairs, however, was entirely failed.

2. *The nauplius stages.*

The present species has six naupliar stages as shown in the previous descriptions by Takeda (1939) and Igarashi (1960), who proposed neither illustrations nor a description of the structure in each stage, though *T. fulvus* investigated by Fraser (1936 a) has five successive stages.

The following descriptions were carried out based upon some cultured specimens which were produced by some individuals collected from Rishiri, Oshoro, Otaru and Hakodate. Anterior three appendages are illustrated in only one of each pair reciprocally.

Before going further, the author must confess that some structures, particularly setal number of antennule, antennal gnathobase or exopodite, were not always able to be observed and clarify exactly in spite of careful examination, because of some technical difficulties together with their minute size. Some minor incorrectness, not so gross, might be present in the following.

2.1. *The first nauplius stage.*

Body (Fig. 3-1) unsegmented, 0.102 mm in length, 0.107 mm in width; ventro-posterior surface with some minute spinules between furcal rami. *Labrum* almost rectangular in shape, about half as long as body, furnished with some hairs along each lateral edge subdistally, distal margin thickly chitinous. *Furcal ramus* represented by a small protuberance with one slender bare seta. *Antennule* three-segmented, tapering distally; first segment with only one diminutive seta; third one with three well-developed setae apically. *Antenna* furnished with well-

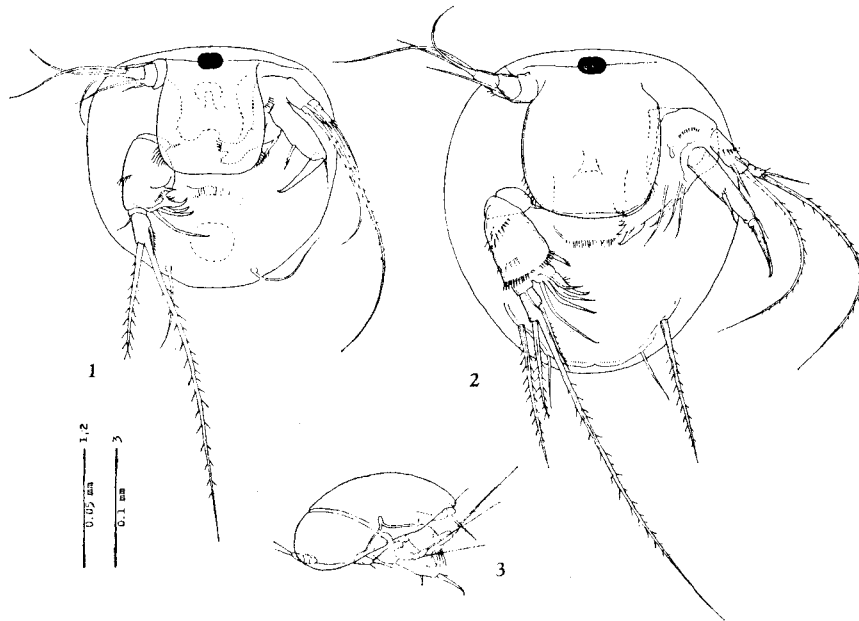


Fig. 3. 1. The first nauplius; 2. The second nauplius; 3. The cast off carapace of the second nauplius.

developed gnathobase, of which distal edge ending into a strong claw and with some spinules and one short seta; one seta on about middle edge. Exopodite three-segmented; first segment longest with one short seta; second one shortest, with one long spinulose seta; third one, which seemingly divisible into more two segments but not certain, furnished with one very long spinulose subterminal seta, some spinules and one bare seta on distal end. Endopodite one-segmented, furnished with one strong claw accompanied with one minute seta on distal end, and with one seta on middle inner edge. *Mandible*. Coxa small, with one short bare inner seta. Basis well-developed, with one short spine on inner subdistal edge, and some spinules ornamented as in the figure. Exopodite exactly two-segmented; first

segment shorter and with one minute seta on distal edge; second one furnished with one long spinulose terminal seta, about 1.3 times as long as the body length, not separable from the segment; one short seta, inner margin spinulose, on middle inner edge; one thick spinulose seta on outer distal corner. Endopodite very short, one-segmented, furnished with one pectinate claw and three spiniform setae, outermost one longest.

2.2. *The second nauplius stage.*

All segmentations in antennule, antenna and mandible, are not changed in the present stage and all following stages.

Body (Fig. 3-2) slighter in appearance, 0.137 mm in length, 0.124 mm in width. Abdomen recognized ventrally, but seemingly without distinct segmentation. *Antennule* almost same as in the preceding stage. *Antenna*. Gnathobase with more spines on cutting edge, and added three setae on middle part. First segment of exopodite with some spinules, and one short seta added near distal end. Terminal claw of endopodite accompanied with one additional short seta. *Mandible*. One spiniform seta added on endopodite. *Maxillula* represented by one strong spinulose seta.

2.3. *The third nauplius stage.*

Body (Fig. 4-1) two-segmented, with two spinular rows on each lateral edge, 0.169 mm in length, 0.147 mm in width. *Labrum* more rounded. *Furcal ramus* with two spinulose setae, outer one longer and accompanied with one bare slender seta dorsally. *Antennule*. Several minute setae added on third segment. *Antenna*. Gnathobase with six setae, not exact, near and along outer edge. *Mandible*. Endopodite with one additional seta. The seta, representing maxillula, a little shortened, on a small protuberance.

2.4. *The fourth nauplius stage.*

Body 0.185 mm in length, 0.169 mm in width. Posterior segment with an arched spinular row on each ventro-lateral surface. *Furcal ramus* with one additional bare seta on distal end. *Antennule*, *antenna* and *mandible* not changed remarkably in shape. *Maxillula* accompanied with several spinules near base, and with two spinulose setae, terminal one a little shorter than outer one.

2.5. *The fifth nauplius stage.*

Body (Fig. 4-2) three-segmented, 0.194 mm in length, 0.172 mm in width; middle segment bare. *Labrum* more rounded. *Antennule*. Several setae added on third segment. Other appendages and furcal ramus almost same as in the preceding stage.

2.6. *The sixth nauplius stage.*

Body (Fig. 5-1) three- or indistinctly four-segmented, 0.232 mm in length, 0.199 mm in width. *Labrum* about a third as long as body, thinned in appearance,

without hair. *Furcal ramus* with one additional bare seta on middle outer edge. *Antennule* almost as in the preceding stage. *Antenna*. Gnathobase lacking almost distal half, with only some spinules and a short seta. *Mandible*. Coxa without inner seta. *Maxillula* almost same as in the preceding stage. *Maxilla* represented by a small protuberance pointed apically. *Maxillipede* represented by a lamella, of which outer distal end minutely pointed, ending into two apparent spiniform protuberances. *Leg 1* represented by a trapezoid lamella, of which outer distal corner pointed, furnished with two short terminal setae, inner one a little shorter.

