Studies on Gyrocotyle rugosa Diesing, 1850, A Cestodarian Parasite of the Elephant Fish, Callorhynchus milii.*

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ABSTRACT

Gyrocotyle rugosa is a common parasite of the elephant fish in New Zealand. G. urna also occurs in the elephant fish, but less commonly. A description is given of the adult G. rugosa and its lycophore larva. Very small postlarval stages are common in the mucus scraped from the spiral valve of the host, although not more than six adults were found in one host.

Eggs of G. rugosa taken from the uterus of adult worms hatch almost immediately in sea water. They did not infect a snail (Buccinulum), a bivalve (Aulacomya), or a hermit crab. They do penetrate, in large numbers, scrapings of mucus from the spiral valve of an elephant fish. They also penetrate pieces of the wall of the spiral valve, usually entering the muscular layers, and may reach and enter

blood vessels within an hour.

INTRODUCTION

Gyrocotyle is a genus of cestodarian flatworm occurring in the spiral valve of chimaeroid fishes. Due to the large size of the adult worms they have been known for many years. A review of the genus by Dollfus (1923) has a bibliography of 75 papers. In this literature a surprising amount of controversy developed regarding which end of the parasite was anterior. The study of numerous postlarval stages by Lynch (1945) seems to prove definitely that the characteristic, ruffled "rosette" is posterior. The history of the genus will not be repeated here since it is well summarized by Watson (1911), Dollfus (1923), and Lynch (1945).

Three species of Gyrocotyle are now recognized: Gyrocotyle rugosa Diesing, 1850 (the type species); G. urna (Grube and Wagener, 1852); and G. fimbriata Watson, 1911. Of these species G. rugosa is least well known. Spencer's (1889) description of this species from the elephant fish is unreliable since he compiled it from specimens of both G. rugosa and G. urna. The purpose of this paper is to present certain additions to the description of the adult worm; describe the lycophore larva, some postlarval stages, and a few experiments with these larvae. Most of the study was made at Victoria University College, Wellington, but some of the experimental work with larvae was done at the Portobello Marine Station near Dunedin.

Gyrocotyle rugosa is a common parasite in the spiral valve of the elephant fish, Callorhynchus milii Bory (= C. antarcticus Lacépède) in New Zealand waters. Of 16 hosts examined all except three were infected with Gyrocotyle species,

^{*}This study was conducted during the tenure of a Fulbright Grant as a Research Scholar,

usually G. rugosa. The uninfected fish had been dead some hours and in one case two Gyrocotyle were found in the container near the fish. It is well known that upon death of the host these parasites often migrate to the exterior either by way of the anus or mouth. Thus, the actual incidence of infection in New Zealand must be very high.

Gyrocotyle urna also occurs in Callorhynchus in New Zealand but is much less common. It, but not G. rugosa, occurred in two of the 16 hosts examined. Three specimens occurred in one host, two in the other. Only one specimen was stained and cleared. These specimens agreed with G. urna and differed from G. rugosa in several easily recognized characters, viz.: the lateral frills or undulations of the body; the presence of body spines; the eggs containing undeveloped embryos; and the small extent of the lateral coils of the uterus. The lateral extent of the uterus was 14 to 22 per cent. of greatest body width (in three specimens). The extent of body undulations and relative width of the rosette were like that described for G. urna rather than fimbriata. The extent of the left testicular field in a 50 mm. specimen was 6 mm, or 12 per cent, of the body length, as in G. urna. Vitellaria were not observed posterior to the dorsal pore but their exact posterior boundary was not clear. In a few respects, however, my material does not agree with G, urna. The number of acetabular spires was 50 to 60 on each side, rather than 17 to 25, a number more like that of G. limbriata. The largest acetabular spine was only 0.214 mm. or 7.7 per cent. of acetabular length and smaller than the largest body spines. Thus, both number and size of these spines agree better with G. fimbriata. The size, however, is nearly that of G. urna forma parvispinosa. The male pore was rather far to the right nearer the edge of the body than to the midline. Excretory pores could not be seen. While study of more specimens might possibly indicate a new species for this material it is considered for the present to be G. urna.

