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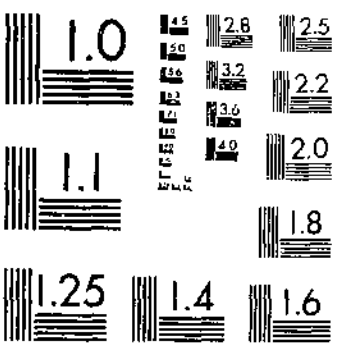

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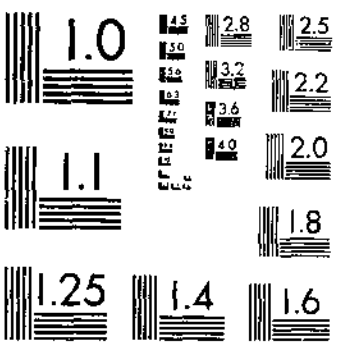

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STUDIES ON THE DEVELOPMENT OF THE PIGEON CAPILLARID, *CAPILLARIA COLUMBAE*[1]

By EVERETT E. WEHR

Associate zoologist, Zoological Division, Bureau of Animal Industry

CONTENTS

INTRODUCTION

There has been a dearth of information on the biology of nematodes of the genus *Capillaria*, as well as on the effects of these parasites on their hosts. The species *C. columbae*, discussed in this bulletin, has been responsible for deaths among pigeons in Europe. In view of the increasing importance of pigeon raising in the United States, experiments were conducted to obtain fundamental information that might lead to the formulation of satisfactory control measures. Experiments were also conducted to determine the transmissibility of the parasites to chickens and turkeys under natural conditions. The data obtained as a result of these investigations, together with indicated control measures, are presented in this bulletin.

REVIEW OF LITERATURE

Capillaria columbae was first described, in 1819, under the name *Trichosoma columbae*, by Rudolphi (*12*),[2] who states that he obtained specimens from the large intestine of the pigeon (*Columbae domesticae*).

[1] Submitted for publication December 1, 1938.
[2] Italic numbers in parentheses refer to Literature Cited, p. 18.

Eber (*2*) and Schlegel (*13*) reported *Trichosoma tenuissimum* (synonym of *Capillaria columbae*) as being the cause of a number of deaths among pigeons in Europe. In the course of necropsies on parasitized pigeons, these authors observed that an intensive intestinal inflammatory condition developed as a result of a heavy infestation with *C. columbae*. Eber (*2*) further reported that the entire intestinal mucosa was swollen and destroyed, and that, in severe cases, masses of the sloughed mucosa sometimes blocked the lumen of the large intestine so completely as to cause the retention of large quantities of fluid in the posterior part of the small intestine.

Levine (*8*) reported having successfully produced heavy infestations with *C. columbae* in chickens by the direct feeding of the infective eggs. Eber definitely showed that this parasite was pathogenic to chickens and that heavy infestations in these birds caused loss of weight, emaciation, and death. Definite lesions consisting of a catarrhal enteritis with desquamation of the intestinal epithelium were recorded by this author, who found also that pigeons became infested with this parasite through the ingestion of contaminated feed and water. He suggested that the droppings be collected daily and either burned or buried deeply as a possible control measure.

Graybill (*3*) reported finding specimens of this parasite in the chicken and the turkey. Stubbs and Crawley (*16*) reported specimens of an undetermined species of capillarid from the intestines of three young White Wyandotte chickens that had been brought to their laboratory for examination. According to these authors, the females of this worm varied in length from 11 to 13 mm. and the eggs measured 45μ by 25μ. It is not possible to determine from their report whether the worms reported by them were *C. columbae*, but the length of the females and the size of the eggs suggest that the species involved was probably *C. columbae*.

DISTRIBUTION AND HOSTS

Capillaria columbae was first reported by Rudolphi (*12*) from the large intestine of the domestic pigeon in Europe. This parasite has since been reported from the same host species in Australia, Brazil, Canada, Ceylon, Cuba, France, Hungary, Ireland, Yugoslavia, Scotland, and United States.

Although normally a parasite of the small intestine of the domestic pigeon (*Columba livia domestica*) and the wild pigeon (*C. livia*), *Capillaria columbae* has been reported from the intestines of the mourning dove (*Zenaidura carolensis*) by Skrjabin (*14*), Travassos (*17*), Leidy (*5*), and Stiles and Hassall (*15*); from the chicken (*Gallus domesticus*) by Graybill (*3*), Morgan (*9*), and Levine (*6, 8*); and from the turkey (*Meleagris gallopavo domestica*) by Graybill (*3*) and Pérez Vigueras (*11*).

In the United States, *Capillaria columbae* has been collected from the pigeon in Maryland, New Jersey, New York, South Carolina, and the District of Columbia; from the chicken in New York, New Jersey, Pennsylvania, and the District of Columbia; and from the turkey in New Jersey.

EXPERIMENTAL PROCEDURE

The pigeons used in the study of artificial and natural infestations were supplied by the Animal Husbandry Division of the Bureau of

Animal Industry, and the strain of *Capillaria columbae* was obtained from infested pigeons supplied by a pigeon raiser in one of the southern States. The work was carried out in the laboratory of the Zoological Division at the Agricultural Research Center, Beltsville, Md.

Material for experimental purposes was made available by confining uninfested with infested pigeons of this species under conditions simulating those usually employed for the rearing of these birds. The room used for this purpose had a dirt floor, roosts, and other equipment necessary for the successful rearing of pigeons. To insure heavy infestations in the birds, conditions in the room were maintained as nearly ideal as possible for the perpetuation of *C. columbae*. The droppings were allowed to accumulate on the floor of the room, and the soil was kept slightly moist to provide adequate moisture for the development of the eggs passed with the droppings of infested birds. Occasionally, the topsoil with the accumulated droppings was turned under in order to build up a heavy infection in the soil. Feed for the pigeons was scattered promiscuously over the surface of the soil so that particles of fecal material containing infective eggs might cling to the food particles and later be swallowed by the birds.

Whenever experimental or dead birds were removed from the infection pen, they were replaced by clean birds. All birds placed in the infection pen were leg-banded, the band numbers and the ages of the birds being recorded for future reference. All dead birds and those otherwise removed from the room were examined post mortem, and estimates of the number of worms present in the intestines were made.

