STUDIES ON NORTH AMERICAN HELMINTHS OF THE
GENUS CAPILLARIA ZEDER, 1800 (NEMATODA)

BY

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The First of Two Theses Submitted to the Faculty of the
William Marsh Rice Institute
In Partial Fulfillment of the
Requirements for the Degree of
Master of Arts

Houston, Texas
1948
44-4933
ACKNOWLEDGEMENTS

This investigation was done under the direction of Professor Asa C. Chandler, to whom I wish to express my appreciation for his encouragement and for his valuable suggestions. Thanks are also due to Dr. Robert Rausch, of the University of Wisconsin, for the loan of many specimens; to Dr. E. W. Price for the loan of specimens from the U. S. National Museum; to Professor E. S. Hathaway, of Tulane University, for laboratory space during the summer of 1947; and to my wife, Leota W. Read, who spent many hours typing this manuscript.
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Introduction

The genus *Capillaria* was established by Zeder in 1800 with *Capillaria anatis* (Schrank, 1790) as the type species. In 1819 Rudolphi originated the name *Trichosoma* to replace Zeder's generic name. Creplin (1839) designated the genus *Trichosomum*. Dujardin (1845), in an attempt to split up this group, erected the genera *Calodium*, *Lemniscus*, *Thominx*, and *Eucoleus*. Stossich (1890) included the members of the genus *Capillaria* in the genus *Trichosomoides* which he divided into three subgenera.

Travassos (1915) demonstrated that *Capillaria* Zeder is the correct name for this genus and erected two subgenera, *Capillaria* and *Thominx*, which were characterized by the presence or absence of spines on the spicule sheath. Hall (1916) erected the genus *Hepaticola* for the reception of *Capillaria hepatica* (Bancroft, 1893) which had been described by previous workers as lacking a spicule. Baylis (1931) demonstrated a spicule in this species and concluded that *Hepaticola* is a synonym of *Capillaria*. Further, Baylis felt that Travassos' subgeneric division of the genus had dubious taxonomic or phylogenetic significance. Teixeira de Freitas and Lent (1935, 1936) and Teixeira de Freitas and Almeida (1935) have made extensive studies of members of the genus and have reviewed the species found in various host groups. Cram (1936) has reviewed the species occurring in the upper digestive tract of birds. Madsen (1945) made an elaborate study of capillarids from Danish gallinaceous and anatine birds.
The genus contains many species which are inadequately described as has been pointed out by Travassos (1915), Hall (1916), Teixeira de Freitas and Lent (1936), and other authors. Because of this and because many species have been described from only a few specimens it is almost impossible to determine the limits of variation of many members of the genus. A thorough restudy of the genus is needed, but it is probable that such a task could better be undertaken by some worker with access to large collections of material, such as that of the United States National Museum, or some of the larger European institutions.

Important contributions to the knowledge of the life cycles of various species have been made by Nishigori (1925), Wehr (1937, 1939), Morehouse (1944), and other workers.

The present study is limited to those species parasitic in North American mammals and in the lower digestive tract of North American birds. None of the writer's material from the upper digestive tract of American birds revealed features which were not covered in the excellent work of Cram (1936). Most of the material examined in the course of this work was collected by Dr. Robert Rausch of the Department of Veterinary Science, University of Wisconsin, who kindly made the material available. Some additional specimens were collected by the writer at Houston, Texas, and New Orleans, Louisiana.

Representatives of the genus have been reported as parasites of the alimentary canal, respiratory tract, genito-urinary tract, and subcutaneous tissues of various
North American mammals. A review of the literature reveals that ten species have previously been reported from North American mammals and seven from the lower digestive tract of North American birds. A questionable record of an additional mammalian species, *C. putorii*, is discussed below. In the present work seven species are added to the known mammalian parasitic fauna and four are added to the capillarids known from American birds. Further, several new hosts are recorded for capillarids previously known from this continent.
CAPILLARIDS FROM NORTH AMERICAN MAMMALS

*Capillaria linearis* (Leidy, 1856)

This helminth was not encountered during the course of this study. However, during the revision of this paper it has been called to the attention of the writer that this species has been subjected to a rather curious misdescription by various workers. Leidy (1856) gave a fragmentary description of *Trichosomum lineare* from the intestine of a cat. He gave the lengths of the male and female as 1 1/2 and 3 inches respectively. Neveu-Lemaire (1912), Baylis (1929), and Teixeira de Freitas and Lent (1936) gave the lengths of the male and female of Leidy's worm as 3.8 and 7.6 mm. These measurements, evidently due to the misplacing of a decimal point in converting from inches to millimeters, are ten times smaller than the measurements given by Leidy. A search of the literature has revealed no correction of Leidy's original description by that author, and no mention of a correction has been made by other authors. Using Leidy's measurements, *C. linearis* is much larger than any other North American species.

Lewis (1927) reported *C. linearis* from the urinary bladder of cats in Wales. Lewis's specimens and *Capillaria* sp. reported from the urinary bladder of Canton cats by Chen (1934) are probably referable to *C. felis-cati* (Diesing, 1851), Travassos, 1915, rather than to *C. linearis*. It seems highly unlikely to the writer that these specimens from the urinary bladders of cats are co-specific with Leidy's *Trichosomum lineare* from the intestine.
Capillaria hepatica (Bancroft, 1893) Travassos, 1915

This cosmopolitan species is here reported for the first time from the cotton rat, Sigmodon hispidus, taken at Houston, Texas.

Capillaria putorii (Rudolphi, 1819) Travassos, 1915

Sprehn (1932) includes the U. S. in the geographical distribution of this species. The writer has been unable to locate any report of this worm from a North American mammal and has failed to find it in any of the material examined during the course of this study. It has been reported from at least eight species of mustelids in Europe and it would not be surprising to find this worm in the North American fauna. It is possible that some of these European records of *C. putorii* were actually *C. mustelorum* Cameron and Parnell, 1932, described from mustelids in Scotland, which resembles *C. putorii* closely. Petrow (1928) redescribed *C. putorii* and Christensen, Olsen, and Roth (1946) have recently reported it from a Copenhagen cat.

Capillaria mustelorum Cameron and Parnell, 1932

Worms of this species were recovered from the small intestine of two of eight weasels, Mustela frenata nova-boracensis, at East Lansing, Michigan, and from one of thirty-six mink, Mustela vison, at Horicon Marsh, Wisconsin, and from one of two mink at Houston, Texas. This species has not been previously reported from North America.

Capillaria spp. reported from Mustela vison in North America by Law and Kennedy (1932), Allen (1934), Sealander (1943),
and Erickson (1946) probably belong to this species. Since the material at hand shows a range of variation not covered in the description of Cameron and Parnell, a description of the worms seems warranted.

Description: Bacillary lines not visible. Cuticle transversely striated. Mouth simple.

Female: 4.3 to 12.1 mm. long; 45 to 54 μ wide just posterior to vulva. Esophagus 2.5 to 3.3 mm. long. Vulva slightly posterior to termination of esophagus, without appendages or with small cuticular bosses marking the labia. Vulva divides body 1:1.1 to 1:2.6. Ova 52 to 60 by 24 to 30 μ, outer shell smooth, prominent plug at each end. Posterior extremity rounded. Anus subterminal.

Male: 3.6 to 8.0 mm. long; 33 to 38 μ wide. Esophagus 1.7 to 3.7 mm. long. Spicule 290 to 406 μ long, 3.8 to 4.5 μ wide near proximal end; spicule sheath transversely striated. Cauda provided with lateral cuticular alae, 98 to 120 μ long. Body terminated by two stout papillae, supporting a membranous cuticular bursa. Termination of esophagus divides body 1:1.1 to 1:1.3.

Certain features serve to differentiate this species from C. putorii (Rudolphi, 1819) Travassos, 1915. The female worms differ in the position of the vulva and in the size of the eggs. The males differ in the length of the spicule and in the relative lengths of the esophagus. Teixeira de Freitas and Lent (1936) mentioned the possible synonymy of C. mustelorum with C. erinacei (Rudolphi, 1819). The vulva of C. erinacei,
as described by various workers, differs from that of *C. mustelorum* in possessing markedly salient labia; the spicule of *C. erinacei* has not been adequately described and cannot furnish a distinctive character for the separation of the two species.

*C. micronuta* (Molin, 1858), an insufficiently described species from the urinary bladder of *Martes foina* in Europe, is probably a valid species although it is certainly similar to the forms mentioned above.

**Capilleria muris-sylvatici** (Diesing, 1851)

Worms of this species were recovered from the small intestine of the vole, *Microtus p. pennsylvanicus*, examined at Madison, Wisconsin. No previous record from this host nor from any North American host has been found in a search of the literature. Since the worms show some features not recorded by other workers, a description of this material seems warranted.

**Description:** Lateral bacillary lines visible. Mouth simple. Cuticle striated transversely.

Female: 13.4 to 16.1 mm. long; maximum width in posterior region 70 to 75 μ. Termination of esophagus 3 mm. from anterior end. Vulva just posterior to termination of esophagus, 3 to 3.2 mm. from anterior end, with cuticular vulvar flap projecting from region of anterior labium. A discoid cuticular projection is located anterior to vulvar flap at level of esophageal termination. Vulva divides body 1:3.5 to 1:3.7. Ova 47 to 60 μ long by 24 to 26 μ wide.
inner shell bends to form collar at each end; outer shell smooth. Anus slightly subterminal.

Male: 9.1 to 10.8 mm. long; maximum width 45 to 47 μ. Termination of esophagus 2.7 to 2.9 mm. from anterior end. Lateral caudal alae present, about 70 μ long. Spicule 204 to 225 μ long by 11 to 13 μ wide. Spicule sheath without spines or transverse striations. Everted spicule sheath divided into four portions: Distal portion delicate, membranous, usually wrinkled; subdistal portion bulblike, muscular; proximal portion bulblike with rugose markings on lateral aspect; proximal and subdistal portions joined by short, wrinkled tubular projection of proximal bulb. Cuticular bursa supported by pair of bifid papillae. Cloaca subterminal. Termination of esophagus divides body about 1:2.7.

