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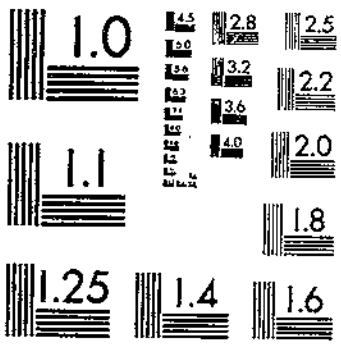

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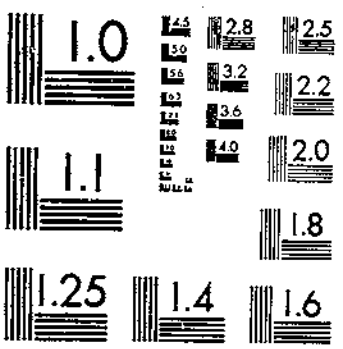

MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS-1963-A

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SPECIES OF CAPILLARIA PARASITIC IN THE UPPER DIGESTIVE TRACT OF BIRDS

By ELOISE B. CRAM

Zoologist, Zoological Division, Bureau of Animal Industry[1]

CONTENTS

	Page
Introduction	1
Genus *Capillaria* Zeder, 1800	2
Capillaria annulata (Molin, 1858) Cram, 1926	4
Capillaria contorta (Creplin, 1839) Travassos, 1915	8
Capillaria cheradrii (Rudolphi, 1819) Travassos, 1915	19
Capillaria corvicula (Wassilkowa, 1930) Baylis, 1931	19
Capillaria cylindrica (Eberth, 1863) Travassos, 1915	20
Capillaria dispar (Dujardin, 1845) Travassos, 1915	20
Capillaria laricola (Wassilkowa, 1930) Baylis, 1931	21
Capillaria laphortygis Baylis, 1934	21
Capillaria obtusiuscula (Rudolphi, 1819) Travassos, 1915	22
Capillaria perforans Kotlán and Orosz, 1931	22
Capillaria trilobu (Linstow, 1875) Travassos, 1915	23
Summary	24
Literature cited	25

INTRODUCTION

Within the past decade there have been found, in the United States, nematodes belonging to the genus *Capillaria* which occur in the upper digestive tract of birds, that is, anterior to the intestine. The infestations have frequently been severe. The stomachs have never been involved, but the entire esophagus and, more especially, the crop have been affected. The birds have been chiefly galliform, but passeriform species also have been infested, the birds in both classes being of importance to commercial rearers and to sportsmen. Such infestations were not recorded in the United States until 1925; since then the increasing frequency of their occurrence and the widening range of bird hosts affected, in several different areas, indicate that these parasites present a problem of growing importance.

The writer has identified the nematodes as belonging to two species: *Capillaria annulata* (Molin, 1858) Cram, 1926, and *C. contorta* (Creplin, 1839) Travassos, 1915. The former species is easily recognized because of certain morphological characteristics to be discussed later. The latter species is more difficult to recognize. The American material allocated to this species shows considerable variation, and it is proposed to describe these variations and to give the reasons for considering the worms as *C. contorta*. Data concerning natural cases and experimentally produced cases of infestation are presented, including observations on the life history and pathogenicity of the parasites. Nine additional species are also considered; only two of

[1] Transferred to United States Public Health Service April 1, 1936.

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these, namely, *C. perforans* Kotlán and Orosz, 1931, and *C. lophortygis* Baylis, 1934, involve the same bird hosts as those of the American findings.

Except when otherwise noted, classification of birds, as given in this bulletin, is based on that in the following publications: Check-List of North American Birds (*3*)[1] for all species there included; and List of the Vertebrated Animals Exhibited in the Gardens of the Zoological Society of London, 1828–1927, volume 2, Birds (*32*) for other species.

GENUS CAPILLARIA ZEDER, 1800

Synonyms.—*Trichosoma* Rudolphi, 1819; *Trichosomum* Creplin, 1839; *Calodium* Dujardin, 1845; *Thominx* Dujardin, 1845; *Liniscus* Dujardin, 1845; *Eucoleus* Dujardin, 1845; *Hepaticola* Hall, 1916.

The genus *Capillaria* belongs to the group of nematodes which Ward (*50*) has called the order Trichosyringata, which group comprises forms defined as having a tubular capillary esophagus. The tube is embedded in, or otherwise related to, a single row of cells (Zellkörper of Eberth (*20*)) finely granular in appearance. Each cell has a conspicuous nucleus, and the cells extend almost to the head end of the body, the tube itself continuing to the mouth. On the other hand, Chitwood (*10*) has found that the esophagus does not differ fundamentally from that of the Myosyringata; it has a triradiate lumen surrounded by a muscle layer, is enclosed in a membrane and is pressed against or embedded in the row of cells; each cell communicates with the esophageal lumen through a small orifice.

Mouth simple, unadorned. At posterior end of esophagus, on each side a pear-shaped appendage of finely granular appearance. Portion of body containing esophagus commonly called anterior portion of body, and postesophageal portion called posterior portion of body. Cuticle with longitudinal "bacillary" bands, so called because of rod-shaped polygonal and cylindrical cells (Stäbchen of Eberth) of which they are composed, the number and relative size of the bands—dorsal, ventral, and lateral in position—varying.

Male genital organs consisting of single tubular testis, followed by a vas deferens, the latter sometimes constricted into two or three parts, the posterior part serving as a seminal vesicle; posterior to this, tube becoming narrower, forming an ejaculatory duct, this being followed by a tube provided with gland cells and with more or less strongly developed muscular wall, the tube extending to the cloaca and opening here along with the intestine. A membranous spicule sheath, of varying appearance, present within the muscular tube, in some species showing delicate transverse folds or numerous spines, the latter anteriorly directed when sheath is extruded. A single spicule, relatively long and slender, present in most species, sometimes only very slightly chitinized, if at all; sometimes absent. Cloacal aperture at tail end, more or less ventral, bounded by more or less prominent cuticular swellings of varying size and shape.

Female with a single ovary and uterus, simple in nature, the latter opening on ventral side of body near junction of esophagus and intestine; vaginal opening at same level as body cuticle or elevated, transversely elongate or circular, simple or with cuticular appendages. Eggs lemon shaped, with opercular plugs, without visible evidence of beginning development when deposited; outer surface of shell smooth or ornamented.

Location.—Digestive tract, liver, urinary bladder, or respiratory passages of all groups of vertebrates.

Type species.—*Capillaria anatis* (Schrank, 1790) Travassos, 1915.

DISCUSSION

Attempts to split up the genus *Capillaria* have not proved satisfactory because of the fact that no differential characters of an unvarying nature, on which to base such a subdivision, have yet been found.

[1] Italic numbers in parentheses refer to Literature Cited, p. 25.

Baylis (*4*) analyzed the situation and concluded that the genera proposed by Dujardin (*19*) and by Hall (*24*) must be considered synonymous with *Capillaria*, as previously listed. These new genera were based on the nature and length of the spicule sheath and the presence or absence of a spicule. Baylis pointed out that great variation is possible in the appearance of the spicule sheath, even within a species, and therefore it cannot be relied upon as a generic differential character. As regards presence or absence of a spicule, he stated:

> In the writer's experience it is not unusual to meet with forms of "Capillaria" in which the spicule appears to be so feebly chitinized that it is extremely difficult to detect, and it seems by no means improbable that in some cases the statement that a spicule is absent may be erroneous. It may, in fact, in any given form, prove impossible to state definitely either that a spicule is present or that it is absent.

He adds also that "the same observation applies to the presence or absence of bacillary bands."

There is perhaps no other group of nematodes, certainly not among nematodes of birds, for which existing descriptions are on the whole so inadequate and of which the characters considered to be of specific value are so few in number, owing to the apparently simple organization of the nematodes, and so variable within a species. There is great need for a monographic study, including examination of a large number of specimens, in an effort to discover more definite specific characters than are now known.

The following key indicates the distinguishing characters which are to be found in the descriptions of the 11 species included in this bulletin.

KEY TO SPECIES OF CAPILLARIA IN THE UPPER DIGESTIVE TRACT OF BIRDS

1.	No description; nomen nudum	C. charadrii (p. 19).
	Description given	2.
2.	Head with bulbous swelling and neck with cuticular thickenings	C. annulata (p. 4).
	Head and neck simple, without above structures	3.
3.	Female with large, bell-shaped, vaginal protuberance at vulva	C. cylindrica (p. 20).
	Female without such vaginal protuberance	4.
4.	Posterior part of body much thicker than anterior part, especially in female	C. dispar (p. 20).
	No such marked change in width of body	5.
5.	In gizzard	6.
	In esophagus, including crop	7.
6.	Spicule sheath unarmed; male tail simple, without lateral lobes	C. obtusiuscula (p. 22).
	Spicule sheath thickly covered with spines; male tail with 2 lateral lobes	C. triloba (p. 23).
7.	Esophagus of male unusually short, measuring 410μ to 480μ in specimens 12.8 to 15.6 mm long	C. corvicula (p. 19).
	Esophagus of male considerably longer than above	8.
8.	Tail end of male with 3 pairs of lobular projections, each with a pair of papillae, and the whole hidden by a bell-shaped bursal structure	C. laricola (p. 21).
	Tail end of male simpler than above, having dorsolaterally 2 prominences or papillae	9.
9.	Spicule apparently absent	C. lophortygis (p. 21).
	Spicule present, although sometimes difficult to see	10.
10.	Spicule very long, measuring more than one-third body length	C. perforans (p. 22).
	Spicule length much shorter than above; when determinable, not more than one-tenth body length	C. contorta (p. 8).

CAPILLARIA ANNULATA (MOLIN, 1858) CRAM, 1926 [2]

Synonyms.—*Trichosoma annulatum* Molin, 1858; *T. strumosum* Reibisch, 1893; *T. delicatissimum* Perroncito and Tomiolo, 1899; *Capillaria strumosa* (Reibisch, 1893) Travassos, 1915; *Thominx strumosa* (Reibisch, 1893) Travassos, 1915; *T. annulata* (Molin, 1858) Cram, 1925; *Eucoleus strumosa* (Reibisch, 1893) Wassilkowa and Gouchanskaja, 1930. *Capillaria semiteres* Zeder, 1803, described from the chicken but without location specified, is sometimes listed as the correct name for this species, but Zeder's species is considered unrecognizable by the present writer.