Eggs of *Capillaria columbae* intended for experimental infections were obtained by cutting gravid females into small pieces in Petri dishes containing a small quantity of tap or distilled water and then allowing the prepared cultures to remain at room temperature (20° to 24° C.) until embryonation of the eggs was completed.

The birds used for artificial infections were given infective eggs in a small quantity of water by means of an ordinary medicine dropper. Following infection and throughout the course of the experiments, all birds were confined in wire cages provided with wire-mesh floors beneath which were metal pans. Feed and water were placed in metal troughs attached to the outside of the cage so as to avoid contamination with droppings.

The following procedure was used in the examination of the infested birds: The small intestine was slit open in a large dish containing a small quantity of water, and the intestinal contents, including the mucosa, were scraped loose from the wall of the intestine with a scalpel or knife. The scrapings were usually examined immediately for the presence of worms, but if for any reason the material could not be examined at once, it was preserved in 2 to 4 percent of formalin for later examination. Sedimentation of the fresh intestinal contents for the purpose of concentrating the worms was unsatisfactory owing to the tendency of many of the worms to remain near the surface of the water in the settling dish. Consequently, it was necessary to examine a small quantity of the sediment at a time. A few drops of the material were pipetted into a small Petri dish and then diluted with a small quantity of water. The larger particles of mucus were broken up by repeated withdrawal from and expulsion of the material into the tube with a wide-mouthed pipette. This procedure also

served to release many of the worms that were entangled in bits of mucus and that otherwise might have been overlooked. The diluted material was then placed under a binocular microscope equipped with a medium-powered objective, and the worms were removed by means of a needle or a fine pipette.

Larvae intended for morphological studies were usually examined in the preserving fluid, since the addition of a clearing agent obliterated the outlines of the internal organs by making them too transparent. Some of the structures were brought out more clearly by adding to the solution containing the larvae a drop or two of a weak solution of iodine or some other intra-vitam stain.

DESCRIPTION AND DEVELOPMENT OF EGGS

The eggs of *Capillaria columbae* (fig. 1) are lemon-shaped, yellowish in color, with thick, punctate shells provided at either end with a "plug."

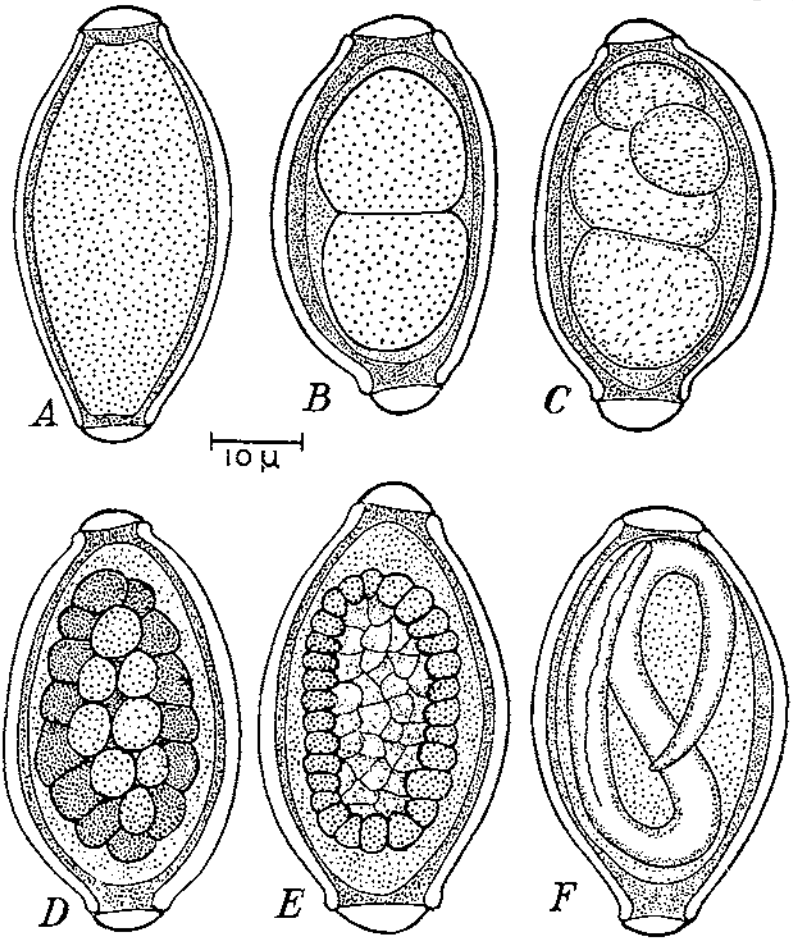

FIGURE 1.—Eggs of *Capillaria columbae*: *A*, Egg as found in freshly deposited feces of pigeon; *B*, egg 48 hours after incubation at 24° C.; *C*, egg 48 hours after incubation at 24°; *D*, egg 65 hours after incubation at 24°; *E*, egg 89 hours after incubation at 24°; *F*, egg 192 hours after incubation at 24°.

In a series of measurements involving 25 eggs, the variation was from 50μ to 55μ in length and from 27μ to 31μ in width. Morgan (*9*) found the eggs to be from 48μ to 55μ long and 22μ to 27μ wide, whereas Graybill (*3*) reported them to be 50μ to 62μ long and 20μ to 27μ wide.

The contents of the freshly deposited egg (fig. 1, *A*) are homogeneous in character. After 48 hours of incubation under conditions affording a suitable supply of oxygen, moisture, and heat, cleavage had progressed to the two-celled stage (fig. 1, *B*) and, in some instances, to the four-celled stage (fig. 1, *C*). Within 65 to 89 hours, development had progressed to the morula stage (fig. 1, *D* and *E*), and 6 to 8 days were required for the eggs to become infective (fig. 1, *F*). Graybill (*3*) found that the eggs contained embryos in 7 days when cultures were kept in physiological saline at a temperature ranging from 23° to 25° C. He noted infective eggs in 6 days when the cultures were kept at a temperature of from 24° to 25°. The present writer found that eggs cultured in tap or distilled water contained completely formed embryos in 6 days when kept at room temperature during August 1936, and in 8 days when kept at room temperature during October 1936, at Washington, D. C. Eggs cultured in 1 to 2 percent of formalin likewise contained fully formed embryos as early as those cultured in tap or distilled water.

EFFECTS OF LOW TEMPERATURES AND AIR DRYING ON THE VIABILITY OF EGGS

The effects of environmental factors on the viability of the eggs of *Capillaria columbae* were determined by a series of experiments that involved the exposure of both nonembryonated and embryonated eggs suspended in a small quantity of water, or in a completely dried state, to various temperatures for different periods.

