ON THE DEVELOPMENT OF PARASITIC COPEPODA I. *SARCOTACES PACIFICUS* KOMAI (CYCLOPOIDA : PHILICHTHYIDAE)[1]

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With Text-figures 1–25

The parasitic copepods must have adapted themselves to respective parasitic mode of life, exhibiting deformation and degeneration in different degrees. Especially reduction of appendages, chiefly of the mouth-parts, has taken place in the course of evolution, and this seems to be responsible for excessive confusion in explaining the interrelationships between the various groups of parasitic copepods. It is, however, usually suggested that the earlier larval stages may retain more phylogenetic, essential features of the group than adult forms. Therefore, in addition to examinations of adult morphology, the ontogenetic studies are very desirable in order to elucidate the natural relations between the different groups of parasitic copeopds and to speculate about their course of evolution. So far a considerable number of works have been made on the developmental stages of parasitic copepods inclusive of fragmentary descriptions of larvae. There remain still, however, many groups, in which any larval stages are unknown. For these reasons, the present author is going to describe the larvae, especially the free-living stages, of different groups of parasitic copepods, dealing with in the present paper those of *Sarcotaces pacificus* Komai.

Sarcotaces is a genus of the most deformed parasitic copepods, which lives in the gall produced underneath the skin of fishes. The female is maggot-shaped and considerably large, attaining 70 mm in body length at the maximum in *S. arcticus*. On the contrary, the male is incomparably smaller than the female and is living in the narrow space between the female and the wall of the gall. Sometimes numerous eggs or the first nauplii are found in the space. Thus, only the first nauplius stage has been illustrated in *S. arcticus* by Hjort (1895) and Kuitunen-Ekbaum (1949), in *S. pacificus* by Komai (1924), and in *Ichthyotaces pteroisicola*, another genus closely related to *Sarcotaces*, by Shiino (1932), but further development of these nauplii has never been seen in the gall nor described so far. It seems that the first nauplii probably develop

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further after they have escaped from the gall to the sea through a pore, the only opening of the gall to the exterior.

Material and Methods

The larvae used for this study were reared at the Seto Marine Biological Laboratory in November 1971. The frogfish, *Antennarius tridens* (Temminck & Schlegel), parasitized with *Sarcotaces pacificus,* were found in the laboratory aquarium. They were collected from Tanabe Bay, to which the laboratory faces. The gall containing the parasite was carefully incised to release the eggs or the first nauplii into a glass finger-bowl of sea water. Those were then washed in fresh sea water to remove host-tissues to prevent bacterial infection. Larvae were reared in the running sea water of the laboratory filtered through cotton wool, the bowl being placed in a water bath to keep the water temperature at 20–22°C. Neither aeration nor circulation of water was applied, but the water was renewed two or three times a day by using pipette. As the larvae contain a large amount of yolk and seem to be lecitotrophoic, no consideration was needed as to the food supply. Metamorphoses of the larvae were recognized at sudden appearances of cuticular moults on the bottom of the bowl. Sufficient numbers of larvae and castoff exoskeletons of respective stages were fixed in a 10% solution of formalin in sea water and then stored in 70% ethyl alcohol. The preserved specimens were then examined in lactic acid by using the wooden slide of Humes & Gooding. The castoff exoskeletons were observed for detailed morphology, especially of appendages. Drawings were made by using Abbe's drawing apparatus.

Development

A 13 mm long female was found together with about 10000 eggs or nauplii in the gall. The eggs are ovoid, approximately 0.14 mm long and 0.11 mm wide, and colored yellowish due to a large amount of yolk contained within. When hatching draws near, they become slightly transparent, but the color remains unchanged as no pigment spots appear. The hatching rate of this brood was low under laboratory conditions and the first nauplii failed to develop further; success of hatching seemed to depend mainly upon whether the embryo had fully developed inside the egg membrane or not. Further developmental stages were obtained by rearing the first nauplii released from another gall. Though not actively, the first nauplii was able to swim, and began to moult shortly after released into the bowl. They passed through five nauplius stages in all within 45 hours and then grew to the first copepodid stage. The rate of the first nauplius survived through the stages to the first copepodid was high. The nauplii notably reacted to an intermittent lighting and were attracted by the directed lighting, but the continuous illumination did not cause any reaction of nauplii.