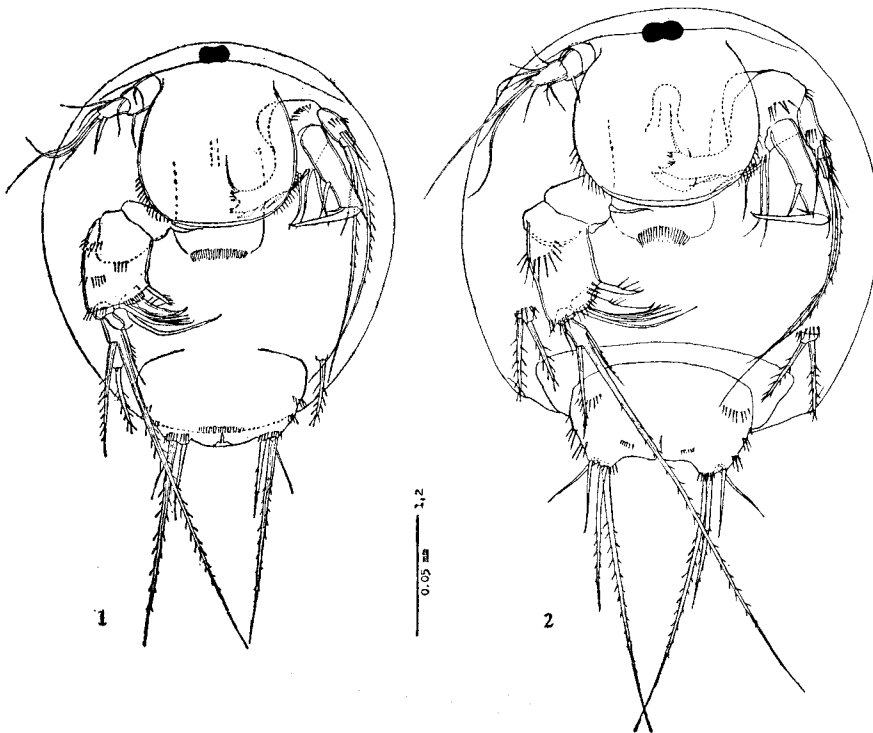


Fig. 4. 1. The third nauplius; 2. The fifth nauplius.

2.7. *Discussion*. The manner in the appendage formation through all naupliar stages except for the fourth one coincides with that of *T. fulvus* described by Fraser (1936a). Fraser, however, did not refer to the following structures; the deformation of labrum through all stages, the shortening of antennal gnathobase in the last stage, the presence of inner seta on mandibular coxa and small bud of maxilla in the last stage. Probably he overlooked these structures. The shor-

tening of antennal gnathobase is not so far reported within the harpacticoids. The inner seta on the mandibular coxa seems to be exactly present also in the following species, *Longipedia coronata* by Nicholls (1935), *Sumaristes paguri* by Gurney (referred by Lang 1948), *Canthocamptus staphylinus* by Dietrich (ref. Lang), further *Epischura massachusettsensis* (Calanoida) by Humus (1955) and *Eucyclops serrulatus* (Cyclo-

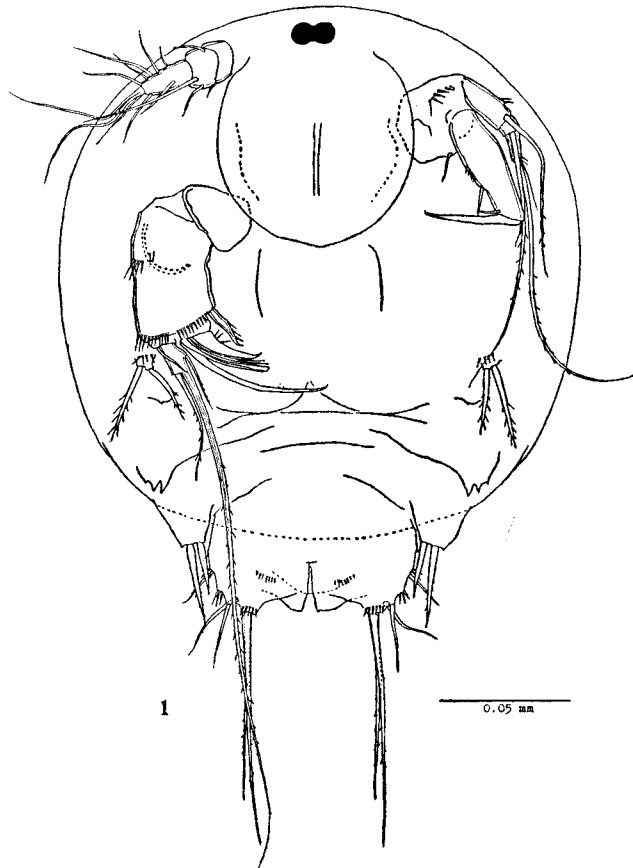


Fig. 5. 1. The sixth nauplius.

poida) by Auvray & Dussart (1966), but not in, *Diarthrodes cystoecus* by Fahrenbach (1962), *Macrosetella gracilis* by Tokioka & Bieri (1966), *Bryocamptus zschokkei*, *Br. pyrenaicus* and *Antrocamptus catherinae* by Rouch (1968). In above mentioned species, only *Macrosetella gracilis* has very peculiar shape in the appendages, unsegmented antennule, no distinct exopodite on antenna, and mandible, extremely different from one of all other harpacticoids. In the species, inner seta of antennal

coxa might not be furnished as in the description and figures by Tokioka & Bieri, but in all other species, at least some of them, it will be probably recognized by further minute examinations.

3. Copepodid stages.

Because of the difficulty in making good preparations in very delicate and smaller stages, it was failed to represent minute structural successions of all oral appendages in each stage. But in the following characters, rostrum, antennule, antenna, maxillipede, legs, furcal ramus and body segmentation, the successions are clarified through all copepodid stages. Further, some new knowledge in developmental point of view, some of which has been treated only briefly or entirely overlooked by Fraser and also others, will be discussed.

