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Title THE LIFE HISTORY OF NEOECHINORHYNCHUS RUTILI (MUELLER, 1780) AND ITS DEVELOPMENT IN THE INTERMEDIATE HOST (ACANTHOCEPHALA; NEOECHINORHYNCHIDAE)

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Abstract approved
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The fish of Suttle Lake, Oregon, have been found to harbor an acanthocephalan parasite, which lives attached to the mucosa of the intestine. Between July 1961 and January 1963, several hundred of these fish were examined and nearly every one was infected with this parasite, which was identified as Neochinorhynchus rutili (Mueller, 1780).

Since relatively little is known about the life cycle and post-embyonic development of N. rutili, it was decided to study these problems in the laboratory.

Of 267 ostracods (Cypria turneri) examined, 64 or 24 percent were found to harbor the cystacanth or juvenile stage. Some of these ostracods were fed to two small infection-free cutthroat trout. The first fish was fed five and the second was fed nine. Two weeks later one male acanthocephalan was found established in the

intestine of the first fish and four, including three females in the second.

It was possible to follow the development of the parasite from the emergent embryo to the infective cystacanth. Several infection-free ostracods from a local pond were infected by allowing them to feed on shelled embryos from the body cavity of an adult worm. The ostracods were then dissected periodically and the stages of development were studied and drawn.

The life cycle can be summarized in the following way. The shelled embryos are released by the adult worm into the intestinal lumen of the fish and they pass out with the feces. These "eggs" are ingested by ostracods (Cypria turneri). The embryo emerges as an acanthor and penetrates the wall of the gut into the hemocoel where it metamorphoses through acanthella to the cystacanth or juvenile stage in 48 to 57 days. This final stage is infective when eaten with the ostracod by the fish.

THE LIFE HISTORY OF *NEOECHINORHYNCHUS RUTILI* (MUELLER, 1780) AND ITS DEVELOPMENT IN THE INTERMEDIATE HOST (ACANTHOCEPHALA; NEOECHINORHYNCHIDAE)

by

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INTRODUCTION

Neoechinorhynchus rutili (Mueller, 1780), an acanthocephalan worm parasitizing the small intestine of fresh water fish, was redescribed adequately by Van Cleave in 1950 (25, p. 166-167). The synonyms which he listed are well substantiated by his discussions of the historical development of the species. They are as follows:

Echinorhynchus rutili Mueller, 1780
Neorhynchus rutili (Mueller, 1780)
Eorhynchus rutili (Mueller, 1780)
Echinorhynchus clavaeceps Zeder, 1800
Neorhynchus clavaeceps (Zeder, 1780)
Echinorhynchus tuberosus Zeder, 1803

In the same paper the distribution of Neoechinorhynchus rutili was shown to be continuous in fresh water fish throughout the northern Holarctic Region, including Sweden, Finland, Russia, Central Europe, Wisconsin, within the Arctic Circle of the Canadian Northwest Territories, off the coast of Alaska, and into Washington.

The adult worm is found in 14 families of fishes including Salmonidae, Thymallidae, Cyprinidae, Catastomidae, Cobitidae, Esocidae, Gadidae, Gasterosteidae, Centrarchidae, Percidae, Labridae, Gobiidae, Cottidae, and Zorarcidae (6, p. 39-45).

G. M. Vevers (1920) reported finding Neoechinorhychus clavaeceps (= N. rutili) in a turtle which had died in the London

Zoological Gardens, but later corrected the identification to Neoechinorhynchus emydis in a personal letter to Van Cleave (25, p. 169).

Van Cleave implied that occurrence of adults in frogs and turtles is probably due to accidental infections (25, p. 169).

In 1956 and 1957 Dyk made an ecological study of N. rutili and Crepidostomum farionis in the fish of the Tatran Lakes of Czechoslovakia (3, p. 33-42; 4, p. 333-351).

