



The life cycle of *Cotylurus erraticus* (Rudolphi, 1809) Szidat, 1928 (Trematoda: Strigeidae) and the effect of the metacercaria on rainbow trout (*Salmo gairdneri*)  
by Robert Eldon Olson

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of  
DOCTOR OF PHILOSOPHY in Zoology  
Montana State University  
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Abstract:

The life cycle of the strigeid trematode *Cotylurus erraticus* (Rud., 1809) Szidat, 1928 was completed experimentally in the laboratory. Eggs were obtained from laboratory infected immature *Larus californicus*. Most eggs hatched in 15-16 days at 24 C and the miracidium. was similar in morphology to other strigeoid miracidia.

Mother and daughter sporocysts developed in the operculate snail *Valvata lewisi* and the pharyngeate, furcocercous cercaria usually emerged 35 days after infection. The metacercaria is tetracotyliiform and was originally described as *Tetracotyle intermedia* by Hughes (1928). It encysts in the pericardial cavity of salmonid fishes and was found in *Salmo gairdneri*, *Salvelinus fontinalis*, *Oncorhynchus nerka*, *O. kisutch* and *Thymallus arcticus* collected from Georgetown Lake. When ingested by immature gulls, the metacercariae developed in the small intestine to patent adults in four days. This study is the first complete life cycle for a fish infecting *Tetracotyle*. The effects of *C. erraticus* metacercariae on *S. gairdneri* were studied by comparing the swimming performance, hematocrit value, high temperature tolerance and low oxygen tolerance of parasitized trout with parasite-free trout. No difference between parasitized and control fish was found in any of these tests.

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THE LIFE CYCLE OF COTYLURUS ERRATICUS (RUDOLPHI, 1809) SZIDAT, 1928  
(TREMATODA: STRIGEIDAE) AND THE EFFECT OF THE METACERCARIA  
ON RAINBOW TROUT (SALMO GAIRDNERI)

by

ROBERT ELDON OLSON

A thesis submitted to the Graduate Faculty in partial  
fulfillment of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Zoology

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## ABSTRACT

The life cycle of the strigeid trematode Cotylurus erraticus (Rud., 1809) Szidat, 1928 was completed experimentally in the laboratory. Eggs were obtained from laboratory infected immature Larus californicus. Most eggs hatched in 15-16 days at 24 C and the miracidium was similar in morphology to other strigeoid miracidia. Mother and daughter sporocysts developed in the operculate snail Valvata lewisi and the pharyngeate, furcocercous cercaria usually emerged 35 days after infection. The metacercaria is tetracotyloform and was originally described as Tetracotyle intermedia by Hughes (1928). It encysts in the pericardial cavity of salmonid fishes and was found in Salmo gairdneri, Salvelinus fontinalis, Oncorhynchus nerka, O. kisutch and Thymallus arcticus collected from Georgetown Lake. When ingested by immature gulls, the metacercariae developed in the small intestine to patent adults in four days. This study is the first complete life cycle for a fish infecting Tetracotyle. The effects of C. erraticus metacercariae on S. gairdneri were studied by comparing the swimming performance, hematocrit value, high temperature tolerance and low oxygen tolerance of parasitized trout with parasite-free trout. No difference between parasitized and control fish was found in any of these tests.

## INTRODUCTION

During the fall of 1965, a number of salmonid fishes were collected from Georgetown Lake, near Anaconda, Montana. Examination of these fish revealed a high prevalence and intensity of a trematode metacercaria in their pericardial cavities.

This metacercaria proved to be Tetracotyle intermedia which was described by Hughes (1928) from the round whitefish (Prosopium cylindraceum) and the cisco (Coregonus artedii) collected in Lake Huron. Hoffman (1960) lists 15 species of Tetracotyle that infect fish, none of which has a completely described life cycle. Van Haitsma (1930a) reported the life cycle of Cotylurus platycephalus (syn. C. michiganensis and C. communis), but this was later shown to be in error by Olivier and Cort (1942). The present study is the first complete life cycle for a fish-infecting Tetracotyle.

Georgetown Lake is an impoundment formed by a dam athwart Flint Creek constructed in 1894. According to Fred Beal (unpublished, undated manuscript) the dam was raised 5 feet in 1919 and another 3 feet in the 1940's, resulting in a lake of 1120 hectares and an average depth of 5.5 meters. This lake is situated at an elevation of 1942 meters and is usually ice covered from mid-November to mid-May. It is highly eutrophic and supports a large variety of plant and animal life. In recent years, rainbow trout (Salmo gairdneri) have been regularly planted in the lake. Arctic grayling (Thymallus arcticus) were stocked in 1966 and 1967 and coho salmon (Oncorhynchus kisutch) in 1967.

Other fish which are numerous are: brook trout (Salvelinus fontinalis), kokanee salmon (O. nerka), longnose sucker (Catostomus catostomus) and redbreast shiner (Richardsonius balteatus). Large areas of mucky bottom and decaying vegetation in Georgetown Lake make conditions favorable for the eight species of snails found during the study period.

The purpose of this investigation was to determine the adult stage and life cycle of T. intermedia and to study the effects of sublethal infections of the parasite on swimming performance, high temperature and low oxygen tolerance of young rainbow trout. Study on this project extended from September, 1965 to June, 1968.

## MATERIALS AND METHODS

### Life Cycle

A number of aquatic birds were collected at Georgetown Lake. One of these, an immature California gull (Larus californicus) was infected with Cotylurus erraticus in the intestine. In addition, four young California gulls were collected from breeding islands at Freezeout Lake, Teton Co., Montana. These birds were checked for natural trematode infections and although negative, were given 1 cc. doses of  $\text{CCl}_4$  to ensure that they were free of parasites. One of these birds died after receiving a laboratory infection. The remaining three gulls served as a source of parasite eggs throughout the study. Gulls were fed fish from Georgetown Lake, principally longnose suckers and salmonids that had been frozen.

All C. erraticus eggs used were obtained from laboratory-infected California gulls. Fresh fecal material from infected birds was placed in quart jars and mixed with distilled water. After settling for about 10 minutes, the supernatant was decanted and more distilled water added. This process was repeated until the sample consisted only of eggs and larger particles of fecal material. Distilled water was again added but since the remaining fecal particles settled faster than the eggs, a settling period of less than one minute allowed the still-suspended eggs to be decanted into finger bowls along with a small amount of fecal material. Eggs were then removed with a pipette, using a dissecting microscope, and placed in a finger bowl with clean water where they were incubated at room temperature, approximately 21 C.

Some eggs were incubated in finger bowls floated in a constant temperature aquarium. Eggs were agitated and the water was changed daily during the incubation period. Hatching of eggs was delayed when desired by placing them in a refrigerator at 5 C when fully embryonated (Harris, Harkema and Miller, 1967). Miracidia were studied alive, both unstained and supravitaly stained with neutral red. Methyl cellulose was used to inactivate living individuals. The excretory system was most easily studied by allowing miracidia to dehydrate slowly under a coverslip. Permanent mounts were also made after fixation in hot AFA and staining in Semichon's carmine. The epidermal plate pattern was determined using the silver nitrate method described by Lynch (1933).