MORPHOLOGICAL STUDIES

Gyrocotyle rugosa. Adults (Figs. 1, 2)

Body size and proportions vary considerably with contraction. The worms are strongly muscular and it is difficult to preserve them in their normal shape. Living specimens are soft and flabby, creamy-white in colour. Watson (1911) noted that in freshly killed hosts the worms were a pinkish, translucent flesh colour. Measurements of 22 specimens were: length 32 to 82 mm., greatest width 6.5 to 22 mm. A dead specimen, greatly extended, was 130 by 15 mm. Moderately contracted worms were 42 to 71 by 16 to 20 mm. Lateral undulations of the body are lacking. The lateral edges tend to curve slightly inward ventrally but the striking undulations present in other species do not occur. The rosette is highly frilled, fully as much so as in G, urna although usually less than is true for G, fimbriata. The diameter of the rosette is $33\frac{1}{3}$ to 50 per cent, of greatest body width, thus resembling G, urna.

The body surface is rugose even in extended or compressed specimens. The rugae are transverse except in the anterior half of the body ventrally where short longitudinal folds occur irregularly so that the surface is incompletely broken into irregular segments. Body spines such as occur in G. urna and G. fimbriata are lacking, but numerous exceedingly minute spines or points occur on the tips of small papilla-like elevations (Fig. 2). These papillae and spines are best observed by reflected light when the body surface is exposed to the air. They are invisible in cleared specimens. They are arranged more or less in transverse rows on the

body ridges. Where the rugae or ridges are irregular the spines are also irregular. They occur on both the dorsal and ventral surfaces and on the rosette but appear to be lacking anterior to the vaginal pore.

The acetabular spines occupy a subtriangular area on each side opposite the posterior half of the acetabulum. In two specimens, the length of the spiny area was 71 per cent. and 74 per cent. of the acetabular length. The spines are lateral and ventral and perpendicular to the body surface. The area is longest on the edge of the body and tapers as it extends ventrally almost to the acetabulum. The largest spines are 0.357 by 0.065 mm. or 13 per cent. of the length of the acetabulum. The number of spines, estimated to be approximately 100 on each side, is greater than in either G. urna or G. fimbriata.

The genital notch is conspicuous on the right side of the body a little posterior to the acetabulum. The uterine pore is median about 1/6th body length from the anterior end. The male pore is at the tip of a pointed, cone-like elevation of the body surface, the genital papilla or genital cone. Fresh, living specimens may show this structure only slightly elevated, but after a few minutes outside the host and during killing and fixation it extends toward the right, usually to and even through the genital notch. Here it bends dorsally and may almost reach the vaginal pore. As has been noted by previous authors, it evidently can serve in self-copulation. It appears not to be a true cirrus or any specialized structure but merely an elevation of the body wall. When the cone is retracted, the male pore lies just median to the right longitudinal nerve and only slightly posterior to the genital notch. The vaginal pore is dorsal, well to the right of the longitudinal nerve, and near the genital notch. Excretory pores were not observed but the excretory tubes were seen to approach the edges of the body 14 mm. from the anterior end of a specimen the acetabulum of which was 2.5 mm. long. This distance of more than five times acetabular length is considerably more posterior than in the other species. In another specimen 44 mm. long and with acetabulum 2.2 mm. long, a diagonal excretory tube extended to each side of the body 16 mm, from the anterior end.

Testes are numerous, estimated 400 to 500 on each side, and close together. They extend anteriorly to near the base of the acetabulum and posteriorly well beyond the uterine sac, to about the tenth lateral coil of the uterus. Approximately half the longitudinal extent of the testes is posterior to the uterine sac. In a 32 mm. specimen with acetabulum 1.90 mm, long, the testicular field was 10 mm, or 31 per cent. of body length and more than five times acetabular length.

The ovary is approximately 26 per cent, of body length from the posterior end. The lateral coils of the uterus are much longer and much more numerous than in other species. In 22 specimens measured, the width of the uterus was 40 to 81 per cent, of greatest body width. In only one specimen was it less than 50 per cent, and the average was 60 per cent. Since the gravid uterus is visible from the surface, this character alone easily distinguishes G. rugosa from G. urna and G. fimbriata which have short uterine coils. The vitelline follicles extend from about midacetabular level to a short distance posterior to the ovary. They are not limited to the lateral fields but extend across the body both ventral and dorsal to the acetabulum, the testes, and most of the uterus. Medianly they tend to be more sparse and are few or lacking opposite the ovary and the terminal eight or ten coils of the uterus. The distance between the posterior limit of the vitellaria and the posterior end of the body was 7.8 mm. in a 70 mm. specimen, and 7 mm. in a 40 mm. specimen, a greater distance than occurs in the other two species.