3.1. *The first copepodid stage.*

Body (Pl. VIII, Fig. 7) 0.35 mm in length, remarkably top-heavy in appearance, five-segmented; third free segment shortest, without any trace of appendage; fourth free one (anal segment) about two times as long as preceding one, with many spinules along ventro-posterior edge and on ventral surface near posterior end transversely. *Rostrum* (Fig. 6-1) rounded rectangular, with a hair on each distal corner. *Anal operculum* very prominent, flap-like. *Furcal ramus* (Fig. 6-6) about 1.5 times as long as greatest width, slightly tapering posteriorly, with some spinules along ventro-distal edge; one prominent bifurcate terminal seta, somewhat spinulose; two outer setae, anterior one hair-like, on about two-fifths of furcal ramus, posterior one near distal corner, and each accompanied with some spinules around the base; three dorsal setae on posterior half, anteriormost being biassed a little to outer side, middle one to inner, and posteriormost one spinulose and almost just dorsally near distal end.

Antennule (Fig. 6-1) six-segmented; first segment with only one seta as in the adult; second one about same length as preceding one, furnished with one aesthetasc, very alike to usual seta and not bifurcate; succeeding three segments each much shorter than others; sixth one about same length as in first but more slender, with one trifurcate terminal seta as in the adult. *Antenna* (Fig. 6-2) almost same as in the adult female excluding following structures; only three geniculate and one hair-like setae on apical end of endopodite-segment instead of four and three in the adult; third exopodite-segment with some spinules around the base of terminal seta instead of one. *Mandible*, *maxillula* and *maxilla*, each seemingly almost same as in the adult but more delicate. *Maxillipede* (Fig. 6-3) same as in the adult.

Leg 1 (Fig. 6-4): Outer part of coxa relative to basis not larger than in the adult; spinular row on border between coxa and basis absent; basis with many spinules on inner half of distal edge and one strong spinulose outer seta, but no inner seta. Exopodite one-segmented, as long as basal two segments combined, inner margin slightly rounded, about two times as long as greatest width, with one outer spiniform seta on middle edge accompanied with some spinules around the

base; two outer spines near distal edge; two spines and one long spiniform seta on distal end; one oblique row of spinules between proximalmost outer seta and the base of the segment. Endopodite one-segmented, length and greatest width as in exopodite, but width clearly reduced distally at middle part with one long inner seta; one slender inner seta near distal end; three setae, innermost one longest and outermost shortest, on distal end; all setae spinulose or hairy; four groups of spinules along outer margin. *Leg 2* (Fig. 6-5): Segmentation as in leg 1. Basal two segments same as in the adult. Exopodite about 2.5 times as long as greatest width; width slightly reduced distally near middle, with three outer spiniform seta; two long setae on distal end; one long inner seta near distal edge; all setae

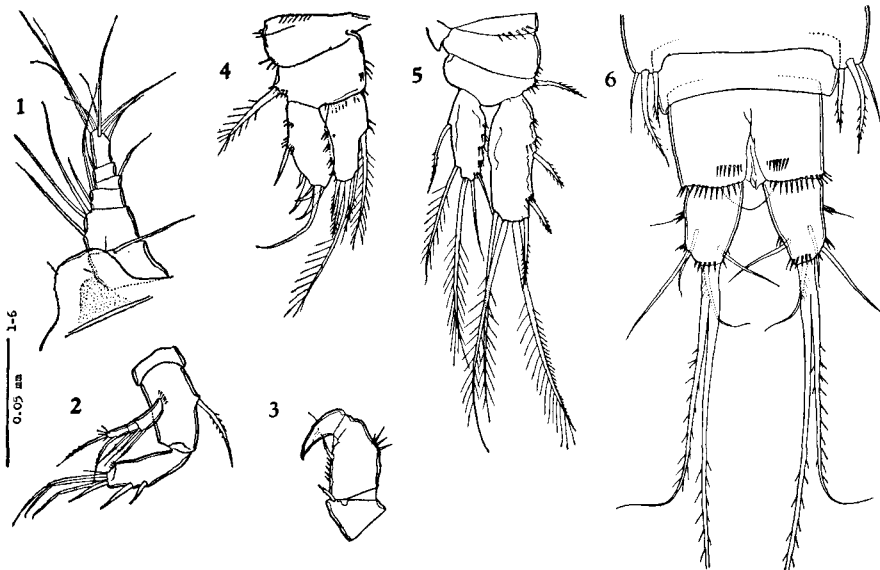


Fig. 6. The first copepodid. 1. Rostrum and antennule; 2. Antenna; 3. Maxillipede; 4. Leg 1; 5. Leg 2; 6. Leg 3 and abdomen.

spinulose or hairy. Endopodite about three-fourths as long as exopodite and slightly tapering distally, with one outer and one terminal bare setae; three hairy setae along inner margin, distalmost one longest; some groups of spinules along outer margin. *Leg 3* (Fig. 6-6) a slight flap-like protuberance with one bare slender outer and two sparsely spinulose setae.

3.2. *The second copepodid stage.*

Body 0.38 mm in length, seven-segmented; fourth free segment without any buds of legs and spinules; fifth free and anal ones, each with many spinules along

ventro-posterior end. *Rostrum* (Fig. 7-1) more rounded. *Anal operculum* prominent, but a little reduced. *Furcal ramus* (Fig. 7-8) entirely as in the adult.

Antennule (Fig. 7-1) seven-segmented; second segment about 1.3 times as long as first, furnished with one aesthetasc as in the adult. *Antenna* (Fig. 7-2) and *maxillipede* (Fig. 7-3) as in the preceding stage.

Leg 1 (Fig. 7-4): Coxa remarkably increasing the size and with many slender spinules along outer margin. Basis with one spinulose inner seta as in the adult.

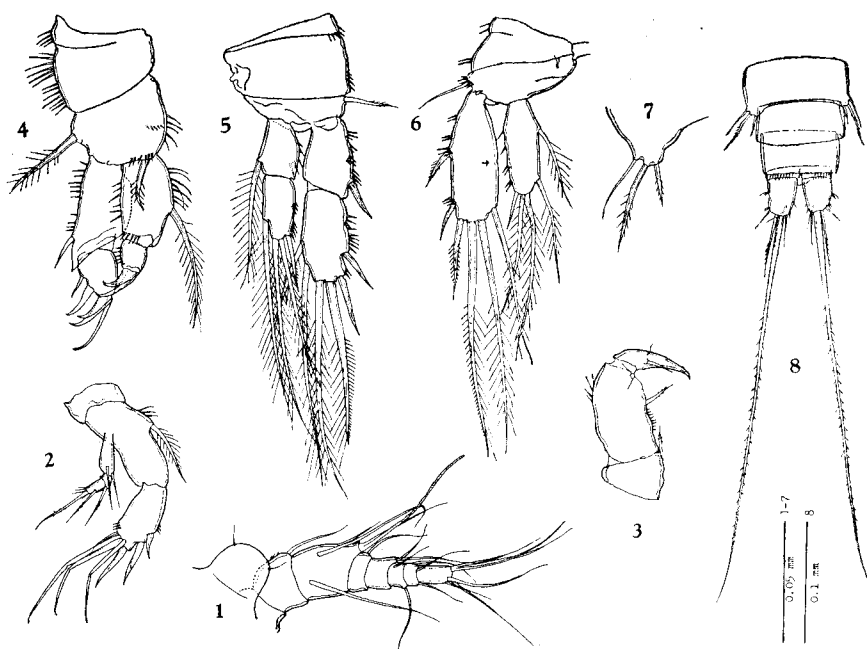


Fig. 7. The second copepodid. 1. Rostrum and antennule; 2. Antenna; 3. Maxillipede; 4. Leg 1; 5. Leg 2; 6. Leg 3; 7. Leg 4; 8. Leg 4 and abdomen.

