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# Experimental Infections of Sparganum pseudosegmentatum Vergeer (Cestoda) and Diphyllobothrium laruei Vergeer (Cestoda) in the Golden Hamster

Dennis W. Sutton
*Northern Michigan University*

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by

Dennis W. Sutton

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Marquette

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This thesis is recommended for approval by the student's thesis committee.

Lewis Peters
Chairman

Orland B. Reynolds

Gordon D. Hall

Approved by Albert A. Feig, Dean of Graduate Studies

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ABSTRACT

Hamsters were force-fed either 1 or 10 excysted plerocercoids with a stomach tube in order to determine infectivity, growth rate, region of attachment of scolices, and onset of egg production of Sparganum pseudosegmentatum Vergeer and Diphyllobothrium laruei Vergeer.

D. laruei was found to have very low infectivity, 1% when fed in groups of 10 and none when fed singly to the hamsters.

In single worm feedings only the larger plerocercoids of S. pseudosegmentatum were infective; in groups of 10, 43% of the worms survived for 24 hours or more, with no significant difference in the infectivity of small or large worms.

The growth rate of S. pseudosegmentatum was exponential between the first and fifth day of infection, with the growth formula $\frac{W_2}{W_1} = 0.66e^{0.56t}$, where $W_1$ is the larval weight at time of infection, $W_2$ is the weight of the worm recovered, and t is the time in days. Worms first established their scolices 10-11 cm beyond the pylorus, but by the third day had migrated to within 4 cm of the pylorus. Eggs were first found in hamster feces on the fifth day and normal-appearing eggs on the sixth day.

These results are compared with D. norvegicum Vik and D. latum (L.) to demonstrate differences among species.

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# INTRODUCTION

Sparganum pseudosegmentatum was mentioned but not named by Vergeer (1928). He later named (1934) and described (1942) the plerocercoid stage from burbot (Lota lota Le Sueur) without knowledge of the corresponding adult. Mongrain (1967, unpublished) demonstrated that the larvae can be reared to adults in the hamster and identified them as a species of Diphyllobothrium, and Robertson (1966, unpublished) demonstrated the probable definitive host to be the herring gull (Larus argentatus Pontoppidan) and succeeded in raising ovigerous adults in these piscivorous birds.

Vergeer (1942) also named and described the larvae of Diphyllobothrium laruei, obtained from cysts on the stomach and mesenteries of the lake herring (Leucichthys artedi Le Sueur). Vergeer (1934, 1942) attempted to infect dogs and cats with these larvae but obtained inconsistent results. Thomas (1938) fed unnamed plerocercoids (which may have been D. laruei) from lake herring to young gulls; retention in these birds was less than one month.

It has been considered for a number of years that species of the genus Diphyllobothrium Cobbold can never be satisfactorily classified on the basis of morphologic criteria alone (Vik, 1964). The lack of hooks or other solid structures in the adult and the great intraspecific variation in morphology, due to variation in the host-parasite relationship and to methods of fixation, make taxonomic identification at the species level nearly impossible. Stunkard's (1949) opinion was that no species of Diphyllobothrium from mammals can be positively and fully characterized at the present time and that until this problem

is clarified, further taxonomic work on species of this genus is pointless.

Keys to species of adults of Diphyllobothrium use such characteristics as number of uterine loops, number and size of testes, egg size, and various measurements of scolex, mature segments, etc. Use of these criteria alone was criticized by Vik (1964). Markowski (1949) also considered such characters as dimensions of the strobila, number of segments, and size of the scolex and neck too variable to be used as specific criteria in identification of species. Meyer (1966) reported that because of size range identification of species of Diphyllobothrium on egg size alone is worthless. Rausch (1954) had previously concluded that species cannot be effectively differentiated solely by means of adult morphologic features. He also recommended that adult cestodes be reared in a variety of piscivorous birds and mammals so that comparative material of known age can be obtained and physiological data can be acquired on rate of growth, time required for sexual maturity, onset of apolysis, and normal life span.

