STUDIES ON THE LIFE HISTORY AND THE HOST-PARASITE RELATIONSHIPS

OF THE FOWL TAPEWORM RAILLIETINA CESTICILLUS (MOLIN)

by

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TABLE OF CONTENTS

INTRODUCTION

During the last half century much progress has been made in the control of parasitic diseases of man and his domestic animals. These advances are dependent upon a thorough knowledge of the nature of each individual parasite, its life history and the mechanisms of resistance which control the interactions between a host and its parasites.

Our domestic chicken is possibly parasitized with more different kinds of parasites than any other domestic animal. This is primarily due to two factors. First, the barnyard fowl has a diet consisting of grain, garbage, meat scraps, green plants, insects and other small animals, and the dirt or sand which is taken into the gizzard to aid in mastication. Such food habits make possible the entrance of numerous parasites which are dependent upon the food canal for entrance into the body. Second, our domestic fowl usually lives in a crowded house and frequently is confined in pens. This crowding makes possible ready transference of ectoparasites from fowl to fowl and also concentrates the eggs or larvae of internal parasites into comparatively small areas.

A study of poultry parasites is especially pertinent in Kansas since poultry raising is one of the more important minor industries in the state. Much is known about the ectoparasites and the nematodes of poultry but the problem of fowl tapeworms has had comparatively little attention. It was to make available important information upon the tapeworms of chickens that the present studies were undertaken.

ACKNOWLEDGMENTS

MATERIAL AND METHODS

Experimental Feeding of Intermediate Hosts

The principal intermediate hosts studied were various species of coleoptera, especially ground beetles. These insects were taken on sidewalks, under rocks and boards and near street lights. In order to avoid natural infestations, the beetles were collected some distance from chicken pens.

The gravid proglottids from the tapeworms in infested chickens were obtained for feeding purposes by the decantation method of fecal examination. An infested fowl was confined in a small pen, the floor of which was covered with course screen. Beneath the screen was a wet paper to catch the droppings and keep them from drying out. After a few hours the feces were collected and broken up in a large glass dish. Water under considerable pressure from the tap served to further break up the material. After allowing the heavier particles to settle, the supernatant fluid and débris were poured off and the whole process re-peated several times until only the heavier material remained. The shiny white proglottids of <u>Raillietina</u> <u>cesticillus</u> can be distinguished readily from débris if the dish is held over a dark background.

In feeding, the proglottids which contained numerous hexacanth embryos were given to beetles in Petrie dishes where each beetle could be observed. In most cases a beetle consumed at least one entire pro-

glottid, and in some cases several proglottids were taken. Because of
the cannibalistic habits of the carabidae, each beetle was placed in a
separate pint Mason jar. About three inches of dirt and a piece of
moist filter paper were put in the jars after which the lids were loose-
ly placed upon them. The jars were inspected daily for moisture content
and condition of food which was supplied semi-weekly in the form of meat
scraps.

On the sixteenth to twenty-first day after the beetles had been
parasitized, they were examined for cysticercoids. Of the various meth-
ods used in killing the beetles, drowning was found most satisfactory
because the viability of the cysticercoids seemed to be less affected
than when chemicals were used.

The beetles were examined by being pinned face downward through the
thorax to a blackened dissecting dish which contained 0.1 per cent
physiological salt solution. The elytra and membranous wings were pin-
ned back and the thin membrane covering the viscera was broken by sharp
dissecting needles. The viscera were then pulled out into the salt
solution and examined for cysticercoids with a low power binocular
microscope. The cysticercoids when present usually floated free from
the viscera. They were then transferred from the dissecting dish to
watch glasses by means of a dropping pipette especially modified for the
purpose. The tip of the pipette was drawn out to form a long narrow
tube. Attached to the bulb end was a Hoffman screw compressor. By
slight manipulation of the screw, the cysticercoids could be drawn up

into the narrow end of the pipette and held there until released by
turning the screw in the opposite direction. This apparatus eliminated
previous difficulties encountered in the transfer of cysticercoids from
one dish to another.