Nonembryonated eggs were obtained from females collected from the small intestines of freshly necropsied pigeons. These gravid females were placed in a dish containing a small quantity of either tap or distilled water and cut into fine pieces with a pair of scissors. The dish was then exposed to the desired temperature. Embryonated eggs were obtained by exposing to room temperature, until the eggs embryonated, freshly cut up, mature, gravid females suspended in a small quantity of tap or distilled water.

EFFECT OF COLD ON NONEMBRYONATED EGGS

Freshly prepared cultures were exposed to varying degrees of cold and examined after they had incubated for a sufficient time at room temperature to permit embryos to develop. In each experiment a control culture, prepared in the same manner as the experimental cultures, was maintained at room temperature. In all cases the control cultures yielded large numbers of embryonated eggs after incubation for periods of from 7 to 10 days. The data relating to the cultures that were subjected to low temperatures are given in table 1.

The data in table 1 indicate that nonembryonated eggs of *Capillaria columbae* may survive the winter in most of the States of the southern part of the United States, as the winter temperatures in this section are seldom less than the lowest temperature indicated in the table. However, these eggs probably would not retain their viability from

one warm season to another in many States of the northern part of the United States, since the winter temperature in many areas is lower than −9.4° C.

TABLE 1.—*Effect of low temperatures on the viability of nonembryonated eggs of Capillaria columbae*

Experiment No.	Temperature to which culture was exposed	Duration of exposure	Duration of subsequent incubation at room temperature	Embryonated eggs found in culture after incubation	Experiment No.	Temperature to which culture was exposed	Duration of exposure	Duration of subsequent incubation at room temperature	Embryonated eggs found in culture after incubation
	°C.	*Days*	*Days*			°C.	*Days*	*Days*	
1	−5.6 to −9.4	5	14	Numerous.	7	2.5 to 5	7	8	Numerous.
2		15	20	Few.	8		14	8	Do.
3		24	11	Do.	9		22	8	Do.
4		35	7	Very few.	10		96	12	Do.
5	−2.2 to −5.6	3	8	Numerous.	11		170	8	Do.
6		5	14	Do.					

EFFECT OF COLD ON EMBRYONATED EGGS

Levine (7), carrying on experiments in the State of New York, exposed embryonated eggs of *Capillaria columbae* to natural conditions in the shade from October 21, 1935, to November 9, 1936, a period of 385 days, and found that the eggs were capable of producing light infestations when fed to chickens. He also found that embryonated eggs survived an exposure to natural conditions in the sun from November 2, 1935, to March 27, 1936, a period of 146 days. In another test, he exposed embryonated eggs contained in fecal residue (50-percent moisture) to a temperature of −1° C. and found that they survived continuous freezing for 316 days but not for 346 days.

To determine the effect of cold on embryonated eggs of *C. columbae*, and to determine whether such exposed eggs were capable of producing an infection, cultures were exposed to different temperatures and subsequently fed to uninfected pigeons. The results of these experiments are shown in table 2.

TABLE 2.—*Effects of low temperatures on the viability of embryonated eggs of Capillaria columbae*

Experiment No.	Temperature to which culture was exposed	Duration of exposure	Date of feeding eggs to pigeon	Date of examining pigeon	Worms recovered
	°C.	*Days*	*1937*	*1937*	
1	−5.6 to −9.4	7	Aug. 18	Oct. 5	Few.
2	−6.7 to −12.2	14	Sept. 10	Nov. 15	Very few.
3	−2.2 to −5.6	7	Aug. 18	Oct. 5	Many.
4	2.5 to 5	7	(1)	----------	Embryos very active.
5		170	(1)	----------	Embryos dead.

[1] Not fed.

From the data given in table 2 it is evident that some embryonated eggs of *C. columbae* survived a continuous exposure to a temperature of — 6.7° to — 12.2° C. for as long as 14 days. It is apparent, however,

that a slightly longer exposure to this temperature may have been detrimental to these eggs, since only a very few worms were recovered from the intestine of a previously uninfected pigeon as a result of the feeding of a large number of these eggs. At the same temperature, embryonated eggs are apparently viable for a shorter time than nonembryonated eggs. Cultures of both types of eggs were exposed continuously to a temperature of 2.5° to 5° for 170 days. At the expiration of this period none of the embryonated eggs contained live embryos, whereas the nonembryonated eggs developed completely formed embryos when exposed for 10 days to room temperature.

EFFECT OF DRYING ON EGGS

Newbigin and Morgan (*10*) reported that poultry runs which had been left unoccupied for 8 months still harbored viable eggs of *Capillaria* spp. Levine (*7*) found that embryonated eggs of *C. columbae* which had been thoroughly dried by means of an electric fan were dead when examined 14 days later. The following experiment was conducted by the writer to determine the resistance of *C. columbae* eggs to drying under laboratory conditions:

Eggs in which the developing embryo had reached the morula stage were contained in small Petri dishes to which a little water had been added and permitted to dry in air at room temperature. The time at which the water had completely evaporated from the dishes was noted. The eggs were then allowed to remain at room temperature for 24 hours. Water was then added to the dry dishes and the cultures were allowed to remain at room temperature for several days to determine whether development of the embryos would be resumed. The effects of air drying for 24 hours were apparently lethal, since no further development of eggs was observed.

DESCRIPTION OF EMBRYOS

The embryo, or unhatched larva, (fig. 2, *F*) is regarded as the first-stage larva since it was not observed to molt within the egg. In order to make a detailed study of the morphology of the embryo, it was necessary to free it from the eggshell. This was most easily accomplished by placing eggs on a slide, covering the preparation with a cover slip, and then carefully rotating the cover slip under gentle pressure with the tip of the finger. If the excess water underneath the cover slip was allowed to evaporate or was drawn off with a piece of filter paper before attempting to release the embryos, less difficulty was encountered in obtaining embryos in perfect condition.

As shown by a series of measurements involving 12 embryos, variation in size is from 123μ to 150μ in length and from 8μ to 10μ in width. A distinct stylet (fig. 2, *F*) is present at the anterior end of the esophagus in specimens subjected to slight pressure, and this structure is sometimes seen protruding from the oral opening (fig. 2, *C*). The esophagus is slightly swollen in the head region and also just anterior to the beginning of the cell body, the posterior swelling being the most pronounced. Numerous cells are present in the coelomic cavity anterior to the cell body. The short cell body is about 35μ long and consists of two rows of opposing cells. The intestinal tract

posterior to the cell body is not well differentiated. Three or four vacuoles and a few undetermined structures are the principal structures present in this region. The posterior end of the body is bilobed.