Life history studies on N. rutili have been sparse and incomplete. Robin (22, p. 777) found a worm in the leech Nephelis octoculata which was identified from his woodcut by Villot (25) as Echinorhynchus clavaeceps (= N. rutili). In 1884 Villot reported finding Echinorhynchus clavaeceps encysted in the adipose tissue of the larvae of Sialis niger (26). Finally in a research note Levander mentioned finding larvae in ostracods, but he neglected to record the genus or species (12).

The early embryology of Neoechinorhynchus rutili has been studied in detail by Meyer (15, p. 103-126). He traced the cleavage and cell lineage up to the development of the shelled acanthor, which is shed by the adult female and is infective to the intermediate host. No study has been made of the complete development in the intermediate host. There have been, however, a few developmental studies carried out on other species of Acanthocephala. The

scattered observations made prior to 1940 have been very well discussed by Ward (27, p. 327-347). A review of the recent literature reveals that the following studies have been made on the development in the intermediate host from the acanthor stage through the cystacanth:

Order Archiacanthocephala

Macracanthorhynchus hirudinaceus (Pallas), by Kaiser (10, pt. 2, p. 1-148), Meyer (17, p. 131-242), Kates (11).
Macracanthorhynchus ingens Meyer, by Moore (19, p. 387-399).
Mediorhynchus grandis Van Cleave, by Moore (21, p. 76-86).
Monilformes dubius Meyer, by Moore (20, p. 257-271).

Order Palaeacanthocephala

Leptorhynchoides thecatus (Linton), by DeGiusti (2, p. 437-460)
Polymorphus minutus (Goeze), by Hynes and Nicholas (9, p. 380-391)

Order Eoacanthocephala

Neoechinorhynchus cylindratus (Van Cleave), by Ward (27, p. 327-347)
Neoechinorhynchus emydis (Leidy), by Hopp (7, p. 284-299)

Moore (21, p. 84) pointed out the need for more information about the acanthor types and their subsequent development to aid in establishing phylogenetic relationships.

The present study was undertaken to determine experimentally the life cycle in local hosts and to make a descriptive study of the

development in the intermediate host from the ingestion of the sheathed acanthor to the cystacanth or juvenile stage, which is infective to the definitive host.

MATERIALS AND METHODS

Adult worms were obtained from the intestine of several fish, including German Brown Trout (Salmo trutta), Rainbow Trout (Salmo gairdnerii), Kokanee (Oncorhynchus nerka nerka), and Whitefish (Prosopium transmontanus) of Suttle Lake, which is a small oligotrophic lake situated on the eastern slope of the Cascade Range in Jefferson County, Oregon. Some of these worms were used as a source of eggs while others were placed in tap water and allowed to relax overnight in the refrigerator. The latter were then fixed in FAA and stained with either Grenacher's Alcohol Borax Carmine (Lynch's precipitation method) or Delafield's Hematoxylin and mounted in Canada Balsam.

The eggs or sheathed embryos were removed from gravid females by rupturing the body wall in the posterior region. The eggs were then washed with tap water, centrifuged, and rewashed. They were stored in the refrigerator in the tap water where they remained viable for up to six months.

Infected ostracods, identified as Cypria turneri Hoff, were collected from Suttle Lake by means of a bottom skimmer designed to capture small organisms living in the epibenthic region (5). A supply of these living ostracods was maintained in a refrigerated laboratory by placing them in well aerated aquaria along with the

original lake bottom sediment as a substrate. A few hundred were dissected to determine the rate of infection.

In order to check the possible need for a second intermediate host several of the ostracods were fed to some small cutthroat trout (Salmo clarkii) which had been obtained from a local fish hatchery where the infection was not present. The ostracods were introduced into the esophagus of the fish with a small pipette. The trout were then placed in a small container of water which was later examined to determine whether or not the ostracods had been regurgitated. The parasites were later recovered from the experimentally infected fish.

Once it was determined that the cystacanths found in the ostracods were directly infective to the fish it remained only to follow the infection from ingestion of the shelled acanthor by the ostracod up to the infective cystacanth stage.