Experimental Feeding of Chickens

The chickens used for the experimental feeding were secured as
day-old chicks and raised in experimental pens under conditions modi-
fied slightly from those found by Herrick, Ackert and Danheim (1923) to
be adequate for growing normal chickens in confinement. Extreme effort
was made to keep these pens free from insects. All openings were
screened and the two entrances were protected by vestibules with double
screen doors. After entering a vestibule through the outside door, all
flies were killed and collected before opening the second door. Creep-
ing insects were eliminated by the concrete floors of the pens. That
these measures were adequate for eliminating accidental infection was
shown by the fact that all control chickens were negative for helminths
during the year and a half in which the experiments were in progress.

The cysticercoids were given to the chickens in gelatine capsules,
on pieces of filter paper, or in water by means of a pipette.

Upon post-mortem examination of a chicken, several methods were
used to remove the tapeworms from the intestine. The following method
was found most satisfactory. The small intestine stripped of its mes-
enteries was taken from the body cavity, placed in lukewarm water and
opened with blunt scissors on the side opposite the mesenteries. The

incision was begun at the duodenal end of the intestine and after about an inch of the intestine had been cut, the debris was washed away and search made for tapeworms. When a tapeworm was found, the point of attachment was located by further washing of the intestine. The scolex was usually so deeply imbedded in the mucosa that it was not visible. The portion of the mucous membrane which surrounded the scolex was then cut out with a quick movement of a scalpel. Very frequently the scolex was entirely freed from the intestine by this operation, but if it remained attached to a small piece of intestine, it could be freed by putting the worm on a piece of glass and teasing the mucous membrane. Although a few of the scoleces were lost by this method, after some practice about 90 per cent of the worms could be recovered unbroken.

The worms were killed and fixed in Gilson's solution and preserved in 70 per cent alcohol for further study.

REVIEW OF LITERATURE

The adult form of the fowl tapeworm <u>Raillietina</u> <u>cesticillus</u> was first described by Molin in 1858 from <u>Phasianus</u> <u>gallus</u> in Patavium, Italy. Molin placed it in the genus <u>Taenia</u> where it remained until 1891 when the genus <u>Taenia</u> was divided by Blanchard and this parasite removed to the genus <u>Davainea</u>. In 1920 Fuhrmann subdivided the genus <u>Davainea</u> placing this cestode as the type species of the genus <u>Raillietina</u> subgenus <u>Skrjabinia</u>. In 1929 Lopez-Neyra removed this parasite to the genus <u>Brumptiella</u> but this nomenclature has not been generally accepted

and the classification here adopted is <u>Raillietina</u> (<u>Skrjabinia</u>) <u>cesti-</u><u>cillus</u> (Molin, 1858) Fuhrmann, 1920.

Specific diagnoses or redescriptions have been made by various writers, among which the ones by Stiles and Hassall (1896), Ransom (1905), Gutberlet (1916a), and Lang (1929) are fairly complete. The parasite is cosmopolitan in distribution and very high incidence has been reported by Gutberlet (1916b) and Ferry (1935) in fowls from different regions. According to Ransom (1909) this tapeworm has been found in <u>Meleagris</u> <u>galloparo</u> <u>domestica</u> and <u>Gallus</u> <u>gallus</u> <u>domesticus</u>. Jones (1931) reported experimental infestations of <u>Raillietina</u> <u>cesti-</u><u>cillus</u> in the guinea fowl (<u>Numida</u> <u>meleagris</u>).

Gutberlet (1916b) reported negative results from attempts to parasitize flies with onchospheres of <u>Raillietina</u> <u>cesticillus</u>. Ackert (1918) found adult forms of <u>Raillietina</u> <u>cesticillus</u> after feeding large numbers of house flies to young chickens. Joyeux (1920) was unable to recover the cysticercoid stage from flies after feeding large number of onchospheres to adult and larval stages of house flies.

In 1928 Cram found cysticercoids of <u>Raillietina</u> <u>cesticillus</u> in the beetles <u>Anisotarsus</u> <u>agilis</u> and <u>Choeridium</u> <u>histeroides</u>. Since that time numerous beetles have been found in which cysticercoids develop. These beetles are listed with the name of the worker and the date when first reported.