This study attempts to determine aspects of the host-parasite physiological relationship for two species of Diphyllobothrium that occur in the area of Marquette, Michigan. The investigation is patterned after one reported by Bråten (1966), in which he studied infectivity, growth, onset of egg production, and site of attachment of the scolex of D. norvegicum Vik in the golden hamster (Mesocrisetus auratus Waterhouse). Others who have studied experimental infections of species of Diphyllobothrium in the

golden hamster are Meyer and Vik (1963) with D. sebago (Ward), Nyberg (1964) with D. latum (L.), and Archer and Hopkins (1958) with a species from Coregonus clupeoides Bleeker. Gnezdilov (1957) reported on experimental infections of D. latum in the Transcaucasian hamster.

## MATERIALS AND METHODS

Fish hosts were procured from local commercial fishermen or from gill nets set five miles north of Marquette Harbor. Plerocercoids of Sparganum pseudosegmentatum were carefully excised from cysts in the stomach wall or attached to the pyloric ceca of burbot, and plerocercoids of D. laruei were dissected from smaller, thinner-walled cysts on the stomach wall of lake herring. After removal, the worms were placed in 0.7% saline and kept refrigerated until used, usually within three days and never more than five days. These larvae were assumed to be in satisfactory condition for feeding experiments; in fact their outward appearance remained normal after periods as long as a month if the saline was changed every two or three days.

The golden hamsters were raised from breeding stock obtained at a retail pet shop in Marquette. They were fed a diet of Teklad commercial hamster food and were given water ad libidum throughout the experiments. Male hamsters of six to fourteen weeks of age were used for the tests.

After excess water was removed by touching plerocercoids several times to a dry glass plate, they were weighed to 0.1 mg on a Roller-Smith balance, examined under a dissecting microscope to make certain they were undamaged, and then immediately implanted into a hamster's stomach. The hamster to be infected was lightly anesthetized with ether and a medical venous intracatheter was passed down the esophagus into the stomach. The worms were forced

into the stomach through the catheter with a hypodermic syringe. One or ten plerocercoids were placed into each hamster. When ten plerocercoids were used, worms were selected with similar weight and only in five of 35 tests was the standard deviation of weight greater than 3 mg. The weight of the Sparganum pseudosegmentatum plerocercoids used in these studies varied between 3.3 and 100.2 mg (mean = 23.4 mg). The weight of the D. laruei plerocercoids used for implantation ranged between 0.3 mg and 4.5 mg (mean = 1.8 mg). After infection the hamsters were held in a small container for 15 minutes to be sure there had not been a loss of worms through emesis after which they were placed into isolated cages.

After 1 to 58 days, each hamster was killed by cervical dislocation and the intestinal tract was immediately removed, its length recorded, and opened lengthwise to reveal the position of any scolices. The worms were then removed from the intestine, washed in 0.7% saline to remove debris, freed of excess water as before, and weighed. All hamsters were sacrificed at the same time of day, 12:00-3:00 p.m. CST, to take into account the effect of the host's eating habits on the glycogen content of the helminth (Reid, 1942; Read, 1949).

To determine the number of days required for initiation of egg production, clean papers were placed each day under the hamster cages to collect fecal samples. The feces were softened in a small amount of tap water, blended with a stirring rod, and the liquid poured through eight thicknesses of cheese cloth to remove excess debris; after rinsing with tap water, the suspension

was left for about 20 minutes to settle. After discarding about 80% of the supernatant, a drop of the remaining liquid was examined microscopically for eggs, which were readily identified if present.

## RESULTS

### I. Survival

*D. laruei* has a very low infection rate in hamsters. Fourteen hamsters, each infected with a single larva, yielded no recoveries when autopsied 1 to 10 days after implantation. Ten hamsters that were infected with 10 larvae each were autopsied after 24 hours, and a young worm of 3.0 mg was the only one of the 100 plerocercoids recovered.

Among the 36 hamsters fed single *S. pseudosegmentatum* larvae, 4 infections were established for an infection rate of 11%. No single worm weighing less than 56.4 mg succeeded in infecting a hamster. Of the 12 plerocercoids with initial weights over 56 mg, 4 became established for 24 hours or more. This infection rate of 33% is comparable to that of hamsters fed 10 larvae each. In the 34 hamsters given 10 plerocercoids each, 143 larvae survived in 26 hamsters for an infection rate of 42%.