Hosts.—Galliformes: *Bonasa umbellus, Chrysolophus pictus, Colinus virginianus, Gallus gallus, Lyrurus tetrix, Meleagris gallopavo, Numida sp., Perdix perdix, Phasianus colchicus torquatus, Syrmaticus reevesi,* and *Tetrao urogallus.*

Location.—Esophagus, especially the crop.

DESCRIPTION OF PARASITE

Capillaria (p. 2): Threadlike worms. Just behind head (fig. 1, *A*), in adult specimens, a bulbous swelling of the cuticle and somewhat more posteriorly, in cervical region, wavy transverse folds giving the appearance of bladderlike swellings in optical section; the enlargement and folds lacking in very young specimens and sometimes collapsing or shrinking in adult specimens with change of pressure during preservation. Molin's (*35, 36*) description is very meager but includes mention of the cervical swelling, which is clearly shown in his illustration, and which is here regarded as diagnostic for this species. Bacillary bands dorsal and ventral, the former two-fifths to one-half as wide as body, the latter three-fourths as wide as body, the rodlike cells of ventral band more thickly set than those of dorsal band.

Male usually 10 to 25 mm long, exceptionally up to 37 mm long, by 52μ to 80μ wide. Esophagus 3.15 to 4.25 mm long. Tail end with two inconspicuous, round, lateral flaps united dorsally by a cuticular flap; cloaca somewhat ventral. Spicule sheath usually 1.12 to 1.63 mm long (2.5 mm, according to Adams and Geiser (*1*)) by about 13μ wide, beset with spines 2μ long. Cram's (*18*) description of the sheath as 225 mm long was a typographical error on the part of the printer, the manuscript having specified 1.26 mm, as derived from Ciurea's (*11*) description. Sheath seldom extruded; Ciurea (*11*) found only one extruded specimen (fig. 1, *B*) out of many examined by him. The present writer has found none extruded; it has been observed, however, that in unpreserved specimens the spines of the sheath are very conspicuous and that there appears to be a nonspinous area, with spinous areas anterior to and posterior to it. In two unusually large specimens from the chicken, one measuring 36 and the other 37 mm, the total length of spicule sheath of the first was 1.42 and of the other 1.63 mm; of these lengths, spines were present on an anterior or proximal area measuring 240μ and 304μ, were absent on a mid-area measuring 240μ and 280μ, and were present on a distal or posterior area measuring 944μ and 1.048 mm, respectively. These observations confirm similar findings of Wassilkowa and Gouchanskaja (*51*); in a specimen 23.17 mm long, from *Lyrurus tetrix*, a proximal portion of the sheath, 101μ in extent, had small spines, then for an area of 197μ there were larger spines, the extremities of which were turned proximally; the following area of 275μ was devoid of spines, after which the last 950μ length had large spines, the dimensions of which diminished gradually toward the distal end. Ciurea referred to a spicule as being 4μ wide but too indefinite in outline to be measured for length; Wassilkowa and Gouchanskaja have interpreted Ciurea's measurement as undoubtedly applying to the diameter of the lumen of the sheath; spicule lacking, according to Wassilkowa and Gouchanskaja and to others, including Orosz (*38*) and the present writer.

Female usually 25 to 60 mm long, exceptionally 15 to 80 mm long, by 77μ to 120μ wide. The largest specimens seen by the writer were from the chicken, with a maximum length of 60 mm; the largest from the turkey was 37 mm; the largest from the bobwhite quail, 30 mm. Posterior portion of body about seven times as long as anterior portion. Esophagus 4.29 to 8 mm long. Circular vulva located to left of median line, between bacillary bands, about opposite termination of esophagus, or 22μ to 93μ (or 560μ, according to Reibisch (*42*)) posterior to it; vulva usually elevated slightly but in young specimens said to open through a cylindrical appendix. Eggs usually 60μ to 66μ long (55μ to 58μ

[2] Cram (*16*) credited the combination to Michalka, 1924, but reexamination of the latter's article (*34*) indicates the combination was not made there.

long, according to Wassilkowa and Gouchanskaja (*51*)) by 26μ to 28μ wide; a small accessory knob usually present on one operculum, rarely present on both opercula.

DISTRIBUTION AND INCIDENCE

North America (Canada and United States), South America (Brazil), Europe, and Asia (Philippine Islands and Siberia).

Before its discovery in North America, *Capillaria annulata* had been known for many years, chiefly in Europe, in several countries on the Continent, the parasite being found mainly in chickens but also in pheasants. The first North American report appears to be that of Wickware (*52*) in 1922, in which report this nematode from the esophagus of the chicken was included in a list of parasites collected in Canada; no descriptive data were given. In 1925 it was recorded briefly from the United States by Cram (*12*), who the following year (*13*) published a general account of the case, at the same time that Hung (*27*) described the pathology; large numbers of the nematode had been found in the esophagus of five turkeys in Maryland and were apparently responsible for the deaths of these and other members of the flock.

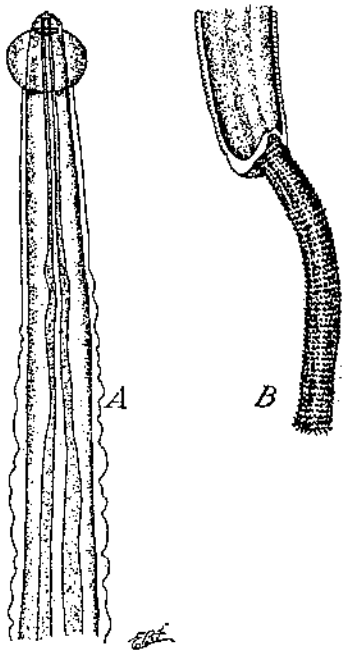

FIGURE 1.—*Capillaria annulata*: *A*, Head end; *B*, male tail. After Ciurea, 1914.

Subsequent reports in this country include the following: In 1926 from six ruffed grouse, five of which were wild birds from southern New England and Columbia County, N. Y., and a captive bird in Tompkins County, N. Y., by Allen and Gross (*2*); in 1927 from a chicken in Puerto Rico, by Cram (*14*); in 1928 from chickens in Maryland, Georgia, Mississippi, and Louisiana and from a ruffed grouse in Michigan, by Cram (*15*), and from pheasants in New York, by Hendrickson and DeVolt (*20*), these last-mentioned authors reporting heavy losses due to infestations; in 1930 from a captive bobwhite quail in Florida, by Thomas (*47*), and in 1931 from considerable numbers of the same host, also captive, in Virginia, by Cram (*16*), both these reports indicating that the parasites were contributory to the death of the birds; in 1930 from chickens in Illinois, by Graham, Thorp, and Hectorne (*23*), losses in two widely separated flocks apparently being caused by the parasites, and from chickens in New York, by Beaudette and Hudson (*7*); in 1931 from three captive Hungarian partridges from 2 sources in the State of Washington, by Hamilton (*25*); in 1933 from two Reeves pheasants in New York, by Gates (*21*), and from chickens in Texas, by Adams and Geiser (*1*); and in 1935 from seven captive ring-necked pheasants suffering from a "diphtheritic" disease in New Jersey, by Graham (*22*). An additional report in 1934, by Nelson (*37*), of a species of *Capillaria* in the esophagus, including the crop, of 30 out of 326 chickens examined

in Kansas, probably dealt with *C. annulata*, although specific identification was not made.

These reports of the 10 years following the original discovery of *C. annulata* in the United States indicate a wide distribution as regards area and the species of gallinaceous birds which are affected. In Europe the finding of this species in the black grouse, *Lyrurus tetrix*, by Wassilkowa and Gouchanskaja (*51*) extends the host list still further.

CLINICAL SYMPTOMS AND PATHOLOGY

European reports of *Capillaria annulata* have not indicated that this nematode is seriously pathogenic to chickens; Ciurea (*11*) noted that the only symptom was an occasional stretching of the neck, that the chickens remained in good flesh and retained their appetites, and that no gross pathological condition was apparent at necropsy. Perroncito and Tomiolo (*39*), however, reported fatal cases of infestation in pheasants in Italy, the symptoms being principally malnutrition and emaciation, associated with a severe anemia.

The principal symptoms which have been noted in connection with the *C. annulata* infestations in the United States are refusal of grain but acceptance of soft feeds by the birds, unnatural position of head, arching or stretching of neck, droopiness, emaciation, and lameness. Allen and Gross (*2*) reported severe anemia in an infected ruffed grouse, shortly before death—

> a count averaging 1,960,000 per c. mm. red cells and 23,600 white cells being obtained. A similar count of an apparently healthy bird gave 2,730,000 red cells and 32,400 white cells per c. mm.

Changes in the appearance of the wall of the esophagus, more especially that of the crop, have been described by Hung (*27*) from the turkey; three general types were observed. In an early stage there were hyperemia and slight thickening of the wall in the vicinity of the worms, which were "threaded" into the mucosa in tortuous patterns; in a subsequent stage, the lymph follicles were enlarged and there were greater thickening and loss of elasticity of the wall; in the third stage there were sloughing of the mucosa and the formation of a fibrinous pseudomembrane. Microscopically, these stages showed hyperemia and lymphocyte infiltration, flask-shaped enlargement and necrosis of lymph follicles, necrosis of mucosa and presence of a pseudomembrane composed of the necrotic substances with fibrin and polynuclear leucocytes. Eggs of the worms were present in large numbers throughout the membrane and the superficial mucosa; the worms had penetrated as deep as the boundary of the muscularis. Graham (*22*) observed approximately the same microscopic pathology in pheasants, except that there was infiltration of plasma cells rather than lymphocytes.