Exopodite two-segmented, almost same as long as basal two segments combined; first segment about two times as long as greatest width, inner margin remarkably rounded; one bare seta on two-thirds of outer margin; some spinules along outer margin sparsely; second segment short, as long as two-fifths of first one, remarkably tapering distally, with one short bare seta and one spine on outer edge; two claws and one long spiniform seta on distal end. Endopodite two-segmented, a little shorter than exopodite; first segment about 1.5 times as long as greatest width, with one strong hairy seta on middle inner edge; some spinules along outer margin and near inner distal end, some hairs along proximal half of inner margin; second segment as long as one-third of first one, with two claws on distal end and some

minute spinules along outer margin. *Leg 2* (Fig. 7-5): Coxa and basis as in the adult. Exopodite two-segmented, about 1.5 times as long as basal two segments combined; first segment with one outer spine; second one a little longer than first, with two outer spines; two long setae on distal end, outer one spiniform; two inner setae, proximal one shorter; each outer margin of two segments with some spinules. Endopodite two-segmented, distal end reaching about half of second exopodite-segment; first segment with one hairy inner seta and some spinules along outer margin; second one with one short spiniform seta near outer distal end; two terminal and one inner setae, each hairy; each middle and distal outer edge with some spinules. *Leg 3* (Fig. 7-6): Almost same as in leg 2 in the preceding stage, except for following characters; exopodite not remarkably tapering distally, and with a small pit at middle outer edge, indicated by an arrow; outer terminal seta of endopodite apparently hairy. *Leg 4* (Fig. 7-7): Same as in leg 3 in the preceding stage.

3.3. *The third copepodid stage.*

Body 0.48 mm in length, slighter in appearance than the first copepodid, eight-segmented, fourth free segment with a row of several long spinules on each ventrolateral surface, posterior three segments ornamented as in the preceding stage. *Rostrum* (Fig. 8-1) slightly produced distally, with more a pair of hairs additionally near middle edge as in the adult female.

Antennule (Fig. 8-1) seven-segmented, first segment with a transverse row of minute spinules; second one extremely elongated, more than 2.5 times as long as first. *Antenna* (Fig. 8-2) same as in the preceding stage. *Mandible* (Fig. 8-3), *maxilla* (Fig. 8-4) and *maxillipede* (Fig. 8-5) as shown in each figure.

Leg 1 (Fig. 8-6): All segmentations as in the preceding stage. Coxa transformed triangularly, with a row of some minute spinules along middle border between the segment and basis. Spinules along outer margin of first exopodite-segment apparently three-grouped as in the adult. Proximal part of second segment in each exo- and endopodite slightly thickened, especially in the latter prominent. *Leg 2* (Fig. 8-7): One outer spine and one slender inner seta added on second exopodite-segment. *Leg 3* (Fig. 8-8) almost same as in leg 2 of the preceding stage, but stronger in appearance. *Leg 4* (Fig. 8-9) almost same as in leg 3 of the preceding stage, but with a slight concavity instead of the pit on middle inner edge of exopodite. *Leg 5* (Fig. 8-10): Only slight protuberance with two slender setae, outer one bare and other sparsely spinulose.

3.4. *The fourth copepodid stage.*

In the present stage, both sexes are recognized in each other morphologically.

Female. Body 0.65 mm in length, nine-segmented; fifth and sixth free segments without any spinules; posterior two segments ornamented as in the preceding stage.

Antennule (Fig. 9-1) eight-segmented, third segment a little longer than

second, with an aesthetasc. *Antenna* (Fig. 9-2): Endopodite-segment with one long geniculate and two minute setae additionally on distal end as in the adult. *Maxillipede* (Fig. 9-3): Each seta increasing in length, to be nearly the same as in the adult.

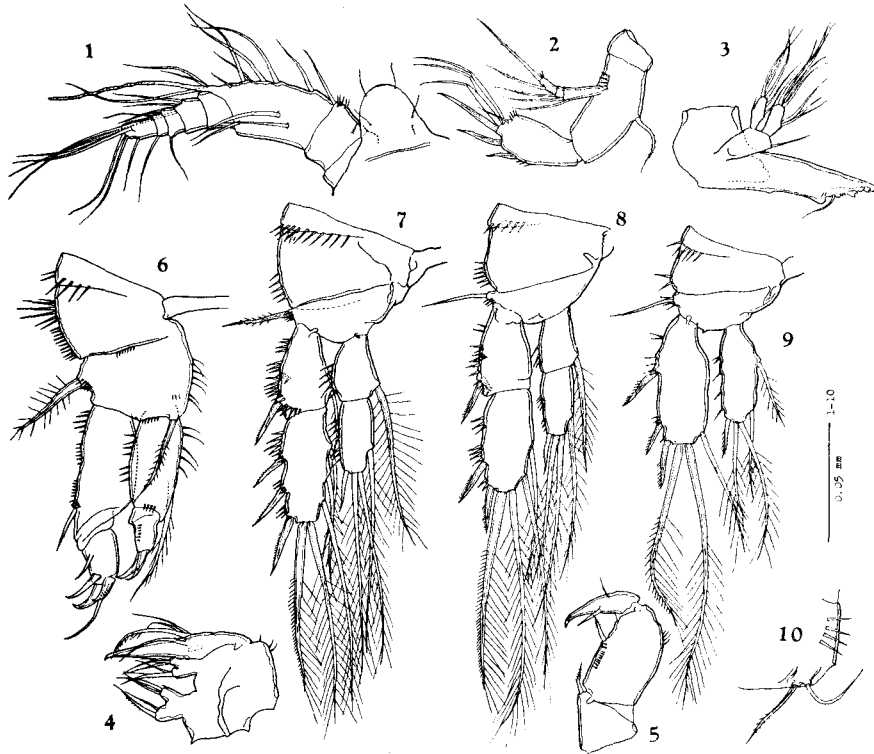


Fig. 8. The third copepodid. 1. Rostrum and antennul; 2. Antenna; 3. Mandible
4. Maxilla; 5. Maxillipede; 6. Leg 1; 7. Leg 2; 8. Leg 3; 9. Leg 4; 10. Leg 5.