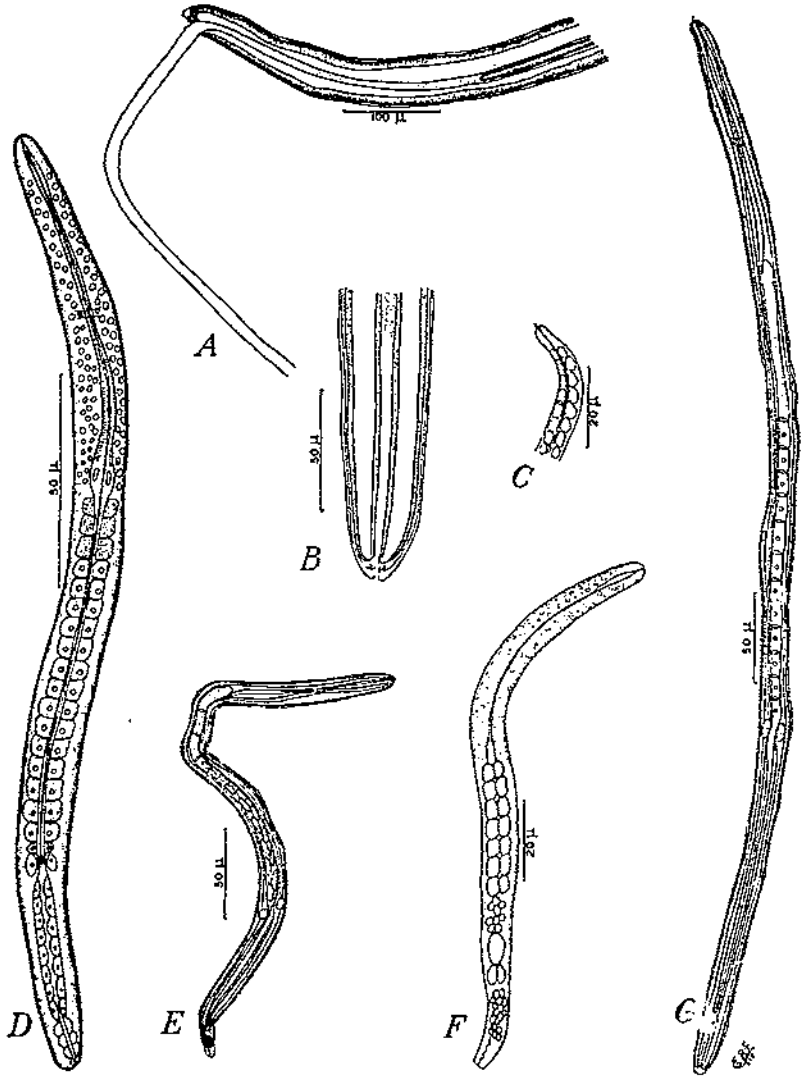

FIGURE 2.—Various stages in the development of *Capillaria columbae*: *F*, Embryo, or unhatched first-stage larva; *C*, anterior end of unhatched first-stage larva showing protruded stylet; *D*, late first-stage larva removed from intestine of pigeon 7 days after infection; *E*, first-stage larva in molt; *G*, second-stage larva; *B*, enlarged drawing of the posterior end of second-stage larva in molt; *A*, posterior end of adult male showing protruded spicular sheath.

The anus opens subterminally. A clear streak, presumably the lumen of the rectum, extends anteriorly from the anal region for a short distance.

DESCRIPTION OF LARVAE

LATE FIRST-STAGE LARVA

Numerous late first-stage larvae, including one specimen in molt (fig. 2, *E*), were removed from the small intestine of young pigeons 7 days after the administration of embryonated eggs of *Capillaria columbae*. Examination showed that larvae of this stage (fig. 2, *D*) vary from 200μ to 292μ in length and from 12μ to 16μ in width. A stylet is present at the anterior end of the esophagus. The esophagus, in a specimen 240μ long, is approximately 175μ long and possesses a slight swelling in the head region and another larger swelling just anterior to the cell body. The esophagus (fig. 2, *D*) lies superficial to and is only partly embedded in the cell body. The cell body is about 84μ long and consists of two rows of opposing cells of which the anterior six appear to be more granular than the others. Two large oval cells of uncertain origin and identity are present at the esophagointestinal junction. The intestine is approximately 65μ long and consists of a single layer of cells. The rectum is 12.5μ long and consists of only a single layer of cells. The anus is located subterminally. The bacillary bands are feebly developed and extend the full length of the body.

The principal measurements of 10 larvae taken at random from a large number of specimens removed from the intestinal contents of a pigeon are shown in table 3.

TABLE 3.—*Measurements of 10 first-stage larvae of Capillaria columbae*

Item	Measurements of larva No.—									
	1	2	3	4	5	6	7	8	9	10
	Microns	*Microns*	*Microns*	*Microns*	*Microns*	*Microns*	*Microns*	*Microns*	*Microns*	*Microns*
Length	200	252	250	220	260	220	260	292	284	240
Maximum width	12	12	14	14	13	12	14	16	14	14
Length of esophagus	125	167	183	149	184	130	175	200	225	175
Length of cell body	92	70	100	100	100	92	105	97	138	84
Length of intestine	75	85	67	71	76	41	85	92	59	65

SECOND-STAGE LARVA

Fully developed first-stage larvae molt and the resulting second-stage larvae complete their development between 7 and 14 days after infection. Larvae recovered from the small intestines of pigeons 1 week after having been fed infective eggs were considered first-stage larvae because of the presence of a double-rowed cell body. On the other hand, larvae recovered from the small intestines of pigeons 2 weeks after infection were considered third-stage larvae, since the cell body consisted of only a single row of cells, the genital primordium extended nearly the full length of the intestine, and the length of the esophagus was 1.7 times as long as that of the intestine. The characters of second-stage larvae, as observed in specimens (fig. 2, *G*) recovered from the intestines of naturally infested pigeons, are given in the following paragraph.