The first copepodids were capable of active swimming, but were already not reactive to the light. They still retained a considerable amount of yolk and many of them survived more than a week unfed, without showing any morphological changes, but only the yolk mass diminished gradually. Thus, the 9 day old copepodids were experimented with to see if they were ready to infest the host fish. An 8 cm long individual of *Antennarius tridens* was kept for 20 minutes in a bowl of 300 ml, in which 100 copepodids had been released in advance. Then, after the fish was removed, only some ten copepodids were recollected from the bowl. This seems to show that the first copeopdid is the infective stage in *Sarcotaces*, too. Unfortuntaely further metamorphoses of copepodids were not observable.

Description of Developmental Stages

First nauplius stage (Figs. 1, 6, 11, 16):

The body length is 0.16 mm and the width 0.10 mm on an average of 24 measurements. Body is plump and ovoid. Labrum is not prominent. Furcal armature on the caudal end consists of a single pair of setae. Through the cuticle on the ventral side are visible two indistinct segment-like structures which are referable to the pairs of the first and second legs of the first copepodid stage respectively.

First antenna (fig. 6) consists of a short basal segment not distinctly separated from the body and an elongate distal segment carrying a median and two apical setae. A short aesthete attached to the base of the longer apical seta plumosed. The surface of distal segment furnished with several short rows of spinules. Second antenna (fig. 11) biramous. Protopodite two-segmented, without any armature. Expopodite five-segmented; first segment as long as endopodite, but without definite joint to protopodite; four distal segments short, each of five segments with a plumose seta at the inner distal corner, but the terminal segment with an additional short seta on the outer distal margin. Ednopodite one-segmented, with a short seta at the middle on the inner side and two plumose setae on the tip. Mandible (fig. 16) biramous. Protopodite two-segmented, with no armature. Exopodite four-segmented, diminishing the length distally and each with a plumose seta at the inner distal corner. Endopodite two-segmented, first segment one third as long as second and furnished with only a short seta on the distal inner margin, second segment with two plumose setae at the tip in addition to a simple seta on the distal inner margin.

Second nauplius stage (Figs. 2, 7, 12, 17):

