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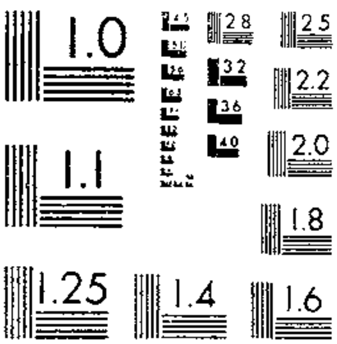

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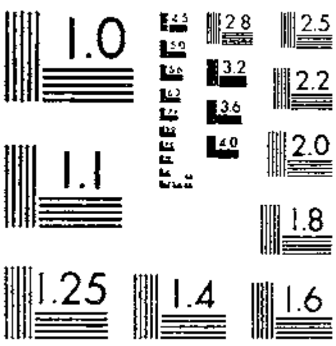

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TECHNICAL BULLETIN No. 227 FEBRUARY, 1931

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DEVELOPMENTAL STAGES OF SOME NEMATODES OF THE SPIRUROIDEA PARASITIC IN POULTRY AND GAME BIRDS

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CONTENTS

REVIEW OF PRECEDING INVESTIGATIONS

Previous investigations conducted in various parts of the world have revealed the life histories of a few of the nematodes belonging to the Spiruroidea which occur in domestic birds. A discussion of these and more recent findings has been included in a paper by the writer.[2] The findings of earlier investigators may be very briefly summarized as follows:

By comparative studies of a morphological nature three crustaceans were shown to be the intermediate hosts of three nematodes.

[1] J. R. Christie, of the Bureau of Plant Industry, and C. H. Popenoe and F. L. Campbell, of the Bureau of Entomology, have assisted the writer most generously by supplying laboratory-reared grasshoppers for the experiments here described. E. A. Chapin, of the Bureau of Entomology, and J. O. Maloney, of the Smithsonian Institution, identified the dung beetles and the isopods, respectively. The Animal Husbandry Division of the Bureau of Animal Industry supplied day-old, incubator-hatched chickens. The investigation of parasites of ruffed grouse was undertaken in cooperation with the New England Ruffed Grouse Investigation Committee; the writer is especially indebted to A. O. Gross of that committee for obtaining the live grouse for the feeding experiments, and for collecting and submitting unpreserved specimens of *Dispharynx spiralis* and *Cheilospirura spinosa* from grouse. The study of parasites of bobwhite quail was undertaken in cooperation with the Bureau of Biological Survey, and the writer is especially indebted to H. L. Stoddard, of that bureau, for aid in obtaining material. W. B. Coleman, of the White Oak quail farm, Richmond, Va., has also been most generous in his cooperation. The Connecticut Game Commission made possible the successful completion of the life-history experiments on *Seurocyrnea colini* by furnishing quail, originating in Mississippi, which were infected with that parasite.

[2] Paper presented at The Fourth World's Poultry Congress, London, July, 1930.

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namely, the isopod, *Porcellio laevis*, serving for *Dispharynx spiralis* as occurring in the chicken; the amphipod, *Gammarus pulex*, and the cladoceran, *Daphnia pulex*, for *Tetrameres fissispina*, as occurring in ducks; and the cladoceran, *Daphnia pulex*, also for *Echinuria uncinata*, as occurring in ducks. By experimental demonstrations two insects were added by the earlier investigators to the list of intermediate hosts for three other nematodes, namely, one of the Isoptera, the termite *Macrohodotermes mossambicus transvaalensis* (synonym: *Hodotermes pretoriensis*), serving for *Hartertia gallinarum* of chickens, and one of the Orthoptera, the roach, *Pycnoscelus surinamensis*, for *Oxyspirura parvovum* and *O. mansoni*, also of chickens.

Investigations carried on by the writer have recently added to this list the names of seven arthropod intermediate hosts, of which five are insects and two are crustaceans, serving for six spirurids. These are as follows: Two members of the Coleoptera, the dung beetle, *Phanaeus vindex* (synonym: *P. carnifex*) and *Copris minutus*, serving for a species of Gongylonema, tentatively identified as *G. ingluvicola* of the chicken; three members of the Orthoptera, the grasshoppers, *Melanoplus femurrubrum* and *M. differentialis*, both serving for *Tetrameres americana* and *Cheilospirura hamulosa* of chickens and for *C. spinosa* of gallinaceous game birds, and the cockroach, *Blattella germanica*, serving for *Seurocyrnea colini* of game birds; and two isopods, the sow bugs, *Porcellio scaber* and *Armadillidium vulgare*, serving for *Dispharynx spiralis* of gallinaceous game birds.

In the case of the species of Gongylonema, a natural infection in the dung beetles was discovered incidental to the conducting of experiments on another spirurid, *Physocephalus sexalatus* of swine, for which those beetles also serve as intermediate hosts; in a chicken a single male specimen and in a rabbit two female specimens of Gongylonema were developed, which were tentatively identified as *G. ingluvicola*, pending further investigation when additional material is available. However, in the case of the other five spirurids, all stages of the life cycle were experimentally produced, and it is planned here to describe the various stages observed in the development of each of these nematodes.

METHODS USED IN THE PRESENT INVESTIGATION

The grasshoppers used as intermediate hosts in the present study were laboratory reared, but all the other arthropods were collected in the wild. The embryonated eggs of the nematodes were obtained from the uteri of the worms and in some cases from the contents of the digestive tract of the infected birds and were fed to the arthropods with green stuff or with finely ground cereals.

The bird hosts used for the life-history experiments were confined indoors throughout the entire period of the experiment. The chickens were hatched in incubators and in all but a few cases were kept on raised wire-mesh floors through which the droppings passed, first in electrically heated brooders and later in cages, but in both instances under an insect-proof cover made of fine wire screening of approximately 2-millimeter mesh. Control chickens were kept in the same compartment as those experimentally fed.

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Tetrameres americana. A, Adult male; B, female. Original

This method has proved to be highly reliable, control chickens being consistently negative as regards the presence of parasites and the chickens which had been artificially infected showing no parasites other than those fed to them. This method was followed in all instances until the life history was definitely established; in a few cases, as in the case of the infections with *Tetrameres americana* and with *Cheilospirura hamulosa*, in order that observations of a more general clinical nature might be made, chickens were released later in indoor pens. The floors of these pens were of concrete, and the windows were screened; the pens were in a new building and had never been used for chickens other than those experimentally infected.

Pigeons were held in cages of the kind described, but the birds other than pigeons and chickens were held in the indoor pens rather than in cages. The quail had been hatched in incubators and reared artificially; the ducks and turkeys were obtained from commercial poultry raisers and the ruffed grouse from a Canadian dealer. Therefore the previous histories in these cases were unknown.

TETRAMERES AMERICANA CRAM, 1927 (*5*)[3]

Synonym: *Tropisurus americanus* (Cram, 1927) Baylis, 1929 (*2*)

Members of the genus Tetrameres and related genera are unique among nematodes in birds in that the females do not conform to the usual shape of roundworms, that is, elongated and cylindrical, but, after entering the glands of the stomach, become globular in shape as the body becomes distended with eggs; there are two small projections, one of which, the head, is at one side, and the other, the tail, on the opposite side. The worm lies in the gland in such a position that the tail protrudes into the duct of the gland, to facilitate the passage of the eggs, and the head is in the fundus of the gland, to facilitate feeding. The female becomes blood red in color (pl. 1), another unusual characteristic. The males, on the other hand, retain throughout life the elongated, slender form of body and are practically without color. This sexual dimorphism in species of Tetrameres, correlated with the life habit, has been compared with that of the chigoe flea, which occurs in tropical America and Africa, the female burrowing into the skin of man and of various domestic and wild animals, becoming engorged with blood, and its body swelling to a globular form as it is distended with eggs.

T. americana is of fairly common occurrence in chickens (*Gallus gallus*) in North America, and in some localities is of considerable pathological significance. It occurs also in bobwhite quail (*Colinus virginianus*).

DEVELOPMENT IN INTERMEDIATE HOST

Embryonated eggs of *T. americana*, when fed to the grasshoppers, *Melanoplus femurrubrum* and *M. differentialis*, hatch in the digestive tract, and the larvae pass into the body cavity, where they can be found in an active, unencysted state for the first 10 days after the feeding. They then penetrate the tissues, chiefly the muscles, and

[3] Italic numbers in parentheses refer to Literature Cited, p. 26.

become loosely encysted; in heavy infestations all parts of the body, including the head and the femurs, contain the larvae. On dissection of the grasshoppers in a shallow layer of water, the larvae excyst quickly and become very active. In 42 days, possibly sooner, the larvae are infective for the final host. The vitality of the grasshoppers appeared to be considerably reduced by the infection; a certain number died, and those which survived were droopy and inactive, a condition which would make them easy prey for food-seeking fowls in nature.