Eggs and Larvae of Gyrocotyle rugosa. (Figs. 3, 4)

Eggs are fully embryonated in the rather short uterine sac and in the adjacent uterine coils. Such eggs, measured in alcohol mounts, are 122 to 135 microns (average 131 microns) long by 76 to 95 microns (average 80 microns) wide, thus being considerably larger than the eggs of G. urna or G. fimbriata. The egg shell is thin and colourless, the operculum inconspicuous. Most eggs show a small knob or boss at the anopercular end. No jelly was noted around the eggs and eggs did not tend to stick together.

Eggs removed by puncturing the terminal region of the uterus and placed in sea water immediately reveal very active embryos. The cilia beat vigorously and the embryo turns, twists, pushes, and struggles. Hatching occurs within a few minutes, apparently largely through the activity of the embryo. The lycophore larva swims very rapidly. It follows a spiral path but turns frequently. In a watch glass, the larvae swim to the top of the water every few seconds then turn and swim to the bottom. In addition, they speed in various directions as if searching for some host, as, indeed, they doubtless are. Since young larvae have been reported in the tissues of adult *Gyrocotyle*, a freshly collected adult was placed in a petri dish with large numbers of recently hatched larvae. No attraction toward the adult was noted and there was no evidence that any larvae adhered to or penetrated the worm. Reactions of the larvae to certain other objects will be discussed later.

Larvae were killed by pipetting into hot formal-alcohol-acetic solution. They were later stained with Delafield's hematoxlyn or with acetic alum carmine, and mounted in balsam.

Description of the lycophore larva of G. rugosa (Figs. 5-8)

Extended specimens, measured in temporary mounts in 70 per cent. alcohol, were 130 to 140 by 50 to 60 microns. The body, tapering from near the middle toward each end, is rounded anteriorly and somewhat truncated at the posterior end. Free swimming larvae as they rotate are seen to be slightly bent or indented near the middle of one surface as noted in the case of *G. fumbriata* by Lynch (1945). The body is completely covered by long cilia of approximately equal length. No evidence of cuticular plates could be seen. Circular muscles lie just beneath the ciliated layer. Except for the posterior hooks, in general appearance and behaviour, this larva certainly resembles a miracidium.

Almost filling the anterior third of the body are three pairs of elongated, pyriform, transparent sacs considered to be glands. The middle pair is almost twice as long as the others and in contracted specimens may be somewhat bent or folded. These structures do not stain but appear as transparent vesicles. The underlying short pair is usually not evident from a dorsal or a ventral view. Each gland opens separately at the anterior end of the body. There is evidence that one of the shorter pairs (the dorsal?) is physiologically different from the others. Among numerous larvae which had penetrated a mass of mucus from the spiral valve of the host, a considerable number, after being stained, showed this pair darkly stained.

Immediately posterior to the glands and just anterior to the midbody lies a large conspicuous bilobed mass of cells. It extends anteriorly lateral to the longer gland cells almost to the base of the shorter glands and posteriorly approximately to the midbody. Near one surface, considered as ventral, the organ narrows to form an isthmus-like band across the body. On each side the cells extend upward and

near the other surface (dorsal) extend medianly but do not meet. This organ is probably a nervous centre. Radiating from the anterior end of the body are six narrow bands of slender nuclei or cells. A central non-cellular cord or tube extends backward between the large gland cells and appears to fork immediately anterior to the isthmus of the cellular mass. Although not granular it is more refractive than the glands. Two finely granular, inconspicuous spherical masses lie side by side immediately dorsal to the isthmus. They are probably not connected with the central cord or tube since they lie at a different level.

Posterior to the bilobed mass, nuclei are more scattered but a central collection and one or two small pairs of cell clusters can usually be observed. At least one pair of flame cells is present. These were not seen in entire specimens either living or stained but were clearly observed in an active state in a crushed, recently hatched specimen. They were located in the posterior half of the body. Each was pointed diagonally backward and inward. Except for the beginning of the excretory tubule near the flame cell, excretory tubules or pores could not be seen. This record of flame cells is the first for lycophore larvae.