Larvae of this stage vary from 700μ to nearly 3 mm. in length and from 17μ to 35μ in width. They appear to have no stylet. The

character of the intestinal tract is similar to that of the first-stage larva. The relative lengths of the esophagus and the intestine differ, however, from those of the first-stage larva in that the intestine is proportionately much longer than the esophagus. This fact is due to the more rapid growth of the intestine. The total length of the esophagus, in a larva 1.18 mm. long, is about 784μ, and that of the intestine about 400μ. The faintly annulated cell body originates about 192μ from the anterior end of the larva and extends posteriorly for a distance of about 592μ. The first cell of the cell body is considerably longer than any of the others. Many large, brown inclusions, apparently of a granular nature, are present in the body wall. Bacillary bands are visible throughout the body but appear somewhat thicker in the region of the nerve ring than elsewhere. The intestine consists of a simple tube, with the anus opening subterminally. An enlarged drawing of the posterior end of a second-stage larva in molt is shown in fig. 2, *B*.

THIRD-STAGE LARVA

Third-stage larvae (fig. 3, *B*) vary from 2.32 to 4.05 mm. in length and from 24μ to 44μ in width. In a larva 3.51 mm. long, the distance from the anterior end of the body to the cell body is 380μ; the length of the cell body is 1.81 mm., of the esophagus 2.19 mm., and of the intestine 1.32 mm. No sex differentiation can be determined in this stage. The genital primordium is almost as long as the intestine, and the well-developed bacillary bands extend throughout the body. Many large brown inclusions, apparently granular in nature, are present in the body wall. Measurements of third-stage larvae are given in table 4.

TABLE 4.—*Measurements of third-stage larvae of Capillaria columbae*

Item	Measurements of larva No.—							
	1	2	3	4	5	6	7	8
Length.....millimeters..	3.51	2.7	3.72	2.34	2.63	3.52	4.05	2.32
Maximum width.....microns..	28	32	44	24	36	42	36	24
Length of esophagus....millimeters	2.19	1.73	2.55	1.66	1.65	2.17	2.70	1.50
Length of cell body.....do....	1.81	1.41	2.15	1.44	1.33	1.79	2.1	1.15
Length of intestine.....do....	1.32	.97	1.17	.68	.98	1.35	1.35	.82

FOURTH-STAGE LARVA

The transition of the larvae from the third to the fourth stage occurs between the second and third weeks of infection. A study of fourth-stage specimens (fig. 3, *G*) showed that they vary from 4.05 to 6.5 mm. in length and from 36μ to 44μ in width. The sexes in the fourth stage are distinct, the length of the males averaging slightly less than that of the females. Both sexes possess well-developed bacillary bands, and numerous large brown inclusions, apparently granular in nature, are present in the body wall. The female organs are clearly differentiated into a vagina and uteri; the position of the vulva (fig. 3, *F*) is indicated by a convexity in the body wall. The vagina appears as a broad clear area about 100μ long, which extends posteriorly from the vulvar swelling. In a female specimen 6.5 mm. long, the esophagus is 3 mm. long and the intestine 3.4 mm. long. In

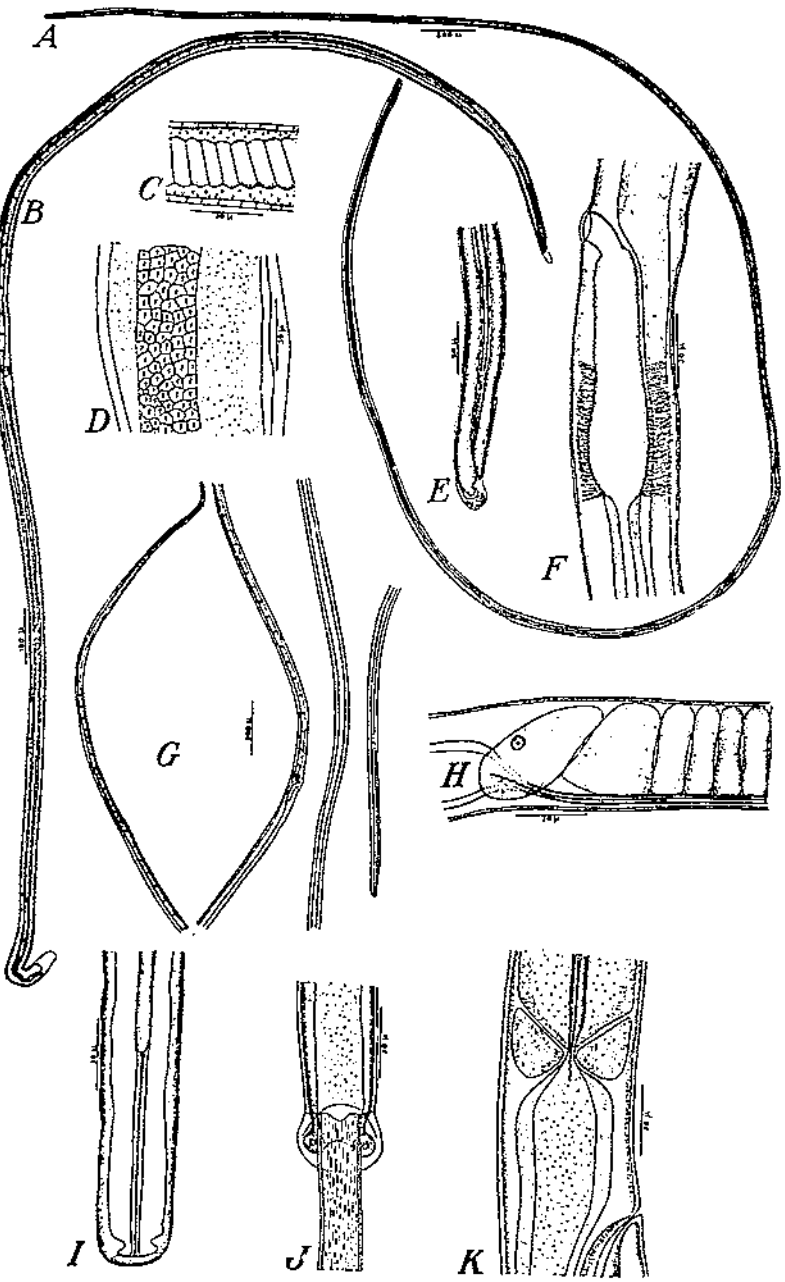

FIGURE 3.—Various stages in development of *Capillaria columbae:* *B*, Third-stage larva in molt; *G*, fourth-stage larva, female; *F*, enlarged drawing of the vaginal region of fourth-stage larva; *I*, ventral view of posterior extremity of male fourth-stage larva showing the two fingerlike processes; *A*, immature adult male; *E*, lateral view of posterior end of immature adult male in molt; *H*, lateral view of body of adult in region of esophago-intestinal junction, showing large triangular cell and esophageal cell annulations; *K*, lateral view of adult female in region of esophago-intestinal junction and vulva; *J*, ventral view of posterior end of male showing extruded spicular sheath and bursa; *D*, portion of bacillary band in surface view; *C*, portion of body in region of esophagus showing columnar cells of bacillary bands.