    Family Scarabaeidae
        <u>Choeridium</u> <u>histeroides</u>   Cram (1928)
        <u>Aphodius</u> <u>granarius</u>   Jones (1930a)

Family Tenebrionidae
    Tenebrio sp.   Jones (1932)
Family Carabidae, Subfamily Harpalinae
  Section Unisetosae

Anisotarsus agilis	Cram (1928)
Anisotarsus terminatus	Cram and Jones (1929)
Selenophorus pedicularius	Jones (1930a)
Selenophorus ovalis	Jones (1930a)
Cratacanthus dubius	Jones (1930b)
Bradycellus collaris	Wetzel (1933)
Harpalus nitidulus	Jones (1932)
Harpalus tardus	Wetzel (1933)
Stenolophus conjunctus	Jones (1932)
Stenocellus debilipes	Jones (1932)
Stenocellus rupestris	Jones (1932)
Triplectrus rusticus	Jones (1930a)

  Section Bisetosae

Pterostichus vulgaris	Wetzel (1933)
Pterostichus niger	Wetzel (1933)
Pterostichus nigrita	Wetzel (1933)
Calathus opaculus	Jones (1930c)
Calathus erratus	Wetzel (1933)
Calathus ambiguus	Wetzel (1933)
Calathus fucipes	Wetzel (1933)
Poecilus cupreus	Wetzel (1934)
Zabrus tenebroides	Wetzel (1934)
Amara (Amara) sp.	Jones (1931)
Amara familiaris	Wetzel (1933)
Amara aenea	Wetzel (1933)
Amara apricaria	Wetzel (1934)
Amara basillaris	Ackert and Reid (1936)

Cram and Jones have recovered adult tapeworms from chickens or guinea fowls after feeding them cysticercoids from most of the beetles they have reported. The coleoptera reported by Wetzel are recorded as beetles from which mature cysticercoids were recovered.

The cysticercoid stage and the life cycle have been described by Wetzel (1933, 1934) and Ackert and Reid (1936).

THE LIFE HISTORY OF <u>RAILLIETINA CESTICILLUS</u>

The Adult Tapeworm

The habitat of the adult tapeworm <u>Raillietina cesticillus</u> is the lumen of the upper third of the chicken intestine. Most frequently the scoleces are embedded in the mucosa about five centimeters below the entrance of the bile and pancreatic ducts. Occasionally, however they occur a short distance above the duodenal loop or as far back as Meckel's diverticulum. The proglottids which form back of the scolex mature in a few days and become gravid in approximately two weeks when the terminal segments break off and pass from the body of the host.

<u>Motility of Voided Proglottids.</u> Numerous gravid proglottids may be found free in the intestine of infested fowls where they are very motile. If such proglottids are kept warm after having been voided in the feces, they will continue to move for some time. The direction of the migration in freshly voided proglottids appears to be to the outside of the fecal mass. Numerous clumps of feces were found in which the proglottids literally covered the whole surface. After removing 18 proglottids from the surface of one such clump, the interior of the fecal material was examined; only one proglottid was found. This phenomenon undoubtedly serves in the life economy of the tapeworm because the proglottids in this way are made accessible to the intermediate hosts. Movement of gravid proglottids of the fowl tapeworm <u>Davainea</u>

<u>proglottina</u> was noted by Wetzel (1932) who concluded that they were positively phototropic. He considered this phenomenon important in bringing the proglottids to the surface of the fecal mass, and even up on a blade of grass.

Numerous tests by the writer on the specific tropistic activities of the proglottids of <u>Raillietina cesticillus</u>, however, have met only with negative results. For example, proglottids were put on a damp filter paper in a Petrie dish and then placed in a closed chamber in which light was permitted to enter only from one side. These proglottids migrated in all directions from the center of the dish regardless of the location of the source of light. Neither did the direction of the movement seem to depend upon the presence or absence of moisture, or upon the effect of gravity. All of the proglottids observed moved forward with the scolex end foremost. Their courses usually were in a straight line although a few curved somewhat to one side. In one case a proglottid moved over eight inches in a straight line. Thus while the living, voided proglottids move out to the surface of the fecal mass, it appears that they do not migrate as a result of light, moisture or gravity stimulation.