According to Teixeira de Freitas and Lent (1936) this species was studied by Kalentarian (1924), whose work has not been accessible to the writer. Kalentarian renamed the species C. halli, which was reduced to synonomy by Teixeira de Freitas and Lent. These workers, following Kalentarian, describe a toothpick-like papilla projecting from the vaginal aperture, and such a structure is shown in the figure taken from Kalentarian. The writer has found that if the female worms are viewed from a dorso-lateral angle the cuticular flap appears as a papilla such as Kalentarian described. Considerable manipulation of specimens is necessary to obtain the true picture of the vulvar anatomy. The male worms agree essentially with Kalentarian's description except that the
writer was unable to find the sub-median papillae mentioned by that worker. The writer at first referred the material at hand to a new species, but the correspondence of the pre-vulvar cuticular projection and vulvar flap in the female and the bifurcate caudal papillae and caudal alae in the male to the described features of *C. muris-sylvestric* seem to warrant the reference of these worms to that species.

Although it is obvious that the everted spicule sheath of capillarids may be highly variable in form, the writer has found that this structure appears essentially as described above in fifteen male worms whose sheaths were everted. This seems to be a rather constant feature.

*Capillaria bovis* (Schnyder, 1906) Ransom, 1911

This worm was described very fragmentarily by Schnyder (1906) from *Bos taurus* in Europe. In 1911 Ransom described a worm, *Capillaria longipes*, from North American prong-horned antelope and sheep. Ransom's adequately described worm differed from the poorly described European form in hostal and geographical distribution. Restudy by Petrow and Orlow (1930) of *C. bovis* from *Bos taurus* in Europe has shown that *C. longipes* is a synonym of *C. bovis*. Teixeira de Freitas and Lent (1936) suggested that restudy of the type material of *C. brevipes* Ransom, 1911, from North American sheep, might show this worm to be cospecific with *C. bovis*.

Through the courtesy of Dr. E. W. Price, the writer has been able to examine the types of *C. longipes* Ransom, 1911, and *C. brevipes* Ransom, 1911, which are deposited in the
U. S. National Museum. The specimens of *G. longipes* conform closely with the description of *G. bovis* as given by Teixeira de Freitas and Lent. The type specimens of *G. brevipes* correspond with Ransom's description in all respects except one. Ransom noted that the shell of the egg of *G. brevipes* was 3 to 4 μ thick, while that of *G. longipes* was 1.5 to 2 μ thick. Ransom's figures of the eggs of the two species also shows this difference in shell thickness. The writer has been unable to find any difference in the thickness of the shell nor has any other difference in the eggs been noted. It would seem that the main differences of the two species are differences in size. The lengths of the male and female of *G. bovis*, following the description of Teixeira de Freitas and Lent, are 11 to 13 mm. and 18 to 25 mm. respectively; the lengths of the male and female of *G. brevipes* are 8 to 9 mm. and 12 mm. respectively. The writer does not feel that the differences in the length of the proximal portions of the caudal papillae in the males of the two species noted by Ransom are of sufficient importance to warrant their separation. Dikmans (1930) has reported *G. brevipes* from cattle. It would be of some interest to compare material from cattle with that from sheep. The writer feels that further study along such lines would probably show *G. brevipes* to be co-specific with *G. bovis*.
Capillaria rauschi n. sp.

Specific diagnosis: Bacillary line not visible. Mouth simple. Cuticle finely striated transversely.

Female: 5.2 to 7.4 mm. long; 48 to 53 μ wide just posterior to vulva; maximum width 61 to 68 μ. Vulva slightly posterior to termination of esophagus, 2 mm. from anterior end, slightly salient or with campanuliform appendage. Vulva divides body 1:1.6 to 1:1.9. Ova 59 to 62 μ by 26 to 28 μ, with outer shell mammillated and with inner shell forming a collar around the opercular plug at one end. Anus subterminal.

Male: 4.8 mm. long; maximum width 50 μ. Esophagus 1.98 mm. long. Spicule sheath transversely striated; spicule 395 μ long and 8 μ wide near proximal end; widened at proximal end and appearing bilobate in lateral view. Body terminated by two stout bilobed papillae supporting a membranous cuticular bursa. Cloacal opening subterminal at base of caudal papillae. Termination of esophagus divides body 1:2.4.

Host: Sorex cinereus Kerr.

Habitat: Small intestine.

Locality: Madison, Wisconsin.


Three females and one male of this species were recovered in the examination of a single masked shrew. This species differs from C. splenaece (Dujardin, 1843) Travassos, 1915, described from Sorex araneus in Europe, and from C. minutus Chen, 1937, from Suncus coerulus in China, in size of eggs and in lack of lateral caudal alae. The
mammillated outer shell of the ova of *C. rauschi* will differentiate it from most species reported from mammals.

The species is named in honor of Dr. Robert Rausch, previously mentioned as the collector of this material.

**Capillaria tamias-striati** n. sp.

Specific diagnosis: Bacillary lines not visible. Mouth simple. Body finely striated transversely.

**Female:** 11.8 to 14.4 mm. long; 45 to 50 μ wide just posterior to vulva. Vulva slightly posterior to termination of esophagus, 3.0 to 4.6 mm. from anterior extremity; labia marked by pronounced cuticular swellings. Vulva divides body 1:2 to 1:3. Ova 53 to 57 μ long by 25 to 27 μ wide; outer shell with reticulate markings; inner shell thin and forming collar at each end around opercular plugs. Posterior extremity straight and conical. Anus subterminal.

**Male:** 6.0 to 7.6 mm. long; 42 to 48 μ wide in posterior region. Esophagus 2.7 to 3.1 mm. long. Spicule sheath striated coarsely in distal portion and finely striated or not striated in proximal portion, 41 to 44 μ wide in proximal portion. Spicule finely striated, 490 to 502 μ long by 7 to 8 μ wide at base; tip of spicule with slender finger-like ending, 26 μ long by 3 μ wide. Cauda provided with lateral cuticular alae, 110 to 160 μ long; alae finely ribbed or not ribbed. Body terminated by two stout blunt projections, supporting a membranous cuticular bursa. Cloacal opening subterminal. Termination of esophagus divides body 1:1.2 to 1:1.4.
Host: *Tamias striatus* L.
Habitat: Small intestine.
Locality: Madison, Wisconsin.

Worms of this species were recovered from two of forty-three Chipmunks examined at Madison. This worm bears a striking resemblance to *C. erinacei* (Rudolphi, 1819), described and reported from European hedgehogs, however, there are certain rather minute differences which seem to warrant referring this material to a new species. The vulva of *C. erinacei* is described as being redundant, and the figure given by Eberth (1863) of *Trichosomum exiguum* Duj., 1845, (= *C. erinacei* (Rud., 1819)) shows the labia as redundant structures quite unlike the corresponding structure of *C. tamias-striati*. Both Eberth (1863) and v. Linstow (1878) described and figured the caudal papillae of the male of *C. erinacei* as two slender finger-like structures. In contrast, the male of *C. tamias-striati* possesses rather stout papillae. Other than these differences, *C. erinacei* possesses lateral bacillary lines which are about one-third the diameter of the body in width. Bacillary lines were not seen by the writer in any specimens of *C. tamias-striati*, although thirty-one specimens were available for study.

*Capillaria michiganensis* n. sp.
Female: 17.5 to 20.9 mm. long; width just posterior to vulva 45 to 46 μ; maximum width 62 to 70 μ. 33 to 35 paraesophageal nuclei. Vulva just posterior to termination of esophagus and 6.7 to 9.0 mm. from anterior end. Anterior labium salient forming flap over vulva. Vulva divides body 1:1.0 to 1:1.6. Eggs 53 to 56 μ by 28 to 30 μ; inner shell bends to form collar around plug at each end; outer shell smooth. Anus subterminal.

Male: Unknown.

Host: Ondatra zibethica.

Habitat: Small intestine.

Locality: Monroe County, Michigan.


Female worms taken from the small intestine of Michigan muskrats are referred to this species. These worms had been examined by Dr. J. D. Tiner and tentatively referred to Capillaria ransomia Barker and Noll, 1915, a species previously recorded from muskrats. However, the worms examined by the writer differ rather markedly from the description of C. ransomia given by Berker (1915). Barker stated that the vulva lay in the anterior fourth of the body in C. ransomia; in the worms examined by the writer the vulva is in the second fourth. Barker gave the egg measurements of C. ransomia as 50 by 20 μ, whereas the eggs from the worms examined in the present study are 53 to 56 μ by 28 to 30 μ. Barker failed to mention an anterior vulvar flap in C. ransomia. This character serves to separate C. michiganensis from all other
species in North American mammals, except *G. muris-sylvatici*. Hall (1916) has already pointed out that the indicated magnifications in Barker's drawings do not agree with the measurements in the text. The error seems to lie in the scale appended to the drawings. Specimens of material from the muskrat identified as *G. ransonia* were loaned to the writer by Dr. E. W. Price. This material consisted of female worms which are identical with the material from Michigan muskrats.

A single male worm recovered from the present series of muskrats has not been accessible to the writer. Tiner (personal communication) examined this worm and stated that the spicule was 1.53 mm. long. Tiner also noted the discrepancy between the position of the vulva in the female worms from this series and those described by Barker. The single male examined by Tiner possibly was *G. ransonia*, since Barker gave the spicule length of this species as 1.36 mm. However, it is impossible to be certain without further information than the spicule length.

It should be mentioned that nine of one hundred muskrats were found to be infected with *Capillaria*. However, the writer examined material from only three of these hosts. It is possible that both *G. ransonia* and *G. michiganensis* occurred in this series of animals and that Tiner's tentative diagnosis was correct for at least part of the worms that he examined.
Capillaria chandleri n. sp.


Female: 15.3 mm. long; 46 μ wide just posterior to vulva; maximum width 72 μ. Body with marked swelling just anterior to vulva. Vulva situated 3.7 mm. from anterior extremity; anterior and posterior labia markedly salient. Ova 57 to 58 μ long by 27 to 28 μ wide; outer shell smooth; inner shell thin and forming collar at either end. Anus terminal. Vulva divides body 1:3.1.

Male: Unknown.

Host: Citellus franklini.

Habitat: Small intestine.

Locality: Madison, Wisconsin.


Two females of this species, one of which was incomplete, were recovered from one of ten Franklin ground squirrels examined. C. chandleri differs from all other species of Capillaria in North America in the peculiar prevulvar swelling of the body. This was seen in both specimens examined.

Capillaria americana n. sp.

Specific diagnosis: Body transversely striated. Thin lateral bacillary lines visible in some specimens. Four minute papillae around mouth.