PREDISPOSING FACTORS

As already noted, reports from countries other than the United States have indicated that chickens are seldom seriously affected by the parasite, as compared with pheasants, in which the infestations may prove fatal. The majority of chicken infestations that have been seen by the present writer have not shown the severe tissue damage seen in turkeys, quail, grouse, and pheasants. Nevertheless, instances have been observed by the writer, by Adams and Geiser (*1*),

and by Graham, Thorp, and Hectorne (*23*) when pathological changes occurred in the crops of chickens similar to those described from turkeys; the last-named authors reported that chickens weighing 2½ to 3 pounds were first to suffer from the disease, death occurring in 10 days to 5 weeks after the first symptoms. The 30 cases observed by Nelson (*37*) were said to indicate that chickens up to 4 months of age were apparently more susceptible to infection, which observations conform with those of Ciurea (*11*) in Europe, that only young chickens became infected and chiefly from May to August, no cases being found by him in winter. It has been suggested by Cram (*13*) that possibly this parasite is normally found in chickens, which have, therefore, an inherent immunity to its effects; its occurrence in other gallinaceous birds may be a more recent transfer from the chicken, and the effects, therefore, more severe. The occasional breaking down of immunity in chickens may be due to lowered resistance of one kind or another. Seifried (*45*) stated that during his investigations in the United States, conducted chiefly at Princeton, N. J., he found heavy infestations with *Capillaria annulata* associated with cases of A-avitaminosis in chickens, and he concluded that penetration of the wall of the esophagus was facilitated by the abnormal condition resulting from the dietary deficiency.

LIFE HISTORY

The protoplasm of the eggs, when they are deposited by the worms, is in the simple unsegmented stage; development of embryos within the eggs is comparatively slow, depending on temperature, moisture, oxygen supply, and probably other factors. Under very favorable conditions, such as an even temperature of 28° to 33° C., in a shallow layer of water, with daily stirring for oxygenation, the first suggestion of vermiform outline within the egg has been noted as early as the thirteenth day and apparently completed embryo development by the twenty-fourth day after eggs were obtained from the crop content of fowls. Under less favorable conditions, 30 and 42 days, respectively, were the usual periods, but if intermittent drying occurred, development was sometimes delayed for considerably longer periods. The addition to the cultures of a bactericide, such as a weak solution of formalin or potassium bichromate, was found to hinder rather than to aid development of the eggs.

Embryos freed from eggs by heat and pressure, in a culture 47 days old, measured 250μ long by 10μ wide.

Attempts to produce experimental infestations by feeding embryonated eggs have been repeatedly unsuccessful. During the years 1929 to 1932 the writer fed cultures of embryonated eggs of *Capillaria annulata*, most of which were derived from infested chickens but some also from infested Hungarian partridges, to 18 young chickens, the age of the chickens at time of experimental feeding being 2, 7, 25 and 28 days and 2½ months in different experiments. In no case were specimens of the capillarids found when the chickens were killed from 1 to 3 months later.

Recently E. E. Wehr of the Zoological Division has ascertained that when the infective eggs of *C. annulata* are fed to earthworms and the earthworms subsequently fed to chickens, the chickens become infested with *C. annulata*.

CONTROL

See recommendations for control of *Capillaria contorta*, page 19.

CAPILLARIA CONTORTA (CREPLIN, 1839) TRAVASSOS, 1915

Synonyms.—*Trichosoma contortum* Creplin, 1839; *Thominx contorta* (Creplin, 1839) Travassos, 1915.

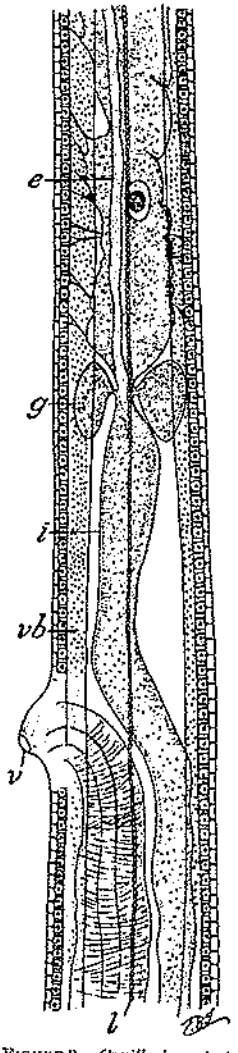

FIGURE 2.—*Capillaria contorta*. Region of vulva: *e*, Esophagus; *g*, gland; *i*, intestine; *l*, lateral band; *v*, vulva; *vb* ventral band. After Eberth, 1863.

Hosts.—Anseriformes: *Anas boschas, A. boschas domestica, A. querquedula* (syn., *A. circia*), *Chaulelasmus streperus* (syn., *Anas strepera*), *Dafila acuta*, "Goose", *Nettion crecca* (syn., *Anas crecca*), *Spatula clypeata* (syn., *Anas clypeata*), *Tadorna tadorna* (syn., *T. cornuta*). Charadriiformes: *Alle alle, Charadrius hiaticula* (syn., *Aegialitis hiaticula*), *Gelochelidon nilotica* (syn., *Sterna anglica*), *Larus canus, L. cachinnans, L. ridibundus, Philomachus pugnax* (syn., *Machetes pugnax, Pavoncella pugnax, Tringa pugnax*), *Recurvirostra avosetta, Sterna hirundo* (syn., *S. fluviatilis*), *Thalasseus maximus*[3] (syn., *Sterna maxima*), *Uria grylle, Vanellus vanellus* (syn., *V. cristatus*). Falconiformes: *Accipiter nisus* (syn., *Astur nisus, Nisus communis*), *Buteo buteo* (syn., *B. vulgaris, Falco buteo*). Galliformes:[4] *Bonasa umbellus, Colinus virginianus, Crossoptilon mantchuricum, Lophortyx californica, Meleagris gallopavo, Orcortyx picta, Perdix perdix, Phasianus colchicus torquatus*). Passeriformes: *Coloeus monedula* (syn., *Corvus monedula*), *Corvus brachyrhynchos* (syn., *C. americanus*), *C. cornix, C. corone* (syn., *Corone corone*), *Corvus frugilegus* (syn., *Trypanocorax frugilegus*), *Erithacus rubecula* (syn., *Lusciola rubecula*,[3] *Rubecula familiaris*), *Oenanthe oenanthe* (syn., *Saxicola oenanthe*), *Phoenicurus phoenicurus* (syn., *Lusciola tithys*,[3] *Ruticilla tithys*[3]), *Sturnus vulgaris*.

Location.—Mouth and esophagus, including crop, usually in mucosa or submucosa.

DESCRIPTION OF PARASITE

Capillaria (p. 2): Original description by Creplin (*17*) in 1839:

First found in *Corvus cornix*. Worms very elastic, twisting in spiral when placed in water. *Male* much smaller and slenderer than female; tail obliquely truncate, with a large opening on the swollen edge, with a protruding spicule enveloped by a comparatively long sheath. *Female* about 1 inch (27 mm) long, the size of a fine hair, very slender anteriorly, slightly enlarged in middle region, and becoming slenderer again posteriorly; tail very obtuse.

Diesing (*18, v. 2*) in 1851, listing several wild birds as hosts of this species, adds to the original description in the following particulars:

Male 13.5 to 15.75 mm long; spicule sheath unarmed, nonstriated. *Female* 18 to 27 mm long.

Eberth (*20*) in 1863 gave a more detailed illustrated (fig. 2) description of specimens from *Corvus cornix:*

Body spirally rolled; ventral longitudinal band three-fourths width of body, dorsal band one-third width of body, both composed of bacillary cells (Stäbchen), these

[3] The writer is indebted to H. Friedmann, U. S. National Museum, for checking the validity of this name.

[4] A single report from *Gallus gallus*, by Rietz (*49*) is considered unreliable, having been based entirely on *Capillaria* eggs in the droppings.

scarcer in dorsal band than in ventral band; lateral lines single, very narrow. *Male* with greatly narrowed posterior end formed into bursalike structure by two small rounded flaps (Lappen), with cloacal opening somewhat ventral; spicule sheath with small, fine, sharp spines. *Female* body becoming thicker posteriorly, again narrowing toward tail, tail ending obliquely; anus terminal; vulva on ventral side, prominent, circular, situated a considerable distance below origin of intestine; inner lamella of outer eggshell with fine punctiform prominences.

Linstow (*31*) in 1877, listing several wild birds as hosts, noted variations which he observed in this nematode; as the body of the female developed, it was only the part of body posterior to the vulva that grew, with the enlargement of the sex organs. In a nongravid female, 16.6 mm long, the ratio of body length anterior to vulva to that posterior to vulva was 4:6, whereas in a gravid female, 26 mm long, it was 4:17. The eggs also he found inconstant in size, ranging from 52μ to 69μ long and 26μ to 36μ wide.

Railliet and Lucet (*40*) in 1889, apparently not having seen Eberth's description, gave one very similar to his, of specimens from *Anas boschas domestica*, which they stated were identical with specimens collected by them from the common crow:

> Body filiform, progressively thicker posteriorly. Cuticle very finely striated transversely. Head very small, mouth characters indiscernible, except for a small terminal prominence or button (bouton). Two longitudinal bands, formed of little rods (batons), originating in subcuticular layer and penetrating cuticle; viewed from side, each batonette appearing as a small hemispherical projection prolonged by an upright point; viewed from the front, batonettes represented by very small circles more or less approximated. Bands unequal in width, exact situation very difficult to determine; one, apparently ventral, about three-fourths width of body, the other, apparently dorsal, more feebly developed, averaging one-third width of body, this latter band tending to disappear at level of vulva. *Male* relatively small, 12 to 17 mm long. Anterior part of body containing esophagus, 3.4 to 4.5 mm long; thus ratio of anterior to posterior part of body about 1:2.6. Tail (fig. 3) at first slightly attenuated, in terminal region slightly swollen and with two lateral more or less prominent projections; cloacal opening slightly ventral. Spicule very slender, about 3μ wide; enclosed in a sheath 20μ wide, cylindrical, and provided with very small bristling (setacées) spines, directed anteriorly. *Female* 31 to 38 mm long by 9μ to 10μ wide at level of head, 80μ to 90μ wide at end of esophagus, and 120μ to 150μ wide in posterior region. Anterior or esophageal part of body 4.5 to 7 mm long; thus ratio of anterior to posterior

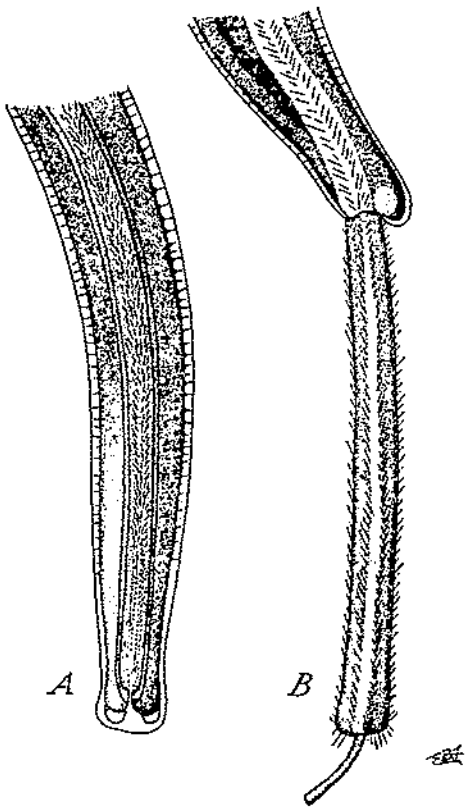

FIGURE 3.—*Capillaria contorta*. Male tail: *A*, With spicule and sheath retracted; *B*, with spicule and sheath extruded. After Railliet and Lucet, 1890.

part about 1:5. Tail very attenuated, ending in slender tip. Vulva 140μ to 170μ posterior to end of esophagus, having appearance of transverse slit, without appendix of any sort. Eggs ellipsoidal, contracted into a neck at the two poles, which are surmounted by a hemispherical, very transparent knob or button; measured from neck to neck, without including knobs, 48μ to 56μ long.