<u>Periodic Expulsion of Proglottids.</u> Another interesting observation upon the proglottids of <u>Davainea proglottina</u> was made by Wetzel (1932). He found that proglottids appeared in the feces in relatively large numbers during the afternoon between 3:00 and 4:00 p. m. while none were passed during the night or early morning. In 1934 he reported similar

results working with R. cesticillus. Observations upon the passing of proglottids of this cestode were made by the writer. Fecal examinations were made at 7:30 a. m., 12 a. m., 3:30 p. m., 5:30 p. m., and 9:30 p. m. over a period of nine days. The maximum number of proglottids obtained from two fowls infected with R. cesticillus was in the 3:30 and 5:30 p. m. examinations. The minimum number of proglottids was found when the 7:30 a. m. examination was made of feces which had been passed during the night. These findings thus confirm the observations of Wetzel (1934).

The Onchosphere

The structure and size of the onchospheres or hexacanth embryos found in gravid proglottids are used in specific diagnosis of tapeworms in live fowls since the entire worm including the scolex rarely is recovered from the feces. For this reason the results of a detailed study are given which include points not heretofore presented.

Each gravid proglottid of R. cesticillus contains about 300 onchospheres. These onchospheres are ovoid to spherical in shape (fig. 1) and range from 74 to 84µ in diameter. These measurements agree closely with those reported by Stiles and Hassall (1896) who reported the size as 75 to 85µ. Joyeux (1920), however, reported the size of the onchospheres as 80 to 100µ when measured in physiological salt solution. It might be noted that measurements must be taken immediately after opening the proglottid as a very slight difference in concentration of the

saline solution will cause dialysis or shrinkage of the onchosphere membranes.

The embryo proper is enclosed in a number of membranes and appears as a clear hyaline structure in which the six embryonic hooks are arranged in pairs. Upon the death of the embryo the hooks become disarranged and the protoplasm assumes a clouded appearance. When a proglottid is teased apart in water, most of the embryos are motionless. However, by adding a weak solution of saline the embryos are activated. Violent movements of the hooks occur which cause the rupture of the membranes, some of the embryos being able to free themselves completely in three or four minutes. The nuclei are prominent under high magnification in living and stained material but the cell walls are difficult to distinguish.

For convenience in discussion, the membranes shown in figure 1 have been lettered beginning with the innermost membrane. This inner membrane, A, is extremely flexible and appears to be similar to the hyaline membrane of an amoeba. The hooks of the embryo continually penetrate the membrane as they go through violent contortions which result in freeing the embryo from its membranes and pulling it through the intestinal wall of its intermediate host. Although the curved part of the hook may extend entirely outside the membrane, yet an enlarged portion at the base of the curve prevents it from going further.

Membranes B and C are so closely associated in living specimens that they appear as one rather thick membrane. Only when the embryo is

dialyzed in distilled water do the two membranes separate. For this reason these membranes previously have been described as one. The size of this inner capsule is fairly constant, measuring from 43 to 59μ in diameter.

Membranes B and D are connected by two small tube-like structures which have been termed filaments by Ransom (1905) and Gutberlet (1916a). The outer connection of this tube or filament is so attached to membrane D as to cause the latter to be drawn in giving the whole structure the appearance of a funnel. Although two of these structures constitute the typical number, three and in a few cases five of them have been noted in one onchosphere.

The two outer membranes, E and F, are closely connected by smaller membranes which cross and recross the area between them. These smaller membranes which are probably the remains of the uterine wall, are seen only in sectioned material. The outer membrane, F, appears much thicker than any of the others.

In concluding the study of the onchosphere it might be well to point out the importance of the funnel-shaped structures in specific diagnosis. The location of these structures is probably more convenient than comparison of the size of the onchosphere with measurements given by other workers.