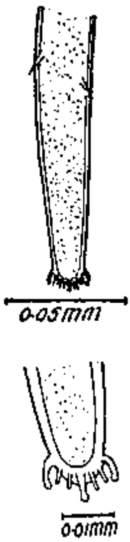

FIGURE 1.—*Tetrameres americana.* Tail of third-stage larva

The most striking characteristics of the third-stage infective larva are as follows: Head end blunt, without lips or other noticeable structures. Cuticle with distinct cross striations. Total length of body, 1.8 to 1.9 mm.; first part of esophagus (muscular portion), 216 to 225μ long; second part of esophagus (glandular portion), 540 to 550μ long; the ratio of total length of esophagus to total body length is therefore as 1 to about 2.4. Anal aperture 170 to 184μ from tail end. Rectum refractive to light, as if chitinized. Tail (fig. 1) with a circle of 12 papillae at its posterior end, the 4 papillae situated in the lateral, ventral, and dorsal fields being larger and more curved than the other 8, of which there are 2 in each of the 4 submedian fields. A pair of slender, sharply pointed papillae are situated in the lateroventral field at a distance of 88μ and 100μ, respectively, from the tail end.

DEVELOPMENT IN FINAL HOST

In the experiments conducted by the writer, the third-stage larvae of *T. americana* obtained from experimentally infected grasshoppers have proved infective for young and adult chickens, for the domestic duck (*Anas platyrhyncha domestica*), for bobwhite quail, and for ruffed grouse (*Bonasa umbellus*), in the cases shown in Table 1.

TABLE 1.—*Development of Tetrameres americana in various bird hosts*

Host	Birds infected after feeding	Nematodes developed per bird	Birds not infected after feeding	Controls (all negative)
	Number	*Number*	*Number*	*Number*
Young chicken	48	1 to 240	9	120
Adult hen	1	10	0	3
Pigeon	1	15	2	4
Young duckling	1	1	0	1
Adult duck	0	0	0	0
Bobwhite quail	2	3 and 6	0	10
Ruffed grouse	1	23	0	5

As regards the negative results in chickens, in seven of the nine negative cases the chickens were not killed and examined until from five to eight months had elapsed after the feeding of the infected-grasshopper parts; the possibility suggests itself, therefore, that the chickens in at least some of these cases may have been lightly infected and that the life of the parasites was not five to eight months long in those cases. This supposition is borne out by the finding of a disintegrated female specimen of Tetrameres in the wall of the proventriculus of one of the chickens, killed eight months after the experimental feeding; the red color had disappeared, and the cuticle was partially disintegrated, but the mass of coiled uteri and the black saclike intestine remained.

The difficulty in producing experimental infections of ducks—only one specimen of parasite, a female, developing in the case of the young duck and no parasites developing in the adult duck—suggests that ducks are not normal hosts of *T. americana*. This observation is substantiated by the fact that natural infestations of domestic ducks with this parasite have never been discovered in this country, so far as the writer knows. This is contrary to the situation in Europe, where the reports of the European species, *T. fissispina*, are as frequent from ducks as from chickens, if not more so. The difference in the intermediate hosts of the two species may be correlated with this difference in final hosts, the species found usually in ducks and other water birds having as intermediate hosts aquatic crustaceans, as noted in the introduction to this bulletin, and the species found normally in chickens having as intermediate hosts terrestrial insects, grasshoppers. Gallinaceous birds would ingest crustaceans accidentally in their drinking water with much greater frequency than water birds would ingest terrestrial insects, such as grasshoppers; the wider range of bird hosts for *T. fissispina* is, therefore, easily understood.

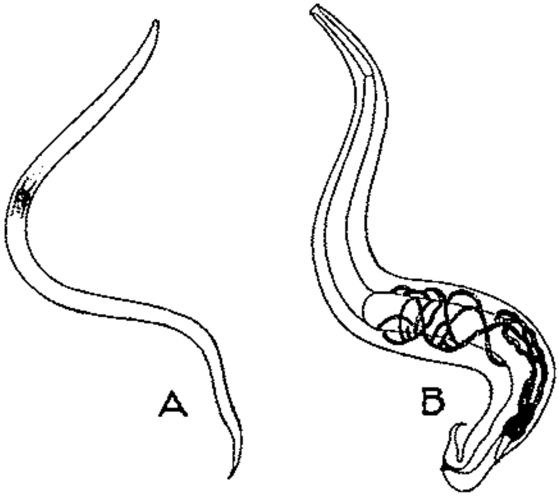

FIGURE 2. Immature forms of *Tetrameres americana*: (A) Male and (B) female, at the end of 14 days in the chicken. About thirty times natural size

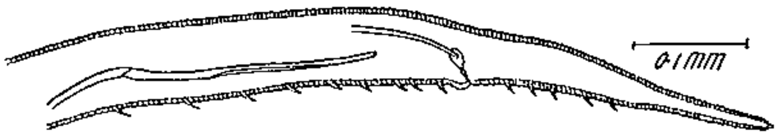

FIGURE 3.—Posterior end of male *Tetrameres americana*

Natural infestations of bobwhite quail with *T. americana* have been noted, but the present report of experimental infestations in the ruffed grouse and pigeon appears to be the first observation of this parasite in these hosts.

RATE OF DEVELOPMENT

As regards the rate of development, the following observations have been made: Eleven days after being fed to a chick the larvae were recovered from the surface of the mucosa of the proventriculus as fourth-stage larvae which were about to shed their cuticles for the last time, or as immature adults with as yet no noticeable sexual differentiation. After 14 days the immature females (fig. 2, *B*) were in the glands of the stomach and displayed primary and secondary sexual characteristics, the most noticeable being expansion of the body and the presence of ovarian and uterine coils confined to the intestinal region; these developments were accompanied by the appearance of the four longitudinal, cuticular bands which later constricted the body. The males (fig. 2, *A*) were at this time still on the surface of the mucosa and as yet showed no adult characters. After 16 days no nematodes were found on the surface, even by gentle scraping of the mucosa, but some were expelled upon squeezing of the glands, the males often appearing simultaneously with the females; the males then showed their adult characters, namely, fully developed spicules and spines (fig. 3), the latter along the entire length of the body. At the end of 19 days and also at the end of 25 days a few males were collected from the surface of the mucosa, but most of them were more deeply embedded. The males had attained their maximum size at that time. The female body had expanded considerably, but its total length had decreased with the expansion in width; the intestine had become saclike, and the coils of the ovaries and uteri had increased but as yet contained no eggs. Both males and females showed evidence at that stage of having fed on blood, the heads of the worms and the contents of their digestive tracts being stained with blood. Small, petechial hemorrhages were to be seen in the glands where worms were situated, and the wall had become greatly thickened and congested.

There is evidence that this period of invasion of the stomach wall is the period that most seriously affects the health of the chicks, as it was then that the largest number of deaths occurred, and in nonfatal cases that the most severe clinical symptoms, emaciation and droopiness, were noted. That the diet may play an important part in the chicks' resistance at this stage is indicated by the fact that of a group of four infected chicks which were being fed a vitamin-deficient diet, that is, one in which no yeast or cod-liver oil was present, all four died, on the eleventh, thirteenth, fourteenth, and twenty-fifth day, respectively, whereas of a comparable group of four infected chicks on a vitamin-sufficient diet, none died. Control chicks on the vitamin-deficient diet survived the period of experimentation, so that the conclusion is justified that the severity of the parasitic infestation was correlated with the vitamin content of the diet. More extensive experimentation along this line is highly desirable, being of considerable practical importance.

By the twenty-ninth day practically all the males had returned to the surface, only an occasional one being found in the glands. At this period the females for the first time showed the bright-red color of the body; the saclike intestine was seen within the body, appearing very black in color, since the uterine coils were not yet sufficiently opaque to obscure it.

At the end of 35 days the females were gravid, but the eggs were not yet embryonated; after 45 days the eggs were embryonated, and development was complete, except that the maximum size had not yet been attained. At 2 months the size was approximately the same as at 45 days, but at 3 months it had increased to the maximum.

These observations as to the location of the male specimens of *T. americana* differ from the descriptions of the behavior of *T. fissispina* in this respect: In the latter species the mating of male and female is said to occur on the surface of the mucosa, the females then entering the canals of the glands of Lieberkuehn and the males remaining in the lumen of the stomach. In the American species, on the other hand, it is evident that the female sex characters appear at an earlier date than those of the male. The female enters the gland before the male becomes adult. The male follows later and, after the period of mating has passed, again returns to the surface of the mucosa.

Table 2 summarizes the rate of development of *T. americana*, as shown in the measurements made at different stages in its development.

TABLE 2.—*Measurements of Tetrameres americana at various stages in its development*

Part measured	In grasshopper at 42 days—third stage	In chicken at— 11 days	14 days ♀	14 days ♂	19 days ♀	19 days ♂
Body length	1.8 to 1.9 mm	2.6 mm	3.0 mm	2.8 mm	3.0 mm	3.8 mm.
Body width	56 to 64μ	72μ	320μ	88μ	546μ.	96μ.
Tail length	170 to 185μ	288μ	248μ.	256μ	280μ	256μ.
Vulva from tail end			456μ.		440μ.	
Spicules				None		312μ and 112μ.
Eggs					Present without shells.	