In order to observe the acanthor it was necessary to first free it from the enveloping membranes. Although the techniques outlined by Manter (13; 14) and Moore (18) for artificial hatching of shelled embryos proved unsuccessful, several were freed mechanically. The most satisfactory technique, however, was that of feeding the shelled embryos to ostracods and recovering them from the intestine after six to twelve hours. These acanthors were much more active and their characteristic behavior could be observed.

Uninfected ostracods from local ponds were used for the developmental study. These were placed in small finger bowls containing a suspension of the shelled embryos and allowed to feed for six to eight hours. If left much longer, overinfection often resulted which killed many ostracods or caused abnormal and retarded development of the parasites. The ostracods were then removed to larger finger bowls which were well aerated and kept at 15° C for the duration of the experiment.

The periodic dissection of the ostracods proved to be rather difficult since their tiny bodies (0.5 to 0.7 mm) are enclosed between two chitinous valves which are impregnated with calcium carbonate. The technique finally adopted consisted of placing a single ostracod in a drop of Ringer's solution on a slide and crushing it with the edge of another slide. The animal was then teased apart with needles. The larva having previously penetrated the gut wall to the hemocoel would fall free from the body.

For subsequent microscopic study a drop of Nile blue A or acid carmine was added to stain the nuclei. After adding a coverslip the edges were sealed with vasoline to prevent evaporation. The seal also served to secure the coverslip while oil immersion was being used. Drawings were then made with the aid of a camera lucida or from photomicrographs.

The complete development in the ostracod was repeated three

times in order to substantiate the observations.

RESULTS AND DISCUSSION

Natural Infection

The rate of occurrence of the adults of N. rutili in the fish of Suttle Lake was essentially 100 percent. Almost every one of over 300 fish examined was infected. The degree of infection fluctuated somewhat with the season, increasing gradually to a peak in the fall. The heaviest infection noted was in a 12-inch German Brown Trout (Salmo trutta) which contained 232 worms when it was posted in October of 1961.

To determine the extent of infection of the intermediate host 267 ostracods (Cypria turneri) were dissected and cystacanth stages were found in 64 to give an average of 24 percent. Most of the infected ostracods contained only one parasite but as many as three were found in some.

Of 154 crayfish (Pacifastacus trowbridgi) examined only three were found to harbor the cystacanth stage. This would indicate that it probably serves merely as a transport or paratenic host and does not play an essential role in the life cycle.

Experimental Infection

To determine whether or not the cystacanths in the ostracods

were directly infective to the fish a feeding experiment was performed. From a sampling of ostracods which showed a high percentage of natural infection several were selected and fed to two infection-free cutthroat trout. The first fish was fed five and the second was fed nine. Two weeks later one male acanthocephalan was found in the intestine of the first fish and four, including three females and one male, were found in the second. The worms had increased their length by about one-half the usual length in the ostracod. Fragmentation of the large ovarian sphere of one female was beginning to take place, indicating the onset of maturity.

Infection of the ostracods by allowing them to feed on the shelled embryos proved very successful, resulting in establishment of the parasite in nearly every case.

Development within Cypria turneri

Acanthor. When the mature egg or shelled acanthor is released into the water from gravid female worm it is oval in shape and usually measures 0.027 mm in length and 0.017 mm in width (Plate I, Figure 1). There are three shell membranes present including the delicate fertilization membrane, the tough inner or middle shell membrane, and the transparent outer membrane. The outer membrane bulges out 0.0028 mm from the middle membrane in the equatorial region while the two are separated by a

distance of only 0.0015 mm at the poles. Another distinctive characteristic of the outer membrane is the presence of tiny circles covering the surface.

Within the shells the cuticle of the acanthor appears to be folded at the poles as though the embryo were being compressed. When the shell membranes were ruptured by applying pressure to the coverslip the acanthor suddenly expanded, presumably by the inbibition of water, to nearly twice its original size. Inside the membranes the acanthor measured about 0.024 mm in length by 0.009 mm in width, but following mechanical "hatching" it increased to 0.040 mm by 0.017 mm. This increase in size has also been observed by other workers (10, pt. 2, p. 127; 13; 27, p. 338; 7, p. 292).