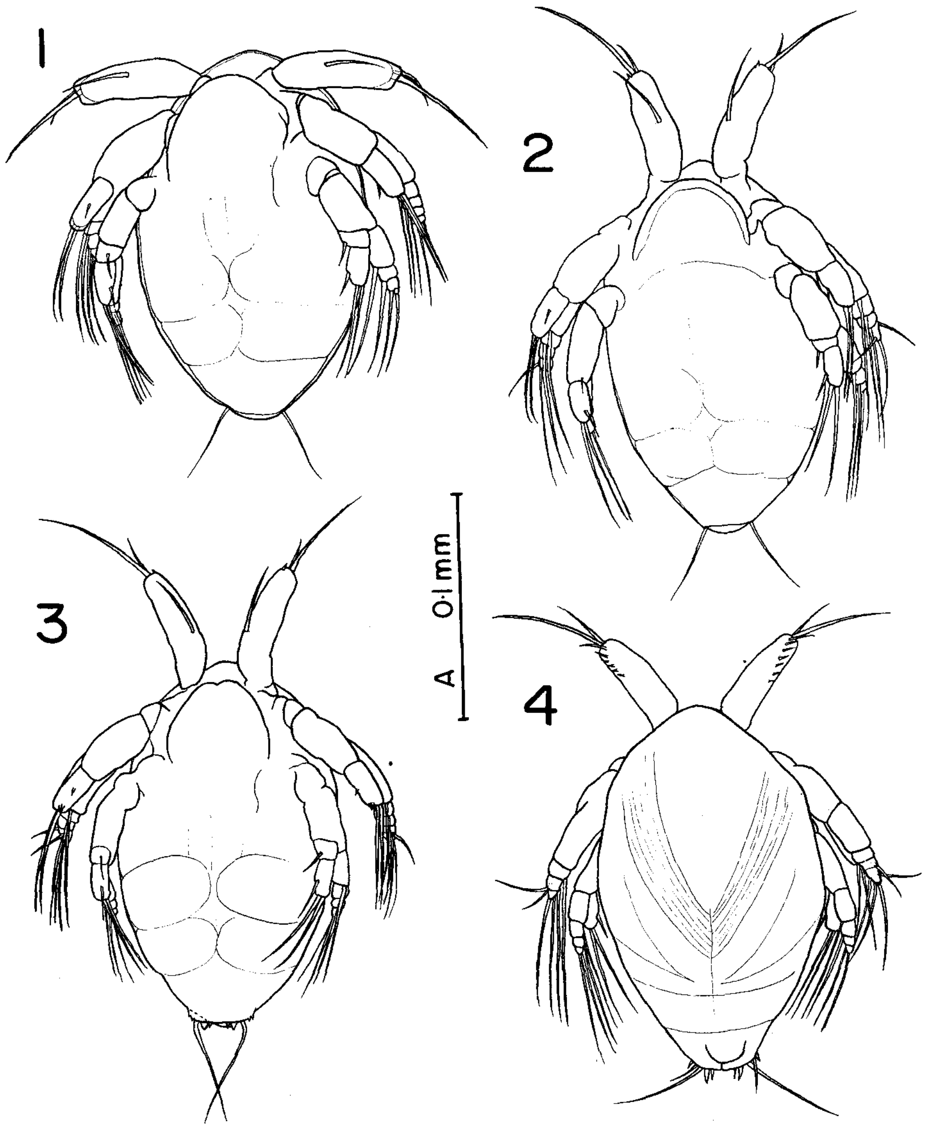
Length 0.16 mm and width 0.10 mm on an average of 32 measurements. This stage is rather difficult to distinguish, as the morphological differences between this and the preceding stages are so exact.

Labrum, mandible and caudal armature as in the first nauplius. First antenna (fig. 7) with an additional minute setule at the antero-distal corner of second segment. Second antenna (fig. 12) altered, but slightly; the joint between the distal two segments of exopodite has disappeared, a short seta on terminal segment in first nauplius moved in this somewhat proximally on the outer side; this seta and penultimate plumose seta on the inner side are issued perpendicularly to the axis of ramus; on endopodite a short medial seta reduced its length.