Railliet and Lucet (*41*) the following year reviewed the earlier descriptions of this nematode but made no changes from their previous description.

Travassos (*48*) in 1915, listing numerous wild birds as hosts, included the following in the description of this nematode:

Male 8 to 15 mm long; size relation of anterior to posterior part of body 3:5; tail (fig. 4) truncate and with two laterodorsal projections; spicule sheath with many spines, measuring about 0.3 (mm ?), capable of being invaginated interiorly in posterior part of body; spicule very delicate and transparent, difficult to see, measuring about 0.8 mm long. *Female* 15 to 30 mm long; size relation of anterior to posterior part of body 1:5; no projection at vulva; eggs 49μ to 56μ long by 24μ to 28μ wide.

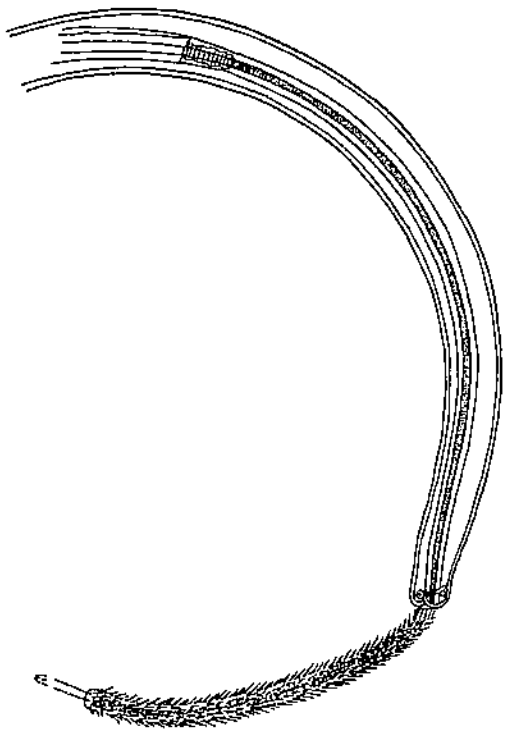

FIGURE 4.—*Capillaria contorta*. Male tail. After Travassos, 1915.

MORPHOLOGICAL CHARACTERS OF NORTH AMERICAN SPECIMENS

The writer has identified as *Capillaria contorta* nematodes from the esophagus of all the species of Galliformes listed previously and of ducks (*Anas boschas domestica* and *Dafila acuta*). The principal characters on which these identifications were based included relative size and nature of bacillary bands and the situation of the vulva on a circular prominence, as described and figured by Eberth, the two rounded prominences or projections of the male tail and the presence of delicate spines on the spicule sheath, the two last-mentioned characters being included in the descriptions of Eberth, of Railliet and Lucet, and of Travassos. These characters appeared constant in the large number of specimens examined; in certain other respects, however, variations were noted, as included in the following observations.

Lot A. Pheasant (*Phasianus colchicus torquatus*); natural infestation.—*Male* 37 to 48 mm long. Spicule sheath (?) about 3 mm long, minutely spined, lying within the ejaculatory duct; the duct longitudinally striated, extending anteriorly for 3 to 5 mm beyond anterior end of sheath, then preceded by vas deferens, thick-walled with transverse contractions giving corrugated appearance, for distance of 8 to 10 mm; at its proximal end a sphincter separating it from seminal vesicle, the latter with dense opaque contents; spicule not discernible. *Female*

70 mm long; vulva on elevation about 184μ posterior to level of origin of intestine; eggs 50μ by 25μ.

Lot B. Pheasant (*Phasianus colchicus torquatus*); natural infestation.—*Male* 18 to 32 mm long. Tail end in dorsoventral view like that figured by Railliet and Lucet (fig. 3); in lateral view similar to that of *Capillaria lophortygis* (fig. 10). Spicule sheath in no case everted; spines not apparent for distance of about 65μ from posterior end, but anterior to that area, an area of about 100μ with spines showing clearly; in a specimen 28 mm long, ejaculatory duct and vas deferens 13 mm long; spicule discernible in one specimen. *Female* 25 to 30 mm long. Location of vulva ranging from same level as origin of intestine to 120μ posterior to it; eggs 54μ by 25μ.

Lot C. Bobwhite quail (*Colinus virginianus*); artificial infestation of 52 days' duration with pheasant strain (lot B).—*Male* 31 mm long. *Female* 45 mm long. Eggs 58μ by 27μ.

Lot D. Duck (*Anas boschas domestica*); probably artificial infestation (see Life History, p. 16) of 48 days' duration, with pheasant strain (lot B).—*Male* 15 to 16 mm long. In two specimens spicule sheath 760μ and 780μ, respectively, or somewhat longer (coiled at anterior end); spines of spicule sheath easily seen, very delicate except in space of 200μ of most anterior area, here shorter and stouter; in a third specimen, the larger anterior spines easily seen but the others discernible only with difficulty except in sectioned specimen, then spines on inner surface of sheath easily seen, the sheath collapsed, 21μ wide, except toward its anterior looped end, where not collapsed and here spicule, 3μ wide, discernible; in fourth specimen, spicule sheath extruded, the spicule discernible within it but not protruding beyond it, the spines very similar to those figured by Railliet and Lucet (fig. 3), except not extending out from edge of sheath so far but lying close to it. *Female* 32 to 35 mm long. Vulva 136μ to 176μ from origin of intestine; eggs 50μ by 29μ.

Lot E. Duck (*Dafila acuta*); natural infestation.—*Male* 15 to 17 mm long; spicule sheath 823μ long, similar in appearance to first two specimens described from lot B. *Female* 21 to 26 mm long.

Lot F. Mountain quail (*Oreortyx picta*); natural infestation.—*Male* about 45 mm long; spicule sheath (?) 6.24 and 6.47 mm long, respectively, in two specimens, lying in ejaculatory duct, latter extending farther anteriorly, with total length of 11.4 mm; spicule questionable. *Female* about 80 mm long; eggs 54μ by 27μ.

Lot G. Turkey (*Meleagris gallopavo*); artificial infestation of 72 days' duration, with strain from bobwhite quail.—*Male* 43 mm long. *Female* 48 mm long.

Lot H. Turkey (*Meleagris gallopavo*); artificial infestation of 80 days' duration, with strain from turkey.—*Male* 41 mm long; spicule sheath (?) about 3 mm long. *Female* 67 to 77 mm long.

Lot I. California valley quail (*Lophortyx californica*); natural infestation.—*Male* 35 to 45 mm long. *Female* 50 to 60 mm long.

The foregoing observations indicate the difficulties encountered when an attempt was made to study the male genital organs in specimens which were all identical, judging from external characters, except for size. The presence or absence of a spicule and, if present, its length are the characters which have been specified as differentiating from *Capillaria contorta* two recently erected species, *C. perforans* and *C. lophortygis* of galliform birds. The writer found that as the size of the specimens examined became greater, and as the walls of the body and of the genital tubes became thicker, there was increasing difficulty in seeing the spines of the spicule sheath and the spicule within the sheath; only by resorting to sectioning was it possible to see the spicule in some instances. In only one of the many specimens examined was the sheath extruded from the body; unless extruded, the spines are on the inner surface of the sheath, flattened against the wall and, therefore, much more difficult to see.

The spicule sheath in specimens from galliform birds appeared to be proportionately longer, ranging from 3 to 6 mm in specimens 37 to 48 mm long, than from anseriform birds, which in specimens 15 to 17 mm long had sheaths up to only 832μ long. The sheaths of

the former specimens appeared to have smaller and more delicate spines than those of the latter specimens, in contradistinction to what might be expected of larger specimens. In no case was it possible to measure the length of the spicule.

In view of the difficulty of distinguishing the internal male genital organs and the finding of intermediate gradations between the smallest and the largest and between the most obvious and the most obscure of these organs, it was concluded that no differentiation of species could be made from those characters, in the material at hand, and that this material must be allocated to *C. contorta* chiefly on the basis of external characters.

These conclusions of the writer conform to those of Baylis, as referred to in the discussion of the genus *Capillaria* (p. 3).

DISTRIBUTION

North America (United States), South America (Brazil), Europe (England (Middlesex), France, Germany, Italy, Poland, Switzerland, Union of Soviet Socialist Republics, and Yugoslavia), and Asia (Taiwan and Russian Turkestan).

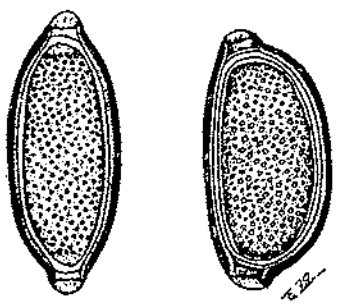

FIGURE 5.—*Capillaria contorta*. Eggs. After Korkhaus, 1935.