Snails were collected at Georgetown Lake by hand-picking them in shallow water and with an Ekman dredge in deeper water. Representatives of all species found in the lake were maintained in laboratory aquaria on a diet of boiled lettuce. Attempts to infect various species of snails were accomplished by placing miracidia and snails together in small Stender dishes for a period of about 12 hours.

Sporocysts were carefully dissected out of infected snails and studied alive unstained. Permanent mounts were also made, but were not as good as living specimens for the study of internal structure.

Cercariae were collected from finger bowls containing infected snails. Methods used to study cercariae were the same as for miracidia.

Cercariae used to infect fish were obtained by placing infected snails in finger bowls containing clean water for a period of 18-24 hours

before infections were attempted. The number of cercariae used in experiments was estimated by the method of Olson (1966). All fish were kept in water slowly tempered to 21 C and then exposed to cercariae for 30 minutes in a small (5.6 liter) aquarium. This aquarium allowed the cercariae and fish to be concentrated and increased the chances of cercarial contact. After exposure, fish were held at 21 C to facilitate rapid metacercarial development.

Metacercariae were collected both from naturally and laboratory infected fish and the parasite cysts were mechanically removed. They were fixed in hot AFA or 10% formalin, stained in Semichon's carmine and mounted in Permount.

Adult worms were obtained from the infected immature California gull from Georgetown Lake and from a laboratory infected California gull that died during experiments. The intestines were slit open and the contents washed into a quart jar. This material was decanted several times until the supernatant was clear. Worms were then recovered and whole mount slides prepared in the manner described for metacercariae.

All measurements of parasite stages are given in microns. When length and width measurements are given, length is given first. Ranges are given in parentheses.

#### Experimental

Fish were procured from a single stock of 50-85 millimeter rainbow trout at the National Fish Hatchery, Ennis, Montana, on March 8, 1968.

The 500 fish obtained were held in hatchery troughs containing running water (5-11 C) until used in experiments.

A stamina tunnel made by the Bureau of Commercial Fisheries, Seattle, Washington, was used to test the swimming performance of experimental rainbow trout. This apparatus was modified and described by Fox (1965). Briefly, the tunnel was constructed of plexiglass, had a length of 132 centimeters and an inside diameter of 7.6 centimeters. Water was supplied by a centrifugal pump powered by an electric motor. Fish were stimulated to remain in the tunnel by an electrical field produced by three electrodes near the outlet. A sliding gate with three openings of different sizes was located at the outlet of the tunnel. The small opening was used for velocities of 0.12-0.30 m/sec., the intermediate for 0.30-0.76 m/sec., and the large for removing test fish from the chamber.

Fish to be used in tests were transferred from the troughs into 84 liter aquaria in which the water temperature could be controlled at desired levels (Fox, 1965).

Experimental fish were exposed to cercariae in the manner described above. Control fish were treated the same as experimental fish, but were not exposed to cercariae. Control and experimental fish were placed in the same aquaria so that they were indistinguishable until post-test necropsy.

After a period of at least two weeks at 21 C to allow rapid metacercarial growth, the water temperature was lowered to 11 C. Fish were transported about 8 kilometers to the Fish Hatchery Development

Center and were allowed at least two days to acclimate before tests were started.

The stamina tunnel was situated over a hatchery trough which had a continuous flow of water. Water was pumped from the upper end of the trough, through the tunnel and emptied into the lower end. Some reuse of water may have occurred, especially at high velocities when a larger volume was used, but no problems with metabolic waste, increased temperature, lowered oxygen etc. were encountered.

Test fish were held in a trough adjacent to the one on which the stamina tunnel was situated. One fish at a time was netted and placed in the experimental chamber. The water velocity was then raised to 0.30 m/sec. over a period of 5 minutes. At this time, the sliding gate was moved to the high velocity position and the electrical field activated. The water velocity was then slowly increased 0.03 m/sec. every 5 minutes until the test terminated. Fish were allowed two passes through the electrical field. After the first pass, fish were allowed 5 minutes to return to the velocity at which they failed and the test continued. The test terminated when one of the following occurred: 1. The fish passed through the electrical field and failed to return to the experimental chamber after the water velocity was reduced to zero and the electrical field inactivated. 2. The fish returned to the experimental chamber but did not reach the velocity at which it failed within the allowed 5 minute period. 3. The fish passed through the electrical field a second time.

At the completion of each test, the highest velocity attained and the total swimming time were recorded. Each test fish was measured to the nearest millimeter and a blood sample taken. Blood samples for use in hematocrit determinations were collected from the caudal artery after severing the caudal peduncle. Heparinized capillary tubes containing the blood sample were centrifuged at 12,500 r.p.m. for 5 minutes and hematocrit values obtained with a microhematocrit reader. All test fish were labeled and taken to the laboratory, frozen and later examined for parasites.

The ability of parasitized fish to withstand high water temperatures was compared with that of parasite-free fish using the constant temperature aquaria mentioned earlier. Experimental fish to be used in temperature stress tests were handled and exposed to cercariae as described above. Control fish were treated similarly but were not exposed to cercariae. A number of infected and control fish were then placed in each of two aquaria and held at 21 C. Oxygen was maintained at high levels throughout the experiment by bubbling air through an air stone. After allowing two weeks for metacercarial development, the temperature in each tank was raised 1 C every 24 hours. When a fish died, the temperature was recorded and the fish was frozen and later examined for parasites.

Fish used in experiments testing the ability to withstand oxygen depletion were handled and exposed as described above. After the period allowed for metacercarial development, 50 experimental fish (half infected, half control) were placed in a 84 liter aquarium and the air and inflow water turned off. The water temperature was 20.5 C. The oxygen level was

checked about once an hour with a Precision Galvanic Cell Oxygen Analyser. When a fish died, the oxygen level was recorded and the fish frozen and later examined for parasites.

## HISTORICAL ACCOUNT OF C. ERRATICUS

A historical account of Cotylurus erraticus (Rud., 1809) Szidat, 1928 is given by Dubois (1938). Some confusion arose among the early workers, due in part to the number of different hosts in which the parasite was found. All of the early work on C. erraticus was done in Europe and can be summarized as follows: The parasite was first described by Rudolphi in 1809 as Amphistoma erraticum from specimens that he found in the intestine of the red-throated loon, Larus septentrionalis (now Gavia stellata). Later, he observed specimens of the same parasite from the arctic loon (G. arcticus). In 1844, Bellingham described trematodes from the intestine of the common loon (G. immer) as A. gracile; these were actually C. erraticus. In 1845, Dujardin changed A. erraticum of Rudolphi to Holostomum erraticum. The name was changed again in 1909 to Strigea erratica by Lühe who reviewed the work reported by Brandes in 1888. Finally, in 1928, Szidat placed the parasite in the new genus Cotylurus characterized by vitellaria confined to the hindbody and a muscular bursa copulatrix.