<center>Intermediate Hosts</center>

The next step in portraying the life history of the tapeworm R. cesticillus is to trace the entrance of the onchosphere into the inter-

mediate host and follow its development in this animal. Various species
of beetles were used in the present studies of intermediate hosts.
These insects were artificially infected by placing them in a Petrie
dish to feed on gravid proglottids which contained onchospheres or R.
cesticillus. Most of the beetles were singularly attracted to the
proglottids especially after having been without food for a day or two.
The beetles seemed to detect the presence of proglottids by means of
their sense of smell. Although the material in the proglottid was
rather viscous, yet the beetle was usually able to masticate the
material well enough with its mandibles to permit entrance into the
esophagus. A few beetles became so entangled in the material that
considerable difficulty was encountered in extricating themselves. The
larger species of beetles were able to take a whole proglottid in a
remarkably short time. The migration of the onchospheres through the
intestinal wall of the intermediate host and the early development of
the cysticercoid stage in the body cavity of the beetle have been
studied by Wetzel (1934). Further discussion of the cysticercoid stage
of the tapeworm will be deferred to a later section.

In order to determine the important intermediate hosts of R.
cesticillus in this region, and at the same time to furnish cysticer-
coids for other studies, a large number of experimental feedings were
carried out. The results of these feedings are recorded in table I.
Of the 570 beetles to which onchospheres were fed, records were made
only for those which lived long enough to permit cysticercoids to
mature.

Table I. Coleoptera Tested as Possible Intermediate Hosts of
Raillietina cesticillus.

Genus and Species	Positive	Negative	Maximum Number of Cysticercoids
Family Carabidae, Subfamily Harpalinae			
*Pterostichus (Eumolops) torvus Lec.	1	0	Numerous
*Pterostichus (Abacidus) permundus Say	2	3	75
*Pterostichus (Anaferonia) sp. near			
constrictus Say, following Casey	18	11	626
Pterostichus (Poecilus) calictes Say	0	11	0
*Amara (Percosia) obesa Say	3	0	91
*Amara (Curtonotus) laticollis Lec.	1	0	4
*Amara (Celia) muscula Say	1	0	50
*Amara (Amara) fallax Lec.	3	0	37
*Amara (Amara) basillaris Say	2	0	Several
Amara (Curtonotus) pennsylvanica Hayw.	0	1	0
Amara sp.	21	9	177
Dicaelus elongatus Bon.	0	1	0
*Anisotarsus subvirens Csy.	5	1	150
Anisotarsus sp.	21	11	100
Selenophorus (?pedicularius Dej.)	1	0	20
Cratacanthus dubius Beauv.	56	44	360
*Chlaenius tomentosus (Say)	1	0	70
*Anisodactylus (Triplectrus) rusticus Say	2	1	200
Anisodactylus (Triplectrus) ovularis Csy.	0	1	0
Anisodactylus (Triplectrus)			
carbonarius Say	0	1	0
*Harpalus pennsylvanicus Degeer	1	2	5
Harpalus faunus Say	0	1	0
Harpalus caliginosus F.	0	1	0
Harpalus (actiosus Csy., or very near)	0	1	0
Harpalus sp.	0	12	0
Family Carabidae, Subfamily Carabinae			
Scarites subterraneus F.	0	2	0
Calosoma sp.	0	1	0
Family Tenebrionidae			
Alphitobius piceus (Oliv.)	0	9	0

* Genera or species that have not been previously reported.

With one exception all of the species of beetles tested as possible intermediate hosts of the cestode R. cesticillus belong to the family Carabidae. Several beetles belonging to the family Tenebrionidae which were found around the feed boxes in the experimental pens were tested, but the results from the tests on these beetles were negative in all cases. All of the beetles found by the author to be infective belong to the subfamily Harpalinae[1]. The infective coleoptera reported by Wetzel (1935) belong to this same subfamily, but Cram (1928) and Jones (1930a and 1932) also reported infective beetles of the families Scarabaeidae and Tenebrionidae.

It is noteworthy that a considerable amount of variation in infectivity is found within a single genus. Within the genus Pterostichus some species were good hosts while all Pterostichus calictes were negative for cysticercoids after being fed a number of proglottids. Only one beetle of 18 Harpalus produced cysticercoids. This phenomenon can be noted in the same genera by a study of Wetzel's data (1934). The genus Amara is well adapted as an intermediate host as was shown in the present results from experimental feedings and the number of species of Amara reported as intermediate hosts by other writers.