The dependence of infection rate on worm size in multiple infections is difficult to ascertain; however, I believe it is possible to make comparison because of the small deviation from the mean weight of the larvae in each group, as expressed in Table 1.

Student's t test showed that there is no significant difference in the infectivity of worms in different weight groups.

Established worms survived for at least 58 days. An examination of data in the appendix reveals that the length of the experimental infection appears to have little effect on the number

Table I. Establishment of plerocercoids of *Sparganum pseudosegmentatum* in hamsters after introducing 10 plerocercoids into each hamster.

| Weight group (milligram) | Mean weight (milligram) | Total larvae fed | Number of larvae established in each group | % infection |
|---|---|---|---|---|
| 5.0-14.9 | 9.5 | 70 | 16 | 23 |
| 15.0-24.9 | 20.7 | 120 | 48 | 40 |
| 25.0-34.9 | 29.2 | 110 | 65 | 59 |
| 35.0-40.4 | 37.0 | 40 | 14 | 35 |
| Total | 23.2 | 340 | 143 | 43 |

of worms surviving in a hamster. For example, 2 infections of 58 days duration had 3 and 8 worms surviving out of 10 introduced, whereas 3 infections of 1 day had 5, 1, and 8 worms surviving. The critical period for establishment seems to be in the first 24 hours.

II. Growth

In order to make all observations comparable and independent of the weight of the plerocercoids at the time of infection, the growth rate of S. pseudosegmentatum is expressed as the ratio of weight of the worm recovered to the original weight of the plerocercoid when fed to the hamster (Fig. 1). Multiple infections are plotted the same as a single worm using the mean weight of worms recovered divided by the mean weight of plerocercoids introduced.

The adult worm reached its maximum weight at about the fifth day after which the weight remains constant. The largest worm recovered was taken on the 48th day of infection, weighed 872.1 mg, and had not yet had its first apolysis (shedding of exhausted tissue).

A higher growth index was obtained when unusually small worms were implanted; the two with indices over 100 were from the two smallest groups of plerocercoids introduced. Archer and Hopkins (1958), using a species of Diphyllobothrium from Coregonus clupeoides to infect rats, obtained similarly high growth rates when using exceptionally small plerocercoids.

For the period of exponential growth, the growth formula is $\frac{W_2}{W_1} = 0.66e^{0.56t}$, where $W_1$ is the mean initial weight of the pler-