Female: 23 to 28.4 mm. long; 106 to 118 μ wide just posterior to vulva; maximum width 136 to 144 μ. 56 to 39
paraesophageal nuclei. Vulva slightly posterior to termination of esophagus, 6.8 to 7.5 mm. from anterior extremity; labia slightly salient; heavily muscular ovejector present. Body cavity filled by gravid uterus. Ova 46 to 52 μ by 23 to 27 μ; outer shell lightly striated; inner shell forming slight collar for opercular plug at each end. Anus slightly subterminal. Vulva divides body 1:2.4 to 1:2.7.

Male: 12.2 to 15.4 mm. long; maximum width 84 to 103 μ. 41 to 45 paraesophageal nuclei. Termination of esophagus 5.4 to 6.5 mm. from anterior end. Spicule sheath smooth. Spicule stout, transversely striated, 209 to 258 μ long by 11 to 14 μ wide. Cauda terminated by two poorly developed lobes; single minute papilla on ventrum of each lobe. Bursa lacking. Cloacal opening slightly subterminal. Termination of esophagus divides body 1:1.0 to 1:1.7.

Hosts: Glaucomys volans volans (type), Sciurus carolinensis leucotis, Peromyscus maniculatus bairdii, Peromyscus leucopus noveboracensis.

Habitat: Small intestine.


Worms of this species were recovered from the small intestine of seven flying squirrels at McHenry, Illinois, and Marysville, Ohio, from one of forty-six prairie white-footed mice at Madison, Wisconsin, from two of twenty-seven gray squirrels at Madison, Wisconsin, and from one of one
hundred and twenty-nine northern white-footed mice at Madison, Wisconsin. The distribution of this worm in squirrels under the designation "Capillaria sp." is discussed by Rausch and Tiner (1948).

The posterior end of the male of C. americana shows some similarity to that of males of C. aerophila from the lungs of carnivores, but the two species are quite different in other respects. The stout spicule and the cauda of the male are quite adequate for differentiation from other mammalian species of Capillaria.
Keys to the Species of Capillaria Parasitic
in North American Mammals

**Females**

1. **a.** From alimentary canal ..........................2.  
   **b.** From location other than alimentary canal ......4.

2. **a.** Worms about 75 mm. long. Tail with two conical 
   projections on ventral surface ........................
   .......................... *linearis* (Leidy, 1856).
   **b.** Worms considerably less than 75 mm. long .....3.

3. **a.** Vulva in anterior fourth of body ...............7.  
   **b.** Vulva not in anterior fourth of body ..........10.

4. **a.** From skin of primates. Vulva divides body about 
   1:5. Ova 67 to 70 by 40 to 42 u ......................
   .......................... *cutanea* (Swift, Boots, and Miller, 1922).
   **b.** From viscera .................................5.

5. **a.** From trachea, bronchi, and lungs of carnivores. 
   Vulva at level of termination of esophagus, 
   without appendage..... *aerophila* (Creplin, 1839).
   **b.** From liver. Vulva with tubular appendage.....
   .......................... *hepatica* (Bancroft, 1893).

6. **a.** Vulva with campanuliform appendage. Posterior 
   end obtuse with anus terminal ......................
   .......................... *plica* (Rudolph, 1819).
   **b.** Vulva with slightly salient labia. Posterior 
   end with three slight lobes surrounding terminal 
   anus............. *felis-catii* (Diesing, 1851).
7. a. Vulva with anterior cuticular flap and a discoid cuticular prevulvar projection. Ova 47 to 60 by 24 to 26 u. \textit{C. muris-sylvatici} (Diesing, 1851).

b. Vulvar anatomy other than as in a. \textbf{8.}

8. a. Body with marked prevulvar swelling. Labia salient. Ova 57 to 58 by 27 to 28 u. From Sciuridae \textit{chandleri} n. sp.

b. Body without marked prevulvar swelling. \textbf{9.}

9. a. Anus terminal. Ova 64 to 72 by 28 to 32 u. From carnivores \textit{putorii} (Rudolphi, 1819).


10. a. Anterior labium forms a vulvar flap. Ova 53 to 56 by 28 to 30 u. From \textit{Ondatra zibethica} \textit{michiganensis} n. sp.

b. Vulvar anatomy other than as in a, with or without appendage. \textbf{11.}

11. a. Vulva with tubular appendage. \textbf{12.}

b. Vulva without tubular appendage. Labia slightly salient or not salient. \textbf{13.}

12. a. Worms 21 to 22 mm. long. Vulva divides body about 1:2.2. Ova 47 to 50 by 31 to 32 u. From Vespertilionidae \textit{palmata} Chandler, 1938.

b. Worms 5.2 to 7.3 mm. long. Vulva divides body 1:1.6 to 1:1.9. Ova 61 by 27 u. From Soricidae \textit{rauschii} n. sp.

13. a. Vulva with salient or slightly salient labia. \textbf{14.}

b. Vulva without salient labia. \textbf{16.}
14. a. Vulva with slightly salient labia. Heavily muscular ovejector present. Body filled by gravid uterus ...

................................. americana n. sp.

b. Vulva with markedly salient labia. Body not filled by gravid uterus ................................. 15.

15. a. Worms 18 to 25 mm. long. Ova 45 to 52 by 21 to 30 u. From Ungulata ........... bovis (Schnyder, 1906).

b. Worms 10.5 to 15.5 mm. long. Ova 50 to 57 by 25 to 27 u. From Sciuridae .............. tamias-striati n. sp.

16. a. Anus terminal. Ova 50 by 25 u. From Ungulata ....

................................. brevipes Ransom, 1911.

b. Anus subterminal. Ova 52 to 60 by 24 to 30 u. From Carnivora ....... mustelorum Cameron and Parnell, 1932.

Males

1. a. From alimentary canal ................................. 2.

b. From location other than alimentary canal ......... 11.

2. a. Worms about 36 mm. long. Cloaca considerable distance from posterior end ...... linearis (Leidy, 1856).

b. Worms less than 20 mm. long. Cloaca terminal or subterminal ................................. 3.

3. a. With lateral caudal alae ................................. 4.

b. Without lateral caudal alae ................................. 9.

4. a. Spicule sheath smooth. Membranous bursa supported by two papillae; distal portion of each papilla turned cephalad at right angles to proximal portion. Found in ruminants ................................. 5.
4. b. Spicule sheath transversely striated. Membranous bursa supported by papillae which are different from a. Not found in ruminants ....................... 6.

5. a. Spicule 1000 to 1200 u long. Termination of esophagus divides body 1:1.7 ........ bovis (Schnyder, 1906).
   b. Spicule 900 u long. Termination of esophagus divides body 1:1.2 ......................... brevipes Ransom, 1911.

6. a. Termination of esophagus in anterior third of body.
   Spicule less than 225 u long ....................... 14.
   b. Termination of esophagus not in anterior third of body. Spicule more than 225 u long .................... 7.

7. a. Tips of caudal lobes bifurcate. Lateral bursal "rays" present. From Vespertilionidae ..............
   .................................................. palmata Chandler, 1938.
   b. Tips of caudal lobes not bifurcate. Lateral bursal "rays" not present ................................. 8.

8. a. Spicule 490 to 502 u long. Lateral caudal alae sometimes ribbed .................. tamias-striati n.sp.
   b. Spicule 290 to 406 u long. Lateral caudal alae not ribbed ........... mustelorum Cameron and Parnell, 1932.

9. a. Cauda with two stout papillae supporting bursa ... 10.
   b. Cauda with two poorly defined lobes. Bursa lacking.
   Spicule 209 to 258 u long by 11 to 14 u wide ......
   .................................................. americana n. sp.

10. a. Worms about 4.8 mm. long. Spicule 395 u long. From Soricidae .......................... rauschi n. sp.
    b. Worms about 19.6 mm. long. Spicule 1360 u long.
    From Ondatra zibethica..ransomia Barker and Noll, 1915.
   b. From viscus other than urinary bladder. Spicule sheath finely spiny ................................. 13.

12. a. Spicule 4 mm. long ............ plica (Rudolphi, 1819).
   b. Spicule 2.5 mm. long ....... felis-cati (Diesing, 1851).

13. a. From trachea, bronchi, and lungs of carnivores.
   Spicule very thin, usually not visible..............
   ........................................... aerophila (Creplin, 1839).
   b. From liver. Spicule well developed ........................
   ........................................... hepatica (Bancroft, 1893).

   b. Spicule 149 to 168 μ long. Caudal papillae stout, not bifurcate .......... C. putorii (Rudolphi, 1819).

Not included in the key to the males are C. michiganensis, C. chandleri, and C. cutanea; only the females of these worms are known.
PLATE IV
CAPILLARIDS FROM THE LOWER DIGESTIVE TRACT OF NORTH AMERICAN BIRDS

*Capillaria caudinflata* (Molin, 1858)

Two female worms of this species were recovered from the small intestine of a starling, *Sturnus vulgaris*, of twenty-five examined at East Lansing, Michigan. Several chickens examined by the writer at Houston, Texas, also harbored this parasite. Since this material conforms closely with the descriptions of *Trichosoma longicolle* of Shipley (1909) and *Capillaria longicollis* of Morgan (1932), no description of the material at hand seems necessary.

Morehouse (1939) reported this helminth for the first time from North American birds, finding it in chickens in Iowa, Minnesota, Ohio, Illinois, Wisconsin, Pennsylvania, Missouri, Kansas, Indiana, and Michigan. Todd (1946) reported it from chickens in Tennessee. Morehouse (1944) described the life cycle and reported the turkey and the English sparrow, *Passer domesticus*, as experimental hosts.

Madsen (1945), in an extensive study of capillarids from gallinaceous and anatine birds, concluded that the correct name for this species is "*Capillaria longicollis* (Mehlis 1831)." Madsen said, "As *Capillaria longicollis* in its modern delimitation occurs only in the small intestine, the species very fragmentarily described by Rudolphi under the above mentioned name does unfortunately not belong to this species. But as Mehlis (1831) has found in the small intestine of the pheasant a species which he named *Capillaria longicollis* and the name in the present delimitation has been
current for a number of years, it seems reasonable to retain it, however, with Mehlis as author."

The writer cannot agree with this opinion of Madsen's. In the first place, it should be said that Madsen is attributing the name to a man who did not make the name. If Mehlis' *Trichosomum longicolle* is not the same species as *Trichosoma longicolle* Rudolphi, 1819, Mehlis created a homonym; this seems to be the case. The worms described by Madsen and other workers from the small intestine are probably not *C. longicolli* (Rudolphi, 1819), described from the large intestine of the pheasant, but a distinct species. As Morehouse (1944) pointed out, the first available name applied unquestionably to this zoological entity from the small intestine was *Calodium caudinflatum* Molin, 1858. Thus, the correct name for this worm is *Capillaria caudinflata* (Molin, 1858). *C. cadovulvata* Madsen, 1945, from the cecum of the pheasant and the quail may be the same species as *Trichosoma longicolle* of Rudolphi.