The most conspicuous feature of the lycophore larva is the presence of 10 large hooks withdrawn into the posterior end of the body. In G. rugosa these hooks are unusually large, measuring 34 to 36 microns in length or approximately 26 per cent. of body length. Eversion of the hooks was not observed. Several specimens possessing eight rather than ten hooks were observed. When the hooks are retracted an appearance of eight might result if certain hooks lie directly over others. Fig. 7 shows eight hooks as seen in a crushed specimen.

The lycophore of G. rugosa differs in several respects from the lycophores of G. urna and G. fimbriata. That of G. urna has ten pairs of unicellular glands extending nearly to the midbody, and relatively shorter hooks. The lycophore of G. fimbriata has hooks 19 to 23 microns long and only about 1/16th body length. It has at least one pair of very long gland cells (Lynch, 1945). The anterior pair of clear vesicles mentioned by Lynch may correspond to what I have considered gland cells in the lycophore of G. rugosa.

Postlarval Stages of G. rugosa. (Figs. 9, 10)

It was discovered more or less accidentally that numerous very small postlarval stages of G. rugosa occurred in the mucus of the anterior portions of the spiral valve of infected fishes. By scraping the wall of this organ with a scalpel living specimens can easily be found. They all possess a posterior, conspicuous, expanded, circular or subcircular, haptor-like organ bearing the larval hooks. The smallest specimens had a body length, not including the haptor, only slightly more than the length of the ciliated lycophore. All were non-ciliated. The total body length, including the haptor, and the greatest width varied from 0.225 by 0.098 mm. to 0.957 by 0.280 mm. The body is uniformly filled with nuclei and shows less differentiation of cellular groups than does the ciliated lycophore. A depression is visible at the anterior end, and in the larger specimens a concentration of nuclei indistinctly outlines the rudiments of the acetabulum. In the 0.943 mm. specimen the acetabulum was 0.143 by 0.072 mm. The haptor contains more scattered nuclei. It was 0.108 mm. in diameter in a 0.686 mm. specimen. The hooks retain their original size but become more widely separated in the larger specimens. No evidence of the overgrowth of the haptor by the body as noted by Lynch for G. fimbriata was seen.

Similar postlarval stages have been described embedded in the tissues of adult specimens of G. urna, G. fimbriata, and G. rugosa. None such were observed in the few specimens stained and cleared. In view of the common occurrence of these larvae in the spiral valve of the host, it seems probable that their penetration into an adult Gyrocotyle is accidental.

Fuhrmann (1930), commenting on the occurrence of young larvae in the tissues of adult specimens, stated: "Die 10-hakigen Larven bohren sich vielleicht normalerweise in die Mucosa des Darmes ein (anomalerweise ins Parenchym des Gyrocotyle), um sich dort zu entwickeln und dann wieder in den Darm zu gelangen, wo sie geschlechtsreif werden." He gave no evidence to support this possibility which he apparently proposed as a theory. It is supported by the above findings of numerous very young larvae in the mucosa. It will be shown below that there is a possibility that these larvae may have reached the mucosa by way of the blood stream rather than by way of the digestive tract.

OBSERVATIONS ON THE LIFE CYCLE OF GYROCOTYLE

The life cycle of only one Cestodarian is known; it is that of Amphilina foliacea (Rud.) parasitic in the body cavity of the sturgeon in Europe. Eggs of Amphilina foliacea pass out through the abdominal pores of the ganoid host. They contain a ciliated lycophore but do not hatch until eaten by amphipods (Gammarus or Dikerogammarus). The lycophore penetrates into the body cavity of the amphipod, loses its cilia, and gradually becomes an organism resembling the adult. Sturgeons become infected by ingestion of infected amphipods (Janicki, 1930).

The order Amphilinidea is quite distinct from the Gyrocotylidea in many respects. Amphilinids never occur in the digestive tract but are parasites of the body cavity. There is evidence that when the host is a teleost fish adult worms bore through the body wall and presumably liberate eggs only after thus leaving their host. At least specimens of Gephyrolina paragonopora have been found protruding from the body wall of their host, an Indian siluroid fish. Baer (1951) states: "One might be inclined to interpret such facts as indicating that the adult worms are free-living or, at least, that they escape from their host when their uterus is filled with eggs and that the latter are liberated when the worm disintegrates." Possibly the digestive tract is a secondary location for Cestodarians.

