SUSCEPTIBILITY OF CHICKENS TO THE NEMATODES, *SYNGAMUS TRACHEA* AND *S. MERULAE*

by

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INTRODUCTION

Syngamus trachea (Montagu, 1811) Siebold, 1836, and Syngamus merulae Baylis, 1926, are nematodes found in the tracheae of avian hosts. S. trachea takes its specific name from the location of the parasite in its host; S. merulae was named after the species of bird from which it was first obtained by Baylis (1926), i.e. Turdus merula, the European blackbird. In both of these species, the male remains permanently attached to the female by the copulatory bursa (Figures 1 and 2), hence the name Syngamus (Gr. syn = together; gamos = marriage).

S. trachea is very important economically because of the disease "gapes" which it causes in chickens, turkeys, and many game birds. Heavy infection by this worm causes the host to gape for air (Figure 3) and may cause asphyxiation due to blockage of the trachea. S. trachea and S. merulae are commonly called "gapeworms."

A controversy exists as to whether wild birds act as reservoir hosts for S. trachea infecting poultry. Madsen (1950) considered S. merulae and S. trachea synonymous, while others (Lewis, 1928; Goble and Kutz, 1945) believed the two were distinct species.

Naturally infected grackles harboring S. trachea and naturally infected robins harboring S. merulae constituted the initial source of gapeworms used in this study. A

series of feeding experiments involving both direct and indirect (via earthworms) methods of infection was undertaken to determine the susceptibility of chickens to eggs or to juveniles of both these species. Experiments involving serial passage of S. trachea from chicken to chicken were conducted to study the varying susceptibility of this host. The immune response of chicken hosts after exposure to either S. trachea or S. merulae juveniles was also investigated.

LITERATURE REVIEW

Syngamus trachea

S. trachea was first reported in poultry by Wiesenthal (1799), who referred to it as a "worm of poultry". Later, it was recovered from pheasants and partridges by Montagu (1811) who named it *Fasciola trachea*, apparently under the impression that it was a trematode. Siebold (1836) was the first investigator to recognize the worm as a nematode and to describe its morphology. Since it did not fit into any previously described genera of nematodes, he established the genus *Syngamus* and named the species *Syngamus trachealis*. Chapin (1925) modified the specific name to *trachea*, and most investigators now recognize the species as *Syngamus trachea*.

Most recent reports of *S. trachea* outbreaks in poultry have come from Czechoslovakia (Zavadil and Dyk, 1966) and from Hungary (Varga, 1967). It has been reported from nine avian orders which testifies to its lack of host specificity (Appendix A). Goble and Kutz (1945) first reported it in grackles, but apparently it has never been used in feeding experiments with this host.

Klee (1903), Lewis (1925, 1926b), and Elton and Buckland (1928) associated the incidence of *S. trachea* in passeriform birds to outbreaks of "gapes" in gallinaceous birds. To clarify the relationship between infections in

wild birds and those in poultry, Lewis (1928) suggested exposing chickens to eggs from gapeworms of various wild birds. Taylor (1928), using intrauterine eggs, reported difficulty in directly transmitting gapeworm infections from starlings to chickens. Morgan and Clapham (1934) reported occasional success in transmitting S. trachea infections from rooks and pheasants to chickens, but obtained negative results when they attempted to infect chickens with S. trachea intrauterine eggs from starlings and partridges. Clapham (1935), however, succeeded in transmitting S. trachea from starlings to chickens when the earthworm, Eisenia foetida, obtained from nature was used as an intermediate host.

Syngamus merulae

Most criteria for differentiating species within the genus Syngamus have been found to be highly variable (Chapin, 1925; Lewis, 1928; and Madsen, 1950). Because of this high variability in morphological characteristics, some investigators feel that many of the species within the genus Syngamus are synonyms of S. trachea. Appendix B summarizes the species of Syngamus reported from avian hosts.

