THE LIFE CYCLES OF
ALASSOCONOPORUS VESPERTILIONIS MACY
AND ACANTHATRUM OREGONENSE MACY
(TREMATODA: LECITHODENDRIDAe)

by

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THE LIFE CYCLES OF ALLASSOGONOPUS VESPERTILIIONIS MACY
AND ACANTHATRUM OREGONENSE MACY
(TREMATODA: LECHIODENDRITIDAE)

INTRODUCTION

Allassogonopus vespertilionis Macy and Acanthatrium oregonense Macy are lechiodendrid trematodes parasitizing the small intestines of various species of bats. Macy described Allassogonopus vespertilionis in 1940, and Acanthatrium oregonense in 1939.

Allassogonopus vespertilionis is the second species described in the genus which was established in 1938 by Olivier with A. marginalis, which is parasitic in muskrats (10, p. 155-160).

The genus Acanthatrium was set up by Faust (3, p. 209-215) in 1919 with A. nycteridis, parasitic in bats. Since the erection of the genus six species have been discovered and placed in it; one described by Looss in 1896, A. sphaerula, has been shifted from another genus. Macy (6, p. 282) gave a key for the known species of Acanthatrium.

Trichopteran larvae are known to serve as the intermediate host for members of the families Plagiorchidae, Lecithodendriidae, Allocreadiidae, and Brachycoceliidae.

Lecithodendrium chilostomum, probably the oldest species in the family, was first described in 1831 by Mehlis under the name of Distoma chilostomum. Braun, in 1900, moved D. chilostomum to a new genus, Lecithodendrium, set up by Looss the previous year when he
described *L. lagena*.

The life cycle of *Lecithodendrium chilostomum* was first investigated by Skriabine in 1915, as cited by Brown (1, p. 517), when he discovered the metacercariae in caddis larvae of the genus *Phryganea*. Brown, in 1933, did more work on the metacercariae found in the caddis larvae. He traced the metacercariae through the caddis larva, pupa, and imago. The life cycles of *Lecithodendrium chilostomum* and *Acantho- trrium oregonense* are very similar.

The aim of this study was to trace the life stages of a cercaria found in *Oxytrema silicula* (Gould), which proved to be *Acanthotrium oregonense*, and of a cercaria in *Fluminicola virens* (Lea), which was found to be *Allassogonoporus vespertilionis*, to determine what the species were and the hosts involved in the life cycles.

Originally the problem included only the cercaria found in *Oxytrema silicula*, but in the process of working out the life cycle of that cercaria another closely connected life cycle was encountered. Within the caddis larvae were found two metacercariae which developed into adults when fed to a hamster, therefore it became necessary to work out both cycles to be certain of either one.

Some additional notes were amended to the original description of the adult *Acanthotrium oregonense* concerning its esophagus and excretory bladder.
METHODS AND MATERIALS

Infected snails of species *Oxytremia silicula* (Gould) were collected as needed from the upper Alsea River near the Alsea fish hatchery fifteen miles west of Philomath, Oregon; from Rock Creek located two miles west of Philomath; and from the upper Yaquina River six miles from Summit, Oregon, in Lincoln County, throughout the period from September 1953 to August 1954. The snails were placed in aquaria of stream water which was aerated by an electric pump to provide air. The aquaria were kept at 11°C., approximately, by placing them in a bath of cold running tap water. To find snails infected with the desired cercariae they were segregated in individual dishes, and the water was allowed to warm to room temperature. After several hours or days a few drops of water from the bottom of the dish, when examined beneath a microscope would disclose whether or not the snail in question was infected with the desired cercariae.