The life cycle of Gyrocotyle is unknown. There is at present no evidence as to the manner in which the definitive host is infected. It has been presumed that eggs pass out in the faeces and that some food animal serves as intermediate host, as is the case for most intestinal helminths. However, Lynch observed almost all stages from lycophore to adult either within the parenchyma of adult worms or in the spiral valve of the host. Yet there must be some part of the life cycle outside the host. The following observations may or may not be relevant to the life cycle.

One of the first impressions one receives from collection of numerous specimens of Gyrocotyle rugosa is the absence of small specimens. Of 34 specimens in 13 hosts, all were of large size and contained eggs in the uterus. No half-grown or quarter-grown individuals were found. Lynch found that infections with G. urna or G. fimbriata usually involved only adult specimens. However, of 104 rat fishes (Hydrolagus) examined by him, seven had mass infections "of small juvenile worms, seven to 203 in a host." Such conditions suggest an immunity by which the presence of adults prevents establishment of additional specimens at least of easily visible size. The large surface area of the adult worms suggests that the immunity might be largely determined by available space. As noted above, large

numbers of postlarval stages are of common occurrence in the spiral valve of the elephant fish. The presence of a few adults seems to prevent the development of these larvae. Presumably, the numerous juveniles found by Lynch would follow multiple exposure by a host uninfected by adults, and only a limited number of these could become adult because of space limitations. The actual fate of the numerous postlarval individuals is, however, unknown. Almost microscopic in size and without cilia, they would not seem well adapted to infect another final host directly. Apparently few if any of them attain appreciable size within the elephant fish so long as adult worms are present. If the latter should leave the host, possibly some of the postlarval forms would replace them.

The spontaneous departure from their living host by parasites is not common except for the purpose of dissemination of eggs. The fact that only the eggs in the terminal coils of the uterus of G. rugosa and none of the eggs of G. urna or G. fimbriata are ready to hatch casts some doubt that adult Gyrocotyle normally leaves the host for dispersal of its eggs. Yet there is evidence that adult Gyrocotyle can live in sea water at least for some days. Watson (1911, p. 365) states that G. fimbriata can "live for some days free." Lönnberg (1891, p. 14) notes that a specimen was found floating free in the sea off the coast of Sweden and that in the Museum at Christiana is a specimen found free on the bottom of the Bergen Fiord. One of the early records of adult "Gyrocotyle rugosa" was from a bivalve mollusc, "Mactra edulis"* from the coast of Chili. Since such a finding has not been confirmed, it has been concluded by most authors that the record involved some error or accident, as is more obviously the case in the record of Gyrocotyle from an African antelope (Diesing, 1850). It does seem evident that Gyrocotyle has unusual longevity in cold sea water, and the possible role in the life cycle of this ability seems worth further investigation. A mature individual of G. rugosa contains thousands of eggs ready to hatch, and it is known to be able to leave a dead host. Whether its eggs normally pass out in the faeces of the host has not been demonstrated.

The intestinal content near the anus of an elephant fish infected with six adult G. rugosa was examined. Three smears revealed no eggs or larvae. Four smears of scrapings of the wall of the spiral valve near its middle revealed one living, postlarval stage with everted haptoral disc. It was not measured, but was evidently three or four times larger than the lycophore.

Numerous hatched larvae were exposed to: (1) a snail, Buccinulum multilineatum; (2) a hermit crab; (3) a bivalve molluse, Aulacomya maoriana; (4) mucus from the spiral valve of the elephant fish; and (5) two pieces cut from the spiral valve. No immediate change in behaviour or distribution of the larvae was noted except in the watch glass containing the mucus. Although not markedly attracted to the mucus, the lycophores reacted positively to contact with it. Upon contact they remained or returned until thoroughly enmeshed. Within the mucus they frequently bent the body or revolved with gradually slowing movement. After about an hour, the mucus was filled with many hundreds of larvae. It was then killed and preserved. Slides made of this mucus show larvae so crowded together as to form in places almost a solid mass. In contrast, no larvae adhered to mucus secreted by the snail equally exposed to the lycophores.