a male 5.45 mm. long, the esophagus is 2.77 mm. long and the intestine 2.7 mm. long. The male organs consist of a testis and a weakly cuticularized spicule that measures about 1.3 mm. long. The posterior extremity (fig. 3, *I*) is rounded and shows, in ventral view, two superficial processes pointing inward.

SEXUALLY IMMATURE ADULT MALE

A single ensheathed male specimen (fig. 3, *A*), 7.9 mm. long, was taken from the small intestine of a naturally infested pigeon. The well-developed spicule measured 1.48 mm. in length, its distal end being about 200μ from the posterior end of the body. The transversely striated spicular sheath extended beyond the spicule to the tip of the posterior extremity. The distance from the anterior end of the body to the beginning of the cell body was 281μ; the cell body was 3.2 mm. long, and the intestine 4 mm. long. The posterior extremity (fig. 3, *E*) appeared to be similar to that of the sexually mature adult male. No female corresponding to this male in the scale of development was found.

DESCRIPTION OF ADULTS

Graybill (*3*) and Irwin-Smith (*4*) have given fairly accurate and complete descriptions of the adults of *Capillaria columbae*. When first removed from their natural habitat, the living worms usually assume a loose corkscrewlike appearance, the posterior extremity of the male usually being coiled. The posterior portion of the body of the female is extremely dark in appearance owing to the presence of the reproductive organs. The distinctly annulated cell body consists of a single row of cells, the shortest and broadest of these being at the posterior end. The annulations of the first few cells are absent or seen only with difficulty. However, these annulations are pronounced in the cells near the posterior end of the cell body (fig. 3, *H*). The two large, somewhat triangular cells (fig. 3, *K*) present at the esophago-intestinal junction are more conspicuous in the male than in the female. The esophago-intestinal junction divides the body into two approximately equal parts, the intestinal region being somewhat the longer portion.

The vulva is located slightly posterior to the terminal cell of the cell body and the posteriorly directed vagina is heavily muscled (fig. 3, *K*). The posterior extremity of the female is rounded, with the anus subterminal.

The spicule (fig. 3, *A*) is surrounded by a transversely striated sheath that extends posteriorly beyond the spicule to the posterior end of the body. The spicular sheath in preserved specimens (fig. 2, *A*) is frequently extruded for a considerable distance from the cloaca. The cloacal aperture is surrounded dorsally by a small spatulalike bursa (fig. 3, *J*) or membrane, which is a continuation of the body cuticle. It is supported on each side by a knob-shaped ray. Measurements of the adult worms are given in table 5.

TABLE 5.—*Measurements of adult worms of Capillaria columbae*

FEMALES

Item	Measurements of worm No.—									
	1	2	3	4	5	6	7	8	9	10
Length.....millimeters..	15	14.4	17.2	15.9	14.5	13.1	12.3	13.8	15.6	13.0
Maximum width.....microns..	108	84	88	76	92	84	76	72	80	80
Length of esophagus.....millimeters..	5.1	5.6	6.6	6.3	5.6	5.3	5.6	5.7	6.2	5.3
Length of cell body.....do....	4.6	5.0	6.0	5.8	5.1	4.7	5.1	5.2	6.7	4.8
Distance from anterior end of body to vulva.....millimeters..	5.2	5.8	6.7	6.4	5.7	5.3	5.6	5.8	6.2	5.4
Length of intestines.....do....	9.3	8.6	10.5	9.5	8.7	7.8	6.9	8.0	9.2	7.5

MALES

Length.....millimeters..	10.1	11.6	13.8	12.4	11.5	11.3	9.6	12	11.3	11.5
Maximum width.....microns..	50	56	70	54	50	48	44	56	46	60
Length of esophagus.....millimeters..	4.7	5.3	6.2	6.0	5.9	6.0	4.8	5.7	5.6	5.7
Length of cell body.....do....	4.4	4.8	5.6	5.6	5.3	5.5	4.3	5.2	5.1	5.2
Length of spicule.....do....	1.2	1.5	1.4	1.7	1.4	1.5	1.3	1.4	1.3	1.5
Length of intestine.....do....	5.3	6.3	7.7	6.4	5.6	5.3	4.8	6.3	5.8	5.8

RECAPITULATION OF DEVELOPMENTAL STAGES

The first-stage larva is characterized by having a recognizable stylet and a cell body consisting of two rows of opposing cells. In the succeeding stages there is no recognizable stylet, and the cell body consists of only a single row of cells that are usually rectangular in shape and annulated. The esophagus, in all stages, possesses two swellings, one immediately back of the head and the other immediately anterior to the cell body. Chitwood (*1*) has shown that, contrary to the prevailing opinion, the esophagus is not surrounded by the cell body (fig. 2, *G*); it lies superficial to but in close contact with the cell body. A large triangular cell of uncertain origin and identity is present on either side of the esophago-intestinal junction. Two bacillary bands (fig. 3, *C* and *D*) located laterally, extend the full length of the body in all stages. In the early larval stages, the esophagus is much longer than the intestine, but in the adult the two regions are approximately equal in length. The approximate ratios of the length of the esophagus to the length of the intestine for each of the stages of *Capillaria columbae* are as follows: First stage, 3.5:1; second stage, 2:1; third stage, 1.8:1; fourth stage, 1.1:1; and adult, 1:1.4.

DEVELOPMENT OF *CAPILLARIA COLUMBAE* IN PIGEONS

Each of five young uninfested pigeons was given a large number of embryonated eggs of *Capillaria columbae* at hourly intervals during a 4-hour period. These birds were held in cages and under conditions designed to prevent extraneous infection and were necropsied 7, 14, 19, and 26 days after infection. The small intestines of two birds examined on the seventh day after infection contained numerous, very small larvae varying from 200μ to 300μ in length and from 13μ to 16μ in width. These larvae were considered to be first-stage larvae because of the presence of a distinct stylet and a cell body consisting of two rows of cells. These larvae were 50μ to 75μ longer than the unhatched larvae.