The acanthor which emerged from the artificially "hatched" egg (Plate I, Figure 2) was very similar to that described for Neoechinorhynchus cylindratus (27, p. 336-338). The freed embryo was spindle shaped with blunt ends. The dark embryonalkern, entoblast, or inner cell mass containing the closely grouped nuclei could be seen. This represented the primordia of all the organs of the adult with the exception of the subcuticula and lemnisci. The vascular space surrounding the inner cell mass observed in N. cylindratus (27, p. 338) and N. emydis (7, p. 292) was present in very few of the acanthors of N. rutili. The surrounding material

appeared granular and contained four to eight indistinct giant nuclei.

In the anterior end the tube-like structure observed by Ward (27, p. 338) in N. cylindratus was also observed in the artificially "hatched" acanthor, but was not seen in those naturally freed in the ostracod intestine.

The embryo free in the ostracod intestine was more slender and pointed at the posterior end. The activity of the acanthor consisted of contraction of the body and invagination of the anterior end which presumably would facilitate attachment to and penetration of the wall of the host's digestive tract. Thin sheets of muscles, which run obliquely in both directions around the body, are probably responsible for the contraction and gross movement of the acanthor.

The absence of rostellar hooks and spines in N. cylindratus and N. rutili has been noted previously by Ward (27, p. 342-343). I was unable to observe any hooks in the latter; although N. emydis, the only other species of the genus which has been well studied, appears from the drawings (7, p. 296) to have six longitudinal rows of four spines each.

Acanthella. By the sixth to the twelth day following exposure of the ostracods to the shelled embryos the parasite was found lying free and immobile in the hemocoel (Plate I, Figure 3). From this time until the worm has developed to the stage which is infective to the next host it is referred to as an acanthella. The early acanthella

had increased little in size in 6 to 12 days now measuring 0. 040 mm by 0. 023 mm. It had become blunt at the ends and was beginning to round up. There was little change in the entoblast, but the giant subcuticular nuclei had become more distinct.

By 15 to 19 days the acanthella had elongated to 0. 50 mm and was about 0. 019 mm wide (Plate I, Figure 4). The nuclei of the entoblast were individually distinct and enlarged slightly. The giant nuclei had increased in size and were now vesicular. The number seen varied from six to nine.

By 24 to 30 days a significant change had taken place. Within the nearly spherical larva the entoblast had differentiated into a discrete cellular structure (Plate I, Figure 5). This inner cell mass displayed a slight curve, and at each end there was a group of three large and distinctive cells. One group represented the primordium of the proboscis and the other the reproductive organs. There were six subcuticular nuclei visible at this stage, including one which was much larger than the others.

The cells of the entoblast had undergone considerable organization by 33 to 38 days (Plate I, Figure 6). In the posterior end the three large cells had disappeared and evidently had become incorporated in the mass of small cells which constituted the genital primordium. From this mass a small group of six slightly enlarged cells seemed to be forming a "bud" which projected into the recently

formed pseudocoel. This was later determined to represent the primordium of the gonads of the male. Peripherally, the myoblastic cells, which would give rise to the muscles of the body wall, were seen. They had migrated anteriorly and arranged themselves in their respective positions.

The proboscis and its receptacle had become well differentiated. The brain was now evident as a group of small cells located within the posterior end of the proboscis sheath. It was surrounded by the nuclei which were to give rise to the muscles of the proboscis and its receptacle.

Posterior to the three prominent nuclei of the tip of the proboscis the cells were drawn into elongated cytoplasmic strands. This phenomenon has been observed previously by DeGiusti (2, p. 446) and Hynes and Nicholas (9, p. 384) in two members of the order Palaeacanthocephala.

Within the pseudocoel was seen a mass of cells the destiny of which was somewhat questionable. It is most probable that it represented the primordium of the ligament sacs of the adult; however it was not possible to follow its development satisfactorily to maturity.

By this time the subcuticulum had become much more granular and opaque. There were seven giant nuclei arranged in random fashion. The acanthella had become cylindrical and had a diameter

of 0.095 mm and a length of 0.177 mm.