Outside of the United States, the records of *Capillaria contorta* appear to have been based for the most part on a single or a few findings, with the following exceptions: Railliet and Lucet (*40, 41*) described an epizootic of this parasite in a flock of domestic ducks, in the Department of Loiret, France. Skrjabin (*46*) in reporting this parasite from *Corvus frugilegus* and *C. corone* stated that, in 1908, 100 percent of the former bird hosts which were examined in the locality of Aoulié-ata, Russian Turkestan, were infected with *Capillaria contorta;* the number of birds examined was not given, however. Korkhaus (*28*) examined 334 specimens of *Corvus cornix* and 4 specimens of *C. frugilegus*, in Germany; in the mucosa of the esophagus in 104 cases was found a species of *Capillaria* which was never found in other parts of the digestive tract. In 105 of 244 fecal examinations of these birds there were found capillarid eggs measuring 60μ to 70μ long by 26μ to 28μ wide. Korkhaus provides illustrations of eggs (fig. 5) at this point in his report, labeling the illustrations as *Capillaria contorta,* but not giving the specific name in the text.

In the United States the first record of *C. contorta* appears to have been that of Rietz (*43*) in 1924 which is now considered unreliable, as it was based entirely on capillarid eggs observed in the droppings of a chicken. In 1929 Van Roekel (*49*) reported *C. contorta* as responsible for deaths of captive California valley quail in California. The nematode was reported in 1931 by Cram (*16*) from game birds in New York, Pennsylvania, Maryland, and Louisiana, and by Canavan (*9*) from the common crow in Pennsylvania, the bird having been in the Philadelphia Zoological Garden for 8 months; in 1932 Beaudette (*6*) reported it from bobwhite quail, presumably of New Jersey. A

record of *C. contorta* from the small intestine of a pigeon of New York State, by Gates (*21*), is considered erroneous, as is also, probably, the listing of *Tetrameres americana* from the proventriculus of a crow, in the same publication.

Table 1 shows the origin and evidence of pathogenicity of specimens of *C. contorta* examined by the writer, from naturally infected cases.

TABLE 1.—*Data regarding natural cases of Capillaria contorta infestations observed by the writer*

Infested birds		*C. contorta* collected			Evidence of pathogenicity
Species	Number	Date	Place	By whom	
Ring-necked pheasant (*Phasianus colchicus torquatus*).	4	April 1928	New York	E. B. Cram	Positive.
Do	3	November 1928	Pennsylvania	do	Do.
California valley quail (*Lophortyx californica*).	?	January 1929	California	H. Van Roekel	Do.
Pintail (*Dafila acuta*)	4	April 1929	Louisiana	E. B. Cram	Do.
Hungarian partridge (*Perdix perdix*).	?	November 1930	Pennsylvania	J. D. Jones	?.
Manchurian pheasant (*Crossoptilon manichuricum*).	4	do	Maryland	E. B. Cram	Positive.
California valley quail	2	December 1930	North Carolina	E. J. Moore	Do.
Do	1	January 1932	New Jersey	J. J. Black	?.
Bobwhite quail (*Colinus virginianus*).	2	do	do	A. A. Allen	?.
Ruffed grouse (*Bonasa umbellus*)	1	do	New York	do	Positive.
Bobwhite quail	1	October 1932	North Carolina	E. B. Cram	Do.
California valley quail	2	November 1932	do	do	Do.
Ring-necked pheasant	1	do	do	do	Do.
Do	1	May 1933	Wisconsin	W. Grange	Do.
Turkey (*Meleagris gallopavo*)	1	October 1933	Virginia	E. B. Cram	Do.
Oregon mountain quail (*Oreortyx picta*).	2	May and June 1933.	Maryland	do	Do.

CLINICAL SYMPTOMS AND PATHOLOGY

Railliet and Lucet (*40*) were the first to describe the pathogenic effects of *Capillaria contorta*, the worms causing "indigestion ingluviale", a type of indigestion resulting from overloading of the crop, whether the crop be of the nature of a diverticulum, as in Galliformes, or merely a fusiform distention of the esophagus, as in Anseriformes. A flock of young ducks, when about 2 months old, were seriously affected; their development was arrested, they grew thin, and walking became painful, with the result that they would fall in epileptiform crises, uttering faint cries. The birds, although usually droopy, maintained their appetite fairly well. Later, the feed which was ingested accumulated in the dilated part of the esophagus, producing an obstruction. Examination of the birds after death revealed that the esophagus alone was altered; there was enormous distention and the walls showed sinuous lines, which under the microscope proved to be worms and their burrows, full of eggs, encircling the glands, the number of worms being as many as 30 in a duckling. It seemed evident that the walls of the organ had been rendered inert, with resulting simple mechanical obstruction; the latter, however, by causing pressure on the pneumogastric nerve, was thought to have led to asphyxiation. Only Pekin ducklings were affected; wild ducks and domestic ducks (mallards?) being reared on the same premises, escaped for 2 successive years. The third year, after removal of all Pekin ducks, 2 out of 30 domestic ducks were affected. It was

concluded, therefore, that the race and age of the ducks might constitute a predisposition to this parasitic infestation.

Symptoms which have been associated with similar infestations in North American galliform and anseriform birds conform generally

FIGURE 6.—Section of crop of bobwhite quail, showing *Capillaria contorta* and damage produced by it. Experimental infestation: *A*, × 45; *B*, × 210.

to those just described, except that accumulation of feed in the crop, with the possibility of resulting pressure on the pneumogastric nerve, has not been consistently present, so that some other explanation of the ultimate cause of death seemed necessary. Muscular incoordination, leg weakness, and symptoms "like those of limberneck in chickens" have been noted preceding death; in a few cases, however,

deaths were sudden, without any symptoms having been noted and the birds being in good flesh at the time. High mortality has resulted from infestations among wild ducks, among galliform game birds being reared in captivity, and among domestic turkeys; bacteriological examinations of the majority of the birds failed to show any other pathogenic agent. In the ducks the number of worms was 25 to 35, approximately that found by Railliet and Lucet, and slight thickening and inflammation of the esophageal wall were the only noticeable changes. In galliform birds, however, the infestations have frequently appeared much more severe, the worms being more numerous and marked thickening of the wall being present, often with a flocculent catarrhal exudate covering the mucosa, and with more or less sloughing of the mucosa; degenerated blood pigment indicated earlier hemorrhages.

As regards microscopic pathology, the following observations have been made on experimentally produced infestations: In a nonfatal case of comparatively long standing (80 days) in a turkey (see turkey B, Life History, p. 17), only slight lesions were present in connection with invasion of the crop wall; there was a slight connective-tissue formation immediately surrounding the areas containing the worms or worm eggs, with occasional small foci of necrosis of the epithelial cells in these areas. On the other hand, in a fatal acute case of 48 days' duration in a bobwhite quail (see bobwhite quail B, Life History, p. 17), the lesions (fig. 6) were extensive, as was to be expected from the macroscopic appearance which was that described for this bird under Life History. Marked necrosis of the epithelium, with extensive sloughing of the inner portions, was present; thin connective-tissue capsules surrounded the areas containing the worms or their eggs. There was extensive cellular infiltration, consisting mostly of lymphocytes and large mononuclear leucocytes. The lesions in some portions extended into the submucosa and even into the circular muscle layer.

It appears from these observations that *C. contorta* causes a catarrhal inflammation, with subsequent sloughing of necrotic epithelium, whereas *C. annulata* (p. 6) causes the formation of a croupous or diphtheritic membrane made up of fibrin and the necrotic tissue.

LIFE HISTORY

DEVELOPMENT OF EGGS OUTSIDE BIRD HOST

The only observations on the life history of *Capillaria contorta* appear to be those made by the present writer. Railliet and Lucet (*41*) attempted to determine the process but were unsuccessful. They did not find eggs in the intestinal contents of infected birds; consequently they were at a loss to know how the eggs were liberated from the galleries in the esophageal wall, and they suggested that decomposition of the cadaver of the host might be necessary to free the eggs. The writer is of the opinion that the young ducklings handled by Railliet and Lucet died from such acute cases of infestation, of comparatively short duration, that discharge of the eggs through the openings of the glands or through abrasions in the esophageal wall had not yet taken place. In the writer's experience eggs have been found abundantly in droppings from infected birds. Railliet and Lucet stated that early segmentation occurred in the eggs while they were in the esophageal wall; their removal to a humid

chamber in an incubator, a method which these workers had used successfully for other nematodes, did not result in further development.

The present writer has observed development of the eggs of *C. contorta*, procured either from passed droppings, intestinal or crop contents, or directly from the galleries in the esophageal wall. The cytoplasm of the eggs has always appeared unsegmented when they were deposited, but cleavage soon began, under favorable conditions of temperature, moisture, and oxygen supply. The following notes were made on cultures of eggs in a shallow layer of tap water, held at room temperature.

Quail strain I (October). After 5 days, two- to four-cell stage; after 8 days, morula with large blastomeres; after 12 days, morula with small blastomeres; after 19 days, very early vermiform stage; after 35 days, well-developed vermiform embryo.

Quail strain II (April). After 28 days, early vermiform stage; after 35 days, well-developed vermiform embryo.

Turkey strain (October). After 27 to 37 days, well-developed vermiform embryo.

Pheasant strain (April). After 28 days, early vermiform stage; after 40 days, well-developed vermiform embryo. The embryos remained alive and proved infective when fed to birds after 11 months, the culture having become so dry at times it was feared the embryos had been killed; considerable resistance to drying is thus indicated.

DEVELOPMENT OF CAPILLARIA CONTORTA WITHIN BIRD HOST

Infestations with *C. contorta* have been produced experimentally by the writer in six turkeys, two bobwhite quail, and, probably as a result of the experimental feeding, in two ducks. The turkeys and quail had been hatched in incubators, reared in electrically heated brooders, and carefully protected from acquiring any parasitic infestation other than that artificially introduced; no spontaneous cases of parasitism were ever encountered. The young ducks were obtained from a market and were held from 1½ to 6 months, with repeated examinations of the droppings, to make sure that they were parasite-free before artificial infection was attempted. In no case have the eight ducks thus procured and handled shown any infestation other than that corresponding to cultures experimentally fed. However, the finding of three specimens of *C. contorta* in a control duck which was being held with an artificially infected duck, as noted later, prevents the records for the ducks being as reliable as those for the turkeys and quail, the controls in these cases being uniformly free from *C. contorta* infestation.