From a study of table I it will be seen that twelve new species of beetles have been added to the list of intermediate hosts of this

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[1]One or more beetles of each species listed was identified by L. L. Buchanan of the United States Bureau of Entomology and Plant Quarantine. Others were identified by comparison with these forms.

parasite. Two of the six genera, <u>Chlaenius</u> and <u>Anisodactylus</u>, are being reported for the first time as intermediate hosts of <u>R</u>. <u>cesticil-lus</u>.

The Cysticercoid

After the experimental beetles had been fed proglottids of <u>R</u>. <u>cesticillus</u> they were kept in jars until the hexacanth embryos had had time to penetrate the intestinal wall of the host and develop into mature cysticercoids. During the hot part of the summer, when the maximum and minimum temperatures were about 110^0 and 60^0 F., respectively, mature cysticercoids were developed in from 14 to 16 days. However beetles which were collected during the late fall did not produce mature cysticercoids for 21 days or longer even though the temperature of the room in which they were kept ranged between 70^0 and 80^0 F. At the end of this time the beetles were examined individually for cysticercoids by the technique discussed in Material and Methods (page 4).

When cysticercoids were present in large numbers, some immediately floated out into the salt solution when the abdominal membrane was ruptured. Others remained hidden in the viscera which had to be separated to remove all of the cysticercoids from a beetle. Large numbers of cysticercoids frequently were found concealed in the anterior part of the abdomen under the scutellum.

Numbers of Cysticercoids. The numbers of cysticercoids per beetle ranged from one to 626 which were found in one Pterostichus (Anaferonia) sp. near constrictus[1]. This particular beetle had been fed four proglottids. The beetles of the genus Amara also had rather large numbers of cysticercoids, over 100 being rather frequently found. Cratacanthus dubius had fewer cysticercoids in most of the specimens, the usual number being from ten to 50. The Cratacanthus dubius which had 360 cysticercoids was rather exceptional. Although comparatively large numbers of cysticercoids were recovered from beetles which had been fed one proglottid, yet the larger infestations were found in beetles which had been fed two or more proglottids.

Invaginated Cysticercoid. The mature cysticercoid of Raillietina cesticillus was distinctly ovoid, the broader end of which presented a conspicuous groove or slit extending into the central cavity. The surface was dimly translucent and yellowish brown in color, making the larva easily visible to the unaided eye. The central region below the groove was darker than the rest of the cysticercoid but the structure of the scolex could not be distinguished in the living specimen. The live cysticercoids ranged in length from 363 to 521μ while the width ranged from 199 to 398μ.

Fixing, staining and clearing facilitated a study of the interior of the cysticercoid. The fibrous walls were rendered transparent enough

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[1]According to L. L. Buchanan the taxonomy of this group has not been clearly defined.

to reveal clearly the closely surrounded scolex which showed four suckers and a double row of contiguous hooks. Probably from pressure of the cyst wall the rows of hooks were forced into irregular loops (fig. 2). The scolex appeared in various positions as was found by Wetzel; however, the position shown in fig. 2 was more frequently found in the present studies.

Evaginated Cysticercoid. Some of the cysticercoids readily evaginated in water (fig. 3). These evaginated forms showed the typical broad rostellum which was inconspicuous in the invaginated stage. The double row of hooks forced into loops in the invaginated stage here assumed its natural position and formed a regular circle. Comparison of the cysticercoid scoleces with those of adult R. cesticillus showed that both the suckers and the hooks of the former were more conspicuous than those of the latter. Measurements of evaginated forms gave the following: length of scolex, 205μ; width of rostellum, 150μ; diameter of sucker, 39μ; length of cyst, 395μ; width of cyst, 253μ.

Considerable variation in the size of the cysticercoids from different beetles was noted. In heavy infestations the cysticercoids were very much smaller than in light infestations in the same species of beetles. In a few cases malformed cysticercoids were found along with others that were apparently normal.

Development of Cysticercoids into Adult Tapeworms

The last link in the life cycle is accomplished in nature when an infected beetle is eaten by a chicken. The cysticercoids are then

freed in the duodenum where they search with hooks and suckers for anchorage in the intestinal wall. In the experimental work, the cysticercoids were given to a chicken in a gelatine capsule, on a piece of filter paper, or in water by means of a pipette.