Leg 1 (Fig. 9-4): Coxa, basis and first exopodite-segment with more spinules. Second exopodite-segment with one short seta additionally between the short bare seta and the spine on outer edge in the preceding stage. Second endopodite-segment with one hair-like seta additionally on distal edge. *Leg 2* (Fig. 9-5): Second endopodite-segment with one hairy seta additionally on a third of inner margin; one spine, instead of the spiniform seta in the preceding stage, on inner distal edge of the segment. *Leg 3* (Fig. 9-6): Exopodite with one short hairy inner seta on each distal edge of first segment and a third of second one; one spine added on a third of outer edge of second. Endopodite; second segment a little longer than first one, with one hairy seta additionally on a third of inner edge. *Leg 4*

(Fig. 9-7) almost same as in leg 2 in the preceding stage, but spinules on all outer margins only sparsely. *Leg 5* (Fig. 9-8): Border between basal segment and exopodite indistinct. Basoendopodite with one bare outer seta on a small protuberance accompanied with some spinules; three setae, minutely hairy and middle one longest, on inner expansion which produced slightly. Exopodite about half as long as greatest width, with five setae, all minutely hairy, outermost one accompanied with some minute spinules near base.

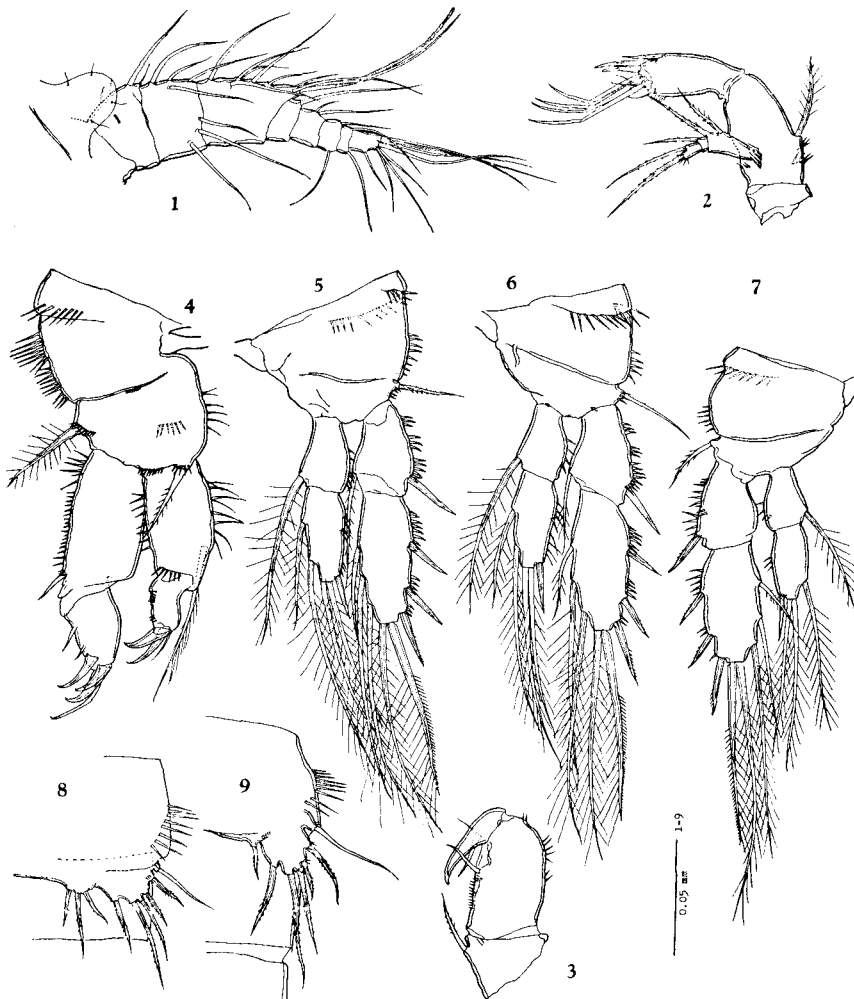


Fig. 9. The fourth copepodid. (♀) 1. Rostrum and antennule; 2. Antenna; 3. Maxillipede; 4. Leg 1; 5. Leg 2; 6. Leg 3; 7. Leg 4; 8. Leg 5; (♂) 9. Leg 5.

Male. Segmentation and ornamentation of body same as in female. Principal terminal seta of furcal ramus a little longer than in female. *Leg 5* (Fig. 9-9) almost same as in adult in appearance, border between two segments indistinct, but inner part apparent and with some minute spinules along it. Basal common plate (fused basoendopodite) not prominent, with one long bare outer and one short hairy inner setae, each on a small protuberance. Exopodite with five hairy setae ornamented as in the adult.

3.5. *The fifth copepodid stage.*

In the stage, the structure of all appendages the segmentation, spinal and setal number or situation, is constructed as in the adult except for the leg 6 in both sexes which is differentiated in the following stage. Further, the secondary sexual dimorphism is apparently recognized in the structure of antennule, leg 2 and principal terminal seta of furca.

Female. Body 0.71 mm in length, 10-segmented; each fifth and sixth free segment with some spinules ventro-laterally, seventh one bare. Rostrum (Fig. 10-1) more produced apically. Anal operculum reduced relatively.

Antennule (Fig. 10-1) nine-segmented; first segment with more spinules on anterior edge, second one almost same as long as third one; fourth one shorter than third one, furnished with one strong aesthetasc. *Antenna* (Fig. 10-2) as in the preceding stage, but the seta on anterior edge of allobasis relatively reduced in length. *Maxillipede* (Fig. 10-3) as in the adult.

Leg 1 (Fig. 10-4) almost same as in the adult except for less spinules equipped along each margin than its in the adult. *Leg 2* (Fig. 10-5) and *leg 3*. All segments more stumpy in appearance than in the adult. All spines thickset. *Leg 4* (Fig. 10-6): Second endopodite-segment without seta as in the adult. The comments above mentioned in the preceding two legs are also applicable in the leg. *Leg 5* (Fig. 10-7): Each basoendopodite forming a common plate. Inner expansion more prominent than in the preceding stage, with five setae, relatively short. Exopodite distinctly separate from basoendopodite, almost as long as width, innermost seta thickset.

Male. Body 0.72 mm in length, cephalothorax slighter in appearance than in female. Rostrum with four hairs as in the female. Principal terminal seta of furca a little longer than in female.