The transition from the first- to the second-stage larva occurs between the first and second weeks after infection, probably very early in the second week, since larvae removed from the small intestine of one pigeon, which was necropsied 14 days after infection, were apparently in the third stage. These larvae varied from 3 to 5 mm. in length and from 30μ to 36μ in width. The cell body consisted of only a single row of cells. A stylet was apparently absent.

A few sexually mature adults, the females containing well-developed eggs, and many sexually immature adults were removed from the small intestine of a pigeon necropsied 19 days after infection, and a large number of sexually mature adults were removed from the small intestine of a pigeon necropsied 26 days after infection. Fecal examination of this pigeon at time of necropsy showed the presence of eggs. No fecal examination was made of the pigeon necropsied 19 days after infection, but this bird was found to harbor a few gravid females.

DURATION OF INFECTION IN PIGEONS

To determine the duration of the infection in pigeons, three young birds that had not been previously exposed to *Capillaria columbae* were infected as follows: Pigeon 6303 was given a single dose of embryonated eggs on September 3, 1936, and pigeons 7069 and 7983 were given embryonated eggs on September 24, 1936, and again on September 26. Fecal examinations of these birds, made from 1 to 2 months after the dates of infections, disclosed the presence of capillarid eggs. Pigeon 6303 was killed about 7 months after the date of infection, and five male *C. columbae* were recovered. Pigeon 7069 was killed 4 months after it was infected, and a few specimens, mostly males, were found. Pigeon 7983, in a post-mortem examination about 3 months after the date of infection, gave negative results.

From these results, therefore, it is evident that pigeons may remain infested for 7 months or longer. Levine (*8*) obtained mature specimens of *C. columbae* from the intestines of chickens 294 days after feeding of embryonated eggs. The experiments recorded by the writer show that there is a tendency for the male worms to survive longer in an infected bird than the female worms.

LOCATION OF WORMS IN INTESTINE

Necropsies of many pigeons experimentally and naturally infested with *Capillaria columbae* showed that these worms usually occur in the anterior half of the intestine. In light infestations, a few worms are found in that portion of the intestine anterior to the bile duct. In heavily infested birds, however, worms are found as far anteriorly as the beginning of the duodenum and nearly as far posteriorly as the ceca. When mature and immature worms are present in abundance in the same bird, the greatest numbers of adults are found in the anterior half of the small intestine. The mature worms are usually encountered somewhat more forward in the intestine than are the immature forms, the latter usually being most abundant in the middle region of the small intestine beginning at a point about 4 or 5 inches back of the duodenal opening.

The worms are usually embedded more or less deeply in the intestinal mucosa, and ordinarily only a few of them are removed from

the intestinal tract by the usual method of drawing the opened intestine back and forth through water in a dish. Some of the adult worms may be freed by this method, but few, if any, of the immature forms can be recovered in this way owing to the deeper position that they occupy in the mucosa. The immature worms can be successfully removed only by scraping the mucosa from the intestinal walls and then examining the scrapings with the aid of a binocular microscope.

ADAPTABILITY OF *CAPILLARIA COLUMBAE* TO TURKEYS AND CHICKENS

Capillaria columbae has only occasionally been reported from the small intestines of chickens and turkeys raised under natural conditions. Graybill (*3*) stated that as a result of many autopsies of chickens and turkeys for a period of several years, *C. columbae* was never observed in these birds in large numbers. As already noted, Stubbs and Crawley (*16*) reported an undetermined species of capillarid from the intestines of three young White Wyandotte chickens that had been brought to their laboratory for examination. According to these authors, the female worms varied in length from 11 to 13 mm. and the eggs measured 45μ to 25μ. Reasons for regarding these worms as *C. columbae* have already been given.

To obtain information concerning the degree of adaptability of *C. columbae* to chickens and turkeys a series of experiments was conducted that involved the exposure of these birds to infection under natural conditions. Four turkeys from 2 to 3 months old and seven chickens about 1½ months old were confined in a small room with a number of heavily infested pigeons. A summary of this experiment is given in table 6, which shows that *C. columbae* was successfully transmitted to both chickens and turkeys.

TABLE 6.—*Data on the susceptibility of chickens and turkeys to infestation with Capillaria columbae*

Species and bird No.	Date of infection	Date host was killed	Duration of infection	Worms present at necropsy
			Days	
Turkey 5015	June 29, 1937	Aug. 13, 1937	45	1 mature female.
Turkey 4960	do	Oct. 8, 1937	101	Fragments of 2 worms.
Turkey 4143	May 25, 1937	June 29, 1937	35	Few mature males and females.
Turkey 248	Oct. 23, 1936	Jan. 22, 1937	91	None.
Chicken 209	Apr. 7, 1937	May 21, 1937	44	Many mature males and females.
Chicken 713	do	June 7, 1937	61	Few mature worms.
Chicken 419	do	May 4, 1937 [1]	27	Many mature worms.
Chicken 277	Oct. 20, 1936	Dec. 13, 1936	54	None.
Chicken 287	do	do	54	Do.
Chicken 388	do	do	54	Do.
Chicken 693	do	do	54	Do.

[1] Bird died on this date.

The negative findings for the one turkey and the four chickens in the experimental pen in October 1936 are attributed to failure of the eggs passed in the droppings of the infested pigeons to become infective. This assumption seems plausible because of the prevailing low temperatures at the time of the year that the birds in question were exposed to infestation.

SYMPTOMS OF INFESTATION

Birds heavily infested with *Capillaria columbae* show definite symptoms of emaciation, listlessness, and diarrhea. They spend much of their time huddled on the ground underneath the roosts or in some corner of the room away from the rest of the birds. The head is drawn back close to the body and the eyes are usually closed. The feathers appear ruffled and soiled around the vent, and the skin and visible mucous membranes are more or less pale. Food and water are partaken of sparingly. Death usually occurs as a result of heavy infestation.