By 38 to 45 days both testes had been formed (Plate I, Figure 7). The anlage of the syncitial cement gland and the bursa were seen to have produced a slight bulge in the posterior end of the larva, which had reached a length of 0.305 mm and a width of 0.146 mm.

Along the walls of the pseudocoel the cells had assumed the typical spindle shape of young muscle cells. It is interesting to note, however, that there was a double row on one side and only a single row on the other. It is very possible that the pair of retractor muscles of the proboscis sheath, which had not yet made their appearance, arise from the double layer and insert into the base of the sheath.

Within the proboscis sheath the brain had become well defined, occupying a position at the base where it would remain through maturity of the parasite. Surrounding the proboscis, anterior to the brain was a circle of three giant nuclei in the subcuticulum. According to DeGiusti's observations (2, p. 447) of the development of Leptorhynchoides thecatus this ring separates the body into an anterior region devoted to proboscis development and a posterior region devoted to the development of the remainder of the body. A circle of smaller nuclei representing the nuclear ring of the proboscis were seen surrounding the proboscis sheath just anterior to the

brain.

Due to the delicacy of the acanthella at this stage it was very difficult to gain accurate information up to the infective cystacanth stage. The observations from this point onward were based on fragmentary evidence and will, therefore, be rather incomplete.

The complete development of the proboscis was not observed, but certain features suggest that it is similar to that observed for Leptorhynchoides thecatus (2, p. 437-460) and Polymorphus minutus (9, p. 380-391). DeGiusti has shown that in L. thecatus the immature proboscis gradually elongates and everts as it develops (2, p. 446). Hynes and Nicholas reported that the proboscis of P. minutus also begins its development inverted (9, p. 384).

In N. rutili the three large apical nuclei were observed to have moved forward as had the nuclear ring of the proboscis from the positions they occupied a few days earlier. Secondly, at the anterior most end of the developing proboscis the cytoplasmic strands appeared to be doubled back over the "rim" as though the whole were evaginating. These observations have led me to postulate that the proboscis of N. rutili begins its development while inverted as has been shown to occur in the order Palaeacanthocephala, but not in the Archiachanthocephala.

Another interesting question occurs concerning the fate of the three apical nuclei. I believe that these nuclei remain to form

the apical organ of the adult. This is a trinucleate sense organ of uncertain function, which is located in a small invagination at the tip of the proboscis.

The formation of the lemnisci was not observed in the present study. It has been observed by some other investigators that in the Archiacanthocephala the lemnisci bud inward from the subcuticulum and the nuclei of the lemniscal ring migrate down these organs (17, p. 165-171; 19, p. 393; 20, p. 264; 21, p. 83). One might postulate that the same thing occurs in N. rutili since one of the lemnisci in the adult contains one giant nucleus and the other contains two. Another fact supporting this theory is the disappearance of these three subcuticular nuclei before the cystacanth stage.

Cystacanth. By 48 to 57 days the acanthella reached the cystacanth or juvenile stage which varied from 0.400 to 1.0 mm in length (proboscis inverted), depending upon how long it had been in the ostracod (Plate I, Figure 8). The cystacanth stage possesses all the structures characteristic of the adult and they are identical except for size. The only obvious change which takes place as maturity approaches is the fragmentation of the large ovarian sphere of the female into smaller ovarian balls.

Comparison with Life Cycles of Other Species of Neoechinorhynchus

Only two previous studies have been made concerning the life

cycle of the genus Neoechinorhynchus. In her work with N. cylindratus Ward (27, p. 332) found very light infections of only 0.30 percent in the ostracod (Cypria globula). Most of the bluegills (Lepomis pallidus) examined were found to harbor young juveniles encysted in the liver and these fish were considered to be the second intermediate host. The definitive host, the large-mouthed bass (Huro salmoides) was shown to acquire infection by ingestion of the bluegills.