The cysticercoids very quickly develop into adult worms. In one case gravid proglottids were found loose in the ileum 11 days after the experimental feeding was made. Proglottids were frequently obtained from fecal examinations 13 days after experimental feedings.

HOST-PARASITE RELATIONSHIPS

Effects of the Parasite on the Host

Few investigators have studied taeniasis due to R. cesticillus sufficiently to report on the effects of this cestode upon its host. Wetzel (1934) reported that chickens showed a diminished appetite on the days immediately following experimental feeding with cysticercoids. Stafseth (1935) in studies made on treatment of chickens for tapeworms, considered R. cesticillus as a comparatively harmless parasite. These conclusions were based on observations upon individual fowls infested with this tapeworm.

In the present work carefully controlled tests were made to deter-mine effects of this cestode on parasitized and control chickens of the same original weights kept under the same conditions. Although in most cases 50 cysticercoids were used to parasitize each fowl, the infesta-

tions acquired by the chickens usually ranged from one to 20 tapeworms which was a comparatively light infestation. In studies involving over 100 chickens no constant differences could be detected in the gain in weight between the parasitized and the control chickens. From these tests it is inferred that light infestations of R. cesticillus have little or no effect upon the weights of fowls approaching maturity.

Records were made also of the amount of food consumed by the parasitized birds as compared with that taken by the controls. In preliminary studies three chickens, which had 5, 6, and 37 tapeworms, respectively, consumed more food per fowl than did two control chickens which had no tapeworms. In later studies a larger number of chickens was used, and daily weight records were taken on the fowls and the amount of food consumed for a period of two months. No constant differences were evident but this may have been due to the lighter infestations of tapeworms. During the course of the experiment one of the six parasitized fowls lost all of its worms and upon post-mortem examination none of the fowls had more than four tapeworms.

A similar experiment was begun a few weeks later and an effort made to parasitize the fowls more heavily. Larger numbers of cysticercoids were fed at different intervals to four fowls. Records were again kept on the amount of gain and the food consumed by these chickens and their controls. At the end of two months the fowls were killed and examined for parasites. The numbers of worms in the parasitized fowls ranged from one to 16 while the controls were without worms. No sig-

nificant differences between these two groups could be observed in the amounts of food consumed or the gains in weight. The light infestations in the second experiment may be attributed in part to the fact that the cysticercoids were fed at different times and the later feedings may have been inhibited by resistance which the host built up against super-infection. Hunninen (1935) showed conclusively that mice build up marked resistance to superinfection with the tapeworm Hymenolepis fraterna.

From these studies it is inferred that light infestations of R. cesticillus have little or no effect upon the amount of food consumed or the gain in weight of growing fowls.

Effects of the Host on the Parasite

The factors that affect resistance of hosts to nematode infestations have been studied extensively by Ackert and his associates. These studies were reviewed by Ackert in 1935. Due to the complicated life cycle of tapeworms, however, relatively little study has been devoted to the effect of a host upon its tapeworm parasites.

Shorb (1933) has shown that rats and mice acquire more resistance to the tapeworm Hymenolepis fraterna as they grow older. Rats five months of age are highly resistant to this tapeworm and mice are much less susceptible at seven months than at two.

Since no studies had been made on the factor of age resistance to poultry tapeworms, an experiment was carried out upon helminth-free

Table II. Age Resistance of Chickens to the Cestode

Raillietina cesticillus

Age of Chickens in days	Number of Hosts	Number of Worms	Mean	Standard Deviation	Error of Mean	Difference of Mean	Probable Error of Mean	Ratio, Act. Diff. P. E. D.
				Number of Worms				
20-51	15	73	4.87	1.76	.31	1.65	.33	5.07
71-150	27	87	3.22	.11	.11			
				Number of Proglottids				
20-51	15	67*	94.91	38.56	3.18	15.61	3.73	4.19
71-150	27	84*	79.3	26.47	1.95			

* Only the tapeworms which were entire upon removal
from the gut were used for the proglottid count.

chickens of two age groups: (1) from 21 to 50 days and (2) from 71 to 150 days of age. Usually 50 cysticercoids from the same beetles were fed to individual chickens under comparison.