The two pieces of the spiral valve, each about 8 mm. in diameter, were also exposed to lycophore larvae for approximately one hour, then fixed in formolacetic-alcohol solution. Study of cross-sections of this tissue revealed that a

^{*}Dollfus (1923, p. 216) notes that the correct name for this mollusc is Mulinia edulis.

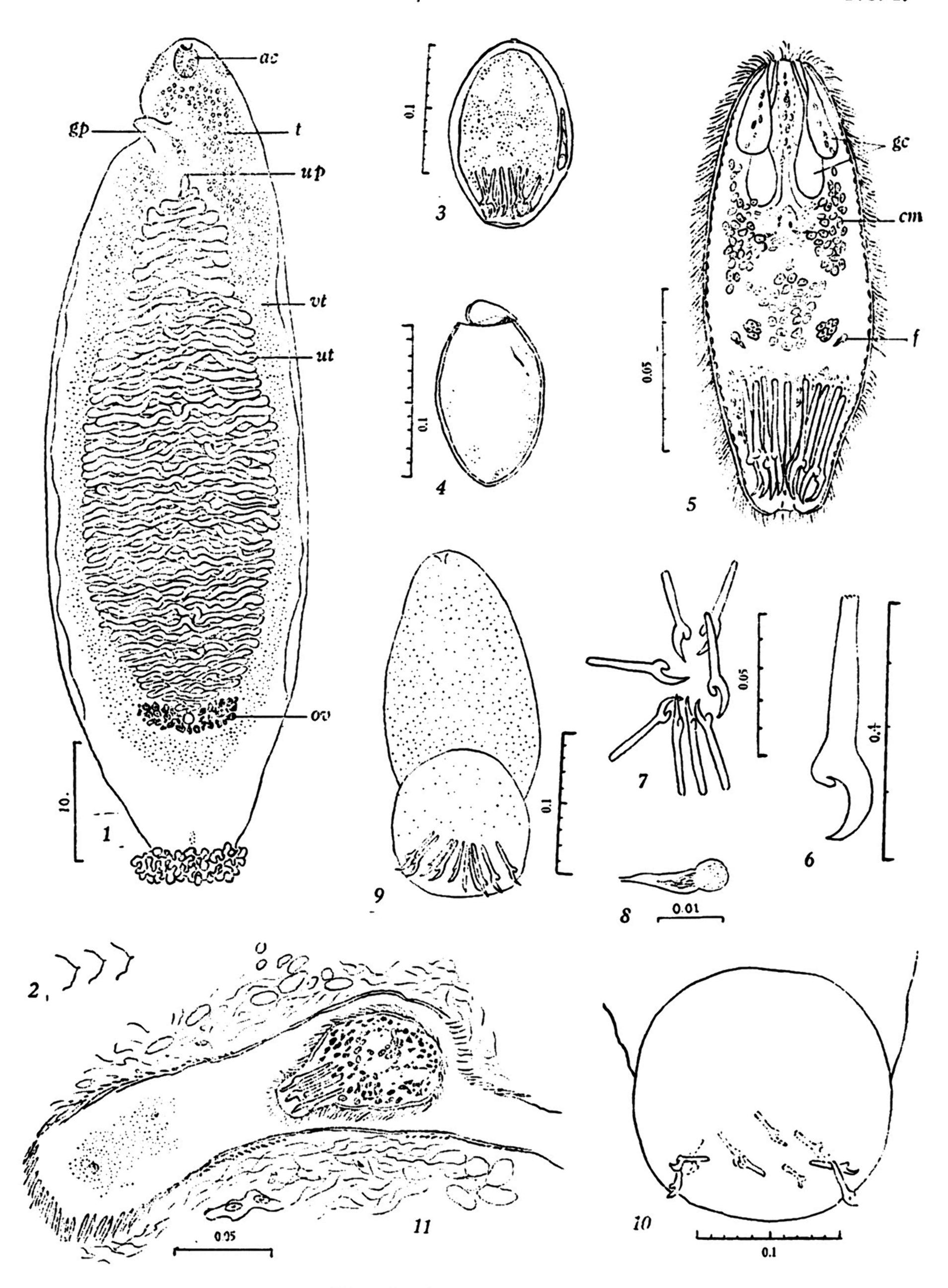


Plate I-Gyrocotyle rugosa.

considerable number of lycophore larvae had penetrated into the tissues of the spiral valve and that at least four larvae had entered the lumen of blood vessels. Oddly enough, the inner mucosal lining was not the area of chief attraction. Practically all the larvae had entered the muscular layer from a cut end of the tissue and were found near the outer surface of the organ. All the larvae observed retained their cilia and held their hooks retracted.