N. emydis, a parasite of the map turtle (Graptemys geographica) has also been shown by Hopp (7, p. 288-289) to utilize commonly two intermediate hosts in its life history. The first host was an ostracod (Cypria maculata) which showed an infection rate of 0.83 percent. The second host was a snail (Campeloma rufum). About 87 percent of the snails studied contained encysted juveniles which matured in the intestine of the turtles.

It is interesting to compare the very low incidence of infection in the ostracods of these cycles, which probably require two intermediate hosts, with the relatively high incidence (24 percent) in N. rutili which requires only the ostracod as a single intermediate host.

The development of a "two intermediate host cycle" in these acanthocephalans is probably due to the preferential feeding of the definitive host. A greater opportunity for infection would exist with

large-mouthed bass feeding on bluegills than if the parasite were obliged to depend upon the bass ingesting an occasional ostracod. The cycle involving snails as paratenic hosts contains a similar set of circumstances. It would seem probable that the turtle would devour more snails in its natural feeding than it would ostracods.

There is a very distinct difference in the cycle of N. rutili in Suttle Lake. The fish here involved feed, as larvae or adults, on the small arthropods including ostracods, comprising the planktonic and benthic fauna of the lake. There is, therefore, no conflict between the requirements of a "single intermediate host cycle" and the feeding habits of the definitive host.

These three species of Neoechinorhynchus seem to follow a similar process of development in the ostracod. The acanthors have been compared previously (page 11). There is a significant difference in the time required for development from acanthor to the infective cystacanth stage among the three species. N. emydis required only 21 days, while N. rutili often took as long as 57 days. N. cylindratus was not maintained to completion in the ostracod, but at 20 days it very closely resembled N. rutili at the same stage (27, p. 337).

Whether the larva of Sialis niger is involved in the life cycle in Suttle Lake has not yet been determined.

SUMMARY

The life history of Neoechinorhynchus rutili was demonstrated experimentally. It was found that shelled embryos are released by the adult worm into the lumen of the digestive tract of fresh water fish and subsequently pass out with the feces. These "eggs" are ingested by ostracods (Cypria turneri). Within the intestine of the ostracod the acanthor hatches, penetrates the wall of the intestine, and enters the hemocoel where it metamorphoses through the acanthella to the cystacanth or juvenile stage which is infective to the fish.

The development in the ostracod has been followed and comparisons have been made with the other two species of the genus which have been studied.

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APPENDIX

Plate I

AON = Apical organ nuclei, B = Brain, BP = Brain primordium, CBP = Copulatory bursa primordium, CGP - Cement gland primordium, CS = Cytoplasmic strand, E = Entoblast, FM = Fertilization membrane, GB - Gonadal bud, GP - Genital primordium, GSN = Giant subcuticular nucleus, ICM = Inner cell mass, ISM = Inner shell membrane, L = Lemnisci, LSP - Ligament sac primordium, MC = Muscle cells of the body wall, NLR = Nuclei of the lemniscal ring, OB = Ovarian ball, OSM = Outer shell membrane, PN = Proboscis nuclei, PP = Proboscis primordium, PrS = Proboscis sheath, Ps = Pseudocoel, RM = Retractor muscle, S = Subcuticulum, T = Testis, UB = Uterine bell.

Figure 1. Shelled embryo from the body cavity of an adult female.

Figure 2. Artificially "hatched" acanthor.

Figure 3. Acanthella from an ostracod which had been exposed 6 - 12 days.

Figure 4. Acanthella from an ostracod which had been exposed 15 - 19 days.

Figure 5. Acanthella from an ostracod which had been exposed 24 - 30 days.

Figure 6. Acanthella from an ostracod which had been exposed 33 - 38 days.

Figure 7. Male acanthella from an ostracod which had been exposed 38 - 45 days.

Figure 8. Infective female juvenile or cystacanth from an ostracod which had been exposed 48 - 57 days. (The proboscis is inverted.