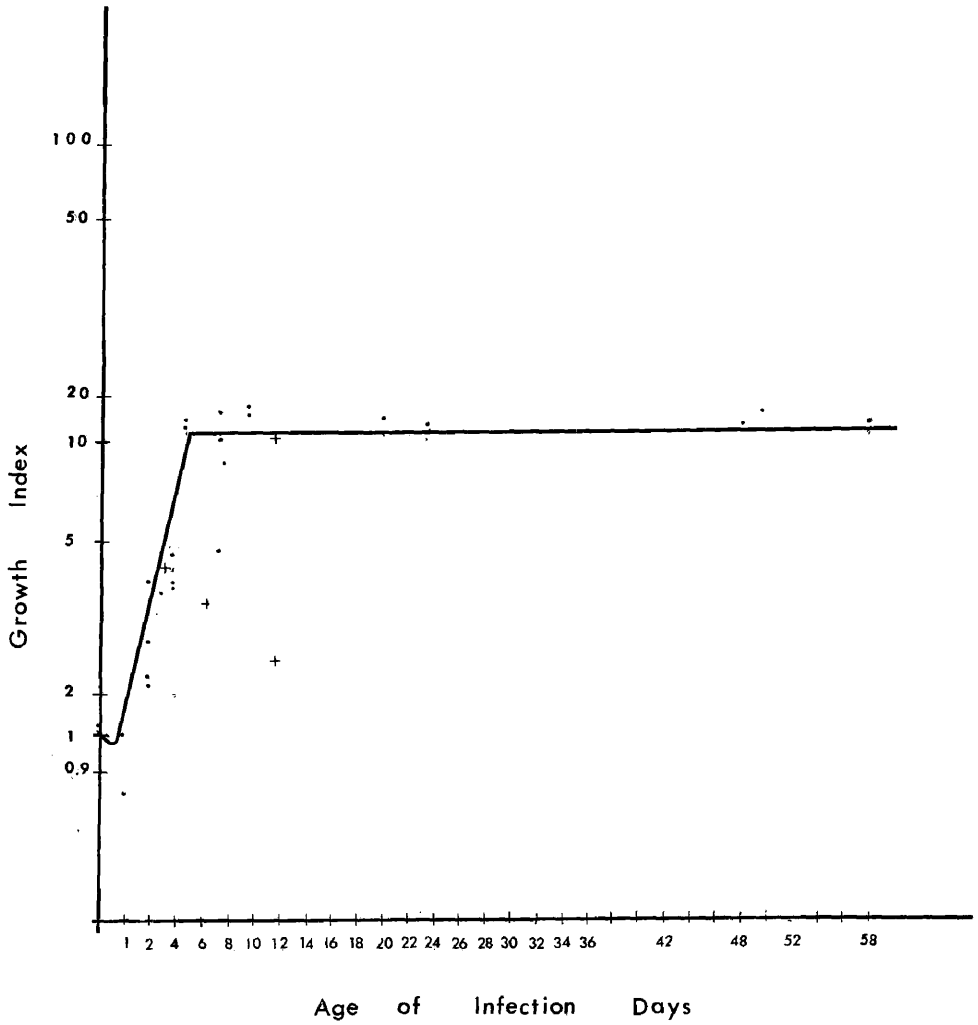


Fig. 1. Semilogarithmic growth curve for Sparganum pseudosegmentatum in hamsters. Each + represents a single infection and each · represents a recovery of from 1 to 10 plerocercoids. The line drawn from the first to fifth days is the calculated line of regression for the observations during this period. The growth index is the ratio of the weight of worms recovered divided by the weight of plerocercoids introduced.

ocercoids fed, $W_2$ is the mean weight of the worms at time of recovery, and t is the time in days.

III. Site of Attachment

Worms recovered 24 and 48 hours after introduction into the hamster were found 10 to 11 cm beyond the pylorus and those recovered on and after the third day of infection were found attached approximately 3 to 5 cm beyond the pylorus. This evidence indicates that the larvae, when first introduced into the hamster, are swept toward the posterior region of the small intestine and then migrate forward so that by the third day of infection they reach a point of permanent attachment about 4 cm from the pylorus. This phenomenon was also noted by Bråten (1966) for similar infections using D. norvegicum and by Archer and Hopkins (1958). Bråten, and also Archer and Hopkins, indicated points of attachment as percent distance from the pylorus to the caecum. It would be impractical to compare S. pseudosegmentatum in this manner due to intestinal length changes when heavy infections are present for three or more days. Hamsters harboring four or more worms three days or more after implantation had small intestinal length of 21 to 39 cm (mean = 33.4 cm), whereas noninfected hamsters had small intestine lengths of 39 to 45 cm (mean = 43.5 cm).

IV. Egg Production

A few eggs, most of them poorly developed and more or less spherical, were recovered from feces five days after implantation; on the sixth day eggs were found in much greater number and were larger and of the normal ovoid shape.

Fertility of some of the eggs was indicated by the finding of empty eggshells with open opercula after 14 days of incubation in tap water, although no coracidia were found. No attempt was made to enumerate the eggs or determine percent fertility.

## DISCUSSION

In comparing Sparganum pseudosegmentatum with Diphyllobothrium norvegicum, the greatest single difference appears to be the inability of small, singly-introduced S. pseudosegmentatum plerocercoids to infect the hamster, whereas Bråten (1966) found that there was no significant difference in infectivity of D. norvegicum larvae of different weight groups. The data for S. pseudosegmentatum indicate that small plerocercoids are capable of infecting hamsters only when introduced as multiple infections. It is possible that a certain critical mass or unit of surface area of larval tissue is necessary to enable the larvae to survive in the digestive tract. The role of antienzymes was discussed by Von Brand (1952; 1966), who found it difficult to ascribe to them a primary role in protecting the helminth from digestion, but thought that impermeability of living membranes may be of prime importance. It would follow that a helminth with an injured tegument might well be digested by the host. Evidence to the contrary is provided by Bråten (1966), who fed to a hamster a plerocercoid of D. norvegicum from which he had cut the posterior end; there was no digestion of the worm at time of autopsy four days later. This evidence suggests that an intact tegument is not the only factor protecting the worm from digestion.