These positive experimental findings are summarized as follows:

Bobwhite quail A (adult). February 26, 1929, fed eggs of *C. contorta* obtained from pheasant April 2, 1928. Fecal examination of quail April 12, 1929—many *Capillaria* eggs present. Bird killed April 19; necropsy findings—heavy infestation of esophagus, including crop, with *C. contorta*. Six control quail negative.

Ducks, 2 Pekins (young). Purchased early in February 1929; fecal examinations made on February 14 and 26, March 21 and 26—negative. March 26—1 duck (A) fed eggs of *C. contorta* obtained from pheasant (same source as eggs fed to bobwhite quail A); other duck (B) held in same pen as control. Fecal examination of duck A, May 11—*Capillaria* eggs present. Ducks killed on same day; necropsy findings—duck A, numerous specimens of *C. contorta* in esophagus; duck B, three specimens of *C. contorta* in esophagus.

As noted in the previous discussion, the presence of *C. contorta* in the control duck raises a question as to the infestations being of experimental origin. In view of the following facts, namely, that *C. contorta* has never been found in domestic ducks in this vicinity or any other part of this country, that the ducks had been held in

confinement for 40 to 50 days before the experimental feeding was made and repeated fecal examinations during that period had been negative, and that the control duck ate and drank from the same vessels as the experimentally fed duck, the evidence appears to be good, although not entirely conclusive, that the few specimens of *C. contorta* in the control duck represented an accidental infection of the same source, that is, the culture of the pheasant strain, as the comparatively heavy infestation in the other duck; regurgitation of a small quantity of the culture by duck A, soon after feeding, might easily have led to contamination of the feed or water.

Turkey A (adult). January 19, 1931, fed *C. contorta* eggs obtained from bobwhite quail October 31, 1930. Turkey killed May 2—a few specimens of *C. contorta* in esophagus.

Turkey B (adult). November 21, 1933, fed *C. contorta* eggs obtained from crop of turkey October 6. Fecal examination January 31, 1934—many *Capillaria* eggs present. Turkey killed February 9—*C. contorta* fairly numerous in esophagus; as regards distribution, the worms occurred throughout the entire length of esophagus, from the area just posterior to the mouth down to the proventriculus. Nine worms extracted from the anterior slender part of esophagus and 44 worms from the posterior slender part; of the latter, about half the number were concentrated in the area just anterior to the proventriculus, a thickened ring of mucosa resulting. Several times as many worms noted in crop as in slender portions of esophagus. *Males* about 35 mm long; *females* 70 to 80 mm long and, although gravid, the eggs in uteri were fewer in number and the body consequently more slender than in females collected from some natural infestations, so that it was concluded that the worms had not reached complete development. (See paragraph on the microscopic pathology of this bird, p. 15.)

Turkey C (adult). May 2, 1934, fed *C. contorta* eggs obtained from droppings of turkey B on February 5. Turkey killed June 25—*C. contorta* numerous in crop; thickening of mucosa in areas where worms were located; tunnels with eggs, leading to surface apparently at gland openings.

Turkey D (adult). May 2, 1934, fed *C. contorta* eggs obtained from droppings of turkey B on February 9. Fecal examination June 26—many *Capillaria* eggs present. Turkey killed June 30—*C. contorta* fairly numerous in esophagus.

Turkey E (young; hatched July 18). August 9, 1934, fed *C. contorta* eggs obtained from mountain quail May 9. During latter part of September, turkey became lame; October 1, prostrate, too weak to stand; fecal examination—numerous *Capillaria* eggs present. Turkey died October 2; necropsy—*C. contorta* numerous, mostly in crop, a few in undilated esophagus. *Males* 38 to 42 mm long; *females* about 98 mm long. Crop wall thickened; blood vessels all engorged. Catarrhal inflammation of mucosa.

Turkey F (young; hatched July 18). August 9, 1934, fed *C. contorta* eggs obtained from mountain quail June 4. October 1, fecal examination—*Capillaria* eggs fairly numerous. Turkey killed October 12; necropsy—*C. contorta* fairly numerous; findings similar to those on turkey E, but infestation not so severe in turkey F.

Bobwhite quail B (young; hatched July 2). August 9, 1934, fed eggs of *C. contorta* obtained from mountain quail May 9 (same culture as turkey E). September 26, quail very droopy, feathers ruffed; fecal examination—many *Capillaria* eggs present. Quail died September 27; necropsy—blood vessels of connective tissues of outer surface of esophagus all highly engorged. Wall of esophagus thickened, inelastic; catarrhal inflammation of mucosa; areas of sloughing of mucosa; tunnels with worms and their eggs appear as dense network. *C. contorta* numerous, distributed from the very upper to the very lower end of esophagus. *Males* 42 mm long; *females*, length undetermined as no complete specimens could be extracted. Intestinal contents meager, stained green black with bile. (See paragraph on microscopic pathology of this bird, p. 15.)

In addition to the foregoing experiments, in which artificial infestations with *C. contorta* were successfully produced, a considerable number of similar feeding experiments gave negative results. Table 2 summarizes the latter and shows their relation to the experiments previously reported.

TABLE 2.—*Results of attempted experimental transmission of Capillaria contorta*

Year	Source of parasite	Experimental birds			Result
		Species	Number	Stage of development	
1929	Ring-necked pheasant (*Phasianus colchicus torquatus*).	Pekin duck	1	Young	Positive.
		Bobwhite quail A	1	Adult	Do.
		Chicken	19	7 to 30 days	Negative.
1930	Bobwhite quail (*Colinus virginianus*)	do	3	1 to 2 months	Do.
1931	do	Turkey A	1	Adult	Positive.
		Chicken	2	Young	Negative.
1931	Manchurian pheasant (*Crossoptilon manchuricum*).	do	3	do	Do.
1931	California valley quail (*Lophortyx californica*).	Guinea fowl	1	Adult	Do.
		Chicken	2	5 months	Do.
1932	Ruffed grouse (*Bonasa umbellus*)	do	6	Young	Do.
1933	Turkey (*Meleagris gallopavo*)	Duck (cross, Pekin and Mallard).	1	Adult	Do.
		Pigeon	1	do	Do.
		Turkey B	1	do	Positive.
		Chicken	3	Young	Negative.
1934	Turkey B[1] (ante-mortem cultures of droppings).	Crow	1	Adult?	Do.
		Pigeon	1	Adult	Do.
		Turkey C	1	do	Do.
		Turkey	2	do	Do.
		Mallard duck	1	do	Do.
1934	Turkey B[1] (post-mortem cultures from crop).	Guinea fowl	1	do	Do.
		Turkey	2	do	Do.
		Turkey D	1	do	Positive.
1934	Turkey D[1]	Turkey	2	55 days	Negative.
		Guinea fowl	2	12 days	Do.
1934	Oregon mountain quail (*Oreortyx picta*).	Chicken	5	Young	Do.
		Guinea fowl	2	40 days	Do.
		Turkeys E and F	2	22 days	Positive.
		Bobwhite quail B	1	38 days	Do.
1934	Turkey F[1]	Pigeon	3	Adult	Negative.
1934	Bobwhite quail B[1]	do	4	3 adult, 1 young	Do.

[1] Details for this bird are reported on p. 17.

As noted in table 2, one duck, two bobwhite quail, and five turkeys were successfully infected. No chickens, guinea fowls, pigeons, or the one crow were infected.

Attempts to observe the early stages of the invasion of *Capillaria contorta* in the esophageal wall were unsuccessful; included in the negative results in table 2 are several such cases. Prolonged microscopical search of the esophagus of a turkey, killed 9 days after the feeding of *C. contorta* eggs, failed to bring to light young capillarids, although from another turkey (turkey D) fed the same culture at the same time there were collected at a considerably later date fairly large numbers of *C. contorta*. Similarly, a microscopical search of a turkey 22 days after feeding failed to show infestation. In a young pigeon, the last one included in table 2, embryonated eggs of *C. contorta* were found to have passed through the digestive tract unhatched; the bird was killed 28 hours later, and search of the entire digestive tract failed to reveal larvae of this parasite. Additional and more critical studies are needed before negative results can be interpreted. It must be kept in mind that on the one hand the development of the embryos within the eggs of *C. contorta* may not have been normal or complete for infectivity, and that on the other hand experimental birds, reared under the most favorable conditions, such as isolation from sources of infection and provision of strict sanitation, optimum temperature, and plentiful and well-balanced feed, may be less susceptible to infection than birds reared under conditions that tend to lower the birds' resistance. On the other hand, in view of the recent discovery of

Wehr (see p. 7) that *C. annulata* is transmitted by earthworms, these annelids should be looked upon with suspicion as possibly serving as facultative intermediate hosts for *C. contorta*, in which case the infectivity of the larvae might be influenced as it is in the case of *Syngamus trachea* of wild and domestic birds.

CONTROL

No medicinal treatment for the removal of *Capillaria contorta* is known; the usual location of the nematodes, in galleries within the wall of the esophagus, protects them from contact with drugs administered by mouth, so that removal or killing of the worms in situ would be a difficult matter. At present, nursing treatment alone may be recommended for clinical cases, and stringent preventive measures for the protection of other birds which have been, or are to be, on infected premises. Such measures include isolation of young birds from adult birds or areas ranged by them and from wild birds which may be the source of infection; the provision of soft, easily digested feed in sanitary containers which prevent contamination, similar containers also being used for the water supply; the draining and drying of damp or swampy areas; and rotation of runs, with the scraping off of the contaminated surface and the sowing of green feed in runs while not in use.

CAPILLARIA CHARADRII (RUDOLPHI, 1819) TRAVASSOS, 1915

Synonym.—Trichosoma charadrii Rudolphi, 1819.

Rudolphi (*44*) listed this nematode under "Species dubiae", as follows: "Trichosoma Charadrii. Hab. inter *Charadrii minoris* et *Himantopodis* tunicas ventriculi. Cat. Ent. V. mscpt." Later authors listed with this specific name hairworms from the following hosts: *Aegialitis minor*, *Charadrius dubius* (syn., *Aegialitis dubia*), *C. hiaticula*, and *Himantopus himantopus* (syn., *H. melanopterus*).