There has been some question as to the taxonomic status of the gapeworm from robins. Manter and Pinto (1928) first described this gapeworm and named it Syngamus tenuispiculum on the basis of the structure of the copulatory bursa. How-

ever, they noted its similarity to S. merulae Baylis, 1926, on the basis of its size and of measurements of buccal capsule, egg, and spicules. In a footnote they mentioned that Lewis' (1928) work on the variability of the copulatory bursa in S. trachea suggested S. tenuispiculum to be synonymous with S. trachea. Ripple (1941) considered gapeworms that he collected from robins to be S. trachea. Goble and Kutz (1945) obtained one pair of gapeworms that Ripple had worked with and identified it, as well as those they had recovered from robins, as S. merulae. They concluded that S. tenuispiculum is a synonym of S. merulae, but that it is not synonymous with S. trachea. A search of the literature indicates that no other investigations have been conducted on the robin gapeworm.

MATERIALS AND METHODS

Natural Infections

Naturally infected common grackles (Quiscalus quiscula) livetrapped at Iowa Lakeside Laboratory, Milford, Iowa, during the summer of 1968 were the initial source of gapeworms for experimental studies on Syngamus trachea. Syngamus merulae used in experimental studies were obtained from naturally infected robins (Turdus migratorius) shot or collected as road kills near Iowa Lakeside Laboratory during the same period. Of the 98 grackles and 34 robins examined, 10 grackles and 11 robins were found to harbor gapeworms.

Birds were taken to the laboratory where tracheae were removed and placed in avian ringer's solution. Gapeworms were removed from the tracheae by carefully dissecting away the tracheal cartilages with microforceps. Some gapeworms were fixed in hot glyerine-alcohol and mounted in glyerine jelly for morphological study, and others were sacrificed for eggs.

Experimental Infections

Eggs from gapeworm uteri and from host feces were used to experimentally infect intermediate and definite hosts. To obtain intrauterine eggs, uteri were removed from gapeworms and eggs were expressed using microforceps. Eggs were incubated at room temperature for 10 days as suggested by

Wehr (1937), after which time juveniles could be seen within them. Eggs were then either fed to experimental hosts or were mixed in an earthworm-rearing medium for subsequent exposure of earthworms (Lumbricus terrestris).

Fecal eggs were separated from the feces of grackles and chickens experimentally infected with S. trachea and from robins experimentally infected with S. merulae. Separation involved a 1:5 dilution of feces with tap water, followed by gentle agitation of the solution and subsequent vacuum filtration through a 150-mesh copper screen sieve. The filtrate was diluted 1:5 with tap water and allowed to stand in 2-liter graduates for 6 hours. Five milliliters of sediment were layered onto 10 ml of a saturated NaCl solution in a 15-ml centrifuge tube and centrifuged at 1700 rpm for 10 minutes (centrifuge temperature 4 C). The top 6 ml was diluted 1:5 with tap water and placed in petri plates at room temperature until eggs were embryonated (about 22 days), after which time they were stored in the refrigerator.

Earthworms (Lumbricus terrestris) reported to be from Canada were obtained from commercial sources. Three worms of each dozen were examined for nematode juveniles by making body-wall press preparations and examining them at 100X. No nematodes were found in these earthworms. Earthworms used in experimental studies were reared at 15-20 C in boxes (9 x 9 x 16 cm) containing 400 gm of Buss-bedding (Buss

Manufacturing Co., Lanark, Ill.). Three worms were reared in each box.

Earthworms were exposed by adding 500-1,000 embryonated intrauterine eggs or 2,000-10,000 embryonated fecal eggs to the medium in which they were reared. Earthworms were exposed for 10 days and then were fed to hosts.

Avian hosts were exposed via the direct cycle by feeding them 0.5 cc of a water suspension of either embryonated intrauterine eggs or embryonated fecal eggs. Dosages were estimated by counting the number of eggs in a 0.5 cc sample of these suspensions.

Avian hosts were exposed via the indirect cycle by feeding them juveniles developed in earthworms. The approximate number of juveniles fed to hosts was determined by making press preparations of pieces of earthworm body wall and by counting the juveniles at 100X, as suggested by Wehr (1937).