Part measured	In chicken at— 25 days ♀	25 days ♂	35 days ♀	45 days ♀	90 days ♀
Body length	2.8 mm	5.2 mm	3.7 mm	3.5 to 4.2 mm	4 mm.
Body width	1.1 mm	112μ	1.6 mm	2 mm	3 mm.
Tail length	268μ	288μ	234μ.	256μ	312μ.
Vulva from tail end	368μ.		546μ	600μ.	620μ.
Spicules		312μ and 112μ.			
Eggs	With shells but not embryonated.		48 by 24μ; not embryonated.	48 to 56μ by 28 to 32μ; embryonated.	Same.

CHEILOSPIRURA HAMULOSA (DIESING, 1851) DIESING, 1861 (8)

Synonyms: *Spiroptera hamulosa* Diesing, 1851 (7); *Dispharagus hamulosus* (Diesing, 1851) Stossich, 1890 (13); *Spiroptera perforans* Centoscudi, 1911 (4); *Acuaria hamulosa* (Diesing, 1851) Railliet, 1911 (12)

Cheilospirura hamulosa is cosmopolitan in distribution, occurring most frequently in the chicken but being known also in the turkey. The nematode is found in the gizzard, associated with small, fleshy growths on the surface of the muscular wall, under the corneous lining, or in burrows in the wall. There is an opening leading to the inner surface of the gizzard for the passage of the eggs of the parasite; these openings are often circumscribed by a rough, brown-colored area on the inner surface of the corneous lining.

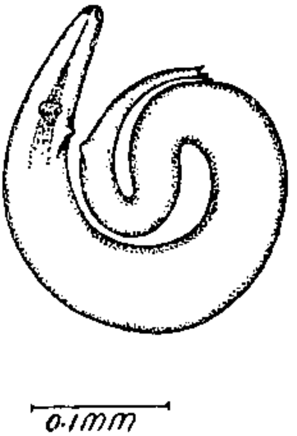

FIGURE 4. *Cheilospirura hamulosa*. Third-stage larva from grasshopper

In the United States *C. hamulosa* is widespread in distribution and in some localities is the cause of numerous fatalities in infected flocks.

DEVELOPMENT IN INTERMEDIATE HOST

Attempts to produce infections in cockroaches, sow bugs, ground beetles, and crickets were unsuccessful; however, as the result of similar feeding experiments, two species of grasshoppers, *Melanoplus femurrubrum* and *M. differentialis*, were found to be capable of serving as intermediate hosts of *C. hamulosa.* The larvae which hatch from the eggs migrate into the body cavity of the grasshopper and develop among the tissues, chiefly in the muscles, to the third stage, which is infective for the bird host. At this stage the nematode is tightly coiled upon itself, and the tissues form a thin-walled cyst around it. The larvae uncoil very slowly when the tissues are dissected in a small quantity of water, and they seldom become more outstretched than the position shown in Figure 4. The coiled form and relative inactivity of these larvae make them strikingly different from the corresponding larvae of *Tetrameres americana*, when the two species of nematodes occur in the same grasshopper. As noted previously, the larvae of *T. americana* quickly uncoil and become very active in water.

The third-stage larva of *C. hamulosa* is 700μ in length by 44μ to 50μ wide. A striking characteristic of this larva, as also that of *C. spinosa* (p. 14) and, therefore, possibly a generic character, is the reversal of the curve of the body which is made by the tail. (Fig. 4.) The head end (fig. 5, A) is rounded but has two prominent lips and four conspicuous submedian papillae. There is no evidence of cordons such as are seen in the adult. The anus is 96μ from the end of the body. The tail end of this larval form of *C. hamulosa* bears four comparatively long digitate papillae (fig. 5, B); one, on the dorsal surface, is larger than the others. The two lateral papillae and the ventral papilla are approximately the same size. On the dorsal surface, at the base of the papillae, the cuticle projects slightly, as a collar. A comparison of these tail structures of the larva of *C. hamu-*

losa with those of *C. spinosa* (fig. 12, B) shows them to be similar in number and in general arrangement but slightly different in shape and considerably different in size; *C. hamulosa*, which is the smaller larva, has the larger caudal papillae.

DEVELOPMENT IN FINAL HOST

As a result of feeding third-stage larvae of *C. hamulosa* dissected from grasshoppers, the remaining stages of the life cycle of the nematode have been obtained experimentally in the final host. The larvae were found to be infective for chickens as early as 22 days and as late as 67 days after the ingestion of the nematode eggs by the grasshoppers. The results of the experiments were as follows:

Young chickens: Positive results, 16 cases; negative results, 15 cases; controls (all negative), 198. Negative results were also obtained when feedings were given to a chicken, a pigeon, a ruffed grouse, a bobwhite quail, and a turkey, all these birds being adult.

In the 16 cases in which chickens were infected experimentally with *C. hamulosa*, the nematodes were collected from the gizzards of the fowls at varying periods, ranging from 11 days to 9½ months; in 7 of the cases the nematodes were adult when collected, whereas in the other 9 cases immature specimens were obtained. Observations made in this way as to the rate and location of development include the following:

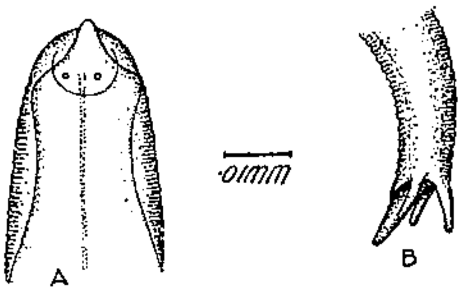

FIGURE 5.—*Cheilospirura hamulosa*: A, head end; B, tail end of third-stage larva

C. hamulosa larvae collected 11 days after the feeding of the chicken from the underside of the corneous lining of the gizzard, possessed the head and tail characters of third-stage larvae, but had attained a length of 1.2 millimeters and a width of 64μ. Sixteen days after the feeding of the chicken, however, larvae collected from this site showed characteristics of immature adults. Sexual differentiation was apparent in that the nematodes were of two sizes; the larger ones clearly showed the primordia of the vulva and ovejector. The cordons were conspicuous in the submedian fields of the cuticle, and the head structures resembled those of the adult. Measurements made of the nematodes at this time were as follows: Male, 2 millimeters long by 72μ wide; anus 200μ from tail end; cordons extending posteriorly from the head end for a distance of 340μ. Female, 2.5 millimeters long by 72μ wide; a primordium of vulva somewhat posterior to middle of body, dividing body length in ratio of 9 to 7; anus 190μ from tail end; cordons strongly developed for a distance of 288μ and discernible for an additional 360μ, from the head end. At the end of 19 days the males were 3 millimeters long, with cordons developed for a distance of 780μ from the head end; the females were 3.8 millimeters long, with cordons 1.2 millimeters long. Throughout this period of development the nematodes remained on the surface of the muscular wall of the gizzard, under the corneous lining; at the end of 25 days, however, they were found to be penetrating the muscular wall, the head end being inserted. Males and females did not enter the wall through the same opening, but one of each sex was often found in close proximity to the other. Measurements made at this time were approximately the same as those made at 19 days: Male, 2.7 to 3 millimeters long by 100μ wide; cordons well developed for a distance of 800μ; cloacal aperture about 218μ from posterior end; spicules and caudal papillae faintly discernible but not well developed. Female, 3.8 millimeters long by 125μ wide; cordons well developed for a distance of 1.4 millimeters; vulva dividing body length in ratio of 3 to 2; anus 225μ from posterior end.

Between the twenty-fifth day and the time when the nematodes became mature, at about 76 days, they were extremely difficult to locate. They had disappeared from the surface of the gizzard but had not yet made any observable tunnels, apparently having penetrated deeper and deeper into the tissue, between the muscle fibers. Females 6.2 millimeters long by 188μ wide were collected at the end of 29 days; the eggs were beginning to form in the ovaries at that time but were still very elementary. The vulva divided the body length in the ratio of 5 to 3; cordons were discernible to a point somewhat posterior to the vulva. Males collected at the end of 61 days were 4.7 millimeters long by 188μ wide; the cordons were discernible to within 880μ of the posterior end of the body; the spicules were well formed, the long, slender spicule, 1.25 millimeters in length, being just six times the length of the short, stout spicule, which measured 208μ. Caudal papillae were well developed. At the end of 76 days both males and females were collected; the tissue reaction was noticeable at that time, a small nodule having formed around the parasites. The males at that time measure 13 millimeters long; the longer spicule is 1.5 millimeters, the shorter spicule 220μ in length; the females are from 15 to 17 millimeters long and embryonated eggs are present in the uteri. Development appears to be complete at this time except for the fact that female specimens collected at later periods, namely, at 8, 8⅔, and 9½ months, exceeded 17 millimeters in length, attaining a maximum size of 22 millimeters.

It is thought probable that the mortality rate is high among the immature specimens of *C. hamulosa* during the period of invasion of the thick, muscular wall of the gizzard. It was found that a comparatively large number of larvae must be ingested by the chicken, in these experimental feedings, in order to obtain an infection. Several of the unsuccessful attempts reported above as negative findings were cases in which only from three to six larvae were fed to the fowl. Others of the negative findings probably do not represent actual noninfection of the chicken but merely failure to locate the larvae during the period when they were buried in the wall and were still so small that they were found only after prolonged microscopical search, if at all. Aside from such considerations, however, the fact that early examinations, that is, up to 25 days after the initial infection, gave positive findings in practically 100 per cent of the experimental feedings, and on the other hand that about one-third of the total negative findings were at a period of two and one-half to four and one-half months after the feeding and thus at a time when the worms would have been fully grown if present, indicates that a certain proportion of the invading nematodes never develop to maturity. It is possible that the general state of health of the fowl may be a factor in determining whether the nematodes successfully accomplish this invasion.