Other European host records were found by Dubois (1938) who studied specimens in the Koningsberg collection. The trematodes found in the common gull (Larus canus) and the lesser black-backed gull (L. fuscus) were identified as C. erraticus.

Guberlet (1922), working in Oklahoma, described Strigea aquavis as a new species from the common loon (G. immer) and from the ring-billed gull (L. delawarensis). Szidat (1928) placed this parasite in the genus

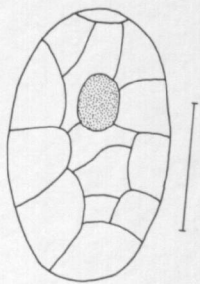
Cotylurus. Dubois and Rausch (1950) found the parasite in G. immer in Wisconsin and suggested that C. aquavis may be the same as C. erraticus. Dubois (1953) placed the two species in synonymy.

## DESCRIPTION AND LIFE CYCLE OF C. ERRATICUS

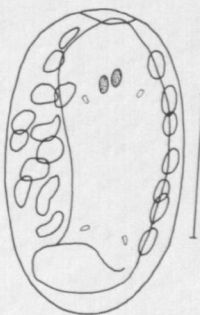
### Egg

The ovoid, operculate egg is amber in color. Ten eggs taken at random averaged 116 X 62 (105-122 X 60-65). These measurements are very similar to those reported by Szidat (1929) and Dubois (1938). Measurements of eggs given by Guberlet (1922) and Dubois and Rausch (1950) were slightly smaller. It may be that the latter were measured in utero since my measurements are slightly less for eggs in utero than for free eggs. An operculum in the open position measured 20 X 7 although the aperture of the hatched egg was 30 across. The aperture may increase in size after the operculum opens.

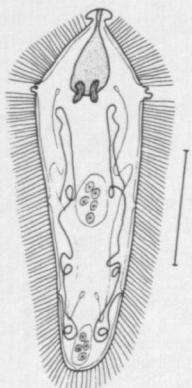
The egg is unembryonated when laid, with the ovum located in the anterior one-third. The rate of egg development depends on temperature as reported for many other strigeid trematodes. Eggs incubated at 24 C began hatching in 13 days, but most hatched in 15-16 days. Hatching was complete in 21 days. Lower temperatures resulted in a corresponding lengthening of incubation time. Eggs allowed to develop almost to hatching and then kept at 5 C for a month before returning to room temperature, showed good survival. Some of the eggs placed at 5 C immediately after collection and held for 1 to 2 months, resumed development upon return to warmer temperatures but survival was noticeably reduced. No eggs survived 12 months at 5 C. Survival was very low when eggs were incubated at 32 C.



1



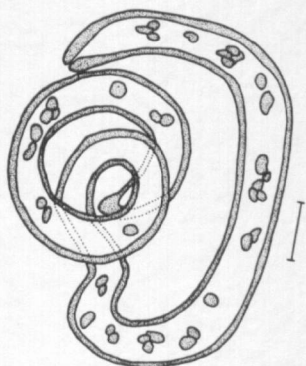
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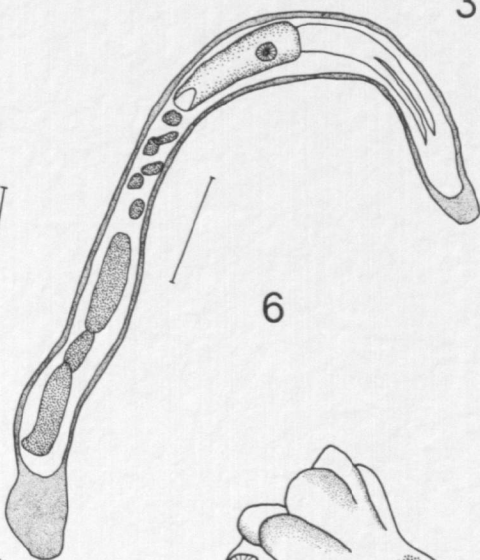
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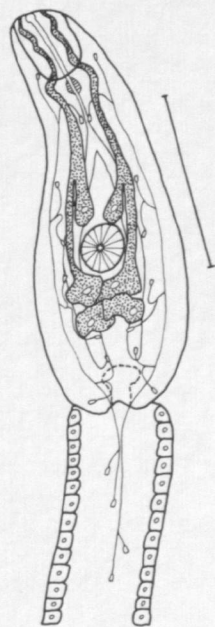
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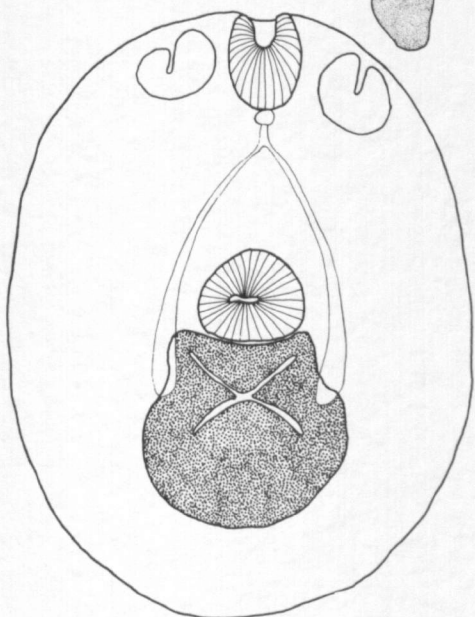
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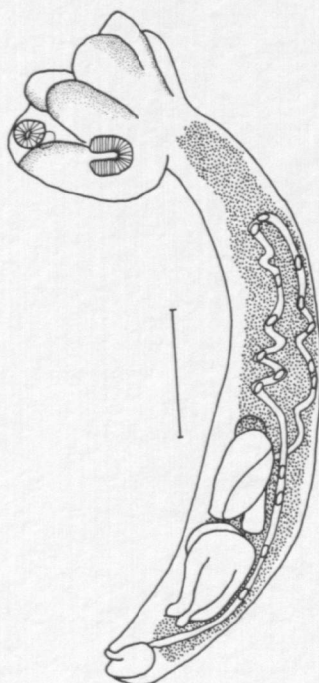
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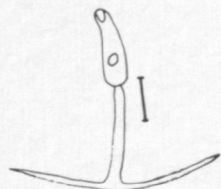
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## Explanation of Figures

All drawings made with the aid of a camera lucida.

- Fig. 1. Unembryonated egg. Scale = 50  $\mu$ .
- Fig. 2. Egg after twelve days of incubation at 24 C.  
Miracidium about ready to hatch. Scale = 50  $\mu$ .
- Fig. 3. Miracidium showing internal structure. Scale = 50  $\mu$ .
- Fig. 4. Miracidium showing epidermal plates. Scale = 50  $\mu$ .
- Fig. 5. Mother sporocyst, 44 days old and contains no developing daughter sporocysts. Scale = 100  $\mu$ .
- Fig. 6. Daughter sporocyst containing embryonic cercariae and one nearly mature cercaria. Scale = 100  $\mu$ .
- Fig. 7. Body of cercaria showing internal structure. Scale = 100  $\mu$ .
- Fig. 8. Entire cercaria showing relative size of furcae to body.  
Scale = 100  $\mu$ .
- Fig. 9. Metacercaria. Scale = 100  $\mu$ .
- Fig. 10. Adult. Scale = 500  $\mu$ .