Fish and copepods were tried unsuccessfully as the intermediate host for the cercaria. Because the cercaria crept about on the substratum rather than swam free, a collection of the animal life existing on the stream bottom was made and examined. Within caddis fly larvae of the genus *Limmophilus* were found metacercariae similar to the cercaria from *Oxytremia silicula*. When the caddis larvae were fed to the hamster, two adult worms, *Allasogonoporus vespertilionis* and *Acantharium oregonense*, developed in the small intestine. Closer examination of the caddis larvae revealed a second, encysted
metacercaria present. Another species of the Limnophilus caddis larvae was collected from the Metolius River in Jefferson County, Oregon; and from Indian Ford, roughly five miles west of Sisters, Oregon, on the Santiam Highway. These larvae proved to be free from any metacercariae of any type. The caddis larvae were placed in bowls of stream water with several Oxytricha silicula discharging the cercaria. When examined next day the Limnophilus larvae contained immature metacercariae which were recognized as the ones giving rise to Acantharium oregonense. A collection of the other common snail, Fluminicola virans (Lea), present also in the same area of the Alsea River, was made to attempt discovery of the cercaria producing Allassogonoporus vespertilionis. The snails were crushed in a watch glass with a few drops of water and examined for cercariae. Several different ones were found, and eventually a cercaria was seen which possessed characters present in the metacercaria and adult. Several Fluminicola virans infected with this cercaria were placed with some uninfected Limnophilus from eastern Oregon, and the next day upon examination the caddis larvae were found to be infected with the metacercaria of Allassogonoporus vespertilionis.

Sexually mature Acantharium oregonense and Allassogonoporus vespertilionis were recovered from the bat Myotis lucifugus (LeConte) captured in an attic near Peoria, Oregon; and one mature Allassogono-
porus vespertilionis was recovered from the bat Eptesicus fuscus (Beauvois) which was shot near Irish Bend on the Willamette River, twelve miles south of Corvallis.
Golden hamsters were used as experimental definitive hosts. They were kept in standard laboratory cages, and were fed Purina Laboratory Chow. The adult flukes were recovered from the small intestine of the hamster by agitating the opened intestine in distilled water.

Measurements and observations were made of living material. The sporocysts, cercaria, and metacercaria were stained with neutral red vital stain in a few drops of water to which enough stain of a 0.1% solution was added to very faintly tint the water.

Adult flukes were fixed in an alcohol-formalin-acetic acid mixture without flattening, and then were stored in the same mixture, except those subsequently stained and mounted. Whole mounts of the adult flukes were stained with Mayer's carmalum or Harris' hematoxylin.

The measurements of the sporocyst, cercaria, and metacercaria were made with a measuring eye-piece. The drawings were made with the aid of a camera lucida or microprojector to assure proper sizes and proportions. Details of anatomy were drawn in free-hand to complete the figure. A pantograph was employed to bring the drawings of a series to the same scale to show relative size.
DATA

_Allassogonoporus vespertilionis_ Macy_

The adult worm. One sexually mature _Allassogonoporus vespertilionis_ (pl. 2, fig. 1) was recovered from the intestine of the bat _Eptesicus fuscus_, and several were recovered from the intestine of _Myotis lucifugus_. In both cases, however, the individuals were considerably smaller and contained fewer eggs than ones which had developed in a hamster for three weeks; possibly indicating that the infection was relatively recent. Six _E. fuscus_ were collected south of Corvallis, Oregon, and one of them had the single specimen of _A. vespertilionis_ along with many flukes of several species within it. Ten _M. lucifugus_ were collected near Peoria, Oregon, and all contained _A. vespertilionis_. Macy (7, p. 43) originally discovered the fluke in _M. californicus caurinus_, collected near McMinnville, Oregon, in 1938. He found 70 specimens in that individual host. Several hundred specimens were collected from hamsters experimentally infected; the hamster appears to be an excellent host for this worm.

The anatomy and size of the worm agree with that given by Macy in his original description of the species.

Ova. The eggs within the uterus are small, ovoid, brown, and at maturity measure 0.027 mm. by 0.012 mm. The eggs are non-embryonated, and an operculum is present. The adult worms could not be forced to
shed their eggs and when placed into distilled water died retaining all of them.

Sporocysts. The sporocysts (pl. 2, fig. 2) obtained from the digestive glands of Fluminicola virens contained cercariae in varying stages of development. No redia were seen at any time, as was expected since Xiphidiocercariae do not develop within redia (2, p. 446). The sporocysts averaged 0.32 mm. long by 0.14 mm. wide, but ranged in size from 0.22 to 0.41 mm. long by 0.12 to 0.15 mm. wide. The number of mature cercariae within the sporocyst varied from 1 to 3 with the larger sporocysts containing larger number of mature cercariae.