The total thickness of the wall of the spiral valve was about 1.474 mm. Of this thickness, the inner half (0.804 mm.) was mucosa thrown into deep folds of flask-shaped pockets, the mucous glands. The mucus-secreting cells were limited to the globular, basal portion of the glands. Although these glands contained mucus, there was no evidence that larvae were being attracted to it. An occasional egg, still unhatched, occurred within a gland, and a single larva free in the lumen was found there.

Of 22 larvae studied from sections of the spiral valve, 14 were found within the muscular layers, 4 were within blood vessels, 2 were within mucosal tissue, and 1 was free in a mucous gland. Those within the blood vessels had probably previously penetrated into the muscular layers. Of the 14 larvae in the muscular layers, 7 had penetrated less than 0.1 mm., and the deepest penetration was 0.165 mm. from the cut edge of the tissue. The distance of the point of penetration from the outer (coelomic) surface of the piece of tissue varied from 0.067 to 0.502 mm., but only four larvae had entered more than 0.2 mm. from that surface and only two were in the inner (mucosal) half of the tissue. The four larvae in blood vessels had more varied locations, showing that locomotion within the vessel was more rapid. Two of these larvae were 0.603 mm. from the outer surface; two others were almost 3 mm. from the nearest cut edge.

These observations indicate that, although lycophore larvae will collect in large numbers in mucus from the spiral valve of the elephant fish, when exposed to a cut piece of the spiral valve, (1) they prefer the muscular layers to the mucosa, and (2) are capable of penetrating not only into the tissues but also into the blood vessels of that organ. Considering this attraction of these larvae to tissues of the final host, their ability to enter blood vessels, and their later appearance in almost as small a size in scrapings of the mucosa, the possibility is suggested that these larvae normally penetrate the gills or some surface area of the elephant fish, be carried to the intestine where they emerge into the lumen, and then for the first time make use of their powerful hooks for anchorage. Their reaction to the gills of the elephant fish, possibilities of which had not occurred to me when fresh material was available, would be of interest to observe. Some experiment which would expose intact gill surface without the distraction of free blood or other tissues is suggested.

Numerous larvae were still living in sea water after $6\frac{1}{2}$ hours. Some were active after 18 hours. All were dead when examined about 34 hours after hatching. Under natural conditions, the larvae probably can live at least 24 hours.

Five days after exposure to larvae, the soft parts of the snail, bivalve, and hermit crab were examined after crushing between slides. No larval stages of Gyrocotyle were observed.

The few experiments recorded above indicate that the eggs G, rugosa hatch immediately in sea water and possibly within the spiral valve of the host; that the lycophore larvae were not attracted to and did not penetrate one species of bivalve, one species of hermit crab, and one species of snail; that they were attracted by, penetrated into, and remained in large numbers in scrapings of mucus

from the spiral valve of the elephant fish; that they also penetrate into the tissues and blood vessels of cut pieces of the spiral valve itself. This attraction to a part of the definitive host suggests a direct life cycle.

Unfortunately, Callorhynchus does not live well in captivity. Furthermore, it is so omnivorous in food habits that it could theoretically be infected from almost any sort of intermediate host. Specimens of elephant fish examined by me had been feeding largely on molluses (both bivalves and snails) or on Crustacea.

Gyrocotyle rugosa is the most favourable species for life cycle studies because its lycophore larvae are so easily obtained in very large numbers.