As regards the site of invasion, the larvae of *C. hamulosa* appeared to burrow under the corneous lining of the gizzard at its anterior end, near its junction with the proventriculus where the tissues are softest. They were found in that area in the early stages, that is, at 11 days. Later, however, they were well distributed over the surface of the muscular wall of the gizzard and were found at 25 days penetrating the musculi laterali as well as the musculi intermedii. On the other hand, in the experimentally produced infections, the final location of adults, with accompanying tissue damage, was always in the musculi intermedii, in the comparatively soft, thin area on the side of the gizzard opposite the openings of the stomach and intestine.

Table 3 summarizes the rate of development of *C. hamulosa*, the measurements having been made at various stages, as indicated.

TABLE 3.—*Measurements of Cheilospirura hamulosa at various stages in its development*

Part measured	In grasshopper 22 days and later	In chicken at—				
		11 days	16 days		25 days	
			♀	♂	♀	♂
Body length	700μ	1.2 mm	2.5 mm	2 mm	3.8 mm	2.7 to 3 mm.
Body width	40μ to 44μ	64μ	72μ	72μ	125μ	100μ.
Length of cordons			648μ	340μ	1.4 mm	800μ.
Tail length	96μ	144μ	190μ	200μ	225μ	218μ.

Part measured	In chicken at—			
	29 days	61 days	76 days and later	
	♀	♂	♀	♂
Body length	6.2 mm	4.7 mm	15 to 22 mm	9 to 13 mm.
Body width	188μ	188μ	400μ to 625μ	300μ to 320μ.
Length of cordons	4.2 mm	3.8 mm	10 to 15 mm	7.2 to 8.8 mm.
Tail length	240μ	336μ	420μ to 590μ	410μ to 488μ.

DESCRIPTION OF ADULT PARASITE

The descriptions of *C. hamulosa* given in the literature have been lacking in certain important respects. Von Drasche (*9*) furnished good descriptions and illustrations of the head (fig. 6, B) and of the

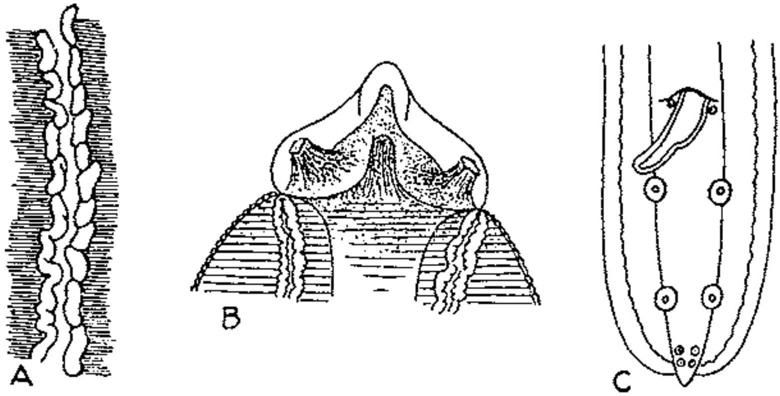

FIGURE 6.—*Cheilospirura hamulosa:* A, Cordon; B, head; C, male tail. After von Drasche, 1884

cuticular cordons (fig. 6, A). The cordons are one of the most important differential characters of this species; the double row of irregularly placed plaques extending posteriorly from the head end for at least two-thirds the length of the body furnish an easily recognizable specific character. Von Drasche explains, however, that on account of the poor condition of the specimens available to him his description of the male tail, especially as regards the preanal papillae, is incomplete. He describes four pairs of postanal papillae, two of which are small and near the tail end, and two other pairs very large and separated from each other by a considerable distance; he pictures (fig. 6, C) an additional small pair just posterior to the cloacal aperture.

FIGURE 7.—Male tail of *Cheilospirura hamulosa*. After Centoscudi, 1911

Centoscudi (*4*) added to these observations made on the male tail, in his description of *Spiroptera perforans*, which species Railliet (*12*) in a critical review of Centoscudi's paper showed to be synonymous with the species, *C. hamulosa*, under discussion here. Centoscudi describes the tail as having two large papillae near its posterior end and eight additional pairs, four of which are preanal and four postanal. His drawing of the tail is shown in Figure 7.

The tail of the male specimens of *C. hamulosa* is tightly coiled; this fact and the density of the underlying structures in the region of the cloacal aperture and immediately anterior to it make discernment of the caudal papillae very difficult. The writer was able to straighten out the tail ends of eight male specimens and by slight staining with gentian violet and subsequent clearing of the specimens in ethylene glycol was able to bring the papillae into sharp relief. Observations made on these specimens, which were from 9 to 13 millimeters in total length, include the following:

Cloacal aperture situated at a point 416μ to 488μ from the tail end, surrounded by an annular projection, refractive to light, chitinous in appearance. Short, thick spicule (fig. 8), in the shape of a chopping knife, 200μ to 220μ long by 64μ wide as viewed from the dorsal surface. Long, slender spicule 1.6 to 1.8 millimeters in length by 12μ in width. Ten pairs of caudal papillae (fig. 9), of which four small pairs are preanal and six pairs postanal. Of the postanal papillae, three pairs occupy the space which makes up the first third of the length posterior to the cloacal aperture; each pair of the papillae of this group becomes progressively somewhat larger in size than the pair anterior to it. A considerable distance separates this group from the remaining three pairs, which occupy the posterior one-half of the tail length. The middle pair of this posterior group is always the smallest. The arrangement of the six papillae which make up these three pairs varies considerably in different specimens, often being asymmetrical. (Fig. 10.)

FIGURE 8.—Short spicule of *Cheilospirura hamulosa*

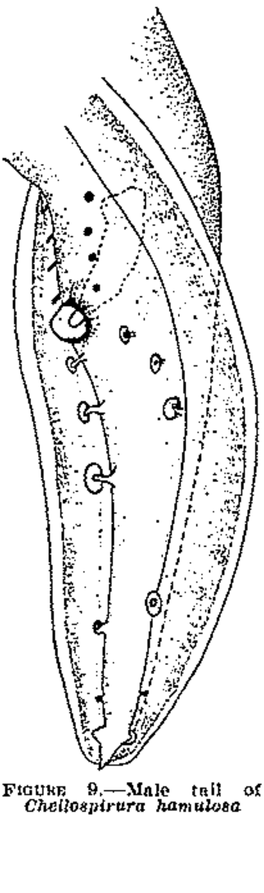

FIGURE 9.—Male tail of *Cheilospirura hamulosa*

In a full-grown female specimen of *C. hamulosa*, 22 millimeters in length, the vulva was located at a point 10 millimeters from the posterior end of the body and was thus slightly posterior to the middle of the body; the anus was about 590μ from the posterior end; eggs dissected from the uterus were 40μ long by 27μ wide.

CHEILOSPIRURA SPINOSA CRAM, 1927

Synonym: *Acuaria (Cheilospirura)* species Stafseth and Kotlán, 1925 (*17*)

This parasite was first reported from the ruffed grouse (*Bonasa umbellus*) of Michigan and was subsequently found in that bird in Minnesota, Wisconsin, New York, Massachusetts, New Jersey, and Pennsylvania (*1*). It has been collected from bobwhite quail (*Colinus virginianus*) of Tennessee and of Virginia, which localities are within the range of the ruffed grouse, but has never been found in quail in States farther south, although an extensive search has been made for it.[4] These findings suggest that the nematode was originally a parasite of the grouse and has spread from it to quail.

In ruffed grouse the percentage of infection was reported by Allen and Gross (*1*) as varying from 14 to 42 per cent in different States. As regards quail, Stoddard [4] found approximately 60 per cent infection of birds from Tennessee, and the writer found approximately 90 per cent infection among quail which were half grown or fully grown, originating from a small area in Virginia, the quail being captive birds of which the original stock had been obtained from the mountainous regions of that State.

C. spinosa is located in the gizzard of the bird host, on the under side of the corneous lining, producing tortuous paths between the lining and the muscular wall. When the nematodes are present in considerable numbers they may produce noticeable damage to the gizzard, as subsequently described.