## Miracidium

The development of the miracidium was studied within the egg and was similar to that observed for the miracidium of other strigeids (Huggins, 1954a, Fox, 1965). The developmental characteristics and measurements of representative individuals incubated at 24 C are described below.

First day: Ovum unembryonated (Fig. 1), 15 in diameter and located in the anterior one-third of the egg.

Second day: Ovum 30 in diameter and vitelline cells scattered throughout egg.

Third day: No apparent change.

Fourth day: Most ova still about 30 in diameter, but more rounded. Vitelline cells decreased in number.

Fifth day: Ovum 35 in diameter, vitelline cells absent, large clear cells surround ovum.

Sixth day: Ovum 45 in diameter and more centrally located within the egg.

Eighth day: Embryo showed form of miracidium. A representative individual measured 58 X 40, the eyespots and flame cells were barely discernible.

Tenth day: A representative embryo measured 88 X 45. Movement was observed for the first time. Eyespots were prominent and flame cells were more easily seen.

Twelfth day: Miracidium fully developed within the egg (Fig. 2). It was longer than the egg and the body was flexed at the posterior end so

that only approximate measurements were possible. One miracidium was 130 X 40. Eyespots had reached maximum size (12 X 5). Movement of the miracidium exerted pressure on the operculum.

Hatching occurred almost exclusively during the early evening hours. This is contrary to the observations of Huggins (1954a) for Hysteromorpha triloba and Van Haitsma (1930b) for Diplostomum flexicaudum. They reported that most miracidia hatched in the early morning hours and suggested that light and heat may play a role in hatching. I did not observe any relationship between either light or heat and hatching time. Temperature was held constant and hatching occurred at approximately the same time whether the room was illuminated or not. After hatching, miracidia appeared to be positively phototactic in that they consistently congregated near the surface and at the edge of the container nearest the light source. Freshly hatched miracidia rapidly swam in a straight line with a rotating motion. After about 6 hours, they swam more slowly and erratically. Most miracidia remained active for 12 hours after hatching and a few were observed to swim as long as 17 hours. Miracidia held at 5 C for 12 hours after hatching were immobilized, but regained activity upon return to room temperature. Most of these swam for as long as 12 hours following refrigeration.

The body of the miracidium is cylindrical and is widest at the level of the lateral papillae (Fig. 3). The anterior end is cone-shaped and contains a protrusible terebratorium. When extended, the terebratorium measures 16 X 10. The body tapers posterior to the lateral papillae and is quite narrow at the posterior end. Living miracidia were difficult to

measure due to their plasticity. Several fully extended individuals measured 175 X 40. Specimens fixed in AFA averaged 161 X 43 and ranged 150-175 X 37-50.

The epidermal plate pattern was 6:8:4:3 (Fig. 4). This pattern has been reported for most strigeid miracidia. Huggins (1954a) reviewed the literature concerning the epidermal plate patterns of strigeids. From this, it is doubtful that an absolute pattern exists.

The entire body of the miracidium is ciliated, with the exception of the area of the lateral papillae. Cilia are very short at the anterior end of the body and increase rapidly in length to about 12 at the level of the eyespots. They then decrease slightly in length to about 10 at the posterior end.

Two cup-shaped eyespots are located 25-30 from the anterior end and are 3-4 apart. They were observed to move within the miracidium, but always maintained their position relative to each other.

Two pair of lateral papillae extend out from the lateral margin of the miracidium at the level of the eyespots. Each anterior papilla measured about 2, each of the posterior pair were larger, and measured 5.

An oval area that appeared clear in living specimens extended back from the anterior edge of the eyespots and measured 30 in its greatest diameter. In mounted specimens, this area did not stain and so was conspicuous. This mass was termed a brain by Lynch (1933) and Huggins (1954a) while Pearson (1956) called it a neural mass.

The apical gland was somewhat flask-shaped and extended from the

terebratorium to the level of the eyespots. It was situated ventrally and, in part, behind the brain mass and was quite easily seen when supravitaly stained with neutral red. The presence of a single gland is consistent with most other strigeid miracidia. The miracidia of other groups of trematodes commonly have more than one gland.

Two clusters of cells contained in ovoid sacs were observed. Similar cells have been termed germinal cells in descriptions of other miracidia (Van Haitsma, 1930b; Cort, Ameel and Van der Woude, 1951; Huggins, 1954a; and Harris, Harkema and Miller, 1967). The miracidium of C. erraticus has a centrally located sac, 22 in length, containing 5 germinal cells and another sac in the posterior portion of the body, 20 in length, containing 4 germinal cells.

The excretory system consists of 2 pairs of flame cells and their connecting tubules. The anterior pair is located laterally and directed anteriorly at the level of the eyespots. The other pair is located in the posterior third of the body and is most often directed medially. The excretory capillaries on each side unite and empty into a main collecting tubule about equidistant between the two flame cells. The main collecting tubule follows a tortuous path anteriorly almost to the anterior flame cell, then bends and continues to the area of the posterior flame cell. The tubule bends anteriorly again for a short distance and empties through the excretory pore located 20 from the posterior end of the miracidium.

## Determination of First Intermediate Host

Eight species of gastropods and two species of sphaeriid pelecypods were collected from Georgetown Lake as potential first intermediate hosts of C. erraticus. These included: Amnicola limosa, Bulimus tentaculata, Valvata lewisi, Gyraulus sp., Helisoma trivolvis, Lymnaea palustris, L. stagnalis, Physa gyrina, Pisidium variable and Sphaerium sp. These molluscs were isolated according to species and checked for cercarial emergence. Furcocercous cercariae, characteristic of strigeid trematodes, were only observed to emerge from H. trivolvis, L. palustris, L. stagnalis, and P. gyrina. Rainbow trout were exposed to examples of all of these cercariae, but no infections with T. intermedia resulted. Determination of the snail host was next attempted by exposing snails to miracidia of C. erraticus in the laboratory. Experimental snails were observed for at least a month for the presence of natural infections and only uninfected individuals were used. Five to 10 miracidia per snail were used in exposure experiments. Infection occurred only in V. lewisi. The resulting furcocercous cercariae were allowed to penetrate rainbow trout. After 3 weeks at 21 C the trout were examined and encysted T. intermedia metacercariae were found in the pericardial cavity.

## Mother Sporocyst

Mother sporocysts were most often found loosely attached to the tissue of V. lewisi between the foot and the head and protruded into the mantle cavity. In a multiple infection, one mother sporocyst was found in the

usual location and two others were found loosely associated with the tissue of the digestive gland. They showed only sluggish movement.