Cercaria. Live cercariae were obtained for study by isolating the snails in different containers of stream water. As the water warmed the snails began to shed the cercariae. The cercariae of Allasagronoporus vespertilionis belong to the cercariae virgulae group established by Lühe (5, p. 199). The cercariae are very poor swimmers, managing only with great difficulty and thrashing of tail to remain suspended in the water even momentarily. More often they settle to the bottom of the container, and creep about on their suckers in a caterpillar-like type of locomotion. When stained with neutral red the cercariae become less active and relax, although they are still not immobile. When contracted, they assumed an ovoid shape with the tail folded in an accordion-like manner. A semi-relaxed individual measured 0.16 mm. in length, the body length being 0.102 mm. The tail when extended was slender and longer than the
body. Most often the tail was contracted and measured 0.04 to 0.06 mm.
long. The tail readily fell off, and many cercariae were seen creeping
about without one. The oral sucker is 0.027 mm. long and 0.025 mm.
wide. The cuticular surface is covered by minute spines which diminish
in number and size posteriorly. Within the oral sucker is a stylet
measuring 0.016 mm. long. It has a rounded protuberance on each side
near the tip when looked at either dorsally or ventrally. A side view
shows the protuberances to be an incomplete ring missing on the ventral
surface, and the tip bending ventrally to make a crook which could not
be seen from a frontal view. A conspicuous virgula which stains a
brilliant red with neutral red vital dye was also found within the oral
sucker. A small pharynx is present at the base of the oral sucker, and
the esophagus and intestinal cæca could vaguely be made out extending
around and dorsal to the ventral sucker. The ventral sucker is in the
approximate center of the body, and slightly smaller than the oral
sucker. Dorsal to, and on either side of the acetabulum, are three
penetration glands which, like the virgula, stain a brilliant red.
The glands each are located one behind the other, but the actual
position varies with movements of the cercaria. The ducts carrying
the glandular secretions pass anteriorly and dorsally, and open to
the exterior just anterior and dorsal to the oral sucker. At the
posterior end of the body lies the excretory bladder which is a
thick walled simple vesicle, showing no indication of a bicornuate
structure. The bladder is very flexible, changing shape as the
cercaria moves. It was observed many times to enlarge, and contract, as if filling and emptying, but no material was seen to be discharged.

Contact of the cercariae with the caddis fly larvae seemed to be merely by chance; no attraction to the caddis was observed. The cercariae were seen crawling about on the surface of the caddis larvae, but the actual penetration by a cercaria was never witnessed.

Metacercaria. The fully developed metacercariae (pl. 2, fig. 4) are found within the larval caddis fly amongst the fat globules of the body. This stage is encysted and the cyst is spherical in shape, measuring 0.142 mm. in diameter. Within the cyst is the metacercaria, appearing very much like the adult worm except that reproductive structures are lacking. The cuticular surface is spinous, more thickly so at the anterior end, and thinning out to bareness at the posterior end. The spines are peculiar in that they resemble minute scales. The oral sucker is unarmed having lost the stylet, also the virgula, and measures 0.043 mm. in diameter. The prepharynx is virtually absent, consisting of an exceedingly short and membranous connection between the oral sucker and the pharynx. The pharynx is nearly spherical and leads into the esophagus. The latter is thin walled and very short, expanding posteriorly into the intestinal forks. The bifurcation of the caeca and the esophagus appears like a T-connection leading into the thick walled caeca from the round pharynx. The intestinal caeca extend from the bifurcation laterally and then rearward almost to the posterior end of the worm. Directly
posterior to the bifurcation lies the ventral sucker, 0.055 mm. in diameter. The most conspicuous structure present in the metacercaria is the simple, sac-like excretory bladder which occupies up to half the volume within the cyst. The excretory pore opening to the exterior seems to be closed because the excretory products found within the bladder do not extend through the pore and into the interior of the cyst. Between the pore and the bladder runs a short stem or canal.

No flame cells were observed in the metacercaria because the opacity of the vacuolated parenchyma of the worm made it impossible to see into the tissues.

The metacercariae are resistant, it appeared, to changes in environment. A caddis fly larva was teased apart in distilled water, and the metacercariae present were found alive several hours afterwards. The cyst wall must provide protection for the metacercaria enabling it to withstand the effects of the water for the long period of time.