*Capillaria tridens* (Dujardin, 1845)

A single male worm of this species was taken from the small intestine of one Red-winged Blackbird of forty-four examined at Prairie du Sac, Wisconsin. A description follows: Diagnosis: Body transversely striated. Bacillary lines absent. Mouth simple.

Male: 13.9 mm. long; maximum width 49 u. Termination
of esophagus 6.2 mm. from anterior end. Spicule 1.275 mm. long, 18 μ wide near proximal end; spicule sheath 1.840 mm. long by 24 μ wide, beset with spines. Cauda broadly terminated by three stout lobes. Slightly developed membranous bursa present. Cloaca subterminal. Termination of esophagus divides body 1:1.3.

Host: *Agelaius phoeniceus*.

Habitat: Small intestine.

Locality: Prairie du Sac, Wisconsin.

This worm has not previously been reported from North America and has been reported only from the type host, *Luscinia luscinia*, the thrush-nightingale, in other parts of the world. The species is easily recognized by the broad trilobed tail of the male.

**Capillaria falconis-nisi** (Diesing, 1851)

Description: Body finely striated transversely. Lateral bacillar lines one-fourth of body diameter or not visible. Mouth simple.

Female: 16.4 to 29.4 mm. long; width just posterior to vulva 60 to 69 μ; maximum width 87 to 100 μ. Vulva transverse slit, 5.0 to 7.7 mm. from anterior end, just posterior to termination of esophagus; labia slightly salient. Ova 65 to 72 μ by 30 to 34 μ; inner shell bent at poles to form collar around plug; outer shell finely reticulated. Anus subterminal. Vulva divides body 1:2.0 to 1:2.7.

Male: 9.6 to 14.8 mm. long; maximum width 54 to 80 μ. Termination of esophagus 3.5 to 6.9 mm. from anterior end.
Spicule lightly striated transversely, 750 to 1250 µ long by 12 to 14 µ wide; tip blunt. Spicule sheath finely striated transversely, 1.20 to 1.35 mm. long when completely everted. Cauda with two stout lobes supporting a slightly developed cuticular bursa; single minute papilla sometimes visible on ventral surface of each lobe. Cloacal opening subterminal. Termination of esophagus divides body 1:0.9 to 1:1.9.

Hosts: *Asio wilsonianus*, *Cryptoglaux acadica*, *Bubo virginianus virginianus*, *Buteo borealis*.

Habitat: Small intestine.

Locality: Wisconsin.

Worms of this species were taken from a single Long-eared Owl at Horicon Marsh, Wisconsin, from a single Saw-whet Owl at Poynette, Wisconsin, from eight of fifty-two Great Horned Owls at Poynette, Wisconsin, and from three of forty-two Red-tailed Hawks at Poynette, Wisconsin.

The male of this species was described as *Trichosomum contortum* from *Accipiter nisus* in Europe by Dujardin (1843). The error was corrected, and the species named by Diesing (1851). It is interesting to note that the female of *C. falconum* (Rudolfí, 1819), described from the same host, is indistinguishable, by extant descriptions, from the female of *falconis-nisi*. Only the female of *falconum* is described; the male is mentioned as having a finely spiny spicule sheath. The inadequately described *C. striata* (v. Linstow, 1879) also differs from *falconis-nisi* in the possession of a spiny spicule sheath. Madsen (1945) has suggested the
synonymy of *falconnum* and *striata*.

It has been found by the writer in examining male capillarids that unless the spicule sheath is everted, it is sometimes almost impossible to determine whether or not the sheath is finely spined. Since *falconnum* and *striata* differ from *falcons-nisi* only in this character, extreme care should be exercised in determining the species involved when reporting one of the three from a new host or locality. It is possible that the three species are synonymous. It should be pointed out that the presence or absence of fine spines on an inverted spicule sheath is sometimes difficult to determine in other species of this genus.

A pertinent example of a mistake of this kind may be seen in the case of *C. collaris* (Linstow, 1873), described as having a finely spiny spicule sheath. Railliet (1895) described a capillarid, *Trichosomum retusa*, which differed from *C. collaris* in lacking spines on the spicule sheath. Later investigators found worms which were obviously *C. retusa*, but which had fine spines on the spicule sheath. Teixeira de Freitas and Almeida (1935) reached the conclusion that *C. retusa* (Railliet, 1895) is a synonym of *C. collaris* (Linstow, 1873). Similar examples will probably be uncovered in this genus by future workers.

**Capillaria quiscali** n. sp.

Specific diagnosis: Bacillary lines absent. Cuticle transversely striated. Mouth simple.
Female: 8.5 to 10.3 mm. long; 65 to 70 μ wide just posterior to vulva; maximum width 84 to 102 μ. Vulva bearing a funnel-shaped cuticular appendage, located 2.9 to 4.5 mm. from anterior extremity just posterior to termination of esophagus. Well developed ovejector, heavily muscular and salient, S-shaped when retracted. Ova 57 to 66 μ long by 25 to 30 μ wide; inner shell forms collar around plug at each end; outer shell roughly mammillated. Anus subterminal. Vulva divides body 1:1.5 to 1:2.0.

Male: 8.2 mm. long; maximum width 72 μ. Termination of esophagus 3.9 mm. from anterior extremity. Spicule smooth with blunt tip, 962 μ long; transversely striated spicule sheath 1.1 mm. long. Cauda provided with lateral cuticular alae continuous with membranous bursa. Bursa supported by two stout papillae; each papilla split into blunt dorsal and ventral rami. Cloaca subterminal, flanked on either side by small papilla. Termination of esophagus divides body 1:1.3.

Host: Quiscalus quiscula aeneus.

Habitat: Small intestine.

Locality: Madison, Wisconsin.


Worms of this species were recovered from two Bronzed Grackles of eighteen examined. This species bears some resemblance to G. caudinflata (Molin, 1858), differing from it in the larger size and rough outer shell of the eggs, the fusion, in the male, of the caudal alae with the membranous bursa, and the somewhat smaller size of the worms.
Capillaria obsignata Madsen, 1945.

Worms of this species were collected from the small intestine of three of forty-nine robins, Turdus migratorius, taken at Columbus, Ohio, and Madison, Wisconsin, and from the domestic pigeon, Columba livia domestica, at New Orleans, Louisiana.

Other workers have reported and described this worm from the small intestine of pigeons in many parts of the world, under the name Capillaria columbae (Rud.). According to Wehr (1939), this worm has been taken from the pigeon in Maryland, New Jersey, South Carolina, and District of Columbia. Miller (1937) has reported it from this host in Quebec. Leidy (1887) reported it from the mourning dove, Zenaidura carolinensis, in Florida. It has been reported from the chicken in at least twelve states east of the Rocky Mountains by Graybill (1924), Levine (1938), Morehouse (1939), and Todd (1946). The turkey was reported as a host in New Jersey by Graybill (1924). Cannon (1939) has reported it from the starling, Sturnus vulgaris, in Quebec. According to Levine (1938) and Morehouse (1944), Cram (1931) experimentally infected a quail with this helminth. Levine (1938) and Wehr (1937, 1939) described the life cycle. Madsen (1945) has shown that C. columbae (Rudolphi, 1819) was originally described from the large intestine and differs from the species from the small intestine in possessing a projecting vulvar appendage. Further, Madsen stated that the first recognizable description of the capillarid from the small
The intestine of pigeons was that of *C. dujardini* by Travassos (1915). This is true. Unfortunately, however, Travassos in 1914 proposed *Capillaria dujardini* n. nom. for *Calodium tenue* Dujardin, 1845, the name *tenue* being preoccupied by page preference by *Trichosomum tenue* Dujardin, 1845.

Dujardin (1845) in his description of *Calodium tenue* places "*Trich. columbae, Rudolphi*" as a synonym. It would appear that the name *C. dujardini* Travassos, 1914 must be applied to a form from the large intestine with a projecting vulvar appendage.

Travassos (1915) in describing the female of *C. dujardini* Trav., 1914 states "vulva circular, de labios ligeiramente salientes." And he gives as the habitat "Intestina delgado de *Columba livia* L. e *Columba livia dom. L.*" It would appear that Travassos in 1915 misdetermined his material, since it is evident that he was not dealing with the same species that Dujardin had described from the pigeon, and yet it was Dujardin's species to which he (Travassos) gave this name in 1914. This being the case, a name must be selected for the species in which the vulva is circular and slightly projecting and which lives in the small intestine of the pigeon.

Madsen (1945) has referred *C. columbae* of Graybill (1924) to a new species, *C. obsignata*. Madsen evidently came to this decision solely on the basis of Graybill's description and differentiated this worm from the capillarid from the small intestine of the pigeon mainly by differences in the structure of the eggs. The writer has been unable to
locate the material from which Graybill made his description, however, Dr. E. W. Price has kindly made available for study material from the pigeon at Washington, D. C. This material (U.S.N.M. Helm. Coll. No. 15144) was identified by Graybill as *C. columbae*, and it seems that this is the material mentioned by Graybill as having been compared with his worms from chickens and turkeys. This material is specifically identical with the writer's specimens from the pigeon. The eggs do not possess a collar as described and figured by Graybill. It seems that Graybill made a misinterpretation of the egg structure in his material, since his description agrees in other respects with descriptions of *C. columbae* of other workers. According to Dr. Allen McIntosh (personal communication) of the Bureau of Animal Industry, the material on slide number 15144 may be considered as a part of the type material of *C. obsignata*.

It is, therefore, concluded that there are two capillarids from the pigeon with the synonomy in part as follows:

1. From large intestine:
   *Capillaria columbae* (Rudolphi, 1819).
   
   Syn. *Calodium tenue* Dujardin, 1845.
   
   *Trichosomum* (*Calodium*) *tenuissimum* Diesing, 1851.
   
   *Capillaria dujardini* Travassos, 1914.

2. From small intestine:
   *Capillaria obsignata* Madsen, 1945.
Capillaria freitasi n. sp.

Specific diagnosis: Body smooth. Bacillary lines absent.
Mouth simple.

Female: Unknown.