Antennule (Fig. 11-1) eight-segmented as in the preceding stage, but furnished with more setae and remarkably enlarged. *Antenna* with the seta on the anterior edge of allobasis as in the female.

Leg 2 (Fig. 11-2): Inner edge of second endopodite-segment produced into a spiniform process as in the adult, but shorter and thickset. Third endopodite-segment not extremely reduced. *Leg 5* (Fig. 11-3): Fused basoendopodite forming a long common plate. Exopodite separated from the basal segment; innermost seta thickset.

3.6. *Discussion.* According to the copepodid development described, some new knowledge concerning with the metamorphosis is proposed. The structure of the rostrum, together with the sensory hairs, is the same as in both sexes through all five copepodid stages, and the difference in the adult seems to be brought to completion in the final molt because of degeneration in the male. Such structural degeneration in the final molt seems to be also in the antenna. In the antennular segments, only the second and third segments in the first copepodid stage participate

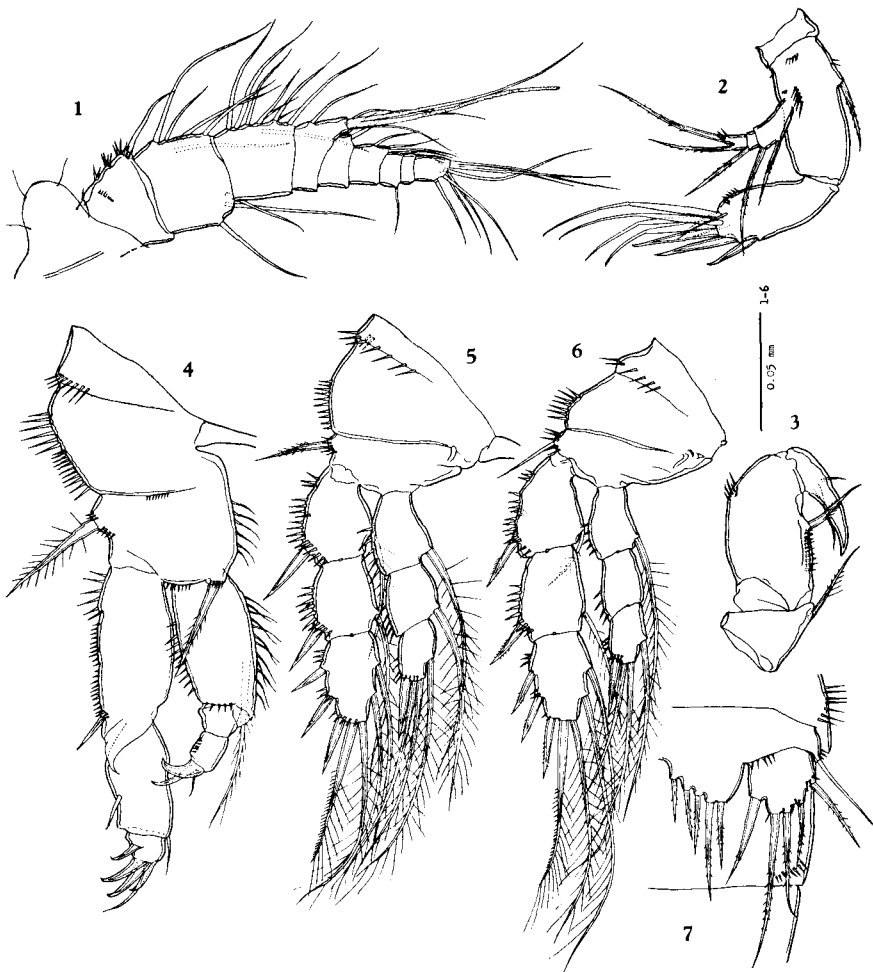


Fig. 10. The fifth copepodid. (♀). 1. Rostrum and antennule; 2. Antenna; 3. Maxillipede; 4. Leg 1; 5. Leg 2; 6. Leg 4; 7. Leg 5.

in the increasing of number of the segment. The manner of such increasing of segment is not mere distal addition of segments, but it is carried out by several successive extentions and subdivisions in certain segments. The second segment and the third one in the first copepodid stage become three and two segments subdivided respectively, in the fifth copepodid female. The manner is schematically shown in Fig. 12. Certain structures in the first segment and apical three ones in the first copepodid stage are maintained through all successive stages without

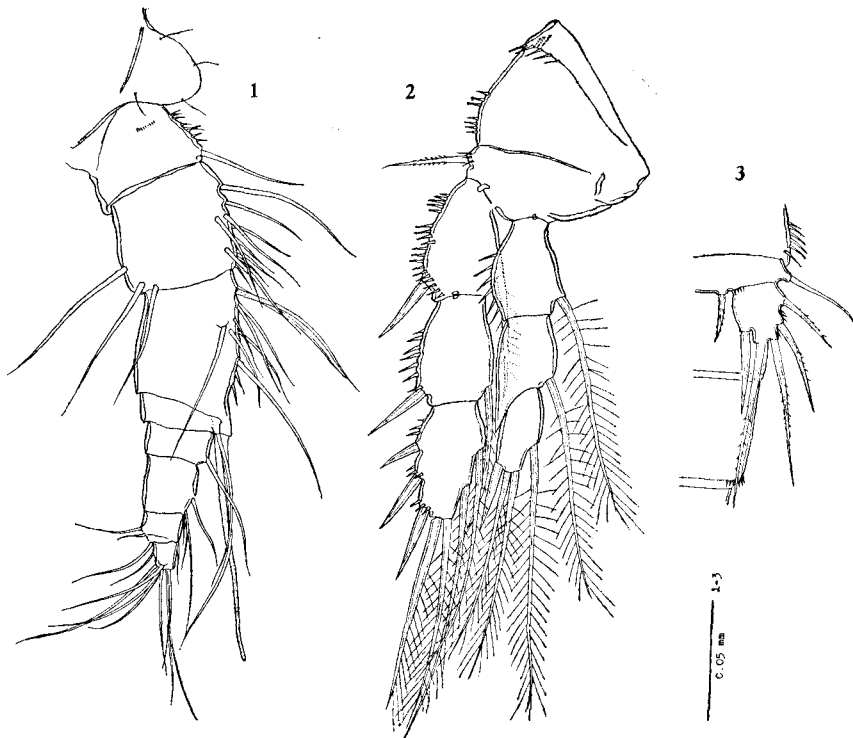


Fig. 11. The fifth copepodid. (♂) 1. Rostrum and antennule; 2. Leg 2; 3. Leg 5.

any remarkable changes, namely the seta of the first segment and the trifurcate seta of the last one. The antennular segmentation in the fifth copepodid male coincides to that in the fourth copepodid. Further, the leg 5 in the male is almost completed in the fourth copepodid stage, and no remarkable change is occurred between the fourth and fifth stages as in the antennule.