Sexually mature adult worms were obtained from a hamster six days after feeding it infected caddis fly larvae. The infections were very heavy (one hundred or more flukes) from a feeding of ten caddis fly larvae. Larvae that had been infected for seven days with the cercariae of *Allassogonoporus vespertilionis* were fed to a hamster, but no adult worms developed. It appears that the period for maturation of the metacercaria is of a longer duration.
Acantharium oregonense Macy

The adult worm. Many sexually mature Acantharium oregonense (pl. 1, fig. 1) along with other trematodes including Allassogonoporus vespertilionis, were recovered from the intestine of the bat Myotis lucifugus. A few specimens were collected from experimentally infected hamsters. Macy originally found Acantharium oregonense in the bats M. californicus caurinus and M. evotis evotis collected at Nelscott, Oregon.

The anatomy of the fluke agrees with the description given by Macy (8, p. 640) for the most part. In the former, Macy stated that the esophagus was apparently absent. In the ones studied for this paper an esophagus was observed which was quite long. It leaves the pharynx, and makes a dorsal loop before entering the intestinal caeca which are located very close to the pharynx. The appearance is given of no esophagus being present since it is doubled back dorsally, sometimes actually over the caeca and pharynx which are brought together to lie adjacently. The excretory bladder was not mentioned by Macy; it consists of a very large, thin walled, V-type occupying nearly half of the posterior of the worm. In preserved and stained specimens these characters are difficult to see, but in living individuals are very obvious.

Ova. The eggs when mature are small, ovoid, brown, and measure 0.03 mm. long by 0.016 mm. wide. While the shell is still soft, and prior to turning brown, it is permeable to stain. Within
the eggs at this stage can be seen 3 to 5 nuclei later obscured by the brown shell, which is impermeable to stain. The eggs are non-embryonated, and an operculum is present on one end. The adult worms never shed eggs when placed in distilled water, as many trematodes do.

Sporocysts. The sporocysts (pl. 1, fig. 2) obtained from the digestive glands of *Oxytremia silicula* contained cercariae in all stages of development. No redia were ever seen, as could be expected, since the cercariae are *Xiphidiocercariae*, and they develop to maturity directly within the sporocyst. The sporocysts measured on an average 0.25 mm. long by 0.178 mm. wide, but they varied in size from 0.24 mm. to 0.43 mm. long and 0.17 mm. to 0.27 mm. wide. The number of mature cercariae within the sporocyst ranged from 1 to 6, the larger sporocysts containing the greater number of cercariae.

Cercaria. The mature cercariae (pl. 1, fig. 3) can be collected for study by isolating the snails in separate receptacles of stream water. The cercariae will be found creeping around on the bottom of the dish as the water warms and they emerge from the snail. Dawes states that during periods of sunny clear weather and high barometric readings *Xiphidiocercariae* are released in great numbers; my laboratory observations tend to corroborate his statement.

The cercaria belongs to cercariae virgulae established by Lühe (5, p. 199). Superficially, it resembles the cercaria of *Allassogonoporus vespertilionis*, both in behavior and gross appearance. Both are poor swimmers, and usually creep about upon surfaces in a
caterpillar fashion. Neutral red vital stain causes them to slow down for study in addition to differentiating structures by staining. In a relaxed position they assume an oval shape with the accordion-like folding of the tail similar to that seen in A. vespertilionis. A semi-contracted specimen measures 0.19 mm. long by 0.07 mm. wide. The tail when extended is slender and naked, measuring roughly 0.10 mm. The oral sucker has a diameter of 0.024 mm., and within it is located a stylet 0.014 mm. in length. This stylet has a frontal appearance like the one of A. vespertilionis with two rounded protuberances near the tip. In a side view the stylet tapers from the base to the pointed tip; it is straight with no bends or crooks, and no protuberances are present on the dorsal and ventral surfaces. A brilliantly staining virgula is present in the oral sucker, and occupies nearly three-fourths of it. The ventral sucker, located 0.046 mm. from the anterior end of the worm, is nearly round and measures 0.012 mm. in diameter.

Laterally, anterior to the ventral sucker on either side are two, adjacentally located, penetration glands. The vital dye stains them bright red, with the prominent nucleus a clear area in the center of each one. The ducts from the two gland cells open to the exterior just dorsal to the oral sucker. No traces of the caeca or excretory bladder were observed.