DEVELOPMENT IN INTERMEDIATE HOST

In attempts to discover possible intermediate hosts of this nematode, feeding the worm's eggs to cockroaches, ground beetles, sow bugs, and crickets gave negative results, whereas in two species of grasshoppers (*Melanoplus femurrubrum* and *M. differentialis*) infestations were successfully produced. Nematodes from quail were first used and the experiments repeated later with nematodes from grouse, with the same results. The larvae which hatched from the nematode eggs migrated from the digestive tracts into the tissues of the grasshopper, chiefly into the muscles of the legs and of the inner surface of the body wall. At the end of 25 days they were loosely encysted and had developed into third-stage larvae, the stage which is infective for the bird host. The larvae uncoiled slowly when the tissues were dissected in water. These third-stage larvae are 850μ long by 40μ wide; the posterior end of the body is bent sharply backward, reversing the curve made by the anterior part of the body (fig. 11), a trait seen also in the third-stage larvae of *C. hamulosa*. (Fig. 4.) The tail end bears four digitiform papillae, three of which, occupying the ventral field, are smaller than the fourth, which is situated in the dorsal field. At the base of this dorsal papilla the cuticle forms a collar with projects slightly as seen in lateral view. (Fig. 12, B.) These tail structures are similar in number and in form to those of *C. hamulosa* (fig. 5, B), but smaller in *C. spinosa* than in *C. hamulosa*. The head end of the larva of *C. spinosa* is provided with two large, lateral lips; at their base the cuticle forms

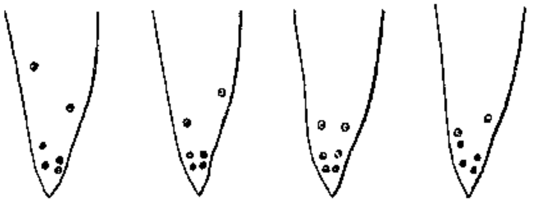

FIGURE 10.—Diagram of variations in arrangement of most posterior group of caudal papillae of *Cheilospirura hamulosa*

[4] H. L. Stoddard examined over 400 quail from the Southeastern States; a report of this study is now in press.

a distinct collar, which projects anteriorly in the dorsal and ventral fields. (Figs. 11 and 12, A.)

DEVELOPMENT IN FINAL HOST

As a result of feeding the third-stage larvae of *C. spinosa* dissected from grasshoppers, the remainder of the life cycle has been artificially produced in the final hosts as follows:

Bobwhite quail: Positive results, 10 cases; negative results, 0 case; controls (all negative), 13. Ruffed grouse: Positive results, 1 case; negative results, 0 case; controls (all negative), 5. In addition, five attempts were made to infect young chickens, all with negative results.

Cross transmission of the parasite from ruffed grouse to quail was accomplished, seven of the experimental infections of quail, as well as that of the ruffed grouse, being produced with larvae which had been developed from material originating from the grouse; in the remaining case of experimental infection of quail the original material was derived from the quail.

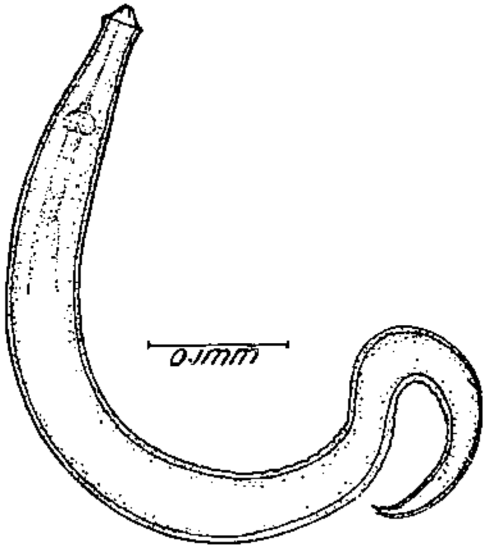

FIGURE 11.—Third-stage larva of *Cheilospirura spinosa* from grasshopper

Observations made in the course of the development of *C. spinosa* in quail include the following: Fourteen days after the feeding of third-stage larvae, the parasites were found underneath the corneous lining of the gizzard as fourth-stage larvae or immature adults. Sexual differentiation was apparent at this time; the larger nematodes, 4.5 mm. long by 120μ wide, displayed a rudimentary vulva and the primordia of the uteri at approximately the middle of the body length. The cordons could be seen extending posteriorly for a distance of 187μ from the head end; the tail was 218μ long. The smaller specimens, apparently males, had not developed sexual characteristics to the extent seen in the females; spicules, caudal alae, and caudal papillae were still lacking. These specimens were 8 millimeters long and 88μ wide; cordons extended for a distance of 125μ from the head end; the tail was 224μ long; primordia of the testes were apparent.

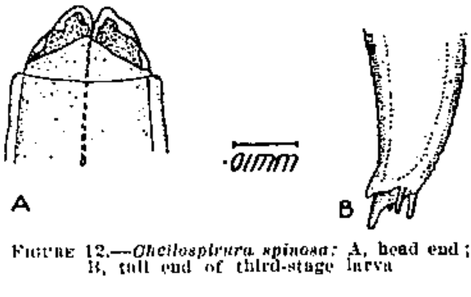

FIGURE 12.—*Cheilospirura spinosa*: A, head end; B, tail end of third-stage larva

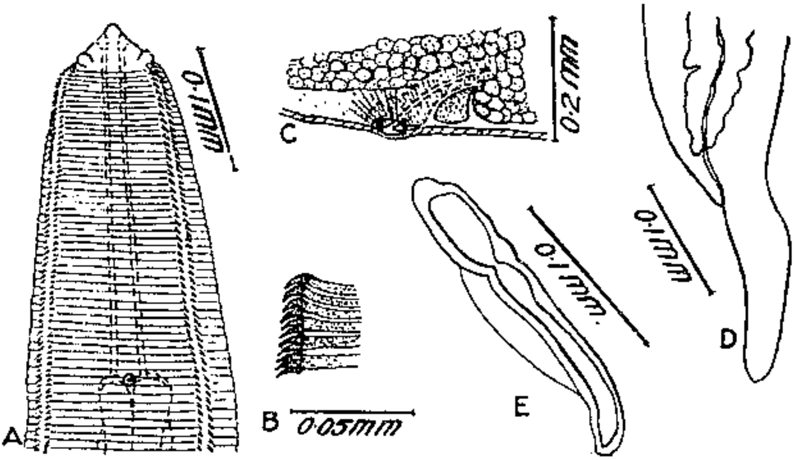

FIGURE 13.—*Cheilospirura spinosa:* A, head end; B, elements of cordon; C, vulva; D, female tail; E, spicule

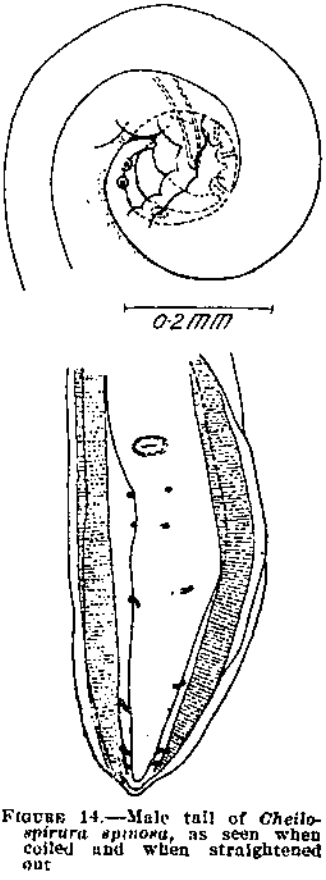

FIGURE 14.—Male tail of *Cheilospirura spinosa*, as seen when coiled and when straightened out

Thirty-two days after the experimental feeding of the bird host, the nematodes had fully developed sexual characteristics; eggs were present in the uteri, but in small numbers and were not yet embryonated. Neither males nor females had reached their full size, however, the males being 8 millimeters long and the females 18 millimeters long at that time. At the end of 45 days, embryonated eggs were being deposited by the females, and the development of both sexes appeared to be complete. The females at that time were 35 millimeters, the males about 12 millimeters long. In ruffed grouse the nematodes attained a greater size, the males being up to 20 millimeters, the females up to 40 millimeters long. The adult characteristics are shown in Figures 13 and 14.

In cases of heavy infestation, both as found in nature and as artificially produced, the gizzard lining may be hemorrhagic and necrotic and the wall flabby (figs. 15 and 16); marked proliferative changes were noted in the gizzard wall in one of the quail, associated with a heavy infection of 84 days' duration. (Fig. 17.)