After being parasitized for 11 days, the chickens whose tapeworms were to be compared were killed and the worms isolated. As the tapeworms R. cesticillus normally mature in 13 or 14 days, their isolation from the hosts at 11 days of age should indicate whether or not the growth of the worms from the older hosts had been inhibited. As the size of living tapeworms in aqueous solutions may vary considerably the criterion for judging the amount of age resistance of the host chickens was the number of proglottids of each tapeworm. To facilitate counting the proglottids a compound microscope equipped with ocular pointer and mechanical stage was used. Only the tapeworms which were complete with scolex and terminal proglottids were used in the statistical consideration.

In table II it may be seen that the younger chickens, 15 in number, averaged 4.87 worms per bird, while the older chickens, 27 in number, averaged 3.22 worms per fowl. This was a difference of 1.65 worms which was 5.07 time its probable error and therefore considered significant.

From these results it may be inferred that older chickens acquire increased resistance which reduces not only the number of worms but also inhibits the rate of growth of the tapeworms Raillietina cesticillus.

SUMMARY

1. The life history of the chicken cestode _Raillietina cesticillus_ (Molin) has been restudied and physiological experiments involving 300 chickens and 570 beetles have been carried out.

2. Observations on the motility of the detached gravid proglottids showed that: (a) gravid proglottids are very motile in the intestine after separation from the tapeworm; (b) they remain motile for some time after leaving the host if they are warm; (c) the proglottids migrate to the outside of the fecal mass in which they are evacuated; (d) one warm proglottid moved eight inches upon moist filter paper; and (e) they are not tropistically activated by light, heat or gravity.

3. The onchosphere stage of _R. cesticillus_ can be distinguished from onchospheres of other species of fowl tapeworms by two funnel-like structures in the membranes which surround the hexacanth embryo.

4. Two genera and twelve species of ground beetles which previously have not been reported can act as intermediate hosts for the fowl tapeworm _R. cesticillus_. These beetles are _Pterostichus torvus_ Lec., _P. permundus_ Say, _P._ (_Anaferonia_) near _constrictus_ Say, _Amara obesa_ Say, _A. latocollis_ Lec., _A. muscula_ Say, _A. fallax_ Lec., _A. basillaris_ Say, _Anisotarsus subvirens_ Csy., _Chlaenius tomentosus_ Say, _Anisodactylus rusticus_ Say, and _Harpalus pennsylvanicus_ Degeer. Nearly all species of _Amara_ which have been tested have proved infective for _R. cesticillus_ but in the genera _Pterostichus_ and _Harpalus_ some species are infective

while others are not.

5. As many as 626 cysticercoids were produced by one beetle which had been fed four proglottids. The size of the cysticercoids is partly dependent upon the number of cysticercoids in a beetle and upon the species of beetle.

6. The mature cysticercoids in the invaginated and evaginated forms are described and illustrated.

7. Cysticercoids usually develop into adult tapeworms in about two weeks, although tapeworms with gravid proglottids were produced in 11 days after the fowl had swallowed cysticercoids.

8. Techniques were developed which facilitated the infection of beetles with onchospheres, the rearing of infected beetles, and the feeding of the fully developed cysticercoids to chickens, thus making possible critical studies of host-parasite relationships.

9. Light infestations of R. cesticillus have comparatively little effect upon the gain in weight of or upon the amount of food consumed by growing chickens.

10. Increased resistance is developed in chickens, two and a half or more months old, to the viability and growth of the tapeworm R. cesticillus. This age resistance limits the sizes of infestations and inhibits the growth of the tapeworms.

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EXPLANATION OF PLATE

Figure 1.   The onchosphere of <u>Raillietina</u> <u>cesticillus</u>,
             somewhat dialyzed to show the membranes. A, B,
             C, D, E, and F are membranes of the onchosphere.

Figure 2.   The mature invaginated cysticercoid of <u>Raillietina</u>
             <u>cesticillus</u>.

Figure 3.   The mature evaginated cysticercoid of <u>Raillietina</u>
             <u>cesticillus</u>, showing characteristic broad rostellum.

2.

100 μ

3.

100 μ

A
B
C
D
E
F

25 μ

1.