Travassos (*48*) pointed out that this specific name is a nomen nudum; it is thus an unrecognizable species. However, given the original host species and location, this name would be available for an undescribed capillarid from such hosts and location if anyone describing the nematode wished to attach Rudolphi's name to it.

CAPILLARIA CORVICULA (WASSILKOWA, 1930) BAYLIS, 1931

Synonym.—Eucoleus corvicula Wassilkowa, 1930.

Hosts.—Passeriformes: *Coloeus monedula* (syn., *Corvus monedula*), *Corvus cornix*, *Garrulus glandarius*, *Pica pica*.

Location.—Esophagus.

Description of parasite.—Capillaria (p. 2): Cuticular bands, covered with small verrucous projections, easily visible in both sexes.

Male body filiform and transparent, 12.77 to 15.63 mm long, with maximum width 100μ. Esophagus 410μ to 480μ long. Tail end bursalike, armed with two large papillae. Spicule sheath 420μ to 520μ long, provided with small spines irregularly arranged along its course; spines on proximal extremity smaller and more serrate, followed by larger but less serrate spines, followed by spines increasing in number considerably in proportion to their diminishing and insignificant size at the distal extremity. Width of sheath also varying—200μ to 240μ at proximal, and 120μ at distal, end; sheath contracted to 8μ in region of few spines (that is, proximal part?). Spicule lacking.

Female yellowish, 14.16 to 18.57 mm long, with maximum width 150μ. Esophagus 3.95 to 4.82 mm long. Vulva one-third of body length, or 4.07 to 5.34 mm, from anterior end. Tail end fairly wide, armed with conical papillae; anus terminal. Eggs typically barrel shaped, 60μ by 30μ.

Distribution.—Europe (Union of Soviet Socialist Republics (Sévéro-Dvinsk)) and Asia (Union of Soviet Socialist Republics (Armenia)). The only report of this species is that given by Wassilkowa (in Wassilkowa and Gouchanskaja (*51*)).

Pathology.—Unknown.

Life history.—Unknown; probably similar in a general way to that of *C. contorta* (p. 15).

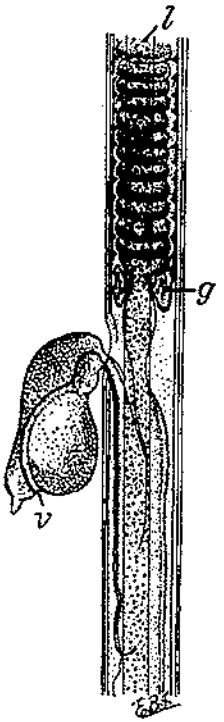

FIGURE 7.—*Capillaria cylindrica.* Region of vulva: *l*, Lateral band; *g*, gland; *v*, vulva. After Eberth, 1863.

CAPILLARIA CYLINDRICA (EBERTH, 1863) TRAVASSOS, 1915

Synonym.—*Trichosoma cylindricum* Eberth, 1863.

Hosts.—Accipitriformes: *Buteo buteo* (syn., *Buteo vulgaris*, *Falco buteo*).

Location.—Esophagus.

Description of parasite.—*Capillaria* (p. 2): *Male* unknown. *Female*, only specimen not fully developed—6 mm long by 54 μ wide in posterior part of body. Body almost equally wide throughout, except for narrower tail end. Cuticle smooth; two lateral bands with bacillary markings, each about one-third body width. Vulva slightly posterior to origin of intestine, with a large bell-shaped (almost balloon-shaped, according to fig. 7) appendix protruding from opening.

Eberth (*20*) placed this description of his new species directly after that of *C. dispar* (see below) from the same host, placing his new species under a heading of Doubtful Species (Zweifelhafte Arten).

Distribution.—Not given (Europe?).

Pathology and life history.—Unknown.

CAPILLARIA DISPAR (DUJARDIN, 1845) TRAVASSOS, 1915

Synonyms.—*Trichosoma contortum* Creplin, 1839, of Dujardin, 1843; *T. dispar* Dujardin, 1845; *Thominx dispar* (Dujardin, 1845) Travassos, 1915.

Hosts.—Accipitriformes: *Buteo buteo* (Syn., *Buteo vulgaris*) and *Falco subbuteo*.

Location.—Tongue, pharynx, and esophagus.

Description of parasite.—*Capillaria* (p. 2): Longitudinal bacillary bands present; according to Eberth (*20*), a ventral band about one-fifth diameter of body and lateral bands about one-half diameter of body, as shown in figure 8; according to Dujardin (*19*), also a dorsal band on anterior part of body.

Male posterior end of body enlarged, with a round superficial elevation on either side of cloacal opening. Spicule sheath with sharp anteriorly directed spines; spicule not observed.

Female about 20 mm long, according to Brüll (*8*). Posterior part of body greatly swollen, narrowed toward the blunt tail end; anus somewhat ventral. Vulva (fig. 9) not prominent, round, situated at beginning of intestine.

Distribution.—Europe (France and Germany).

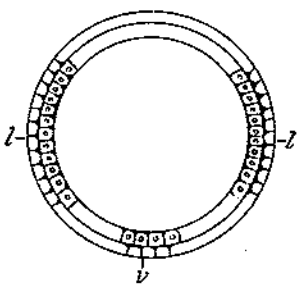

FIGURE 8.—*Capillaria dispar.* Cross section of body: *l*, Lateral band; *v*, ventral band. After Eberth, 1863.

Clinical symptoms and pathology.—Brüll (*8*) reported severe infestation of a passenger falcon (Wanderfalk). The bird was apparently about 5 years old, judging from its feather coat; it had been in captivity for about 5 weeks, at first eating well but later refusing food. Loss of weight followed, so that at the time of death it weighed

only 450 g whereas the normal weight would have been 750 to 800 g. Necropsy revealed that the tongue and the pharyngeal region were swollen as the result of the presence of a large number of nematodes, identified as *Capillaria dispar*, which had burrowed into the mucosa of these regions and of the esophagus. Purulent masses obstructed the passageway into the esophagus, as they protruded from the posterior border of the tongue. Sections of this area showed that in patches the epithelium was completely destroyed so that the underlying connective tissue was exposed; necrotic tissue, loosened, formed the lumpy masses. Between the remaining patches of epithelium were zones rich in nuclei, with abundant leucocytes, a picture of the reaction of the mucosa to destruction. The blood vessels were distended; red blood cells were free in the tissue; a layer of fibrin covered the necrotic mucosa. Deeper layers (connective tissue and musculature) were not invaded by the worms but showed infiltration with leucocytes. Worm eggs were numerous in the masses of destroyed tissue and also in the remaining epithelium.

Life history.—Unknown; probably similar in a general way to that of *C. contorta* (p. 15).

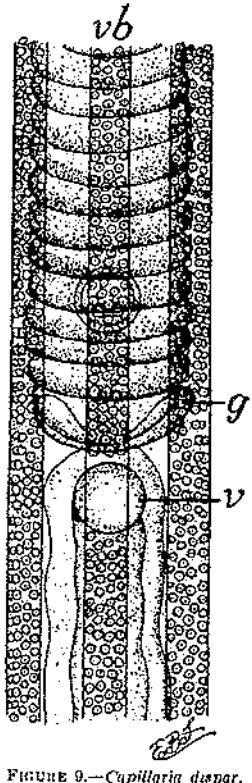

FIGURE 9.—*Capillaria dispar*. Region of vulva: *g*, Gland; *v*, vulva; *vb*, ventral band. After Eberth, 1863.

CAPILLARIA LARICOLA (WASSILKOWA, 1930) BAYLIS, 1931

Synonym.—*Eucoleus laricola* Wassilkowa, 1930.

Hosts.—Charadriiformes: *Hydrochelidon nigra*, *Larus argentatus*, *L. canus*, *L. ridibundus*, *Sterna hirundo*.

Location.—Esophagus.

Description of parasite.—*Capillaria* (p. 2): Body filiform. Cuticular bands, verrucous, conspicuous in female, less easily seen in male.

Male 10.37 to 13.14 mm long by 89μ wide at equator of body. Esophagus 2.54 to 3.33 mm long. Tail end with lobular cuticular projections, two pairs on anterior side and one pair on posterior side, each armed with a pair of papillae and the whole hidden by a bell-shaped bursal structure. Spicule lacking. Spicule sheath 465μ to 595μ long; along its whole length, small spines, obtuse and short at proximal extremity, pointed and 14μ long elsewhere. Spines serrate on anterior third of sheath; less serrate and their distribution more regular on the other two-thirds. Sheath 120μ to 200μ wide at proximal end; dorsal (distal?) end slightly attenuated.

Female 14.62 to 17.48 mm in length by 129μ in maximum width. Esophagus 3.05 to 3.88 mm long. Vulva in anterior third of body, its orifice swollen and simulating lips. Anus terminal. Eggs 56μ to 60μ by 24μ to 28μ.

Distribution.—Asia (Union of Soviet Socialist Republics (Siberia)).

Pathology.—Unknown.

Life history.—Unknown; probably similar in a general way to that of *C. contorta* (p. 15).

CAPILLARIA LOPHORTYGIS BAYLIS, 1934

Host.—Galliformes: *Lophortyx californica*.

Location.—Crop.

Description of parasite.—*Capillaria* (p. 2): Cuticle, at least toward extremities, with fine transverse striations; bacillary bands present. Posterior portion of esophagus composed of very large cells, up to 400μ long.

Male 28 to 30 mm in length by 80μ to 90μ in maximum width. Esophagus 5.8 to 6.5 mm long. Tail end (fig. 10) with two pairs of papillae, a small preanal and a larger postanal papilla on each side. Spicule sheath not seen extruded; its hinder portion, in inverted condition, lined with very minute spines. Spicule apparently lacking.

Female 37 to 39 mm in length by 160μ to 170μ in maximum width. Esophagus 7.7 to 8.8 mm long. Rectum 200μ to 300μ long. Vulva at level 150μ to 200μ behind junction of esophagus and intestine. Eggs averaging 45μ by 22μ, very uniform in size when fully formed; shell thick, apparently sparsely punctate.

FIGURE 10.—*Capillaria lophortygis*. Tail of male, lateral view, showing papillae. After Baylis, 1934.

Distribution.—Australia (in bird imported from America).