Levine (*8*) stated that the first clinical symptoms of *C. columbae* infection in chickens were noticeable on the twelfth day after the feeding of embryonated eggs. At this time much pinkish material composed of mucus, necrosed epithelial cells, and numerous erythrocytes, granulocytes, and lymphocytes were noticed in the feces of the infected birds. During the next 4 days the feces of the birds were fluid owing to an increase in the quantities of epithelium and inflammatory exudate that was being eliminated from the intestinal tract. During the following 2 weeks, however, most of the birds regained their normal appearance and the feces became normal. A number of the birds, however, lost weight steadily, became extremely emaciated, and either died or were destroyed.

GROSS PATHOLOGY

Eber (*2*) and Schlegel (*13*) have observed that an intensive intestinal inflammatory condition developed as a result of a heavy infestation with *Capillaria columbae*. Furthermore, Eber (*2*) reported that the entire intestinal mucosa was swollen and destroyed and that, in severe cases, masses of sloughed mucosa sometimes so completely blocked the lumen of the large intestine that large quantities of fluid were retained in the posterior part of the small intestine.

Levine (*8*) reported that the intestines of chickens heavily infested with *C. columbae* showed a moderate thickening of the mucosa, which contained "reddish areas varying from pinhead hemorrhagic spots to diffuse hyperemia of large portions of the mucosa." In some cases, he reported that the intestinal mucosa was covered with much catarrhal exudate which ranged in color from "opaque white to translucent salmon color." He stated that the intestines of some infected birds showed no changes in spite of the fact that as many as 1,500 to 5,000 worms were found in each.

As observed by the writer, pigeons naturally infested with *C. columbae* under laboratory conditions showed, on post-mortem examination, infestations varying from a few to hundreds of worms each. The largest number of worms removed from the small intestine of a single pigeon raised under these conditions was approximately 1,500. Usually only a few worms were found in the small intestines of fatal cases and most of the worms in such instances were males. Following is an explanation of this occurrence.

In fatal and in severe advanced cases of infestation the intestines showed extensive destruction of the mucosa, frequently with complete sloughing of the mucous membrane. It is assumed that these birds had been heavily infested with capillarids earlier and that the attachment of the worms to the intestinal wall caused necrosis of the

tissue immediately surrounding them to such an extent that both parasites and necrotic tissue were sloughed off into the lumen of the intestine. The intestines contained a large quantity of fluid.

The nonfatal experimental cases did not show a marked destruction of the intestinal mucosa. However, there was considerable thickening of the walls of the intestines owing to edematous infiltration.

The intestines of uninfected pigeons showed no evidence of thickening of the walls or destruction of the mucosa. The intestinal contents were never so fluid as in the fatal cases.

SUGGESTED CONTROL MEASURES

The practice of rearing different species of poultry separately is recommended, since experimental data show that chickens and turkeys, as well as pigeons, are susceptible to infestation with *Capillaria columbae*.

Studies on the viability of the eggs under different environmental conditions indicate that drying is fatal to them. Consequently, pigeon lofts should be located on well-drained soil and the runs exposed to direct sunlight and kept free from vegetation or debris that might provide shade or moisture. The feed should be placed in sanitary troughs, and water pools should not be allowed to form around the drinking troughs.

The adoption of a program of strict sanitation is strongly urged as a control measure for this parasite. Since the experimental data show that freshly passed eggs require from 6 to 10 days to become infective, under favorable conditions of temperature and moisture, the houses and pens should be thoroughly cleaned and all litter removed at least once a week during the summer months.

In case of an outbreak, the houses and adjacent grounds should be cleaned thoroughly and disinfected with hot water or hot water and lye mixed in the proportion of 1 pound of commercial lye containing 94 percent of sodium hydroxide to 5½ gallons of water. This solution is also effective in destroying coccidia as well as the eggs and larvae of other poultry parasites.

SUMMARY AND CONCLUSIONS

In view of the increasing importance of pigeon raising in the United States and the fact that little information was available regarding the biology of *Capillaria columbae* and its effects on the pigeon, an experimental study of the life history of this parasite was undertaken.

Eggs of *C. columbae* were found to develop to the infective stage within 6 to 8 days when kept at room temperature.

Cultures of nonembryonated and embryonated eggs of *C. columbae* suspended in a small quantity of water, were found to be very resistant to low temperatures. Nonembryonated eggs were found to be viable and to complete embryonation after an exposure of 35 days to a temperature of −5.6° to −9.4° C. when subsequently exposed to room temperature. Embryonated eggs were found to be infective to pigeons after an exposure of 14 days to a temperature of −6.7° to −12.2°. Drying for 24 hours at room temperature destroyed the vitality of partly embryonated eggs.

Morphologically, the first-stage larva is characterized by having a recognizable stylet and a cell body consisting of two rows of opposing

cells. A recognizable stylet is absent in all succeeding stages, and the cell body consists of only a single row of cells. The esophagus, in all stages, assumes a position superficial to the cell body and possesses two swellings anterior to the cell body. The relative lengths of the esophagus and the intestine vary with the stage of development. In the first-stage, the esophagus is three to four times as long as the intestine, whereas in the adult the two regions are approximately equal in length.

The life history of *C. columbae* was shown to be of the direct type. The unhatched embryo has not been observed to molt within the egg. The first-stage larva molts and becomes a second-stage larva early in the second week of infection. The second-stage larva completes its development and molts to the third stage before the fourteenth day after infection. The transition from the third to the fourth stage occurs between the second and third weeks of infection, and mature worms may be recovered from the small intestines of experimentally infected birds as early as 19 days after infection. Eggs have been found in the feces of the birds 26 days after infection.

In experimental studies, pigeons necropsied 7 months after infection were still infested with *C. columbae*.

All stages of the worm penetrate more or less deeply in the intestinal mucosa, the larvae being found somewhat deeper than the adults. Necropsies of many birds have shown that most of the worms usually occur in the middle portion of the small intestine.

Heavily infested birds showed symptoms of emaciation, diarrhea, and listlessness; food and water were consumed sparingly; and death was usually the termination of severe infestations. For several days prior to death, infested birds spent considerable time in a huddled position on the ground. The feathers were ruffled and those around the vent were usually soiled with fecal material.

As observed by the writer, pigeons naturally infested with *C. columbae* showed, on post-mortem examination, extensive destruction of the mucosa, frequently with complete sloughing of the mucous membrane. The intestines contained large quantities of fluid.

Control of this parasite should be directed toward prevention by thorough sanitation and selection of well-drained areas for permanent lofts.

Chickens, turkeys, and pigeons should be raised separately, since all three types of birds are susceptible to *C. columbae* infection.

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