Male: 11.5 mm. long; maximum width 46 u. Termination of esophagus 5.9 mm. from anterior end. Spicule smooth with blunt tip, 900 μ long. Spicule sheath smooth, 1.825 mm. long by 13 μ wide when completely everted. Cauda terminated by two stout lobes supporting membranous bursa. Cloaca slightly sub-terminal. Termination of esophagus divides body 1:0.9.

Host: Passarella iliaca iliaca.

Habitat: Intestine.

Locality: Madison, Wisconsin.


A single male of this species was recovered from one of nine fox sparrows examined at Madison, Wisconsin. C. freitasi bears some resemblance to C. falconis-nisi (Diesing, 1851) reported elsewhere in this paper from owls and hawks. However, the spicule and spicule sheath of this species are definitely smooth in contrast to the striated structure of these organs observed in falconis-nisi.

This species is named in honor of Dr. J. F. Teixeira de Freitas who has made many valuable contributions to the knowledge of the helminths of this genus.

Capillaria sp.

Single immature female worms of this genus were recovered from the small intestine of two Scarlet Tanagers of six
examined at Madison and Shawano, Wisconsin. It has not been possible to refer these worms to any known species. Description: Body transversely striated. Lateral bacillary lines one-fourth diameter of body; slight dorsal and ventral bacillary lines present. Mouth simple.

Female: Immature. 11.5 and 20.2 mm. long. Width just posterior to vulva 64 and 76 μ; maximum width 76 and 98 μ. Forty-eight paraesophageal nuclei. Vulva 4.6 and 7.8 mm. from anterior end, with tubular cuticular appendage. Eggs absent. Anus subterminal. Vulva divides body 1:1.5 and 1:1.6.

Male: Unknown.

Host: *Piranga erythromelas*.

Habitat: Small intestine.

Locality: Wisconsin.

The cuticular vulvar appendage resembles that seen in some specimens of *C. caudinflata*, however, females of that species would be expected to have reached maturity before attaining the size of the worms described above. It is possible that *caudinflata* is incapable of reaching maturity in this host, but, in view of the fact that mature female *caudinflata* have been reported from such diverse hosts as chicken, partridge, pheasant, grouse, pigeon, starling, and English sparrow, this would seem doubtful.
Keys to the species of Capillaria parasitic in the lower digestive tract of North American birds.

- Females -

1. a Vulva with well developed appendage........... 2
   b Vulva without appendage............................... 4

2. a Anus terminal, Ova 43 μ long.....................
   ...........................................picorum (Rudolphi, 1819)
   b Anus subterminal................................. 3

3. a Ova 47 to 55 μ long; outer shell smooth.
   A prevulvar notch present.......................
   ............................................. caudinflata (Molin, 1858)
   b Ova 57 to 66 μ long; outer shell roughly mammillated. No prevulvar notch............
   quiscali n. sp.

4. a Body with pre-and post-vulvar cuticular bosses... bursata Teixeira de Freitas and Almeida, 1934
   b Body without pre-and post-vulvar cuticular bosses................................. 5

5. a Inner shell of egg bent to form a collar.. 6
   b Inner shell of egg not bent to form a collar............. obsignata Madsen, 1945.

6. a Ova 65 to 70 μ long; outer shell reticulated
   Small intestine of Strigiformes and Falconiformes....falconis-nisi (Diesing, 1851)
   b Ova less than 62 μ long......................... 8
7. a Ova 46 to 67 μ long (average 53 μ) by 22 to 25 μ wide. Worms 11.2 to 20.9 mm. long. Ceca of Galliformes \textit{collaris} (v. Linstow, 1873)

b Ova 45 μ long by 15 μ wide. Worms 19 mm. long. Small intestine of Piciformes......

\textit{longistriata} Walton, 1923

- Males -

1. a Lateral caudal alae present:.................. 2

b Lateral caudal alae absent.................. 4

2. a Bursa heart-shaped, supported by two lobes.3

b Bursa supported by two dorsal and two ventral lobes. Spicule sheath transversely striated, without spines. Small intestine of Galliformes..........

\textit{bursata}

3. a Spicule sheath transversely striated and provided with minute spines. Small intestine of Galliformes and Passeriformes

\textit{caudinflata}

b. Spicule sheath transversely striated, but without spines. Small intestine of Passeriformes............ \textit{quiscali}

4. a Spicule sheath spiny...................... 5

b Spicule sheath not spiny.................... 6
5. a Tail broad with three lobes. Spicule 1120 to 1840 μ long by 18 to 19 μ wide. Small intestine of Passeriformes.

...............tridens (Dujardin, 1845)

b Tail with two lobes. Spicule 740 to 1890 μ long by 25 μ wide. Ceca of Galliformes....collaris (v. Linstow, 1878)

6. a Spicule sheath smooth......................... 7

b Spicule sheath transversely striated.... 8

7. a Worms about 11.5 mm. long. Spicule 900 μ long, not twisted. Small intestine of Passeriformes........ Treitas n. sp.

b Worms about 14 mm. long. Spicule 1000 to 1600 μ long, twisted. Intestine of Piciformes............... picorum

8. a Each caudal lobe provided with hook-like papilla on ventral surface. Spicule stout 1500 μ long by 100 μ wide. Small intestine of Piciformes.................

...............longistriata Walton, 1923.

b Caudal lobes without hook-like papillae. 9
9.  

a. Spicule transversely striated, 750 to 1250 µ long by 12 to 14 µ wide. Small intestine of Strigiformes and Falconiformes .................. *falconis-nisi* (Diesing, 1851)

b. Spicule not striated, expanded at proximal end .................. *obsignata* Madsen, 1945

Since only the males are known, *C. tridens* and *C. freitasi* are not included in the key to the females.
DISCUSSION

Specificity in the Genus *Capillaria*

Helminths of this genus show no marked degree of host specificity. *Capillaria hepatica* (Bancroft) furnishes an excellent example of this lack of specificity. This species has been reported from a number of species of rodents including rats, mice, prairie dogs, muskrat, beaver, and the European hare. Nishigori (1925) and Wright (1930) have reported this worm from the dog. Foster and Johnson (1939) have reported it from the liver of the peccary, the spider monkey, and the capuchin monkey. A single authentic case of human infection, a British soldier in India, has been reported by MacArthur (1924). Some other species of *Capillaria* exhibit a similar lack of specificity, though to a somewhat less marked degree. The host distribution of *C. americana*, for example, shows a lack of specificity, but all hosts thus far known are rodents. In this respect, the distribution of *C. muris-sylvatici* (Diesing, 1851) is of some interest.

Elton, Ford, and Baker (1931), in a study of the parasites of various rodent populations in England, failed to find this species in *Microtus*, although the worm was found in other rodents from the same areas. Conversely, the writer has found it only in material from *Microtus* in North America, although large collections of material from native rodents have been available for study. It seems probable that the host distribution of this species is mainly limited by the food habits of the rodents concerned. This is a factor which
must be considered in any assay of host specificity.

It should be mentioned that capillarids are restricted in specificity to the various vertebrate classes. No species is known to parasitize animals of more than one class.

Another obstacle to accurate information on distribution of members of this genus is the difficulty with which they are recovered in parasitological examinations. The worms are small and show little movement when removed from the animal body to water or normal saline solution. Those species inhabiting the alimentary canal are often found only when the mucosa is thoroughly scraped. The fact that \textit{C. hepatica} causes a grossly perceptible pathology of the liver may explain why such a wide diversity of hosts are known for this species.

An anecdote from the writer's own experience may serve to emphasize the fact that capillarids are probably overlooked rather frequently in parasitological examinations. In the two year period of 1945 and 1946 the author examined over five hundred vertebrates and encountered only a single worm of the genus \textit{Capillaria}. In the summer of 1947 this study was begun and a number of the forms described herein were subjected to close scrutiny. In the ensuing months after this study was begun, a careful search was made for capillarids in all animals examined by the writer. In several instances capillarids were found, although the number of hosts examined in this period was considerably less than five hundred. Among others, \textit{C. hathawayi} was described by the
writer (1948) from these collections. This was the first adult capillarid to be described from a Selachian fish. Other species probably occur in these fishes, but have simply been overlooked.

On the other hand, capillarids are somewhat more specific in regard to their location in the host animal. A pertinent example may be cited: In the domestic fowl, Capillaria collaris (v. Linstow, 1873) [≡C. retusa (Railliet, 1895)] is invariably found in the cecum, while C. caudinflata (Molin, 1858) is always found in the small intestine. Although C. caudinflata may be found in the terminal portion of the small intestine in extremely heavy infections, these two species are always in the locations noted above, though both may occur in the same host animal.

The foregoing discussion furnishes justification for this statement: The fact that a capillarid is found in the same host species as a previously described member of the genus is a poor criterion for assuming that the worms are specifically identical. It follows that a capillarid which occurs in a mammalian host from which no member of the genus has been previously described should be carefully compared with other described species from mammalian hosts before being considered a new species. Further, the location of the worm in the host animal may be of great significance and should be recorded with accuracy.
The Economic Importance of Capillarid Distribution

It seems appropriate to call attention to the possible economic implications arising from this and other studies which have broadened the knowledge of the distribution of this group of helminths. Of the capillarids known from the lower digestive tract of American birds, at least four species are parasitic in domestic fowl. The finding of any of these worms in a wild bird is highly significant from an epidemiological standpoint; for example, the reporting in the present work of *C. caudinflata* from the starling uncovers a possibly important sanctuary for this worm from the measures currently used against it and its ravages on domestic birds. The starling may be of importance in the actual transmission of this infection to healthy flocks. Thus, formulation of effective control measures must take this reservoir into consideration. It would seem that the starling merits its reputation as a pest.

The same type of relation between wild birds and domestic fowl may be pointed out in the case of the capillarid living in the small intestine of pigeons. This species is known from the chicken over a great part of the eastern half of the United States. Obviously, it would be of great aid in controlling infection of the chicken if pigeons could be excluded from the barnyard. This, with proper veterinary treatment, is now recommended by competent authorities.
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THE LIFE HISTORY AND MORPHOLOGY OF
RHOPALIAS MACRACANTHUS CHANDLER (TREMATODA)

By

CLARK P. READ

The Second of Two Theses Submitted to the Faculty
of the
William Marsh Rice Institute
In Partial Fulfillment
of the
Requirements for the Degree
of
Master of Arts

Houston, Texas
1948
49-4935
ACKNOWLEDGEMENTS

This investigation was made under the direction of Professor Asa C. Chandler, to whom I wish to express my appreciation for his inspiring criticism and suggestions.