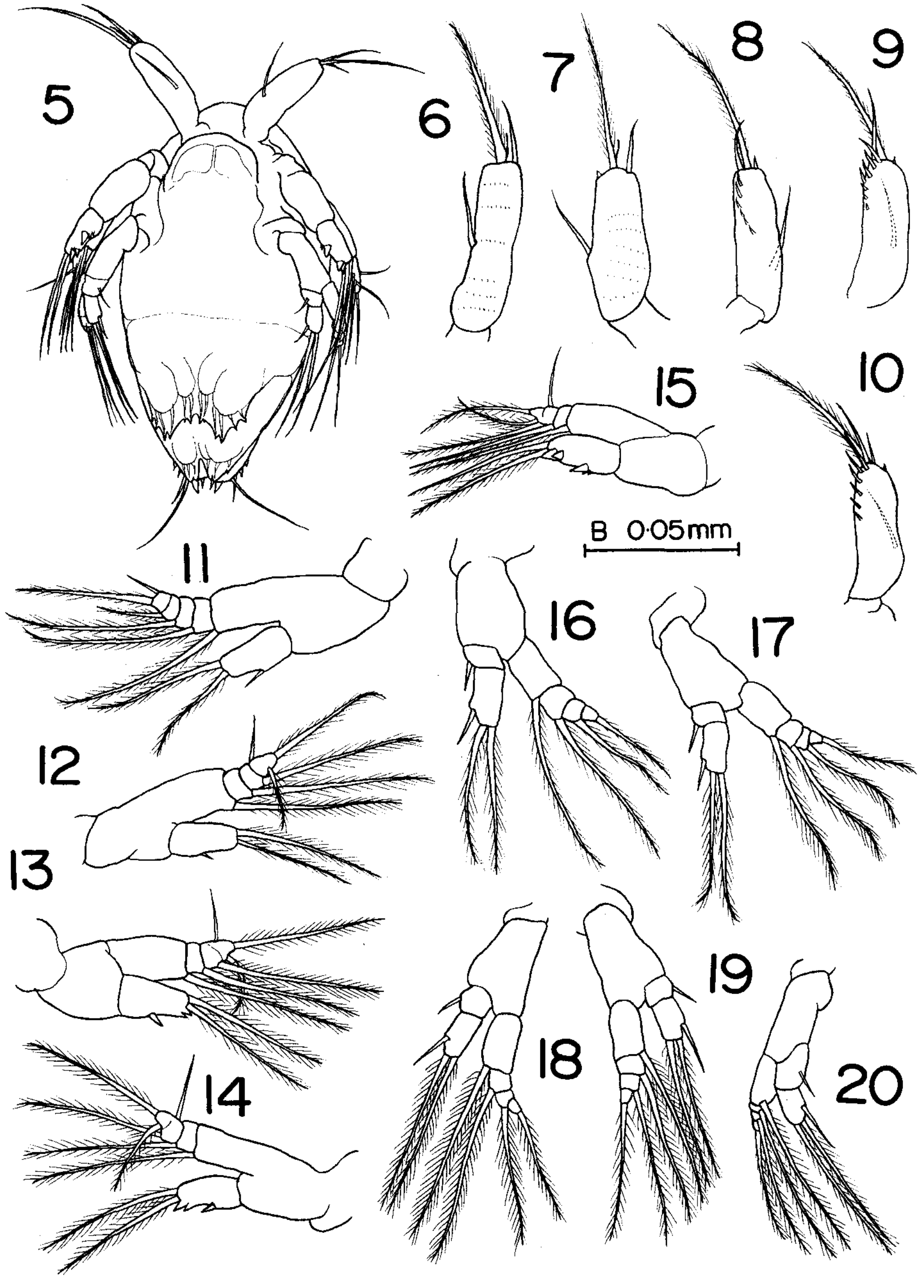
Third nauplius stage (Figs. 3, 8, 13, 18):

Length 0.16 mm and width 0.09 mm on an average of 32 measurements. This stage can be easily distinguished from the preceding stages by eight setules newly appeared on the caudal end in addition to a pair of seta.

Body still ovoid, thoguh slightly narrower. First antenna (fig. 8) furnished



Figs. 1–4. Nauplius stages of *Sarcotaces pacificus* Komai.
1. The first nauplius, ventral view. 2. The second nauplius, ventral view. 3. The third nauplius, ventral view. 4. The forth nauplius, dorsal view. Scale A applicable to all figures.



Figs. 5–20. Nauplius stages of *Sarcotaces pacificus* Komai.
5. The fifth nauplius, ventral view. 6–10. First antennae of the 1st-5th nauplii, dorsal view. 11–15. Second antennae of the 1st-5th nauplii, ventral view. 16–20. Mandibles of the 1st-5th nauplii, ventral view. Scale A for fig. 5 and Scale B for figs. 6–20.

with about six setules arranged in a longitudinal row on the dorsal side of the distal half of second segment, on which several transverse rows of fine spinules have completely disappeared. Second antenna (fig. 13) changed, but slightly; distal three segments of exopodite fused together into one, and two more setules found at the inner distal corner of endopodite. Mandible as in preceding stages.