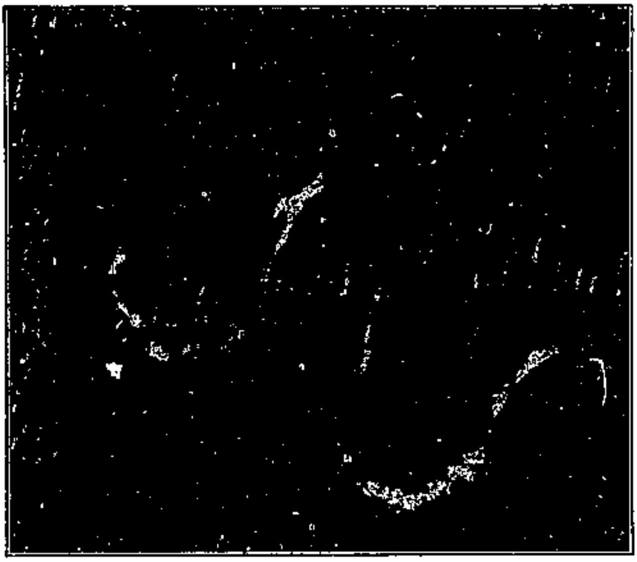

FIGURE 15.—Upper surface of corneous lining of gizzard, showing hemorrhagic necrosis. *Cheilospirura spinosa* protruding from underside. Experimental infection of ruffed grouse

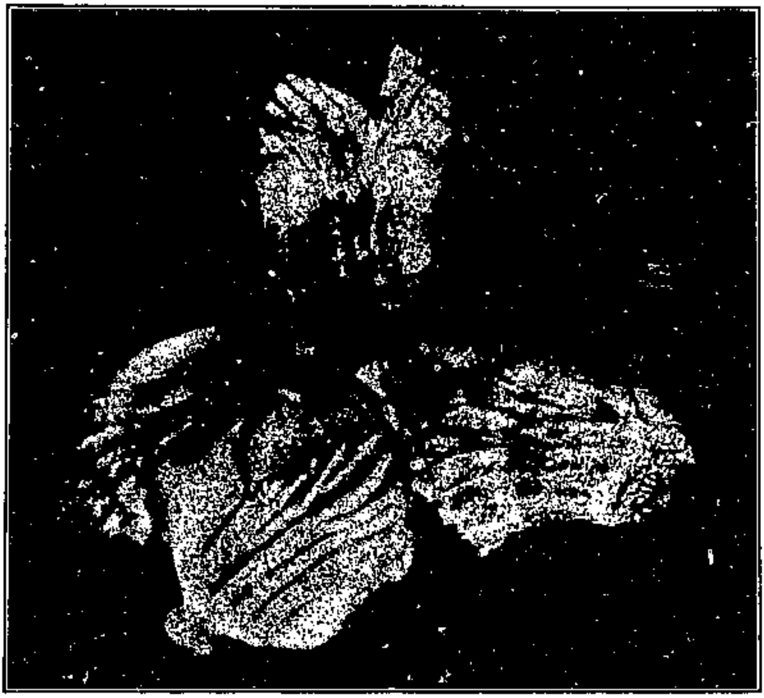

FIGURE 16.—Undersurface of corneous lining of gizzard, and exposed muscular wall, showing *Cheilospirura spinosa* and damage produced by them. Experimental infection of ruffed grouse. Actual size

DISPHARYNX SPIRALIS (MOLIN, 1858) SKRJABIN, 1916 (*16*)

Synonyms: *Dispharagus spiralis* Molin, 1858; *D. nasutus* of Piana, 1897 (*11*); *D. spiralis columbae* Bridré, 1910 (*3*); *Acuaria spiralis* (Molin, 1858) Railliet, Henry, and Sisoff, 1912 (*13*)

The adult forms of these spirurids are short and comparatively thick, white worms, with the body curved or rolled in a spiral.

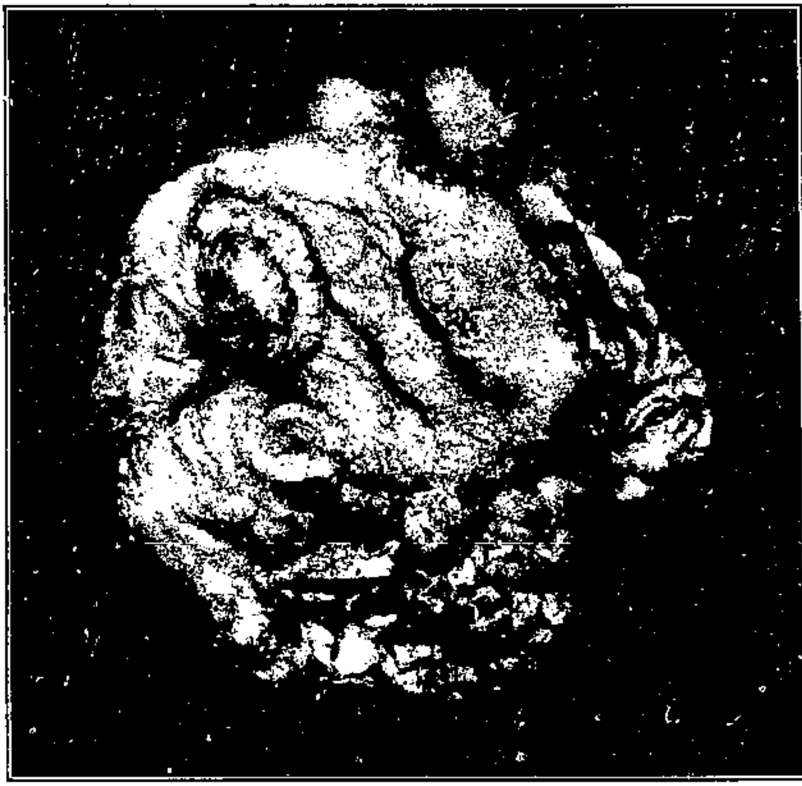

FIGURE 17.—Proliferative changes in gizzard wall of experimentally infected quail, 84 days after infection with *Cheilospirura spinosa*. (Nematodes not to be seen as they were attached to the underside of the corneous lining, which has been removed.) Two times actual size

(Figs. 18 and 19.) Their usual location is the glandular stomach or proventriculus, where their heads may be deeply buried in the wall. The characteristics of the head end of *D. spiralis* may be seen in Figure 20, and those of the male tail in Figure 21.

This parasite is not of common occurrence in the United States, but its distribution covers a wide territory and a wide range of domestic and game birds. It has been collected from the Hungarian partridge (*Perdix perdix*) in Wisconsin, the ruffed grouse in Wisconsin and in the New England States, the bobwhite quail in New Jersey, the turkey in Maryland, the chicken in Louisiana, the pigeon in Texas, and the guinea fowl in Porto Rico. The parasite is potentially, and in many cases actually, highly pathogenic; in the case of pigeons the parasitic disease may result in high mortality among domestic birds, and in the case of ruffed grouse it has been considered the probable cause of deaths of birds in the wild.

DEVELOPMENT IN INTERMEDIATE HOST

In the search for possible intermediate hosts of *D. spiralis* in the United States, cultures of eggs of the nematodes collected from

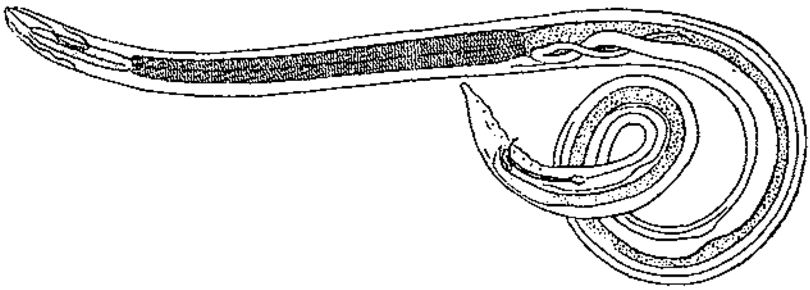

FIGURE 18. Male of *Dispharynx spiralis*. After Piana, 1897

ruffed grouse were fed to snails, slugs, earthworms, millipeds, grasshoppers, leaf hoppers, crickets, cockroaches, ground beetles, beetle larvae, and isopods (sow bugs). All the results were negative except in the case of the isopods, in two species of which, *Porcellio scaber* and *Armadillidium vulgare*, the eggs hatched, and the larvae continued their development. After four days the larvae were found among the tissues of the body cavity of the isopod, distributed throughout the whole body length. They were outstretched, not coiled, and only very slightly active when removed in a small quantity of water; they were from 176μ to 192μ long by 12μ to 14μ wide at that stage of their development. After 14 days in the isopod the larvae were seen to be about to shed their cuticle, the sheath protruding at both ends of the body, or in some cases to have already shed it, these latter larvae (second stage) being somewhat larger than those still retaining the sheath (first stage). The largest larvae were at that time from 1 to 1.2 millimeters in length by 50μ to 56μ in width; this width being comparatively great, they presented a stocky appearance, which was accentuated by the fact that the head end was very bluntly rounded. There were no lips at the mouth; the total length of the esophagus (including the pharynx) was 300μ to 330μ; the excretory pore was prominent in live specimens, being situated about 85μ to 90μ from the head end. The tail was short, tapering very little but with a small point at the end. The larvae were very inactive at that stage, merely giving little jerky movements, chiefly with the anterior part of the body.

FIGURE 19.—Female of *Dispharynx spiralis*. After Piana, 1897

Development of the larvae in the intermediate host was completed within 26 days; that is, the larvae reached the infective third stage. There is no evidence that these larvae were encysted or even coiled, as is often the case with third-stage spirurid larvae, in the tissues of the arthropod host; they emerged from the tissues very quickly when the isopod was partially dissected in a small quantity of water. This third-stage larva is from 2.9 to 3.2 millimeters in length by 65μ to 85μ in maximum width. The head end tapers little or not at all, having a blunt appearance; there are two small, pointed lips and four submedian papillae. (Fig. 22, A.) There is no evidence of cordons such as are present in the adult form of the nematode. A slender, distinct pharynx, 60μ to 70μ long, is followed by a 2-part esophagus; the first part, the muscular portion, is 275μ to 320μ long; the second part, the glandular portion, is about 720μ long; the excretory pore is 175μ to 190μ from the head end. The tail is short (fig. 22, B), the anal aperture being 135μ to 145μ from the posterior end. The rectal glands are very conspicuous. The tail end is without spines or papillae, but the tip is rounded and slightly set off by a constriction from the region anterior to it.