C. erraticus mother sporocysts conform closely with the descriptions of a number of strigeid trematodes given by Cort and Olivier (1941). The body walls are relatively thick and a thick plug of tissue is present at each end. The birth pore is terminal at the anterior end. Two representative mother sporocysts, dissected from a snail exposed to miracidia 24 days previously, were 1500 and 2200 in length. They were not of uniform diameter and contained daughter sporocysts in various stages of development. The shorter one was 50 at the narrowest point and 80 at the widest, while the longer individual was 30 and 90. These mother sporocysts contained 11 and 15 daughter sporocysts respectively. A mother sporocyst dissected from a snail 44 days post-infection differed from the younger individuals in length (2750), in having uniform diameter and in containing no daughter sporocysts (Fig. 5). This individual was probably spent, since the digestive gland of the snail contained many daughter sporocysts and the small amount of cellular material in the body cavity of the mother sporocyst did not appear to be developing daughter sporocysts.

#### Daughter Sporocyst

Four daughter sporocysts obtained from a ruptured 24 day mother sporocyst were studied. None had developed cercariae but all contained round germ masses. These immature daughter sporocysts averaged 222 X 20.

Mature daughter sporocysts were dissected out of laboratory infected V. lewisi from which cercariae were emerging. The walls of the daughter sporocyst are slightly thinner than those of the mother. There are tissue plugs about 40 long at each end and the birth pore is located 175 from one end. Cercariae were often observed protruding from both ends of daughter sporocysts but in these cases, it appeared that the sporocysts were ruptured during dissection. Sporocysts are found in tangled masses throughout the tissue of the digestive gland. Movement of mature cercariae within the sporocysts often gave the appearance that the latter were highly motile. Actually, sporocysts are capable of only sluggish movement like that of the mother.

Five daughter sporocysts which contained mature cercariae (Fig. 6) averaged 1240 X 77 and ranged 800-1750 X 55-90. These contained 1-4 well developed cercariae and 0-8 embryonic cercariae. One young daughter sporocyst measured 300 X 50 contained 12 germ balls. A sporocyst, 2000 in length and unequal in width (25-60), appeared nearly spent. It contained 4 well developed cercariae, but no germ balls or developing cercariae. According to Hunter and Hunter (1935), unequal width caused by constrictions and irregularities is an indication of old age.

The time from snail infection until cercariae first emerged varied from 26-44 days and averaged 35 days. Fluctuations in temperature probably caused this variation.

After cercariae had emerged for about a month, snails usually died; however several individuals produced cercariae for a much longer period.

Cercariae emerged from one snail for 147 days and from another for 127 days. Daughter sporocysts probably remain active for the life of the snail.

### Cercaria

The pharyngeate, furcocercous cercaria of C. erraticus (Fig. 7, 8) is similar in size to that of Bolbophorus confusus (Fox, 1965). Average measurements of 10 cercariae fixed in AFA were as follows: Body 258 X 55 (230-280 X 50-60), tail stem 276 X 32 (270-290 X 30-35), furcae 252 X 22 (220-275 X 20-23), oral sucker 48 X 27 (43-52 X 25-30), and diameter of acetabulum 26 (23-30).

The anterior third of the oral sucker is spinose. Spines surround the oral opening, but heavy forward pointing spines reported at the oral opening of H. triloba by Huggins (1954b) were not observed. A ring of spines surround the acetabular opening. No body spination was found.

The mouth cavity opens subterminally at the anterior end of the oral sucker, runs posteriorly through the sucker and leads into a short pre-pharynx. The pharynx is 11 in diameter. The esophagus leads posteriorly, bifurcating approximately 85 from the anterior end of the body. The two caeca continue posteriorly, dorsal and lateral to the acetabulum, and terminate just anterior to the excretory bladder.

Three pairs of penetration glands are present. These stain readily with neutral red. The anterior pair is pre-acetabular and the two posterior pairs are post-acetabular. This arrangement is similar to that observed by Dönges (1964) in the cercaria of Posthodiplostomum cuticola.

It is interesting that the life cycle reported by Van Haitsma (1930a) for C. platycephalus was questioned by Szidat (1931) because the penetration glands of the cercaria were post-acetabular and not pre-acetabular as in another member of the genus, C. cornutus. The penetration glands of C. erraticus are both pre- and post-acetabular. The ducts of the penetration glands extend anteriorly from the glands, become convoluted, and enter the oral sucker.

There are eight pairs of flame cells in the body and two pairs in the tail stem having a formula of  $2\sqrt{(2+2)+(2+2)}+2=20$ . The position of the body flame cells is as follows: one pair at the posterior end of the oral sucker, one midway between the pharynx and the bifurcation of the esophagus, two just anterior and lateral to the acetabulum, two lateral to the post-acetabular penetration glands, and two in the region of the excretory bladder. The two pairs of tail stem flame cells are situated somewhat in tandem in the anterior half of this structure. The excretory bladder, located at the posterior end of the body, was observed to change shape but was usually ovoid and measured 25 X 15.

The tail stem is bounded by large cuboidal cells and contains centrally located longitudinal muscle fibers. Sensory hairs on the tail stem and spines on the furcae often described for strigeid cercariae were not observed.

Cercariae emerged during the day and night, but greater numbers emerged during the early morning hours than at any other time. The number of cercariae emerging from individual snails varied from 30-50 in a 24 hour

period. Longevity of cercariae was about 22-24 hours, but active swimming began to decrease after 15 hours. The attitude assumed in the water is characteristic of other furcocercous cercariae with the body downward and bent hook-like, the tail stem upward and the furcae spread perpendicular to the tail stem. In 26 C water, the cercariae swim rapidly for 1-3 seconds with a vibratory motion that carries them upward and then they rest for 5-8 seconds.

#### Metacercaria

The metacercaria of C. erraticus was originally described by Hughes (1928). He placed it in the larval genus Tetracotyle and named it T. intermedia because it was intermediate in size between the two other forms (T. communis and T. diminuta) described at the same time. The larval genus Tetracotyle was characterized by Hughes (1927) as strigeid metacercariae having lateral cotylae, a slightly developed hindbody and a reserve bladder consisting of an irregular network of spaces instead of definite tubules. He found the metacercaria in the pericardium of the round whitefish and cisco of the family Salmonidae. Hereafter T. intermedia is referred to as C. erraticus metacercaria. In Georgetown Lake, the metacercaria is also limited to this family including rainbow trout, brook trout, grayling, kokanee salmon and coho salmon. The metacercaria of C. erraticus has also been reported in Russia (Bykhovskaya-Pavlovskaya, et al., 1962), but the key character given, "ventral sucker smaller than oral", does not obtain for either the specimens of Hughes or for mine. The Russian report may not be the metacercaria of C. erraticus.