My thanks are due to Dr. E. W. Price, of the U. S. National Museum for verification of nomenclature; to Dr. J. P. E. Morrison, of the U. S. National Museum, for the identification of snails; to Dr. J. D. Webster for data on the longevity of Rhopalis macracanthus Chandler; to my wife, Leota W. Read, for the typewriting of this manuscript; and to many friends who aided in the collection of snails and other materials.
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INTRODUCTION

The genus **Rhopalias** Stiles and Hassall, 1898, is composed of a small and distinctive group of digenetic trematodes which are characterized as follows:

Medium-sized distome flukes with a retractile spiny proboscis on each side of oral sucker. Oral sucker less than half size of acetabulum. Cirrus sac voluminous. Metraterm and cirrus empty into a common atrium anterior to acetabulum. Ovary anterior to testes, which are tandem. Vitellaria fill lateral fields in hind body and tend to fuse medially in posterior region. Parasites of opossums.

The four known members of the genus are very similar, but are readily distinguished by differences in the armature of the proboscides.

Knowledge of the helminths of this genus goes back to Rudolphi (1819) who described **Distomum coronatum** from a Didelphys sp. in Brazil. Diesing (1850) erected the genus **Rhopalophorus** for Rudolphi's worm and a new species, **R. horridus**, which he (Diesing) described from a Brazilian opossum. Stiles and Hassall (1898) showed that since Diesing's name, **Rhopalophorus**, did not differ essentially from the name of a hymenopteran genus, **Ropalophorus** Westwood, 1840, the name was preoccupied. Stiles and Hassall proposed the name **Rhopalias** with **Distomum coronatum** Rudolphi as the type species. Braun (1901) reviewed the genus and described a new species, **R. baculifer**, from Didelphys palmata in Brazil. Looss (1899) erected the family Rhopaliidae (sic) for the genus. Fuhrmann (1928) accepted Looss' family.
Dikmans (1931) reported a Rhopalias sp. from the opossum in Louisiana. Chandler (1932) described R. macracanthus from Didelphys virginiana at Houston, Texas. Byrd and Reiber (1942) reported this species from D. virginiana at Reelfoot Lake, Tennessee, and described their material in some detail, but failed to find this fluke in any of thirty opossums examined in Georgia.

No work on the life history of any member of this group has been published up to the present time. The study here reported is concerned with the life history of Rhopalias macracanthus Chandler. The observations made throw light on the taxonomic relations of the group.
MATERIAL AND METHODS

Eggs of *R. macracanthus* were recovered from the feces of infected opossums captured in the vicinity of Houston, Texas. It was found that the eggs of the fluke could be recovered most effectively from the feces by a combined decantation and filtration technique: the feces were thoroughly comminuted and diluted in about three liters of tap water. Large particles were filtered out by pouring the mixture through an ordinary kitchen sieve. The suspension was allowed to settle for several minutes, and the supernatant fluid decanted off. This procedure of dilution and decantation was repeated twice more and the residue again diluted, using about a liter of tap water. The suspension was now filtered through silk bolting cloth with a calibrated mesh of 82/in^2, and the residue washed with an additional liter of water, the washings being added to the initial filtrate. The suspension was now subjected to a second filtration through bolting cloth with a mesh of 166/in^2, and the residue on the cloth again washed thoroughly. The suspension remaining was relatively free of putrescible material and contained a high concentration of helminth eggs. The eggs of *Rhopalias* were fairly easily distinguished from those of other worm parasites of the opossum with the exception of *Neodiplostomum lucidum* La Rue and Bosma. It was found, however, that the eggs of *N. lucidum* develop much faster than those of *Rhopalias*, and that hatching and death of most *N. lucidum* miracidia had occurred before hatching of *Rhopalias* eggs began. Eggs of
Echinostoma sp. might be confused with those of Rhopalias, but no worms of this genus were ever found by the writer in a series of sixteen adult opossums examined, nor by Chandler (1932) who studied the helminths of a series of opossums from this area.

Eggs were incubated in 500 cc beakers at temperatures which approximated those found in nature since laboratory windows were left open at all times. The water was changed at weekly intervals in order to maintain freshness. Miracidia were collected from these cultures by inverting a funnel in the beaker. The larvae collected in the narrow neck of the funnel and were easily drawn off in numbers with a pipette. By this method each culture could be rapidly examined daily for swimming miracidia. Development of individual eggs were followed in hanging drop cultures on hollow ground slides.

Snails were exposed to miracidia in some experiments by enclosing the molluscs in coarse cheesecloth bags which were suspended for varying lengths of time in cultures containing miracidia. This method of exposure prevented the snails from feeding on the residue material in the bottom of the container. This feeding was avoided because most cultures contained eggs of Brachlaemus sp. which must be eaten by the snail host in order to liberate the miracidia.

In some experiments snails were fed eggs of R. macracanthus which contained what were apparently fully developed miracidia. These eggs were gathered from a watch glass with a capillary pipette under the binocular microscope.
All snails used in experiments were reared in small laboratory aquaria. Crayfish used in experiments were taken from a small pond in a residential district where opossums have not been observed. Tadpoles were reared from eggs in the laboratory. Young opossums removed from the pouch of a female animal and hand-reared in the laboratory on condensed milk and canned dog food, were used in the feeding experiments. The feces of these young animals were examined daily for at least three weeks to be certain that they were not harboring an infection prior to experimental feeding.

Miracidia and cercaria were studied alive using the albumen method of Krull (1934), and from mounted specimens fixed in hot formalin and stained with carmalum or haemalum. The plate arrangement of the miracidium was demonstrated by the silver nitrate technique. Rediae were studied in the living state and as mounted specimens, fixed in hot formalin and stained with Ehrlich's haematoxylin. Adult worms were studied alive, in whole mounts stained with haemalum or carmalum, and in transverse and sagittal serial sections, 10 μ in thickness, and stained with haematoxylin and eosin.
OUTLINE OF THE LIFE CYCLE

The unsegmented eggs of *Rhopalias macracanthus* are passed in the feces of the opossum host and hatch after 20 to 50 days incubation in water. The miracidium penetrates the snail, *Physa gyrina*, and metamorphoses into a small sporocyst which produces one or two mother rediae. These mother rediae give rise in turn to numerous daughter rediae. About 250 spineless, echinostome-like cercariae are produced two to six at a time in each daughter redia and pass out into the snail's tissues before attaining maturity. Cercariae emerge from the snail 70 to 130 days after infection. They swim vigorously until they come in contact with a tadpole, at which time they crawl over the body and enter the cloaca. They penetrate and encyst in the wall of the cloaca and are infective after about twenty-two days. The worms grow to maturity in the small intestine of the opossum in about seven days after the ingestion of infective metacercariae.
LIFE HISTORY STAGES

Miracidium

Eggs collected from the feces and allowed to incubate in the laboratory hatch in from twenty to fifty days. However, active miracidia are observed in the eggs much earlier. The flame cells and cilia develop several days before the elongate form of the hatched miracidium is assumed. After one week the developing miracidium is spherical, ciliated, and frequently two flame cells may be seen in the center of the body. At this time it is slightly less than half the length of the egg in diameter. At the end of ten days the cuticular plates and the granular pigment in the region of the future eye spots may be seen. The right flame cell is now somewhat anterior to the left one.

After about two weeks, the organism is more elongate, eye spots are clearly defined, and, except for size, the animal has the appearance of the miracidium at hatching. Because it is longer than the egg, the miracidium just prior to hatching is flexed at the posterior end. This flexure is dorsal and the ventral surface of the animal is apparently in contact with the shell. The space not occupied by the miracidium is filled with what are apparently oil globules.

In the hatched miracidium the unicellular, ciliated plates are in four rows of six, six, four, and two plates proceeding from anterior to posterior (Fig. 3). These are arranged in an alternate manner. The eye spots are well defined, with most of the pigment distributed in a crescent
along the mesial portion; a few granules of pigment are scattered through the remainder of the circular eye spot. This distribution of the pigment gives the appearance of an X since the eye spots are in close proximity. The anterior flame cell is on the right side at the level of the second row of plates and is somewhat ventral. The posterior flame cell is on the left at the level of the third row of plates and is dorsal. The ducts from the flame cells empty to the outside through pores between the third and fourth rows of plates. The so-called germ balls lie in the posterior region of the body. A saclike "intestine" may be seen between the protrusable proboscis and the eye spots.

After hatching the miracidia swim almost constantly until a snail host is found or until death ensues. The miracidia live from twelve to twenty-four hours after hatching in laboratory cultures. Penetration of the snail was not observed, but the miracidia disappear in a few hours from a container in which the proper snail host has been placed.

In connection with the hatching of the miracidia an interesting observation was made. It was noted that the miracidia hatched periodically. They appeared in the cultures in "swarms" five to seven days apart. In laboratory cultures of about five hundred eggs, hatching began after twenty-four to twenty-nine days incubation and about forty percent of the viable eggs hatched in a few hours. Five to seven days later a second group of eggs hatched; these numbered about twenty
percent of the original number. Five to seven days after the emergence of this second group, a third group, consisting of about fifteen to twenty percent of the original number, hatched. Additional hatching was not observed. It was thought that fluctuations in temperature might have some bearing on this phenomenon since the experimental work was carried out in a laboratory room with windows open at all times. Fluctuations of twenty degrees in a twenty-four hour period are not uncommon in this area in the winter.

Experiments on the effect of temperature on the eggs showed that they are markedly affected by this factor. When eggs were held at a constant temperature of $18^\circ C$, it was found that although most of the eggs had apparently developed to the stage at which hatching occurs, only a few of the eggs had hatched after thirty-two days of incubation. When the temperature was raised to $22^\circ C$, hatching of almost all viable eggs had occurred after forty-eight hours. When the eggs were incubated at a constant temperature of $24^\circ C$, hatching of almost all eggs had occurred at the end of twenty-five days. At a constant temperature of $30^\circ C$, the mortality rate of the eggs was very high, even though the water was changed every other day to maintain freshness; all viable eggs had hatched at the end of twenty-two days. Eggs kept at $18^\circ C$ hatched after as long as fifty days of incubation if the temperature was raised to $22^\circ C$ at the end of this period. Eggs kept longer than fifty days at $18^\circ C$ failed to hatch when the temperature was raised to $22^\circ C$. Eggs exposed to temperatures
below freezing for as long as seventy-two hours invariably failed to hatch. The hatching of the eggs was not periodic in these cultures which were held at constant temperatures. This seemed to indicate further that temperature changes might be responsible for the periodicity, and additional experiments were done.