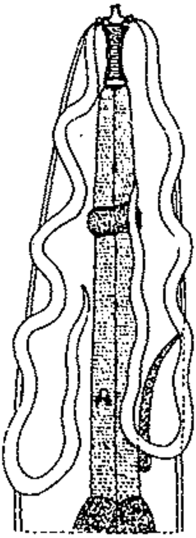

FIGURE 20.—Head end of *Dispharynx spiralis*. After Seurat, 1917

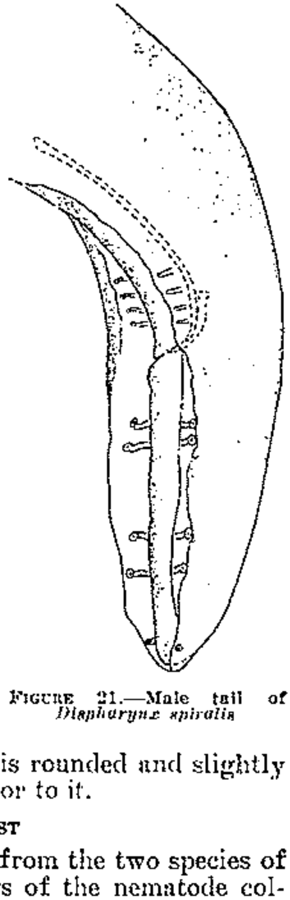

FIGURE 21.—Male tail of *Dispharynx spiralis*

DEVELOPMENT IN FINAL HOST

Third-stage larvae of *D. spiralis* recovered from the two species of isopods, the isopods having been fed on eggs of the nematode collected from the ruffed grouse, were fed to bird hosts, with the results shown in Table 4.

TABLE 4.—*Development of Dispharynx spiralis in various bird hosts*

Host	Positive results		Negative results	Controls (all negative)
	Birds infected after feeding	Nematodes developed per bird	Birds not infected after feeding	
	Number	*Number*	*Number*	*Number*
Ruffed grouse	1	[1] 10	0	5
Bobwhite quail	3	2–12	0	6
Pigeon	3	5– 9	0	2
Chicken	0	0	7	10

[1] Of these nematodes 5 were males and 5 females.

The nematodes were fully developed, the female worms being gravid and their eggs embryonated, 27 days after the ingestion of the larvae by the bird host. In all cases the adult nematodes were concentrated in one area of the proventriculus, and this area was thickened and ulcerated. The heads of the worms were found tightly buried in the wall and on being forcibly extracted were seen to be stained with blood. None of the birds showed serious clinical effects from the infection, possibly because of the small number of nematodes present in each case.

The explanation of the negative results in the case of the experimental feedings of chickens is not apparent. From 2 to 20 larvae were fed in these cases, the larvae originating from several different lots of isopods (all specimens of *Porcellio scaber*), and being fed to young chicks ranging in age from 6 to 29 days at the time of feeding. Specimens collected from the chicken in natural infestations were compared with those from the ruffed grouse, and no morphological differences of importance were to be seen. In these experiments, however, all the material originated from the ruffed grouse, and it is possible that a biological strain has become established in that host and other game birds, the game birds being new hosts, if one may judge by the fact that the records of collection of the parasites from them are all of recent date as compared with those of collections from domestic fowls, which are of many years' standing. The chicken may thus have become much more resistant to infection with this parasite than are game birds.

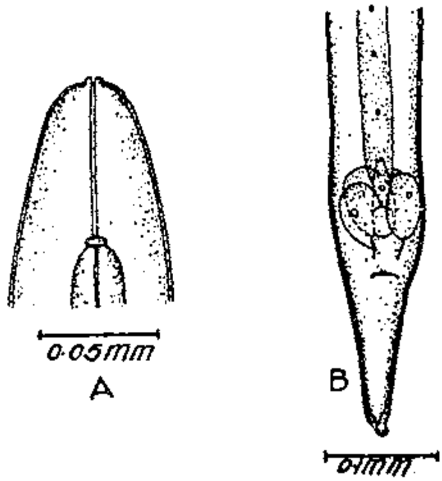

FIGURE 22.—Third-stage larva of *Dispharynx spiralis*: A, head; B, tail

SEUROCYRNEA COLINI (CRAM, 1927) CRAM, 1930

Synonym: *Cyrnea colini* Cram, 1927 (*5*). The genus Cyrnea Seurat, 1914 (*14*) has been changed to Seurocyrnea Strand, 1929 (*19*). Strand points out that the former name was preoccupied by Deshayes in 1858, the latter writer giving a misspelling for Cyrena of Lamark and this error invalidating the name Cyrnea for future use

Seurocyrnea colini is of common occurrence in bobwhite quail of the Southeastern States. It has also been collected from that host in New Jersey and from *Colinus virginianus texanus* in the Philadelphia Zoological Gardens; it occurs in the turkey (*Meleagris gallopavo*) of Georgia, in the prairie chicken (*Tympanuchus americanus*) of Wisconsin, and in the sharp-tailed grouse (*Pedioecetes phasianellus*) of Wisconsin and Montana. As yet it has not been reported from any country other than the United States.

The nematode is located in the wall of the proventriculus, at its junction with the gizzard; it burrows into the wall at this site, but no pathological condition has been found which was definitely attributable to its presence.

DEVELOPMENT IN INTERMEDIATE HOST

The writer undertook an investigation of the life history of *S. colini* as part of a study of the parasites of quail conducted by the cooperative quail investigation (report by H. L. Stoddard, now in press). The nematode is of frequent occurrence in Georgia and northern Florida, and attempts were made there to infect various ground beetles and dung beetles, with no success. The study was resumed at a later date in Washington, D. C., specimens of the parasite having been obtained from quail shipped from Mississippi. Grasshoppers and sow bugs gave negative results in feeding experiments, but in the case of cockroaches (*Blattella germanica*) experimental infections were successfully produced. This species of cockroach is the one commonly found around habitations, but it is probable that other cockroaches, such as occur in fields and woods, are the forms more commonly serving as hosts.

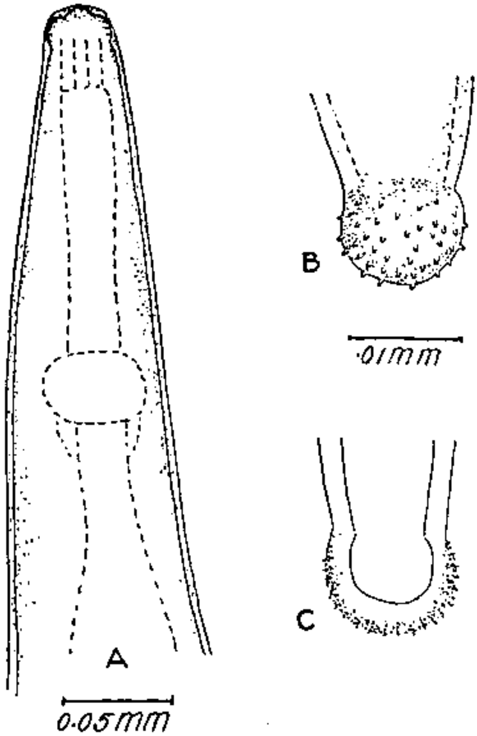

Figure 23.—Third-stage larva of *Seurocyrnea colini*: A, head; B, tail in surface view; C, tail in optical section

The larvae which hatch from the eggs of *S. colini* leave the digestive tract of the cockroach and develop in the body cavity. They do not appear to encyst but develop to third-stage larvae among the tissues, from which they quickly emerge when the cockroach is dissected. These larvae are the largest and the most active of all the third-stage spirurid larvae considered in this study. They can readily be seen with the naked eye, being 3.2 to 3.3 mm. long by approximately 100μ wide. The head end is bluntly rounded; it is without lips, but the structure underlying the cuticle suggests the primordia of lips. (Fig. 23, A.) The pharynx is 24μ deep; the first part of the esophagus 225μ, the second part 1.2 millimeters long. The anus is situated 90 to 95μ from the posterior end. The tail ends in a small, bulbous swelling which is covered with minute, refractive points. (Figs. 23, B and C.)

The larvae of *S. colini* are apparently fully developed at the end of 18 days in the cockroach, as they do not change in size or appearance between the eighteenth and the forty-fifth days; however, it is only at the end of a 45-day period that their infectivity for the final host has been tested, with the results given in Table 5.

DEVELOPMENT IN FINAL HOST

Third-stage larvae of *S. colini* were fed to the following birds with the results indicated in Table 5.

TABLE 5.—*Development of Seurocyrnea colini in various bird hosts*

Host	Killed after number of days shown below	Results	Controls (all negative)
			Number
Quail:			
No. 1	13	Positive; 12 specimens	9
No. 2	30	Negative	9
No. 3	41	Positive; 18 specimens	9
Chicken:			
No. 1	13	Positive; 4 specimens	10
No. 2	30	Negative	10
Turkey	30	do	0

The specimens collected from the quail and from the chicken at the end of 13 days were composed of fourth-stage larvae and immature adults. The former were 4.2 millimeters in length at that time; the head structures were not fully developed, and the bulbous swelling was still present on the tail. Of the immature adults which were also present, the males were 5.5 millimeters long; the caudal alae and the caudal papillae were well formed, there being 10 pairs of the latter, 9 pairs of which were situated laterally and 1 pair, just anterior to the cloacal aperture, situated slightly more ventrally. The females were 6.3 millimeters long; the location of the vulva was 520μ, and that of the anus 175μ, from the posterior end.