All salmonid fishes collected from Georgetown Lake during 1965 and 1966 were infected with C. erraticus metacercariae, but quantitative records were not kept. Most fish collected during 1967-68 were weighed, measured and the number of parasites determined. In infections of 100 or less, accurate counts could be made. Approximate (+ or - 25) counts were made in heavy infections. Based on the opportunity of fish for infection, the data were divided into two parts: 1. Those including fish produced or stocked in the lake--probably present in the lake over one year. These include kokanee salmon, brook trout and rainbow trout over 20 cm in length; 2. Those fish likely to have been recently stocked. These include arctic grayling, coho salmon and rainbow trout under 20 cm. Those with a long period of exposure showed the highest prevalence (100%) and intensity (up to 2500 parasites) of infection (Table I). Those with a short period of exposure

TABLE I. INTENSITY AND PREVALENCE OF C. ERRATICUS METACERCARIAE IN SALMONIDS FROM GEORGETOWN LAKE (Ranges in parentheses)

| Species        | No. of fish | Avg. length (cm) | Avg. weight (g)  | Avg. No. of parasites | % infected |
|----------------|-------------|------------------|------------------|-----------------------|------------|
| Rainbow trout  | 56          | 25<br>(20-36)    | 246<br>(96-682)  | 522<br>(75-2500)      | 100%       |
| Kokanee salmon | 14          | 27<br>(19-37)    | 273<br>(90-558)  | 317<br>(100-800)      | 100%       |
| Brook trout    | 19          | 24<br>(13-38)    | 251<br>(35-1000) | 214<br>(7-1300)       | 100%       |

were divided into two time periods. The first contained fish collected 1-2 months after stocking (July), and the second contained fish collected 4-5 months after stocking (September and October). These data show a greater prevalence (50% to 100%) and intensity (0 to 600) of infection in fish with the longest duration in the lake (Table II). Twenty-two 6-11 cm

TABLE II. NATURAL INFECTION OF FISH WITH C. ERRATICUS METACERCARIAE DURING TWO COLLECTING PERIODS (Ranges in parentheses)

| Species         | No. | Avg. length (cm)  | Avg. weight (g) | Avg. No. of parasites | % infected |
|-----------------|-----|-------------------|-----------------|-----------------------|------------|
| July            |     |                   |                 |                       |            |
| Rainbow         | 13  | 14.7<br>(13-17)   | 48<br>(32-68)   | 2.7<br>(0-13)         | 69.2%      |
| Arctic Grayling | 6   | 16.2<br>(15-18)   | 50<br>(42-67)   | 7.2<br>(0-30)         | 83.3%      |
| Coho Salmon     | 2   | 13.2<br>(12.5-14) | 33<br>(26-38)   | 1<br>(0-2)            | 50%        |
| Sept.-Oct.      |     |                   |                 |                       |            |
| Rainbow         | 17  | 18.6<br>(17-18)   | 87<br>(65-106)  | 97<br>(38-250)        | 100%       |
| Arctic Grayling | 14  | 19.7<br>(18-22)   | 92<br>(65-140)  | 275<br>(85-600)       | 100%       |
| Coho Salmon     | 5   | 17.6<br>(14-19.5) | 80<br>(40-107)  | 160<br>(125-200)      | 100%       |

brook trout were collected on August 31, 1966 and examined for C. erraticus metacercariae. Nine (40.9%) were infected with an average of four parasites per fish. All observations show that the intensity of infection is not high in young trout. The larger and presumably older fish had the greatest

number of parasites. The average number of parasites per fish (rainbow trout) for three length groups is as follows: 56 for 30 fish under 20 cm, 374 for 39 fish 20-28 cm and 844 for 18 fish over 28 cm.

Both living and mounted metacercariae (Fig. 9) were studied. Slight variation in the size of metacercariae may result from development in different host-fish and from the method of fixation. Measurements of living metacercariae from laboratory infected rainbow trout were compared with measurements of those from brook trout, kokanee salmon and laboratory infected rainbow trout fixed in AFA and mounted. Living specimens under cover glass pressure were consistently larger than fixed and mounted specimens. Fixed specimens from naturally infected brook trout and kokanee salmon were slightly smaller than those from laboratory-infected rainbow trout. Average measurements and ranges and those given by Hughes (1928) are given in Table III. Parasite cyst measurements averaged 630 X 445 and ranged 600-700 X 425-475.

According to the key given by Hoffman (1967), the lateral cotylae of C. erraticus metacercariae are "decidedly smaller than the oral sucker". In my specimens, the lateral cotylae are equal to or slightly longer than the oral sucker (Table III). This difference may have resulted because Hughes (1928) reported the size of the cavity of the lateral cotylae and not that of the cotylae themselves. I examined the type specimens (Hughes) and found that the lateral cotylae were not smaller than the oral sucker.

Metacercariae freed from the cyst exhibit very active leech-like movements, but make very little progress in any direction. The reserve

TABLE III. AVERAGE MEASUREMENTS ( $\mu$ ) OF C. ERRATICUS METACERCARIAE  
(Ranges in parentheses)

|  | No. of specimens | Body                                | Holdfast organ                     | Acetabulum                    | Oral sucker                   | Lateral cotylae length |
|--|------------------|-------------------------------------|------------------------------------|-------------------------------|-------------------------------|------------------------|
| Living specimens from laboratory infected rainbow trout  | 10               | 472 X 400<br>(410-530 X<br>290-480) |                                    |                               |                               |                        |
| Mounted specimens from laboratory infected rainbow trout | 5                | 430 X 366<br>(360-460 X<br>300-420) | 92 X 184<br>(80-110 X<br>110-140)  | 51 X 66<br>(40-67 X<br>50-75) | 60 X 54<br>(55-62 X<br>50-60) | 59<br>(55-62)          |
| Mounted specimens from naturally infected brook trout    | 10               | 394 X 300<br>(350-430 X<br>250-340) | 99 X 111<br>(90-110 X<br>90-130)   | 58 X 70<br>(50-60 X<br>60-80) | 57 X 58<br>(50-60 X<br>50-70) | 59<br>(55-62)          |
| Mounted specimens from naturally infected kokanee salmon | 22               | 372 X 300<br>(290-440 X<br>200-360) | 102 X 118<br>(90-140 X<br>100-150) | 50 X 72<br>(50-60 X<br>55-90) | 56 X 56<br>(45-70 X<br>40-60) | 60<br>(56-62)          |
| Living specimens measured by Hughes (1928)               | 5                | 480 X 440<br>(370-590 X<br>300-600) |                                    |                               |                               |                        |
| Mounted specimens measured by Hughes (1928)              | 8                | 380 X 300<br>(300-420 X<br>250-330) | 74 X 105<br>(70-80 X<br>90-110)    | 57 X 66<br>42-66 X<br>56-77)  | 59<br>(43-63)                 | 56*<br>(53-60)         |

\* Measurements made during this study from 5 type specimens (Hughes).

bladder containing small granules and larger calcareous bodies obscures much of the internal structure in living specimens. The pharynx is visible immediately posterior to the oral sucker and a short esophagus leads from it to the caeca which extend to the level of the hold-fast organ and terminate dorsal to it. Numerous flame cells were observed but the number and pattern were not determined. A detailed description of the internal structure of the C. erraticus metacercaria is given by Hughes (1928).