Fourth nauplius stage (Figs. 4, 9, 14, 19):

Length 0.16 mm and width 0.09 mm on an average of 45 measurements. Posterior portion of body has become slightly narrower. Three pairs of appendages almost similar to those of the preceding stage, but the setules on the caudal end are apparently more developed and this makes it possible to distinguish this stage.

Fifth nauplius stage (Figs. 5, 10, 15, 20):

Length 0.16 mm and width 0.09 mm on an average of 45 measurements. The caudal part of body is somewhat prolonged and the posterior end is concaved medially, two more setules in caudal armature. Two pairs of rudimentary legs emerged on the posterior ventral surface, and these are the most noticeable sign for this stage. Labrum as in the fourth stage. Mouth opening and alimentary canal are still unobservable. Any signs of first and second maxillae are not yet recognized.

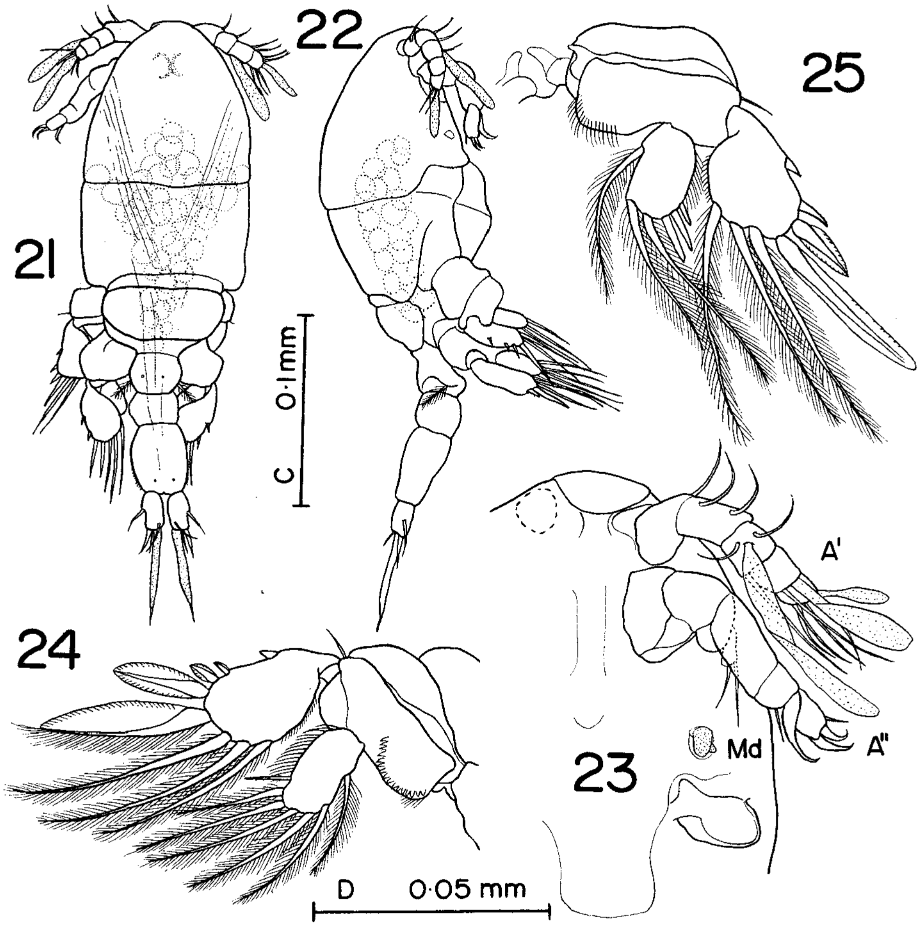
First antenna and mandible as in the preceding stage. In second antenna (fig. 15), the three setules on the inner margin of endopodite a little stouter and with two additional fine setules newly appeared at the base of the most proximal one of the three. Two lamellar sacs, with serrated margin and enveloping two pairs of rudimentary copepodid legs, are projected out posteriorly from the ventral surface of the posterior part of body.