SUMMARY

- 1. A description is given of Gyrocotyle rugosa Diesing, 1850, a cestodarian parasite of the elephant fish, Callorhynchus milii (= C. antarcticus). It is morphologically clearly distinct from the other species in the genus.
- 2. The lycophore larva of *G. rugosa* is described. It has three pairs of transparent vesicles, considered to be gland cells, in the anterior half of the body; a large bilobed organ; relatively large hooks; and one pair of flame cells.
- 3. Numerous postlarval stages, 0.225 to 0.957 mm, in length, were found in the scrapings of mucus from the anterior part of the spiral valve of the host. In 16 hosts examined, no specimens were found between this size and adult specimens.
- 4. Eggs of G. rugosa hatch almost immediately in sea water. The ciliated lycophore larvae showed no interest in one species of bivalve, one species of hermit crab, and one species of snail. They penetrated and remained in very large numbers in scrapings of mucus from the spiral valve of the elephant fish.
- 5. Lycophore larvae readily penetrate into the tissues of pieces cut from the spiral valve of the elephant fish. With few exceptions, they enter into the muscular layers rather than into the mucosal layers. Within an hour, at least four larvae had entered blood vessels, and these had travelled some distance from their point of entry.

EXPLANATION OF PLATE I

All figures except Figs. 1 and 2 were drawn with the aid of a camera lucida. The projected scale has the indicated value in mms. Abbreviations: ac, acetabulum: cm, cellular mass; f, flame cell; gc, gland cells; gp, genital papilla; ov, ovary: t, testis; up, uterine pore; ut, uterus; vt, vitellaria.

- Fig. 1.—Diagram of adult specimen of Gyrocotyle rugosa. Ventral view.
- Fig. 2.—Diagram of the pointed or spined papillae on the ridges of the body surface of *G. rugosa*. Greatly enlarged.
- Fig. 3.—Egg of G. rugosa. From terminal coils of the uterus.
- Fig. 4.—Shell of a hatched egg, showing operculum.
- Fig. 5.—The lycophore larva of G. rugosa. Semi-diagrammatic.
- Fig. 6.—.\ single hook of the lycophore larva.
- Fig. 7.—Hooks of an eight-hooked lycophore crushed to spread the hooks.

- Fig. 8.—Flame cell from the lycophore larva.
- Fig. 9.—Young juvenile or postlarval stage of G. rugosa from scrapings of the mucosa of the spiral valve of the elephant fish.
- Fig. 10.—Posterior end of a somewhat larger juvenile stage.
- Fig. 11.—Lycophore larva of G. rugosa in a blood vessel in the wall of the spiral valve of the elephant fish. From a 10-micron section of a piece of tissue exposed to free-swimming lycophore larvae.

REFERENCES

For a complete bibliography of Gyrocotyle, consult Watson (1911), Dollfus (1923), and Lynch (1945).

- BAER, JEAN G., 1951: Ecology of Animal Parasites. Univ.III. Press. i-x + 224.
- Diesing, Carl M., 1850: Systema Helminthum, Vol. 1, xiii + 680.
- Dollfus, Robert Ph., 1923: L'orientation morphologique des Gyrocotyle et des cestodes en général. Bull.Soc.Zool.France, 48 (4-5), 205-42.
- FUHRMANN, Otto, 1930: Cestoidea, in Kükenthal's Handbuch der Zoologie, Vol. 2, Lief. 7, Teil 2, pp. 141-416.
- Janicki, C. von. 1930: Ueber die jüngsten Zustände von Amphilina foliacea in der Fischleibeshöhle, sowie Generelles zur Auffassung des genus Amphilina G. Wagen. Zool.Anz., 90, 190–205.
- Lönnberg, E., 1891: Anatomische Studien über skandinavische Cestoden. Kongl. Svenska Vetenskaps-Akademiens Handlingar, N.S. 24 (Pt. 1. No. 6), 1–109, pls. 1–3.
- Lynch, James E., 1945: Redescription of the species of *Gyrocotyle* from the ratfish, *Hydrolagus collici* (Lay and Bennet), with notes on the morphology and taxonomy of the genus. *J.Parasit.*, 31 (6), 418-46.
- Spencer, W. Baldwin, 1889: The anatomy of Amphityches urna (Grube and Wagener). Trans. Roy. Soc. Victoria, 1 (2), 138–51, pls. 11–13.
- WATSON, EDNA E., 1911: The genus Gyrocotyle and its significance for problems of cestode structure and phylogeny. Univ. Calif. Publ. Zool., 6 (15), 353-468, pls. 38-48.