Metacercariae became encysted in the pericardial cavity of laboratory infected rainbow trout in 2-3 weeks at 21 C. In heavy infections a few metacercariae were observed to encyst in the mesenteries of the pyloric caeca in close proximity to the pericardium. None were observed elsewhere in the body, but a complete examination of all specimens was not made. No metacercariae were observed in the heart muscle.

#### Determination of Final Host

A number of aquatic birds were collected from Georgetown Lake in an effort to determine the final host and adult stage of T. intermedia. These included: Red-necked grebe (Podiceps grisegena), American coot (Fulica americana), common tern (Sterna hirundo), California gulls and ring-bill gulls. One immature California gull contained over 900 C. erraticus in the small intestine and another, found dead, was infected with over 2500 C. erraticus. To determine the relationship between T. intermedia and C. erraticus in the laboratory, 4 immature California gulls were collected at Freezeout Lake, Montana. After ensuring that

these birds were free of natural trematode infections, they were fed T. intermedia metacercariae. After 4 days, the gulls began passing large numbers of trematode eggs. One bird died and C. erraticus adults were found in the small intestine. It was concluded that the adult form of T. intermedia is C. erraticus.

Some type of immunity develops in gulls infected several times in the laboratory. One bird infected 6 different times gave the following results relative to duration of infection. The first infection lasted 14 days. After 2.5 months, a second infection lasted 10 days and a third infection, after 2.5 months, lasted 5 days. A fourth infection was attempted 10 days after the third terminated and no egg producing adults resulted. Three months later, a fifth infection lasted 5 days and after one year, a sixth infection (extremely light) lasted 3 days. This trend was also observed in two other gulls.

#### Adult

The adult worm (Fig. 10) is divided into a forebody and a hindbody. The forebody is bulbular in shape and is lobulated. The hindbody is cylindrical, often curved and "C" shaped. Measurements of 20 mounted specimens are as follows: Total length 3050 (2310-4080); forebody 590 X 830 (450-880 X 600-1200); hindbody 2450 X 670 (1750-3200 X 530-850); ratio hindbody/forebody 4.16 (3.12-6.33); diameter of oral sucker 127 (100-170); diameter of pharynx 72 (58-90); diameter of acetabulum 195 (140-250); ovary 159 X 193 (130-190 X 180-210); anterior testis 409 X

396 (330-500 X 280-520); posterior testis 586-408 (450-700 X 250-500).

These measurements are consistent with those reported by Guberlet (1922), Szidat (1929), Dubois (1938) and Dubois and Rausch (1950).

The oral sucker is terminal in the forebody, with the pharynx immediately posterior to it. The acetabulum is situated centrally and somewhat ventrally in the forebody.

Vitellaria fill much of the hindbody and extend from the bursa copulatrix anteriorly to the forebody. They usually do not enter the forebody, but appear to extend to its base in a few individuals. The ovary is nearly round and is located about in the middle of the hindbody just anterior to the anterior testis. The uterus originates at the level of the anterior testis, follows a sinuous path anteriorly nearly to the anterior end of the hindbody where it bends back on itself and continues to the posterior end of the hindbody, opening into the genital pore in the area of the muscular bursa copulatrix. The paired testes are situated in tandem just posterior to the ovary. Each is divided into 3 or 4 lobes which are directed posteriorly. The posterior testis is consistently larger than the anterior. Detailed descriptions of C. erraticus are given by Guberlet (1922) and Dubois (1938).

## EFFECTS OF C. ERRATICUS METACERCARIAE ON RAINBOW TROUT

Fish infected with C. erraticus metacercariae in Georgetown Lake showed no gross effects of the parasite. However, it was suspected that infections in young salmonids could be debilitating. Other investigators have found that heavy infection of metacercariae may be lethal to small fish (Krull, 1934; Klak, 1939; Hoffman, 1956, 1958; Hoffman and Hundley, 1957; Bennington and Pratt, 1960; Farrell and Lloyd, 1962; Olson, 1966; and Baldwin et al., 1967). Sublethal effects of metacercariae on fish have also been reported. Wood and Yasutake (1956) stated that salmon fingerlings infected with Nanophyetus salmincola were physiologically weakened. Smitherman (1964) reported that the "functional state" of the bluegill (Lepomis macrochirus) was altered when infected with Posthodiplostomum minimum. This was indicated by increased mortality, decreased growth rate, increased oxygen consumption of liver tissue and decreased hematocrit levels. Fox (1965) studied the sublethal effects of B. confusus metacercariae on rainbow trout. He found that parasitized fish did not swim as long or reach as high a velocity as did parasite-free fish when tested in a stamina tunnel. Average hematocrit values of parasitized trout were lower than those of parasite-free trout and uninfected trout were able to survive at higher water temperatures than were infected trout.

### Swimming Performance

Swimming performance of salmonids has been related to dissolved oxygen and temperature by Gibson and Fry (1954), Katz et al. (1959), and Davis et al. (1963); to dissolved oxygen and carbon dioxide by Basu (1959) and Dahlberg et al. (1968), and to fatigue time and temperature by Brett (1967). The only previous study relating swimming performance to infection with trematode metacercariae was by Fox (1965).

The swimming ability of rainbow trout infected with C. erraticus metacercariae was compared with that of parasite-free trout. Experimental fish were divided into two groups based on the intensity of infection. Although the parasitized fish swam longer and reached a higher velocity than the parasite-free fish in both groups (high and low infection), the differences were small (Table IV). It was concluded that the parasite did not influence the swimming performance of rainbow trout in these experiments.

### Hematocrit

Hematocrit values were obtained for blood taken from each fish at the termination of the swimming performance test. The results showed that the average hematocrit value for 43 parasitized trout was 34.0 and for 45 parasite-free trout, 34.9.

### Temperature Tolerance

The ability of rainbow trout infected with C. erraticus metacercariae to withstand high temperatures was compared to uninfected controls.