First copepodid stage (Figs. 21–25):

Body length (excluding caudal rami) 0.24 mm, carapace length 0.13 mm, and body width 0.08 mm on an average of 45 measurements. Body consists of cephalothorax (cephalosome) and four free segments, metasome, two-segmented urosome and anal somite. Metasome is the second pedigerous segment and the first urosomal segment bears rudimentary third legs each represented by a plumose seta, anal somite carries caudal rami. Cephalothorax broad and thick, divided distinctly into two parts; the anterior part carries two pairs of antennae, a pair of vestigial mandibles and a pair of processes of unknown nature, while the posterior part is the first pedigerous segment. Apparent mouth parts and mouth opening are not yet defined. Vestigial mandible has been confirmed on late fifth nauplii as a small mass of gathered internal tissue of the appendage, which is situated at the base of the appendage.

First antenna uniramous and 5-segmented, with about a dozen setae and three lamellate aesthetes. Second antenna, functional as a prehensile organ, biramous, and consisting of 2-segmented protopodite, vestigial exopodite and 3-segmented endopodite. Exopodite degenerated to a small process tipped with two feeble setae. Endopodite with two claws and a seta at the tip of terminal segment, and a claw and a seta on penultimate segment.

Two pairs of swimming legs biramous and almost the same in size and structure,



Figs. 21–25. The first copepodid stage of *Sarcotaces pacificus* Komai.
21. Dorsal view of the body. 22. Lateral view of the same. 23. Left half of the anterior part of cephalosome, ventral side; A'-the first antenna, A"-the second antenna, Md-vestigial mandible. 24. The first leg, ventral view. 25. The second leg, ventral view. Scale C for figs. 21–22 and Scale D for figs. 23–25.

each consisting of 2-segmented protopodite and one-segmented rami. In first leg, protopodite armed with a seta on the outer side and a row of fine teeth on the inner side; exopodite with eight setae, four spatulate ones on the outer side, three plumose ones on the inner side and the middle largest spatulate one hairy along the inner margin; and endopodite with seven plumose setae. In second leg, exopodite with seven setae, four spatulate ones on the outer side and three plumose ones on the inner side; endopodite with six setae, three spine-like ones on the outer side and three plumose ones on the inner side.

Caudal ramus carries five setae, three of which tipped with a sharply pointed fine blade and the inner-most and longest of them lamellate.

Discussion

Many have been discussed on the systematic position of *Sarcotaces*, because of its peculiar features (Olsson 1872, Hjort 1895, Calman 1909, Komai 1924, Shiino 1932, Heegaard 1947b). Recently Delamare-Deboutteville (1962) included *Sarcotaces* and *Ichthyotaces*, another gall-forming genus, in the family Philichthyidae chiefly on the similarity in the male morphologyl. This family had been established to include all parasites found in the mucous canals or sinuses of various fishes and composed of genera *Philichthys*, *Sphaerifer*, *Leposphilus*, *Colobomatus* and *Lernaeascus*. Delamare-Deboutteville did not, however, refer to the order of Copepoda, to which the Philichthyidae belongs. Yamaguti (1963), without meeting with Delamare-Deboutteville's paper, erected 'Sarcotacidea' and 'Philichthyidea' as new orders, placing them separately at the end of Copepoda and between 'Caligidea' and 'Lerneopoidea' in his work, "Parasitic Copepoda and Branchiura of Fishes."