No attraction seemed evident for the cercariae toward the caddis larvae. Cercariae were seen crawling and swimming about the
larvae within a distance equal to the cercarial length, but no attempts were made to proceed in a direction toward the host. An actual penetration of the caddis fly larva was not observed, although cercariae were watched creeping about on the surface, and newly penetrated cercariae were seen inside the host upon dissection.

Metacercaria. The metacercariae (pl. 1, figs. 4 & 5) can be found creeping and crawling about in the body fluids of the caddis fly larvae. In some cases when the larva was still young and its external surface transparent, the metacercariae were seen through the surface covering, moving about inside the living caddis fly larva. The metacercariae can be collected for study by splitting the exoskeleton of the caddis larva, hence providing a point of exit through which the metacercariae can emerge into the dish of water. Acanthastrium oregonense was never seen encysted. The stylet remains in the oral sucker of the early metacercariae. Intermediate stages of development of the metacercariae in the larval caddis were seen, from newly penetrated ones to mature, infective ones.

The length of the metacercaria is 0.32 mm.; width is 0.26 mm. The cuticle is smooth. In the mature form the stylet and virgula are missing. The diameter of the oral sucker is 0.055 mm. The pre-pharynx is absent or very short. The pharynx is spherical and leads into the esophagus which is 0.045 mm. long. The bifurcation of the caeca occurs a short distance in front of the ventral sucker. The caeca at the base of the esophagus are short and sac-like in
appearance; in some they pass obliquely towards the posterior of the worm, but in others they form a right angle laterally with the esophagus. The exact position of the caeca within the metacercaria depends upon movements being made by the individual being studied. The ventral sucker is located in the approximate center of the body; it is 0.035 mm. in diameter, a little smaller than the oral sucker. Behind the acetabulum and filling the posterior region is the large V-shaped excretory bladder. The walls of this are thick and highly extensible. The bladder was seen many times to fill up and empty itself, discharging its contents to the exterior; but no flame cells were ever seen, although they must have been functioning. Probably they were hidden or obscured by the opacity of the parenchyma and body walls. Lateral to the acetabulum, groups of undifferentiated cells which were the gonad anlagen were noticed.

Mature worms were found in a hamster six days after it had been fed infected caddis fly larvae. Although many infective metacercariae were present in the caddis larvae the number of adults of _Acanthatusrium oregonense_ recovered from the hamster was always small. The ratio of _Alliassogonoporus vespertilionis_ to _Acanthatusrium oregonense_ was something over 50 to 1, although approximately equal numbers of metacercariae were present in the caddis fly larvae. Evidently the hamster is a poor experimental animal for the growth and development of _Acanthatusrium oregonense_. Larvae that had been infected for seven days with _Acanthatusrium oregonense_ cercariae produced
no worms when fed to a hamster. The metacercariae at that time still retained their stylet, and it seems likely that they would be uninfec-
tive or immature metacercariae as long as the stylet is present, hence the period of maturation of the metacercariae is more than a week.
DISCUSSION

Many cases are known in which Trichopteran larvae serve as the intermediate hosts for trematodes. Hall (4, pp. 17-28) made a study of the arthropods as intermediate hosts for trematodes, and found Trichopteran larvae used as the secondary host in four different trematode families. In the Plagiorchidae, *Plagiorchis maculosus* found in passeriforme birds, and *Opisthioglyphe endolobum* in amphibians used caddis larvae for their development. The cercariae of *Dolichosaccus rostellus* encyst in species of *Limnophilus* and *Anabolia* which are eaten by frogs wherein the adults develop. The Trichopteran and Odonatan larvae appeared to be the most important secondary hosts for the family although other arthropod larvae served in the same role.

In the Lecithodendriidae, *Lecithodendrium chilostomum* from bats develop in Trichopteran larvae of the genus *Phryganea*. The flukes in this family using Trichopteran larvae as intermediate hosts are found only in bats.

In the Allocreadiidae, *Allocreadium isoporum* of fish passes the metacercarial stage in *Anabolia nervosa* or *Chaetopteryx villosa*. Within this family of flukes Trichopterans are not as often intermediate hosts as are other insects.