Multiple infections of larger worms or superinfection of small worms probably would not increase the rate of infection or the growth rate. Wardle and Green (1941) subjected dogs to multiple infections of D. latum plerocercoids and found that dogs with

heavier initial infections tend to lose most, if not all, of the tapeworms within 25 days. Chandler (1939) found the average length of Hymenolepis diminuta in laboratory rats to be in inverse proportion to the number of worms present, ranging from an average of 1000 mm in single-worm infections to 300 mm in forty-worm infections. Read (1951) and Roberts (1960) also demonstrated the "crowding effect" that results from increasing the size of the population within a host.

The use of length as a morphometric criterion for measuring plerocercoids was not attempted because of the great variation in length of worms of near equal weight. One worm would often be two to four times the length of another of equal weight due to elongations and contractions. Goodchild and Harrison (1961), working with Hymenolepis diminuta (Rudolphi), considered weighing to be impractical because of the size of the sample and the risk of damage to the worms. They discussed the use of other comparative measurements, such as an index method based upon paper-weight-equivalent, where a specimen is traced upon paper, the paper then being cut out and weighed to obtain a comparative index of area. Length times width measurements were also tested by Goodchild and Harrison and found to be as accurate as the paper-weight method with much less labor involved.

The wide variation found in the weight of adults within the same hamster is probably due to differences in the onset of apolysis. In the present study, apolysis was found to occur as early as the fifth day in one case. Vik (1957) found that the post-

erior end of D. latum in man loosens and is passed in the stool as early as 18 days after infection. Wardle and Green (1941), using D. latum in dogs, found apolysis to occur soon after the first egg discharge, which occurred between the 18th and 20th day. Penfold, Penfold, and Phillips (1937) found a loss of eight to nine proglottids a day in Taeniarhynchus saginata (L.). Growth would be expected to keep pace with apolysis as the tapeworm ages, resulting in a leveling off of weight gain.

This study attempts to present data on host-parasite physiological relationships comparing Diphyllobothrium laruei and Sparganum pseudosegmentatum. These species can also be compared with D. norvegicum because of the close adherance in the present study to Bråten's (1966) methods. Table II compares these three species and D. latum as reported by Gnezdilov (1957); thus, D. laruei differs from the others in its virtual inability to infect hamsters and D. latum from the other two in the much longer period required for onset of egg production. Meyer and Vik (1963) artificially infected one male hamster with plerocercoids of D. sebago from which eggs were obtained on the seventh day postinfection. These eggs were found to have an abnormally high rate of infertility. More data are needed before D. sebago can be compared with the aforementioned species.

Table II. Comparison of four species of *Diphyllobothrium* experimentally introduced in hamsters.

| Species | Infectivity: Single infections | Infectivity: Infections of 10 worms each | Growth rate $\frac{W_2}{W_1}$ | Weight of mature adults (mg) | Eggs in feces found on day | Reference |
|---|---|---|---|---|---|---|
| *D. norvegicum* | 50%; independent of weight of worm | | $0.741e^{.647t}$ | 404-2149 | 5th | Bråten (1966) |
| *S. pseudosegmentatum* | 33%; only worms above 55 mg are infective | 43%; independent of total weight of worm | $0.66e^{.56t}$ | 143-872 (mean, 355) | A few on the 5th day, many on 6th day | This paper |
| *D. laruei* | not infective | 1% | | | No eggs produced | This paper |
| *D. latum* | 30% calculated from 4 infections of 5, 5, 5, and 45 plerocercoids respectively | | | | 13th day | Gnezdilov (1957) |

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Appendix.