Egg cultures were placed in an incubator at a constant temperature of 14° each evening at six o'clock. At eight o'clock each morning the eggs were removed from the 14° incubator and placed in an incubator at 26° and allowed to remain at this temperature until six in the evening, when they were again placed in the 14° incubator. This procedure was carried out for a period of forty days. Under these conditions the eggs exhibited the type of periodicity seen in cultures exposed to natural changes in temperature. Hatching took place in the daytime after twenty to twenty-four days incubation and occurred in groups as described above, the percentage of eggs hatching in each swarm being about the same as observed in cultures exposed to natural temperature fluctuations. The only difference observed was the fact that the period was slightly shorter, being only three or four days. The constant temperature of 26° to which they were exposed in the daytime was probably responsible for this shortening of the period. This was supported by the observation that if cultures which had started hatching under conditions of controlled fluctuation were placed at a constant temperature of 26° C., the miracidia all hatched in a period of about three days without showing any periodicity.
The question, of course, arose as to what value this periodicity might have for the larval trematode. Preliminary observations seem to indicate that this is related to the habits of the snail host. The writer has found that the snails involved do not undergo an extended hibernation period in this region. However, in laboratory cultures they frequently burrow into the sand in the bottom of the aquarium when the temperature is lowered to 18° or less. If this habit is followed in nature, it would obviously lessen the opportunity for infection of the snails at lower temperatures. The staying of the emergence of the miracidia until such time as the maximum number of potential molluscan hosts are available would be of great value to this fluke in perpetuating itself.

The apparent lethal effect for miracidia of temperatures below the freezing point for relatively short periods of time probably explains the fact that this trematode has not been found in opossums in the northern portions of the United States.
Sporocyst

The writer made a number of attempts to find the sporocyst of this trematode, but these were unsuccessful in all cases. However, an indirect demonstration of this stage was possible. Thirty snails were isolated in individual containers and each exposed to a single miracidium of *Rhopalias*. These snails were examined in groups of ten at intervals of fifteen, twenty-five and forty days following exposure. Examination of all snails at fifteen and twenty-five days were negative. However, of the snails examined forty days after exposure, three individuals were found to be infected. Two mother rediae were taken from each of two of these snails and a single redia from the third. The finding of two mother rediae in each of these two snails furnishes indirect evidence that a sporocyst does occur in the life cycle of *Rhopalias*. The only other explanation would require the existence of an additional redial generation, which seems highly unlikely since no trematode is known to produce more than two redial generations. It would seem rather that the miracidium metamorphoses into a minute sporocyst which gives rise to one or two redia.
Rediae

Mother rediae were never recovered from snails earlier than forty days after exposure to the miracidia. In the tissues of the snail host mother rediae measure 0.25 to 0.50 mm. in length and 0.15 to 0.21 mm. in maximum width. They are colored by scattered granules of yellow pigment and contain one or two recognizable daughter rediae and numerous germ balls, varying from round to elongate in shape. The plain collar is readily visible and is about 50 μ from the anterior end. The appendages are usually prominent. The pharynx measures 45 to 55 μ in diameter and is followed by the relatively narrow gut which reaches more than halfway to the posterior end. The birth pore is nearly always visible about 100 μ from the anterior end. The rediae show little movement when removed to normal saline, but tend to contract markedly.

Mature daughter rediae were recovered from the tissues of the gonad and digestive gland of snails 66 to 150 days after exposure to infection. They resemble the mother rediae, but are somewhat smaller and contain from one to six immature cercariae. The daughter rediae are 0.10 to 0.30 mm. long by 40 to 50 μ in maximum width and are colored by yellow pigment granules. The collar is readily visible and the appendages are prominent. The birth pore is easily seen about 30 μ from the anterior end. The pharynx is about 15 μ in diameter. The gut is relatively shorter than in the mother rediae and reaches slightly less than halfway to the posterior
end. It was not possible to count the number of flame cells accurately, but it was determined that there are two groups near the posterior appendages and two groups near the distal end of the gut. There are at least eight flame cells in each group.
Cercaria

In experimental infections the cercariae begin to emerge from the snail about seventy days after exposure to miracidia, and continue to appear daily in cultures for about sixty days. From comparison of the number of cercariae produced during an average infection and the number of rediae present in the snails when dissected, it appears that about 250 cercariae are produced by each redia. When cercariae first begin to appear there are only a few daily for several days. The number emerging gradually increases until about 600 per day are being produced. This maximum peak is reached about forty days after the initial appearance of cercariae. Snails at this time harbor from 90 to 125 rediae which are large enough to find on dissection.

It was found that the emergence of the cercariae is inhibited by lowering of the temperature to 18° C. This is not surprising since such an inhibition has been reported for other larval trematodes.

The cercariae emerge in the afternoon between two and six o'clock and are active for 36 to 48 hours under laboratory conditions. Their swimming movements are very much like those of some other echinostome cercariae and also resemble those of some styleted cercariae, e.g. *Tetrapapillocrema concavocorpa*, which the writer has studied. They swim upward for a few seconds and then fall with the tail held upward over the ventral side of the body. Creeping is infrequent except when the cercariae are in contact with tadpoles.
When creeping, the tail is contracted to about half the length of the body. The body is elongate to oval and is 100 to 145 μ long by 56 to 65 μ in width, depending on the state of contraction. The oral sucker is slightly ventral, spherical in shape, and is slightly smaller than the acetabulum. The acetabulum is at about the anterior limit of the posterior third of the body. Proboscides or proboscis spines are not discernible. There is a mass of glandular tissue on each side of the oral sucker in the region in which the proboscides later develop. No ducts to the outside from these glandular fields could be discerned.

The body has no cuticular spines. The prepharynx is relatively long. The pharynx is cylindrical to spindle-shaped, and is usually about one-half the diameter of the oral sucker in length. The esophagus and the crura are plain with open lumina and are frequently difficult to see. The cystogenous glands are composed of angular masses of fine rod-like structures and are confined mostly to the lateral fields, from the level of the bifurcation of the ceca to the posterior end of the body.

The excretory bladder consists of a single, contractile chamber. The excretory siphons arise on the anterior aspect of the bladder and pass anteriorly to the level of the pharynx where they narrow abruptly. Small tubules and flame cells could not be seen in sufficient number to ascertain their arrangement. The siphon granules are angular, refractile, and about 7 μ in diameter. There are ten to fifteen
granules in each siphon evenly distributed from the excretory bladder to a level about midway between the acetabulum and the pharynx. The powerful tail is attached somewhat ventrally and is 70 to 200 µ long, depending on the state of contraction. About 30 µ from the base of the tail the caudal excretory canal forks into two branches which empty to the outside on the lateral aspects. The cercaria is unpigmented.
Metacercaria

Various species of snails, crayfish, frogs and tadpoles were exposed to cercariae. All attempts to infect the first two hosts were negative, but every attempt to infect tadpoles was successful. Frogs were infected only occasionally.

Tadpoles were placed in shallow bowls with active cercariae for several hours. It was observed under the binocular microscope that the cercaria behave in a manner similar to that of the cercaria of *Echinostoma revolutum*, as described by Beaver (1937). They settle on the tadpoles, begin creeping over the body, and enter the cloaca in a very short time. They creep in a ventro-posterior direction toward the cleft between body and tail or the ventral margin of the tail, and then directly to the cloaca. Examination of tadpoles thus exposed showed that the cercariae penetrate the cloacal wall and encyst here. The tail is shed during penetration. The newly formed cysts have a thin, tough wall, about 2 μ in thickness.

The body of the metacercaria is very similar to that of the cercaria during the day following encystment. The spines of the proboscis become faintly visible about five days after encystment, and some infiltration of host tissue begins to take place. After two weeks the body is larger and is flexed; the ventral sucker has undergone some growth, but the oral sucker has shown little change. The proboscis spines are still relatively small, but are more clearly
defined. The cuticula is beginning to show spination, and
the cyst wall is somewhat thicker. After twenty days the
proboscis spines are about 20 μ long, and the cuticular
spines are well developed. After six weeks the proboscis
spines are slightly larger; other than this the only change
is in the cyst wall which is about 10 μ thick, and unpig-
mented.

In an attempt to determine just when the metacercariae
become infective, four young opossums slightly larger than
mice were each fed 50 metacercariae. These metacercariae
had been encysted for six, ten, sixteen, and twenty-two days,
respectively. Seven days after the feedings, the opossum
which had received the twenty-two day old cysts became
acutely ill, refused to eat, and died about fourteen hours
later. Forty-one adult Rhopalias macracanthus were taken
from the small intestine. The other three animals were
autopsied immediately, and all were free of parasites.
Twenty-two day old metacercariae were fed to three young
albino rats, two guinea pigs, a kitten, and a young barn
owl (Tyto alba). None of these animals were infected at
autopsy one week after the feeding of metacercariae.
Adult

The adult of this worm has been described by Chandler (1932) and by Byrd and Reiber (1942). Some variation in the material of the writer from that of the foregoing workers, as well as some details noted by study of sectioned material, seems to warrant the redescription of this fluke.

The body is elongated and tapers to a blunt point at the posterior end. In most fixed and in all living specimens a constriction just posterior to the acetabulum divides the body into anterior and posterior segments. The posterior segment is more than twice the length of the anterior. When stained with haematoxylin, the anterior segment has a distinctly different staining reaction than the posterior. This was noted by Chandler (1932) in his original description of this helminth. The worm is 2.65 to 4.80 mm. long. The anterior segment is 1.00 and the posterior segment is 1.10 mm. in maximum width. The cuticle is thick, particularly in the anterior region, and is armed with transverse rows of spines which become sparser in the posterior region. No spines were observed posterior to the level of the middle of the posterior testis. The oral sucker is subterminal, usually triangular, and 109 to 200 µ in length with about the same measurements in width. The short proboscis sacs lie on either side of the oral sucker and extend posteriorly to about the level of the anterior part of the pharynx. These sacs are 285 to 350 µ long by 146 to 190 µ wide. Each proboscis bears ten large spines; the spines on the proximal part or base of
the proboscis are 110 to 130 µ long by 20 to 35 µ wide, while
those on the anterior end of the proboscis are somewhat short-er,
measuring 98 to 108 µ long. When the proboscides are
everted the spines point in all directions; there appears to
be no definite pattern of arrangement. When the proboscides
are retracted an irregular row of eight spines may be seen
between the opening of the proboscis sacs and the oral sucker.
These spines are similar to the spines of the proboscis, but
are only about 15 µ long. In sectioned material glandular
tissue may be seen in the basal portion of each proboscis sac.