Pathology.—Unknown.

Life history and control.—Unknown; probably similar in a general way to those of *C. contorta* (pp. 15, 19).

Although agreeing with the general principle that it is better to make a new species than to confuse the records by inclusion in them of misidentified species, the writer feels that *C. lophortygis* is not sufficiently well differentiated to establish it as a valid species. The only character specified by Baylis' (*5*) description by which it can be separated from *C. contorta* is the apparent absence of a spicule in *C. lophortygis*, which according to Baylis (*4*) himself, as noted on page 3, and according to the writer's observations in connection with *C. contorta* (p. 12), is not convincing evidence. Since *C. contorta* has a wide host range, including a number of Galliformes, the writer believes that *C. lophortygis* will prove to be a synonym of *C. contorta*.

CAPILLARIA OBTUSIUSCULA (RUDOLPHI, 1819) TRAVASSOS, 1915

Synonym.—*Trichosoma obtusiusculum* Rudolphi, 1819.

Hosts.—Balaericiformes: *Megalornis grus* (syn., *Ardea grus*, *Grus grus*). Charadriiformes: *Vanellus vanellus* (syn., *V. cristatus*).

Location.—Gizzard, between the corneous and muscular layers of wall, and, according to Diesing (*18*), in intestine also.

Description of parasite.—*Capillaria* (p. 2):

Male with spicule sheath 600μ long, swollen and doubled at extremity (fig. 11); Dujardin (*19*) comments that this illustration by Mehlis (*33*) indicates that the nematode belongs to another genus, a suggestion with which the author cannot agree as it appears possible for the spicule sheath of any species of *Capillaria* to assume this general appearance when extruded; sheath unarmed, according to Diesing (*18*, *v. 2*). Spicule 800μ long, recurved.

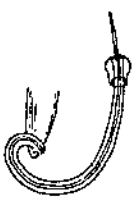

FIGURE 11.—*Capillaria obtusiuscula*. Spicule and spicule sheath, everted. After Mehlis, 1831.

Female 27 to 40 mm long. Vulva situated toward first fifth of body length; tail end somewhat obtuse, recurved.

Distribution.—Europe (Austria (Vienna Museum)).

Pathology.—Unknown.

Life history.—Unknown; probably similar in a general way to that of *C. contorta*, p. 15.

CAPILLARIA PERFORANS KOTLÁN AND OROSZ, 1931 [6]

Host.—Galliformes: *Meleagris gallopavo*.

Location.—Esophagus, including crop, under mucosa.

Description of parasite.—*Capillaria* (p. 2): Posterior end of body of increasing thickness until 5 mm from tail end, after which point gradually narrowing; the last 400μ of length suddenly narrower, coming to a point at end. Cuticle with both longitudinal and transverse striations, the longitudinal ones 2μ to 2.5μ, and the transverse ones 3μ, distant from one another. Longitudinal bands also

[6] Description by Orosz (*38*) translated from the Hungarian with the aid of F. A. Csonka, Bureau of Chemistry and Soils, U. S. Department of Agriculture.

present, extending from head end to tail end, with markings made up of polygonal cells; in middle of each cell a small attachment, the fundus of this facing the cell and the other end toward or in cuticle. Esophagus comparatively short.

Male 37 to 44 mm long (average 39.6 mm). Width at head end, 12μ; 2 mm from head end, 60μ; at end of esophagus, 75μ; 2 mm from tail end, 92μ; at tail end, 30μ. Lateral (?) longitudinal band at end of esophagus, 30μ wide, thus one-half body width; posterior to this point the band becoming narrower, at tail end being 11μ, or one-fifth body width. Esophagus 7.35 to 8.30 mm long (average, 7.76 mm), thus one-fifth to one-sixth body length. Pear-shaped cell at posterior end of esophagus, narrower than in corresponding structure in female. Tail end with two outstanding dorsolateral prominences, touching each other dorsally, on which two circular dorsal projections or outgrowths, measuring 14μ to 18μ in diameter, and with a flatter ventral prominence not extending so far posteriorly as the others. Spicule sheath usually drawn into body, 11μ to 12μ wide throughout most of its length; caudal end notched at edge; on the surface thornlike spines, 1μ long, generally directed toward head, not arranged in any orderly fashion, the largest number and largest in size occurring about 120μ from end, posterior to that point rare, and end apparently entirely devoid of them. Spicule 14 to 16 mm long by 1μ to 2μ wide, ending in fine point, extruded between dorsolateral prominences, supported by the ventral prominence.

Female 50 to 86 mm long (average, 71.8 mm). Width at head end, 14μ; 2 mm from head end, 71μ; at level of vulva, 120μ; 5 mm from tail end, 177μ; 2 mm from tail end, 174μ; at tail end, 35μ. Lateral (?) longitudinal bands very wide, front (dorsal) band taking up from the entire width to one-sixteenth of width (correct translation?). Esophagus 9.9 to 11.76 mm long (average, 10.52 mm), thus one-seventh body length. A pear-shaped cell, about 70μ long, posterior to cells of esophagus; esophagus with an extension 50μ to 70μ (long?) at junction with intestine. Anus directly at end and exactly in center of body. Vulva in anterior part of body, 100μ to 120μ posterior to end of esophagus, thus about one-seventh total body length from head end; projecting very slightly above surface of body; opening circular, 17μ wide, directed slightly anteriorly. Uterus 40μ thick at origin, uneven, crossing intestine several times; its wall, 11μ thick at origin, attaining thickness of 21μ. Eggs 41μ to 51μ by 21μ to 25μ, placed singly for a considerable distance, later in several rows, in no apparent order, pale yellow in color, slender, with no earlike projections but with relatively very small plugs.

Distribution.—Europe (Hungary).

Pathology.—The nematodes were found by Kotlán and Orosz (*29*) in only one turkey; there were 13 females and 11 males, and considerable pathological change had taken place in the mucosa.

Life history and control.—Unknown; probably similar in a general way to those of *C. contorta* (pp. 15, 19).

As noted in the discussion of *C. contorta* (p. 11), the length of the spicule of *C. perforans* is at present the principal character differentiating these two species and, in view of the paucity of data on the length of the spicule of *C. contorta* and the difficulty of determining the same, the writer feels that the validity of *C. perforans* has not been established. The possibility that it is a synonym is noted for further consideration.

CAPILLARIA TRILOBA (LINSTOW, 1875) TRAVASSOS, 1915

Synonyms.—*Trichosoma trilobum* Linstow, 1875; *Thominx triloba* (Linstow, 1875) Travassos, 1915.

Host.—Charadriiformes: *Vanellus vanellus* (syn., *V. cristatus*).

Location.—Gizzard, under corneous lining.

Description of parasite.—*Capillaria* (p. 2): Longitudinal bands present; dorsal band wide, eleven-fifteenths of body width; ventral band narrow, five-eighteenths of body width; no lateral bands observed. Bacillary cells very thickly arranged on dorsal band, with a glistening middle point in a circular outline of each, on the cuticle; in ventral band, bacillary cells less numerous, their points in the cuticle much finer and without surrounding circle.

Male 8.7 mm in length by 60μ in greatest width. Ratio of length of esophageal to postesophageal portion of body, 1:3. Tail end rounded ventrally, with two

small rounded lateral lobes (fig. 12), each carrying a small papilla. Spicule sheath, in retracted condition, 430μ long, thickly covered with spines; spicule not observed.

Female 23 mm in length by 120μ in greatest width. Ratio of length of esophageal to postesophageal portion of body, 7:26. Vulva 200μ posterior to end of esophagus. Eggs 70μ to 74μ by 29μ to 31μ.

Distribution and incidence.—Europe (Germany (Hameln)) and Asia (Union of Soviet Socialist Republics (Russian Turkestan (Aoulié-ata))). Skrjabin (*46*) found this species in 8 of 13 birds, or 62 percent, in the latter area.

Pathology.—Unknown; Linstow (*30*) found masses of the nematodes under the gizzard lining.

Life history.—Unknown; probably similar in a general way to that of *C. contorta* (p. 15).

SUMMARY

The status of present knowledge of 11 avian species of *Capillaria*, occurring in parts of the digestive tract anterior to the intestines, is considered. One species, *C. charadrii*, is a nomen nudum and, therefore, unrecognizable. A morphological description of each of the other 10 species is given. The writer has concluded that external characters rather than an internal character, such as the spicule, are of primary importance in the recognition of *C. contorta*, and on that basis has allocated as that species a capillarid found by her in the esophagus, including the crop, of a considerable number of gallinaceous, and a few anseriform, birds. It is pointed out that the present descriptions of two recently created species, *C. lophortygis* and *C. perforans*, are inadequate for satisfactory differentiation of them from *C. contorta*.

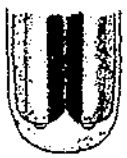

FIGURE 12.—*Capillaria triloba*. Male tail. After Linstow, 1875.

Three species, namely, *C. annulata*, *C. contorta*, and *C. dispar*, are known to produce severe pathological effects, which are described. Of these species, the first two have appeared to be of increasing economic importance in poultry and game birds in the United States during the past decade. Attempts to produce artificial infestations with *C. annulata* were unsuccessful, but experimental proof of the complete life cycle of *C. contorta* was obtained. Vermiform embryos in the eggs in cultures appeared to be fully developed in 27 to 40 days. Their infectivity was demonstrated as early as 46 days and as late as 11 months after culturing; complete development in the bird host, with the capillarid eggs passing in the droppings, occurred in 45 to 54 days. Six turkeys and two bobwhite quail were experimentally infected in such well-controlled experiments that no doubt existed as to the origin of the parasites; the cultures used for these experiments included strains of *C. contorta* from the bobwhite quail, mountain quail, ring-necked pheasant, and turkey. In addition, specimens of *C. contorta* from a domestic duck, a young Pekin, were thought to have developed as the result of an artificial feeding with a culture of the pheasant strain, although the presence of a few specimens of the parasite in a control duck raised the question as to the origin of the infestations. Later attempts to infect ducks were unsuccessful, possibly due to the age or race of the birds used; negative results were obtained also in several cases with turkeys. Only negative results followed repeated attempts to infect chickens, guinea fowls, and pigeons, and a single attempt to infect a crow.

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28

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