Listing of data on implantation trials using 10 Sparganum pseudosegmentatum larvae per hamster. Time in days is the number of days between implantation and sacrifice of he hamster.

| Hamster Number | Time in Days | Mean weight at time of introduction ± standard deviation (mg) | Number recovered | Mean weight at time of recovery ± standard deviation (mg) | Growth index $\frac{X_2}{X_1}$ |
|---|---|---|---|---|---|
| 1 | 1 | 17.2±1.4 | 5 | 16.6±5.3 | 1.0 |
| 2 | 1 | 24.7±1.9 | 1 | 17.6±0 | 0.7 |
| 3 | 1 | 33.8±11.1 | 8 | 32.5±9.6 | 1.0 |
| 4 | 2 | 9.2± 1.9 | 0 | ---- | ---- |
| 5 | 2 | 12.5± 1.6 | 4 | 46.2±1.2 | 3.7 |
| 6 | 2 | 22.7± 1.6 | 0 | ---- | ---- |
| 7 | 2 | 22.9± 2.9 | 3 | 52.7±1.1 | 2.3 |
| 8 | 2 | 24.2± 1.6 | 9 | 53.4±7.6 | 2.2 |
| 9 | 2 | 35.7± 8.6 | 0 | ---- | ---- |
| 10 | 3 | 18.4± 2.7 | 10 | 86.8±15.8 | 4.7 |
| 11 | 3 | 26.4± 0.8 | 5 | 99.6± 6.2 | 3.8 |
| 12 | 3 | 32.3± 2.1 | 9 | 96.0±30.6 | 3.0 |
| 13 | 4 | 14.1± 1.4 | 0 | ---- | ---- |
| 14 | 4 | 17.6± 1.4 | 1 | 64.4± 0 | 3.7 |
| 15 | 4 | 19.3± 1.7 | 0 | ---- | ---- |
| 16 | 4 | 21.6± 1.9 | 9 | 126.4±20.1 | 5.8 |

| Hamster Number | Time in Days | Mean weight at time of introduction ± standard deviation (mg) | Number recovered | Mean weight at time of recovery ± standard deviation (mg) | Growth index $\frac{\bar{X}_2}{\bar{X}_1}$ |
|---|---|---|---|---|---|
| 17 | 4 | 30.9± 2.8 | 7 | 99.4±35.0 | 3.2 |
| 18 | 5 | 19.0± 3.0 | 4 | 296.6±18.9 | 15.6 |
| 19 | 5 | 28.3± 2.1 | 5 | 324.3±113.6 | 11.4 |
| 20 | 6 | 22.2± 2.6 | 0 | ---- | ---- |
| 21 | 7 | 26.1± 1.5 | 2 | 479.0± 16.5 | 18.3 |
| 22 | 7 | 32.1± 1.8 | 6 | 331.9± 70.6 | 10.3 |
| 23 | 7 | 40.4± 3.1 | 1 | 198.1± 0 | 4.9 |
| 24 | 8 | 36.9± 3.0 | 8 | 290.7± 53.7 | 8.0 |
| 25 | 10 | 10.1± 2.9 | 0 | ---- | ---- |
| 26 | 10 | 18.3± 1.5 | 6 | 333.0± 39.5 | 18.2 |
| 27 | 10 | 25.6± 4.2 | 4 | 445.1± 50.5 | 17.4 |
| 28 | 19 | 6.1± 1.2 | 1 | 860.2± 0 | 136.3 |
| 29 | 20 | 33.4± 3.5 | 8 | 483.9± 68.1 | 14.5 |
| 30 | 24 | 27.2± 3.0 | 6 | 388.3±143.4 | 14.3 |
| 31 | 48 | 35.2± 4.9 | 5 | 500.6±231.9 | 14.1 |
| 32 | 50 | 25.4± 4.6 | 5 | 489.8±130.9 | 19.3 |

| Hamster Number | Time in Days | Mean weight at time of introduction ± standard deviation (mg) | Number recovered | Mean weight at time of recovery ± standard deviation (mg) | Growth index $\frac{X_2}{X_1}$ |
|---|---|---|---|---|---|
| 33 | 58 | 5.4± 1.6 | 3 | 557.5±139.9 | 103.6 |
| 34 | 58 | 15.0± 2.5 | 8 | 340.6±122.4 | 22.7 |