The acetabulum is circular to somewhat elongate and is
from 288 to 450 µ in diameter. It is located 0.70 to 1.06
mm. from the anterior end of the body and is just anterior
to the constriction dividing the body. The prepharynx is var-
iable, being 70 to 175 µ in length, depending on the extent
of contraction. The well developed pharynx is 150 to 200 µ
long by 120 to 150 µ wide. The esophagus is short, the ceca
diverging a short distance behind the pharynx. The ceca pass
posteriorly in the lateral parts of the body and are usually
obscured in the posterior region by the dense vitellaria.
In specimens in which they can be traced the ceca end blindly
about 125 µ from the posterior extremity.

The ovary, 145 to 200 µ long by 190 to 240 µ wide, is
located slightly to the left of the midline at the posterior
end of the massive cirrus pouch and from 200 to 350 µ behind
the acetabulum. Between the ovary and the anterior testis
is the large shell gland which is somewhat irregular in
shape and is larger than the ovary. Laurer's canal is present. The uterus is slightly coiled and ascends on the left of the cirrus pouch. Six to twenty-five eggs are present in the uterus. The eggs are 100 to 118 μ long by 48 to 70 μ wide. The distal portion of the uterus is highly glandular in structure, forming a metraterm about half as long as the cirrus pouch, and empties into a slightly developed genital cloaca. The genital pore is located in the midline about equidistant from the acetabulum and the bifurcation of the ceca. The vitelline follicles are large and dense, occupy the lateral fields in the posterior two thirds of the animal, and meet in the midline in the region caudal to the posterior testis. The vitellaria empty into a vitelline reservoir just posterior to Laurer's canal.

The testes are median and tandem in position, located posterior to the ovary. The anterior testis is 218 to 520 μ long by 291 to 400 μ wide and is sometimes slightly constricted in its middle part. The posterior testis is 480 to 700 μ long by 255 to 380 μ wide, is .90 to 1.50 mm. from the posterior end of the body, and usually abuts or slightly overlaps the anterior testis. The large cirrus pouch extends from the genital atrium to the level of the ovary and is 0.968 to 1.580 mm. long with a maximum width of 255 to 370 μ. A coiled seminal vesicle lies in the posterior part of the pouch. This is followed by a pear-shaped glandular pars prostatica and a short stout cirrus.
The excretory vesicle is obscured by the vitellaria in the living animal and in whole mounts, but in sectioned material may be followed very easily. The excretory pore is slightly dorsal in position. The vesicle is large and Y-shaped, bifurcating at the caudal border of the posterior testis. The two arms of the Y extend anteriorly to a level about midway between the ovary and the acetabulum, at which level they branch and become difficult to follow.

This worm is extremely common in opossums taken at Houston, Texas, and vicinity. Of sixteen adults examined by the writer during the winter of 1947-1948, fifteen were infected with this fluke. There were from three to fifty per host. The writer found four specimens of this worm in an opossum which had been in captivity for a period of over eight months. Dr. J. D. Webster, working in this laboratory, found three specimens in an animal which had been confined for over nine months. This would indicate a fairly long period of adult life.
DISCUSSION

The life cycle of *Rhopalias macracanthus* Chandler places the members of this genus very definitely in close relation to the echinostome flukes. This relationship has long been suspected from comparison of the features of the adult worms of this genus with adult trematodes of the family Echinostomatidae.

The 6, 6, 4, 2, arrangement of the ciliated plates, the formation of the X-shaped pigmented areas of the eye spots, and the position of the flame cells in the miracidium of *R. macracanthus* are almost identical with corresponding features of the miracidium of *Echinostoma revolutum* (Froelich) and *Psilostomum ondatrae* Price as described by Beaver (1937, 1939); of *Sphaeridiotrema globulus* (Rudolphi) as described by Szidat (1937); and of *Echinoparyphium recurvatum* (Linstow) as described by Rasin (1933).

The intra-molluscan phase of the life cycle of *Rhopalias* is also echinostome in type. The general structure of the rediae, the yellow pigmentation seen in mature rediae, and the extra-redial maturing of the cercariae in the snail are characters which are held in common with other echinostomes. The difficulty that the writer encountered in actual demonstration of the sporocyst stage in *Rhopalias* is a difficulty which other workers have had in attempting to describe the life cycle stages of various echinostome flukes. Opinions have varied as to whether a sporocyst actually occurs in the life cycle of these flukes. The studies of Mathias (1925)
on the life history of *Hypoderaemum conoideum*, of Rasin (1933) on *Echinoparyphium recurvatum*, and the evidence of the present work indicate that the sporocyst does occur, although only one or two mother redia develop from each sporocyst. Szidat (1939) demonstrated a sporocyst in the life cycle of the *Cathaemasiidae*, which are evidently closely related to the echinostomes. The life cycles of *Parorchis acanthus* Nicoll and *P. avitus* Linton are of some interest in this respect. In these flukes the miracidium contains a single precociously developed redia. Rees (1940) published an exhaustive study of the germ cell cycle of *P. acanthus* and made this statement: "It differs in that the sporocyst is not represented in the life cycle of *P. acanthus* where a single redia is formed in each miracidium from a single germ cell developed directly from the propagatory cell. The miracidium does not become a sporocyst, but disintegrates once it has performed its function of penetrating the molluscan host and depositing the redia there." The writer is not in complete agreement with this statement. It would seem that the sporocyst is not absent in this life cycle, but rather that it is not as well represented as it is in other trematode groups. There is a tendency toward the suppression of the sporocyst, but the suppression is incomplete. A complete suppression of this stage would entail the direct metamorphosis of the miracidium into a redia such as Johnson (1920) postulated for *Echinostoma revolutum*. Such a total suppression has not been demonstrated.
The spineless cercaria of *Rhopalias* resembles the spineless cercariae of the members of the genus *Echinochasmus*. It further resembles these forms in developing spines in the metacercarial stage. The bar-shaped granules of the cystogenous glands, the refractile granules of the excretory siphons, and the behavior of the cercaria are characters which resemble most other echinostome cercariae.

In the course of this work, the variations in the life cycles of flukes of the family Echinostomatidae were studied. Complete or nearly complete life histories are known for about twenty-four species of this family. Most of them fall into a group in which the cercariae swim rapidly and encyst, without penetration, in either snails or tadpoles, or both. These form a heavy cyst and are infective in a few days. Examples of this type are *Echinostoma revolutum* and *Echinoparyphium recurvatum*. A second group is typified by *Parorchis avitus* in which the cercariae encyst in the open or on the shells of molluscs. The third type is illustrated by *Echinochasmus perfoliatus* and *Petasiger nitidus*; in this group the cercariae are of the large-tailed type and is carried to the intermediate host, a fish, in a passive manner, being eaten or carried to the gills by respiratory currents. Further, in this group the cercariae actively penetrate the tissues of the pharynx or gills and form a thick-walled cyst.

The presence or absence of collar or proboscis spines in the cercaria, and the later development of these structures
in the metacercaria, does not seem to be correlated with the
type of life cycle as outlined above. In the life cycles
of *Echinochasmus* sp. of Townsend (1941) and of *Echinochasmus
perfoliatus*, as described by Muto (1921), the cercariae are of
the large-tailed type and spines develop in the metacercariae.
However, the cercaria of *Echinochamus donaldsoni*, as described
by Beaver (1941), which also develops spines in the metacer-
carial stage, is a small gymnocephalous form. On the other
hand, the cercaria of *Petasiger nitidus*, as described by
Beaver (1939), is a large-tailed form which has a well-develop-
ed collar of spines.

Other singularities in the life cycles of trematodes
which are admittedly in close relation to the Echinostomatidae
may be mentioned. In the life cycle of *Cathaemasia hians*,
as described by Szidat (1939), the cercaria possesses a collar
of forty-three spines. The metacercaria also possesses such
a collar. However, the juveniles and adults of this form do
not possess a collar of spines. Szidat (loc. cit.) regarded
*Cathaemasia* as a true echinostome genus in which the head
crown had been lost. The adults of the family Psilostomatidae
do not possess collar spines nor do the cercariae of any
forms for which this stage of the life cycle is known. In
other respects, however, the worms of this family resemble
echinostomes. Beaver (1939) noted the similarities of the
pre-cercarial stages of *Psilostomum ondatrae* Price, *Psilotrema
spiculigerum* (Muhling), and *Sphaeridiotrema globulus* (Rud.)
to corresponding stages in the life cycles of members of the
Echinostomatidae.
Of what significance are these similarities and dissimilarities in the life cycles of these flukes? Further life history studies may tell us whether the psilostomes are echinostomes which have lost the collar of spines, or, being more primitive, have never developed them. It would be of interest to determine whether the Cathamaesiiidae have developed from an ancestral form which possessed collar spines as an adult.

It must be said that the interpretation of the relationships of trematodes by their developmental characters should be done with extreme caution and only when coupled with adequate morphological study of the adults. As pointed out by Stunkard (1946) the classification of the larval stages of the digenetic trematodes has proved even more unsound than those systems which only take into account the adult morphology. Profound modifications of the larval stages occur in single families due to the complications of the life cycles of these organisms, which involves the parasitism of a molluscan host, frequently a second intermediate host, and a definitive host. Stunkard further pointed out that until our knowledge of these animals is more fully developed, classification into groups higher than families has little or no phylogenetic significance.

As pointed out by Beaver (1939), the present classification of the family Echinostomatidae includes three subfamilies and at least a dozen genera which are in isolated positions. In light of the knowledge of the group then available, Beaver
did not feel that a revision of the classification was advisable. The writer does not feel that the situation is yet ripe for such a revision, although it becomes increasingly apparent that a revision will be necessary. Much of the life history data needs confirmation since it is somewhat contradictory in some cases.

The writer was at first inclined to erect a subfamily in the family Echinostomatidae for the reception of the genus Rhopalias, but it seems better in the present status of knowledge of the group to allow it to retain family standing with mere notification of its relationship to the family Echinostomatidae.

The family name given to the group by Looss (1899) is Rhopaliidae. The family name should consist of the ending -idae added to the stem of the name of the type genus. Following this, the name of the family should be Rhopaliasidae, which name is herewith proposed.
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PLATE II