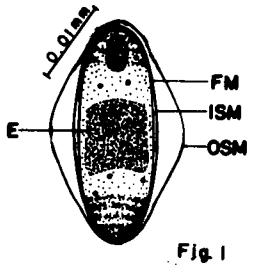

Fig. 1

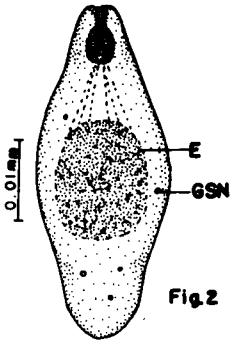

Fig. 2

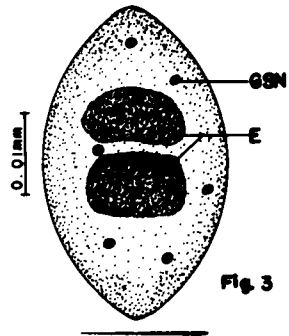

Fig. 3

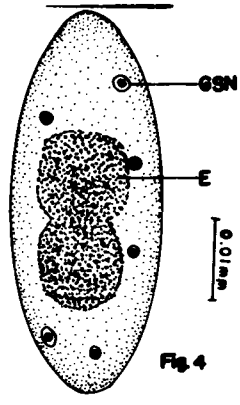

Fig. 4

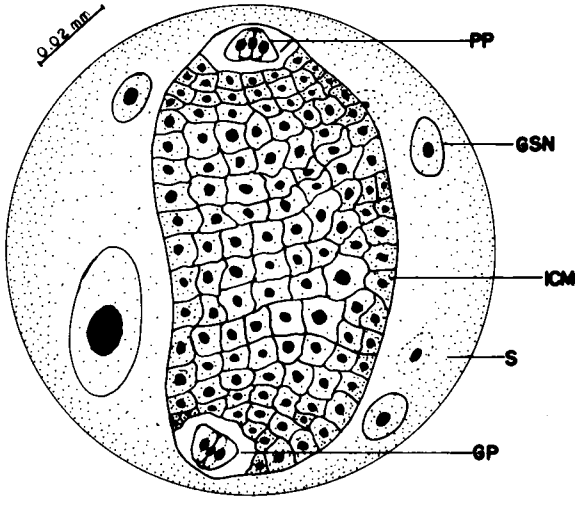

Fig. 5

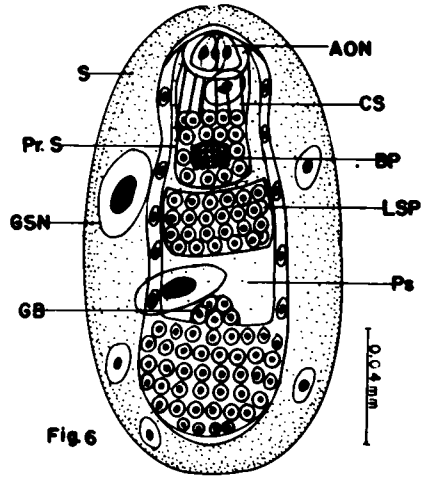

Fig. 6

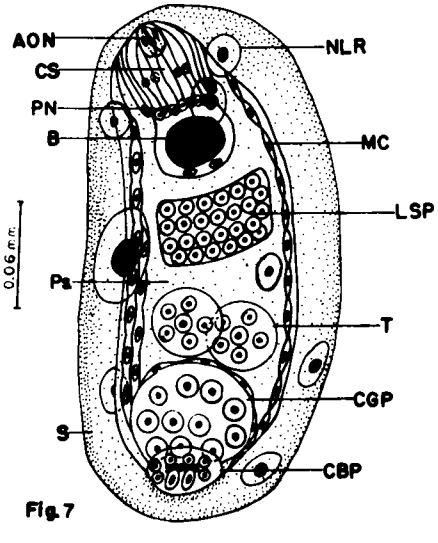

Fig. 7

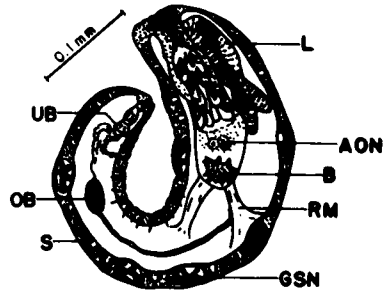

Fig. 8