The morphology of free-living larvae of *Sarcotaces* described in this paper clearly suggests that the genus should belong to the order Cyclopoida. A close relation of *Sarcotaces* to the Philichthyidae is apparently confirmed by the fact that the free-living stages of *Sarcotaces* are quite similar to those of *Colobomatus*, although the first copepodid of the former lacks apparent mouth-parts completely, whereas the mouth-parts of the type of poecilostome cyclopoids are found in the latter (this will be shown in a future paper). And this makes the present author accept Delamare-Deboutteville's classification.

Further, the first copepodid of *Sarcotaces* and also that of *Colobomatus* resemble that of the Chondracanthidae (Heegaard 1947a, pp. 159–162, Figs. 116–117), and then a close relation between the Philichthyidae and the Chondracanthidae seems to be clear, as has been suggested already by Heegaard (1947b), who states that the male of *Ichthyotaces* very much resembles that of *Philichthys* and also in some extent that of the Chondracanthidae.

As described above, the nauplius of *Sarcotaces* is nonfeeding and the body structure is degenerative. In spite of the extremely degenerated morphology of adult forms, the number of nauplius stages is not so much reduced as compared with that of the free-living cyclopoids mostly with six stages. On the other hand, the adult forms are not so much degenerative in the Chondracanthidae as in the Philichthyidae, but there are only three nauplius stages (unpublished data). If it is accepted that the Philichthyidae and the Chondracanthidae are closely related to each other as mentioned above and both have been derived from a common ancestry, how can the difference between them in the number of nauplius stages be explained ? There may be two ways. 1) The number of nauplius stages can depend simply upon the difference in adult habitats. In the Philichthyidae, the first nauplii are protected in the canal or the gall formed on the host body so that they can be free from any stress which will induce some reduction of the nauplius stages, whereas the nauplii of the Chondracanthidae released directly into the sea are subject to many kinds of oppression which will urge them to metamorphose. After all, the difference can be of less phylogenetic significance. 2) The simplification of the nauplius structure and the reduction of nauplius stages might have occurred compensatingly along the course of evolution of parasitic copepods and might be of a phylogenetic significance, not affected by any habitat conditions. If this idea is acceptable, then the Chondracanthidae having three nauplius stages should be placed in more advanced phylogenetic rank than the Philichthyidae which has five stages. The discussion on this problem will be given when the free-living stages of the Chondracanthidae are described in detail in a future paper.

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Summary

1. The free-living larval stages of *Sarcotaces pacificus* Komai are described and figured on the specimens reared under the laboratory conditions.

2. About ten thousand eggs or the first nauplius larvae may be found together with a couple of parasitic copepods in a single gall. Probably, the hatching of eggs takes place inside the gall, but further development does outside it after the napuplii have escaped into the sea through a pore. There are noted five nauplius stages to the first copepodid stage within 45 hours under laboratory conditions at 20–22°C.

3. The nauplii have three appendages typical to usual nauplii, but the appendages are devoid of feeding apparatus, gnathobase and masticatory setae. They are non-feeding throughout all the stages, and no growth of the body is gained. All appendages become gradually simplified and no rudiments of post-mandibular mouth-parts are recognized. The rudimentary first and second legs appear at the fifth stage.

4. The first copepodid is the infective stage. Most of them survive more than a week on the yolk contained in them. The apparent mouth-parts are completely missing. The first pedigerous segment is separated by a distinct suture from the cephalothorax which is provided with only two pairs of antennae.

5. The systematic position of *Sarcotaces* is discussed briefly. The morphology of free-living larvae clearly shows that *Sarcotaces* belongs to Cyclopoida and that the genus is to be included in the family Philichthyidae. Further, a close relation between the Philichthyidae and the Chondracanthidae is ovbious. The difference between these two families in the number of nauplius stages, five in the Philichthyidae and three in

the Chondracanthidae, may depend upon the conditions of the adult habitat or upon the mode of parasitic life, or be referable to the phylogenetic feature.

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