In the abdomen and legs, it is occasionally observed that the situation of next occurring subdivision is already indicated by some spinules or small pit, for example the spinular row on the last body segment in the first copepodid stage and

the small pit on the middle inner margin of exopodite of leg 3 in the second copepodid stage, etc. In the fifth copepodid stage, there are no any traces or buds of the leg 6 in both sexes, and the leg is appeared after the final molting as the primitive shape in the usual bud of legs.

On the other hand, the knowledge described concerning the manner in the structural differentiation, in other word metamorphosis, is not always able to fully put to practical use, at present. In contrast to the species investigated, only two examples within other species are proposed as follows. In *Diarthrodes cystoecus*, the antennular segmentation does not change through three successive stages from the third to the fifth (Fahrenbach, 1962). Further, in *Sacodiscus ovalis*, such seg-

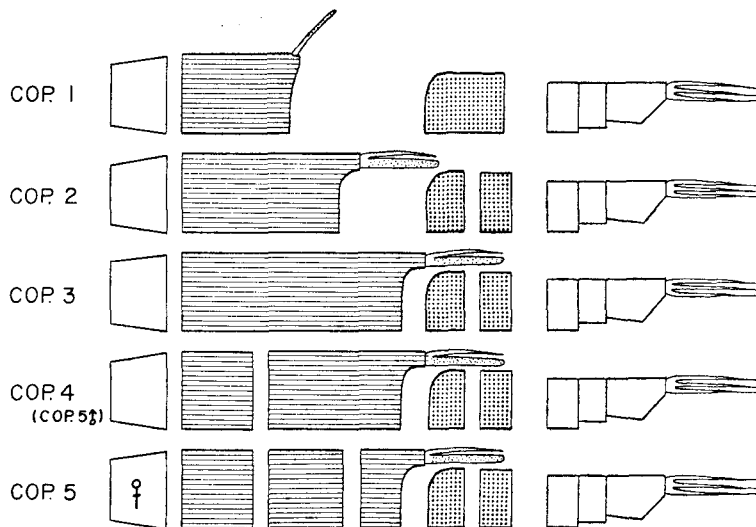


Fig. 12. Differentiation of antennule through the copepodid stages in schema.

mentation is remarkably increased in number, from four in the first stage to seven in the succeeding one, after the first molting (Humus, 1960). Such difference in the metamorphosis as shown within three species including the present one, is probably very useful for considering their phylogenical problems.

4. Abnormalities and variations.

4.1. *Abnormalities in the external structures.* Takeda (1949) reported some structural abnormalities including intersexes in *T. japonicus* and also indicated a possibility that some of which were inheritable. In the present, only four instances of the abnormality are proposed.

The first example. An adult male cultured in laboratory (4-X-'68), produced

by a female collected from Oshoro. The first exopodite-segment of leg 2, one of a pair, was furnished with two inner setae instead of one.

The second example. An ovigerous female collected from Rishiri Island (7-VIII-'68). The setal duplication as described above occurred in both rami symmetrically.

The third example. An adult female collected from Oshoro (18-XII-'69). Body (Pl. VIII, Fig. 9) 0.74 mm in length, very stumpy in appearance. Eye not present in the normal situation, but on a ventral thickset protuberance between rostrum and labrum. The setal duplication was observed on the first exopodite-segment of leg 2 (Pl. VIII, Fig. 8) and, moreover, of leg 3 in each ramus. Basoendopodite of leg 5, in one of a pair, furnished with only four setae instead of five.

The fourth example. A nauplius of the fourth stage (27-III-'70) cultured in the laboratory, originally collected from Otaru. Mandible, in one of a pair, was only coxa with a seta. Maxillula was furnished with only a thick seta, bifurcate apically, instead of two setae.

According to the second example described, it seems to show no indications of correlation between such setal abnormality and certain wrong effect in the ability of reproduction, at least in the female.

4.2. *Colour variation.* The colour of living animals was observed in daylight under a binocular microscope. Colour names were cited from the colour dictionary by Wada et al. (1951).

Naturally, eggs layed are dark green in colour and gradually change to light reddish orange within a few days. On the other hand, it was sometimes observed that the females in the laboratory condition layed pale greenish blue eggs or colourless ones. The eggs seem to correspond with the "blue lethal" and "white" eggs, respectively, described by Igarashi (1964). The females producing such blue eggs were frequently appeared in the cultures in longer artificial condition, but not in the natural one and in the culture containing with an adequate amount of sea weeds, for example *Enteromorpha prolifera*.

The colour of adult body is highly variable, probably connecting with some internal or external conditions, age, foods, presence of eggs in the oviduct, season, etc. The variation is present even in one population. Generally the colours are light reddish orange, yellow orange and light brown in summer, and yellowish red in winter. Younger copepodids are seemingly lighter than adults. Lighter coloured, extremely colourless even in adults, animals are occasionally appeared in the artificial, probably inadequate, cultures. Certainly in the cases, the females produced the pale greenish blue eggs or the white ones described. Hence such colour-lightness in body as well as the eggs in the artificial conditions is probably caused by insufficiency or lack of certain pigments to be produced or deposited in the body. And at least in the eggs, it might be correlated with certain substance contained in the sea weed.

4.3. *Size variation.* The body length is highly variable corresponding with the

nutrition or other environmental factors. The individuals grew in the laboratory, seemingly inadequate condition, were occasionally dwarfed extremely. The present problem will be discussed minutely after an experimental study in future.

Remarks

It was already indicated that the actual copulation probably occurred between the fresh sixth copepodid female and the fully grown adult male. The complete clarification of such problem remains with further study.

The environmental condition in the habitat of Oshoro is not so different from that of Shirahama, at least concerning the annual fluctuation of temperature, but in the lower one particularly during the winter. Remarkable increase of salinity was recorded in winter.

Through all developmental stages, including both naupliar and copepodid ones, some structures seemed not only generating but also degenerating. The degeneration that appeared in the antenna and the mandible in the naupliar stages is very striking. Further, the differentiation of the male structures consists of some degenerative characters occurring particularly in the final molt.

The legs appear successively from anterior one to posterior in each molt. The leg 5 and leg 6 in both sexes, however, are exceptional. The leg 5 is only slightly changed in the structure in the fourth and the fifth molts. While the leg 6 must appear in the fourth copepodid stage supposing that it differentiates in the same order as in other legs, it does not appear in the stage, neither in the next one, but at last in the final stage. Such fact concerning with the leg 6 was not described in *T. fulvus* investigated by Fraser (1936a).