At the time of Hall's writing, the life cycle of one member of the Brachycoeiliidae, *Brachycoeulum retusum* of amphibians was known. Trichopterans (*Phryganea grandis*) were the secondary host.
The metacercariae of *Lecithodendrium chilostomum* were studied by F. J. Brown in 1933 (1, pp. 318-320). *L. chilostomum* is the type genus of Lecithodendriidae to which *Allassogonoporus vespertilionis*, and *Acanthatrium oregonense* belong. Brown found the metacercariae of *L. chilostomum* encysted within the caddis fly larvae of the genus *Phryganea grandis*. The metacercariae overwinter in the caddis fly larvae, and move into the thoracic muscles upon metamorphosis of the caddis.

The *Limnophilus* caddis larvae containing metacercariae of *Allassogonoporus vespertilionis* and *Acanthatrium oregonense* were not maintained long enough to confirm the fate of the metacercariae upon metamorphosis of the *Limnophilus*.

From the evidence presented by Brown, the life histories of *Acanthatrium oregonense* and *Lecithodendrium chilostomum* are very similar, probably parallel. Although it is not known that the metacercaria of *A. oregonense* occurs in the adult caddis fly, it is possible that it does, and that it would be encysted in the thoracic muscles. It would seem necessary that the metacercaria be found in the adult caddis fly in order to be taken by the bat.

*Allassogonoporus vespertilionis* is like the other members of Lecithodendriidae which occur in cysts formed immediately upon penetration of the caddis larvae. The ultimate fate of its metacercaria during metamorphosis of the caddis fly is unknown, but like the previous form it would seem necessary that the metacercaria be found
in the adult caddis fly to be taken by the bats.

Caddis flies along with coleopterans, ephemeropterans, and dipterans form the major bulk of the food for insectivorous bats, hence it is not strange to find the incidence of infection high, and the individuals of a given infection numerous.

It seemed desirable to add certain notes to Macy's description of *Acanthastrium oregonense* inasmuch as I had material that showed anatomical traits not mentioned in Macy's description or illustrations.
SUMMARY

The major larval stages in the life history of *Allassogonoporus vespertilionis* and *Acantharium oregonense*, lecithodendriid trematodes of bats, have been identified and described. Infective metacercariae of both species of trematodes were discovered in the caddis fly larvae of the genus *Limmophilus* and were fed to the hamster under laboratory conditions. Adult trematodes of both species were recovered from the hamster and identified. Caddis fly larvae were separated into two groups, one group was experimentally infected by the cercaria of *Allassogonoporus vespertilionis*, and the other one was experimentally infected by the cercaria of *Acantharium oregonense*. The experimentally produced metacercariae were recognized and identified as the same species which developed into the adult worms.

Sporocysts occur in the digestive glands of *Oxytrema silicula* for *Acantharium oregonense*, and in *Fluminicola virens* for *Allassogonoporus vespertilionis*. No redia are developed in either fluke, virgulae Xiphidiocercariae being produced directly from the sporocyst.

The cercariae find a caddis fly larvae of the genus *Limmophilus* to penetrate for development into metacercariae. Metacercariae of *Allassogonoporus vespertilionis* are encysted, whereas metacercariae of *Acantharium oregonense* are not.

All the stages in the two life cycles that were seen have been illustrated, and anatomical descriptions made.
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APPENDIX
EXPLANATION OF PLATE 1

The scale equals 0.1 mm. in all figures.

Figure 1. Adult Acanthatrium oregonense.

Figure 2. Acanthatrium oregonense sporocyst from Oxytrema silicula showing five mature and two immature cercariae.

Figure 3. Cercaria of Acanthatrium oregonense.

Figure 4. Immature metacercaria of Acanthatrium oregonense possessing stylet.

Figure 5. Mature metacercaria of Acanthatrium oregonense.
EXPLANATION OF PLATE 2

The scale equals 0.1 mm. in all figures.

Figure 1. Adult *Allassogonoporus vespertilionis*.

Figure 2. *Allassogonoporus vespertilionis* sporocyst from *Plumonicola virens* showing two mature cercariae.

Figure 3. Cercaria of *Allassogonoporus vespertilionis*.

Figure 4. Encysted metacercaria of *Allassogonoporus vespertilionis*.