TABLE IV. THE EFFECT OF *C. ERRATICUS* METACERCARIAE ON SWIMMING PERFORMANCE OF RAINBOW TROUT (Ranges in parentheses)

|                  | No. fish | Avg. Length (mm) | Avg. Weight (g)     | Avg. No. parasites | Swimming time (min) | Maximum velocity reached (m/sec) |
|------------------|----------|------------------|---------------------|--------------------|---------------------|----------------------------------|
| Lot I.           |          |                  |                     |                    |                     |                                  |
| Parasite-free    | 25       | 65.4<br>(58-72)  | 2.48<br>(1.30-3.44) | 0                  | 64.7<br>(28-91)     | .62<br>(.40-.76)                 |
| Parasitized      | 25       | 66.4<br>(54-83)  | 2.81<br>(1.39-5.60) | 120.5<br>(33-194)  | 69.8<br>(36-92)     | .65<br>(.46-.76)                 |
| Lot II.          |          |                  |                     |                    |                     |                                  |
| Parasite-free    | 20       | 65.6<br>(56-83)  | 2.77<br>(1.76-5.33) | 0                  | 55.5<br>(11-84)     | .56<br>(.30-.70)                 |
| Parasitized      | 18       | 66.1<br>(60-78)  | 2.94<br>(2.18-5.00) | 414.2<br>(267-526) | 56.1<br>(10-78)     | .57<br>(.30-.70)                 |
| Combined Average |          |                  |                     |                    |                     |                                  |
| Parasite-free    | 45       | 65.5<br>(56-83)  | 2.61<br>(1.30-5.33) | 0                  | 60.6<br>(11-91)     | .59<br>(.30-.76)                 |
| Parasitized      | 43       | 66.3<br>(54-83)  | 2.87<br>(1.39-5.60) | 243.4<br>(33-526)  | 64.1<br>(10-92)     | .62<br>(.30-.76)                 |

Twenty-three infected and 25 control trout were tested. One infected fish died when the water temperature reached 27 C. The other 22 infected and the 25 control fish survived at a temperature of 28 C for at least 8 hours and then died within a 4 hour period (Table V). High temperature tolerance of rainbow trout apparently was not influenced by the parasite.

TABLE V. THE EFFECT OF HIGH WATER TEMPERATURE ON RAINBOW TROUT PARASITIZED WITH C. ERRATICUS METACERCARIAE (Ranges in parentheses)

| Tempera-<br>ture at<br>death<br>(C) | Parasitized Trout  |                        |                       |                       | Parasite-free Trout |                        |                       |
|-------------------------------------|--------------------|------------------------|-----------------------|-----------------------|---------------------|------------------------|-----------------------|
|                                     | No.<br>Fish        | Avg.<br>length<br>(mm) | Avg.<br>weight<br>(g) | Avg. No.<br>parasites | No.<br>fish         | Avg.<br>length<br>(mm) | Avg.<br>weight<br>(g) |
| 21-26                               | No deaths occurred |                        |                       |                       |                     |                        |                       |
| 27                                  | 1                  | 54                     | 1.38                  | 113                   | 0                   | -                      | -                     |
| 28                                  | 22                 | 67.7<br>(54-80)        | 3.66<br>(1.74-6.50)   | 133<br>(81-201)       | 25                  | 68.7<br>(58-83)        | 3.95<br>(2.22-6.22)   |

#### Low Oxygen Tolerance

The ability of rainbow trout infected with C. erraticus metacercariae to withstand low dissolved oxygen levels was compared with uninfected trout in an aquarium in which the water was allowed to stagnate. Twenty-three parasitized and 26 parasite-free trout were tested. The dissolved oxygen concentration was 7.26 ppm at the beginning of the experiment and dropped progressively over the next 8 hours to 1.86 ppm. Four trout (2 infected, 2 uninfected) died when this low level was reached. The dissolved oxygen concentration dropped to 1.74 ppm during the next hour and remained there for 3 hours. Thirty-three fish (17 infected and 16 uninfected) died during this period. The dissolved oxygen increased to 1.88 ppm during the next 8 hours and 10 trout (4 infected and 6 uninfected) died. Two uninfected trout survived the test (Table VI). Ammonia and carbon dioxide concentrations were not monitored during the oxygen depletion test and may have influenced the results. The fish were nevertheless stressed and the parasite was not

shown to influence the ability of rainbow trout to withstand the lowering of dissolved oxygen.

TABLE VI. THE EFFECT OF LOW DISSOLVED OXYGEN ON RAINBOW TROUT PARASITIZED WITH C. ERRATICUS METACERCARIAE (Ranges in parentheses)

| O <sub>2</sub> level<br>at death<br>(ppm) | Parasitized Trout  |                        |                       |                       | Parasite-free Trout |                        |                       |
|---|--------------------|------------------------|-----------------------|-----------------------|---------------------|------------------------|-----------------------|
|   | No.<br>fish        | Avg.<br>length<br>(mm) | Avg.<br>weight<br>(g) | Avg. No.<br>parasites | No.<br>fish         | Avg.<br>length<br>(mm) | Avg.<br>weight<br>(g) |
| 7.26-<br>1.86                             | No deaths occurred |                        |                       |                       |                     |                        |                       |
| 1.86                                      | 2                  | 72<br>(70-74)          | 4.20<br>(3.80-4.60)   | 54.5<br>(44-65)       | 2                   | 67.5<br>(66-69)        | 3.31<br>(3.02-3.65)   |
| 1.74                                      | 17                 | 69.6<br>(55-86)        | 4.01<br>(2.20-7.86)   | 79.5<br>(33-141)      | 16                  | 73.6<br>(61-81)        | 4.59<br>(2.52-5.94)   |
| 1.88                                      | 4                  | 65.7<br>(56-71)        | 3.55<br>(2.22-4.43)   | 74.5<br>(55-92)       | 6                   | 71.1<br>(64-82)        | 4.15<br>(3.06-6.23)   |

## DISCUSSION

According to tests it takes 10-12 weeks for the completion of the C. erraticus life cycle at temperatures near 20 C. Georgetown Lake has a surface water temperature of 18-21 C from July to September. Since the lake is shallow and mixes during the open-water season, it is probably homothermous. These relatively high temperatures may account for the high success of C. erraticus in Georgetown Lake and allow completion of the life cycle in one open-water season. Such favorable temperatures may not be absolutely necessary for the maintenance of the parasite since at least some snails carry infections over-winter as evidenced by fish infected in early July.

Although C. erraticus is well established in Georgetown Lake and V. lewisi is very abundant, no naturally infected snails were found. The snail is most often found associated with vegetation at a depth of 1-4 meters and was collected in large numbers. Collections were confined to relatively small areas and the probability of missing infected snails was high. The incidence of infection in a large population could be extremely low and still include a large total number of infected snails. If other species of fish-infecting tetracotyles utilize Valvata as the first intermediate host, a low incidence of infection could explain why the snail hosts for these parasites have not been reported.

This is the first report of C. erraticus metacercaria from Montana. The parasite may be specific for salmonids (Hughes, 1928), since the other species of fish (longnose sucker and redbside shiner) in the lake

were not infected with this metacercaria. The complete life cycle of C. erraticus may occur in other mountain lakes, but the combination of proper hosts and suitable temperatures is quite restrictive. Temperature was believed to play an important part in the localization of another trematode, B. confusus, in Montana (Fox, 1965 and Olson, 1966).

The apparent immunity produced in laboratory infected gulls and the fact that naturally infected adult gulls were not collected could indicate that the gull is not the best final host. C. erraticus has been reported more often from loons than from gulls (Guberlet, 1922; Dubois, 1938; and Dubois and Rausch, 1950). Although loons are known to inhabit Georgetown Lake, none were observed during the present study. It is possible that loons introduced the parasite into the area and gulls have maintained and intensified its occurrence.

Relatively small summer fish mortalities have been reported in Georgetown Lake on a number of occasions. Based on my limited experimental evidence, the parasite was probably not instrumental in causing these fish kills.

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