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Appendix

After the completion of the manuscript, a paper [Koga, F. 1970. On the life history of *Tigriopus japonicus* Mori (Copepoda). Jour. Oceanogr. Soc. Japan **26**: 11-21. (In Japanese)] has come into the author's notice. Although the paper deals with almost the same subject as the present study, particularly in the metamorphosis, there are some discrepancies between his result and the present, for example, the antennal structure in the last nauplius stage, the leg 3 in the first copepodid stage, the sexual dimorphism in earlier copepodid stages, etc. In these respects, a more minute re-examination is expected in the near future.

Explanation of Plates

Plate VII

Fig. 1. Kabutoiwa, Oshoro. Nearly 20 pools are scattered on the surface. The situation of the rock pool investigated (P-1) is indicated by an arrow. The pool is located at about 6.5 m above high-tide mark.

Fig. 2. P-1 as well as all other pools is entirely covered with ice and snow in mid winter (Dec., '69).

Fig. 3. A small rock pool which is located relatively far from the sea shore about 50 m. Kutsugata, Rishiri Isl. Such porous rocks are abundant along the coast.

Fig. 4. A rock pool near high-tide mark. Kutsugata. Such open and flat pool may be easily affected by even slight change of environmental condition, solar irradiation, rain, wave, etc.

Fig. 5. Pairing. Adult male grasps with his antennules both lateral hind edges of cephalothoracic carapace of his partner, the fourth copepodid female.

Plate VIII

Figs. 1 and 2. Unusual pairing. An adult male (lower one) grasps the thorax of the upper male with his antennules and behaves himself as in the pairing and copulation.

Fig. 3. Rostrum with two pairs of sensory hairs, indicated by arrows, in the female from Oshoro.

Fig. 4. Rostrum with a pair of sensory hairs in the male.

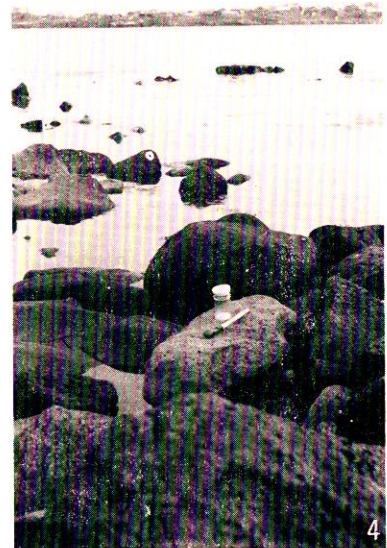
Fig. 5. Trifurcate seta on the apical segment of antennule in the female.

Fig. 6. Spinules and hairs along both edges of a principal furcal seta.

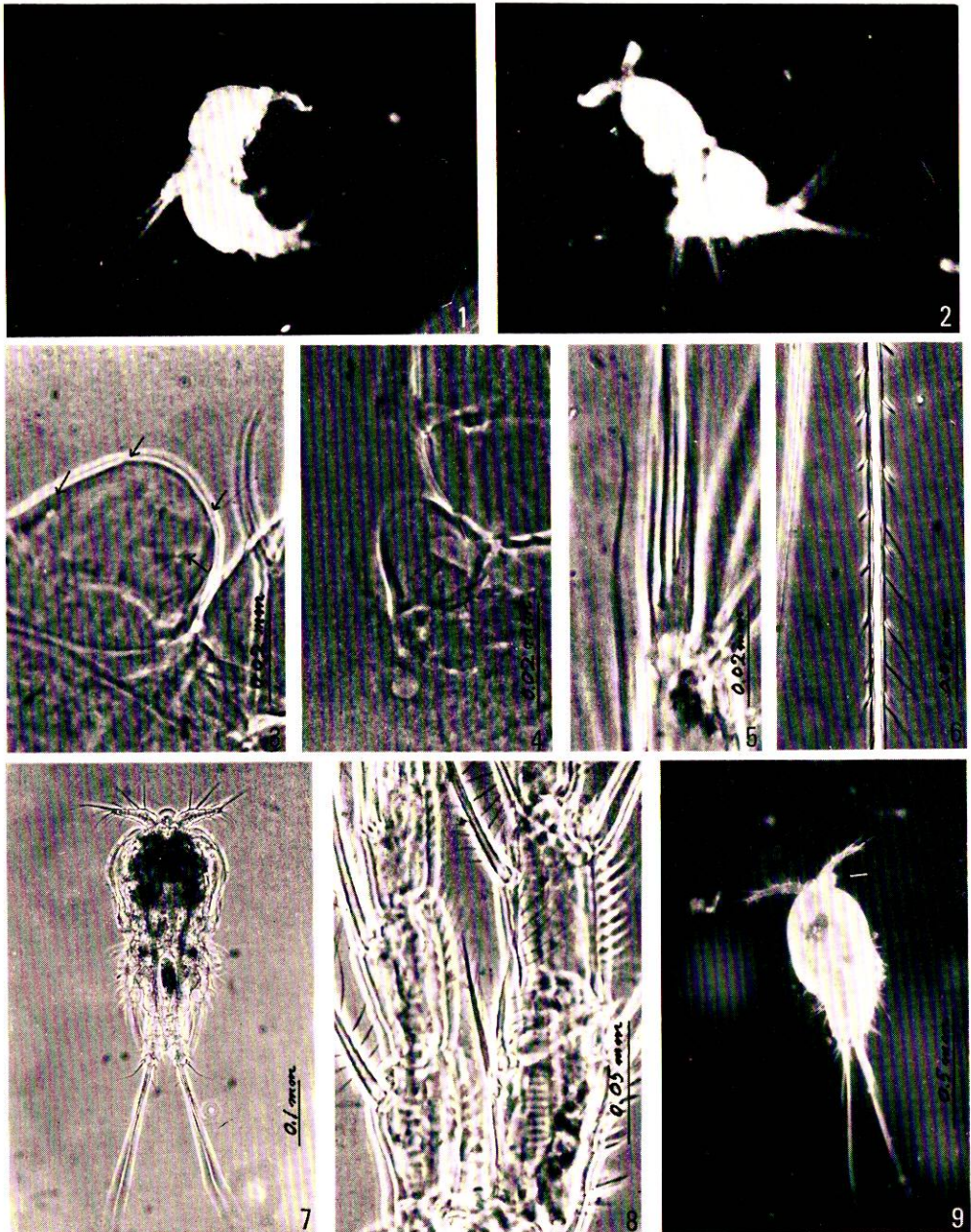
Fig. 7. The first copepodid from Hakodate.

Fig. 8. Setal duplication of the first exopodite-segment of leg 2 in the female described below.

Fig. 9. Abnormal female collected from Oshoro. The nauplius eye is produced ventrally, as indicated by an arrow.



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