The specimens collected from the quail 41 days after the experimental feeding comprised 13 females and 5 males. When collected they were stained with blood pigment, especially in the case of the males; the pigment was most noticeable in the head region. The males were from 7 to 8 millimeters long by 175 to 200μ wide; the spicules were 2 millimeters and 384μ long, respectively. Development was apparently complete at that time; in a considerable number of specimens collected from natural infestations the males were 6 to 10 millimeters long, with the spicules 2 millimeters and 365 to 400μ long, respectively. The females, at the end of the 41-day period, were from 13 to 15 millimeters long; the eggs in the uteri were embryonated and were shown to be infective by experimental feeding to cockroaches, with subsequent development of third-stage larvae in that host. It is probable that the females increase somewhat in size after the forty-first day, as specimens collected in natural infestations had a maximum length of 18 millimeters. The anus in adult female specimens was 260 to 332μ from the tail end, and the vulva was 760 to 960μ anterior to the anus. (Fig. 25, B and C.)

The head structures of adult specimens of *S. colini* are very distinctive. (Fig. 24.) There are four lips, of which those situated dorsally and ventrally are deeply divided into two parts, in such a manner that in lateral view the head appears to bear four conspicuous papillae. Each of the four parts of these lips bears on its outer edge a prominent thumblike extension. The lateral lips are very large; each bears two digitiform processes on its inner surface and two lateral winglike expansions which project into the median groove of the dorsal and ventral lips in such a manner as to give the appearance in some views of being processes from the latter lips.

The male tail (fig. 25, A) is also distinctive, the caudal alae being short and wide, with coarse, transverse striations. The number and position of the caudal papillae vary slightly. Nine or ten pairs may be present, or occasionally 9 papillae on one side and 10 papillae on the other side; they are usually arranged in two practically straight rows, but in some specimens one pair, or occasionally an unpaired papilla, is situated more ventrally and just anterior to the cloacal aperture.

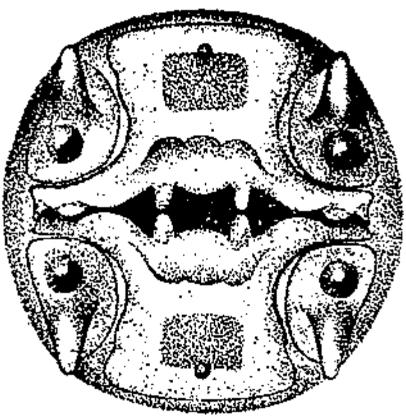

FIGURE 24.—Head of *Seurocyrnea colini*: en face view; semidiagrammatic

The experimental infection of a chicken here described constitutes the first record of the collection of *S. colini* from that host. The chicken was only 2 days old when fed.

That the three negative results, namely, those in a quail, chicken, and turkey, were all cases in which the observations were made 30 days after the feeding, whereas the three positive results, namely, those in two quail and a chicken, were observations made at 13 days in two cases and at 41 days in one case, probably represents merely a coincidence. But the possibility is suggested that at 30 days the nematodes are not in the same location as at an earlier and again at a later date, and that this fact may account for their not being found in those cases. Additional experiments are desirable in order to make further observations at the 30-day period.

SUMMARY

The present study furnishes information concerning the life histories of six nematodes of the superfamily Spiruroidea, occurring in birds; three families, namely, the Spiruridae, Acuariidae, and Tetrameridae, are represented. In one case, involving a member of the Spiruridae, *Gongylonema ingluvicola*, the adult nematodes were developed experimentally in a chicken and a rabbit from larvae found in natural infestations in the dung beetles *Phanaeus vindex* and *Copris minutus*. In the other cases the entire life cycle was artificially produced. For a second member of the Spiruridae, *Seurocyrnea colini*, the cockroach (*Blattella germanica*) was found capable of serving as intermediate host. Of the Acuariidae, two species of

Cheilospirura, *C. hamulosa* and *C. spinosa*, were developed in grasshoppers (*Melanoplus femurrubrum* and *M. differentialis*) as intermediate hosts, and a species of Dispharynx, *D. spiralis*, was developed in isopods (*Porcellio scaber* and *Armadillidium vulgare*). Of the Tetrameridae, *Tetrameres americana* was developed in grasshoppers (*Melanoplus femurrubrum* and *M. differentialis*).

Experimental development of the adult spirurids was accomplished in the following bird hosts: *Tetrameres americana* in the chicken (*Gallus gallus*), domestic duck (*Anas platyrhyncha domestica*), domestic pigeon (*Columba livia domestica*), bobwhite quail (*Colinus virginianus*), and ruffed grouse (*Bonasa umbellus*); *Cheilospirura hamulosa* in the chicken; *C. spinosa* in bobwhite quail and ruffed grouse; *Dispharynx spiralis* in bobwhite quail, ruffed grouse, and the domestic pigeon; and *Seurocyrnea colini* in bobwhite quail and, as immature specimens, in the chicken.

Differential characteristics of the third-stage larvae of the five species of spirurids developed experimentally in the arthropods include size, activity, and encystment. The size of the larvae varies

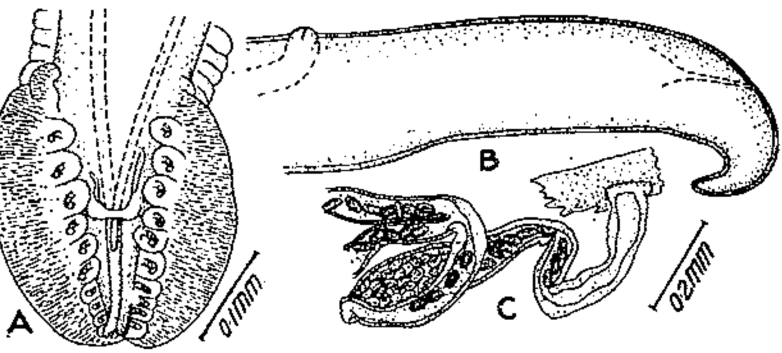

FIGURE 25.—*Seurocyrnea colini*: A, male tail; B, female tail; C, ovejector

greatly, the length being in the case of *Cheilospirura hamulosa* 700μ, in the case of *C. spinosa* 850μ, in the case of *Tetrameres americana* 1.8 to 1.9 mm., in the case of *Dispharynx spiralis* 2.9 to 3.2 mm., and in the case of *Seurocyrnea colini* 3.2 to 3.3 mm. The larger the larvae, the greater the activity shown by them when the intermediate host is dissected; those of *D. spiralis* and *S. colini* are outstretched and emerge from the tissues quickly, crawling and swimming with great agility; those of *T. americana* are coiled rather tightly but soon uncoil and become fairly active; those of *C. hamulosa* and *C. spinosa* on the other hand are tightly coiled and comparatively inactive for a considerable period and seldom become completely outstretched under such conditions. The three smallest larvae, those of *C. hamulosa*, *C. spinosa*, and *T. americana*, all of which are in grasshoppers, are contained in thin-walled cysts, but the larger larvae, those of *D. spiralis* in isopods and those of *S. colini* in cockroaches, appear to be unencysted in the tissues of those hosts.

As regards the length of time for development in the intermediate host, the following observations were made: The infectivity of the larvae for the final host was demonstrated as early as 22 days after artificial infection of the arthropod with *C. hamulosa*, 25 days after infection with *C. spinosa*, and 26 days after infection with *D. spiralis*. With *S. colini* infectivity was demonstrated only at the end of 45 days, but the larvae appeared morphologically as fully developed on the eighteenth day as on the forty-fifth day. The infectivity of *T. americana* was demonstrated after a 42-day period, but it is thought probable that a shorter period would suffice.

With reference to the length of the period of development in the final host, before maturity is reached, *D. spiralis* matured in 27 days, *S. colini* in 41 days, *T. americana* in 45 days, *C. spinosa* in 45 days, and *C. hamulosa* in 76 days. The length of this period of development appears to be correlated with the degree to which the nematodes penetrate the tissues of the final host and, when deep penetration occurs, to be correlated also with the density of the tissue. *D. spiralis* does not penetrate, except for the head end of the worm, which is buried in the mucosa of the proventriculus; the penetration of *S. colini* is shallow and the tissue soft, at the junction of the proventriculus and gizzard; the penetration of *T. americana* is deep but appears to take place through the canals of the glands of Lieberkuehn and to be therefore comparatively easy; that of *C. spinosa* is shallow but through dense tissue, namely, the corneous layer of the gizzard; and finally, the penetration of *C. hamulosa* is both deep and through very dense tissue, that of the muscular wall of the gizzard.

The greatest damage to the final host was observed during the period of invasion of the wall of the digestive tract by the nematodes: clinical effects were most severe and the mortality highest at that stage.

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