Experimentally infected grackles and robins were reared in the laboratory to provide a readily available source for intrauterine and fecal eggs. Four grackles, livetrapped at Ames, Iowa, were reared on cracked corn for 23 days, during which time their feces were periodically examined for gapeworm eggs. No eggs were found in the feces and on the 24th day these hosts were fed about 500 embryonated S. trachea intrauterine eggs that had been stored in the refrigerator

16-45 days. Eggs were first noted in the feces of all these hosts 17-20 days after exposure. Three nestling robins were reared on dog food for 21 days, during which time their feces were periodically examined for gapeworm eggs. No eggs were found in the feces, and on the 22nd day these hosts were fed about 500 embryonated S. merulae intrauterine eggs that had been stored in the refrigerator 8-26 days. Feces of these hosts were examined from the 12th day after exposure until eggs appeared (17-19 days). All robins developed infections.

Chickens used in experimental studies were obtained from two sources. Male chickens (parents: Rhode Island Red x White Rock) were obtained from DeKalb Hatchery, Roland, Iowa, and female chickens (White Leghorns) were obtained from the Poultry Science Department of Iowa State University. Two types of diet were fed to experimental hosts. Most were reared only on scratch grain obtained locally. A selected number were reared on a more balanced diet (Wayne's 26% Egg Balancer, Allied Mills Inc., Chicago, Ill.) to determine if worm burdens differed from hosts fed only scratch grain.

LIFE CYCLES

A direct and an indirect life cycle (via invertebrate hosts) has been reported for S. trachea. Appendix C summarizes published data on experimental intermediate hosts used in transmitting S. trachea infections. In the direct cycle, non-embryonated eggs released by the female are coughed up and swallowed, then pass out with the feces. According to most investigators, juveniles are ingested by avian hosts with their food or water. Juveniles penetrate the gut wall and are carried via the blood to the liver (Wehr, 1937). From the liver, they are carried via circulatory pathways to the lungs where they undergo third and fourth moults to form fifth-stage juveniles (Clapham, 1939a). These become adults without further moults and mate in the lungs. After males and females have united, they migrate up the lung passageways to the trachea where they mature. The indirect cycle involves the same route (Baruš, 1965) except that various invertebrate hosts (including earthworms) may ingest fecal eggs. Such eggs hatch in the intermediate host and live within it as third-stage juveniles (Clapham, 1939a). When this host is ingested by the definitive avian host, development similar to that noted in the direct cycle takes place.

No investigations have been conducted on the life

cycle of S. merulae, a species reported from the European blackbird and the robin.

EXPERIMENTAL STUDIES ON SUSCEPTIBILITY OF CHICKENS TO *SYNGAMUS TRACHEA* FROM GRACKLES

Numerous experiments were conducted on the susceptibility of chickens to *S. trachea* derived from naturally and experimentally infected grackles. These experiments included male chickens 1 or 14 days old, 1-day-old female chickens, and 1-day-old male chickens fed either scratch grain or the more balanced diet noted in materials and methods.

Day-Old Male Hosts

Experiments on 267 1-day-old male chicks were conducted to determine their susceptibility to *S. trachea* from the grackle. Experiments considered the effect of certain factors on susceptibility, namely: 1) source of eggs (host feces and gapeworm uteri); 2) method of exposure (direct cycle using eggs, indirect cycle using juveniles); 3) serial passage of infections from chicken to chicken; and 4) dosage size.

Chicks were exposed by feeding them: 1) embryonated eggs recovered from the feces of experimentally infected grackles; 2) embryonated eggs recovered from the uteri of gapeworms obtained from grackles; 3) juveniles in earthworm pieces, the earthworms having been previously exposed to fecal eggs; and 4) juveniles in earthworm pieces, the earthworms having been previously exposed to uterine eggs. In

serial passage experiments, only intrauterine eggs and juveniles were used. Dosage size in all experiments varied from approximately 150-450 eggs or juveniles.

All eggs obtained from host feces and used in direct transmission studies were stored under refrigeration 5-14 days and were then incubated for approximately 22 days at room temperature before being fed to 1-day-old male chicks. Treatment of fecal eggs used in indirect transmission studies involving serial passages varied; those used for first and second passages were not refrigerated, and those used in third, fourth, and fifth passages were refrigerated for 15, 17, and 13 days respectively (depending upon availability of materials), before being incubated at room temperature prior to exposure of hosts. Storage under refrigeration did not appear to influence viability of fecal eggs, i.e., a similar mean worm burden occurred in second-passage experiments (involving no refrigeration) as in third-, fourth-, and fifth-passage experiments (involving refrigerated fecal eggs).

Uterine eggs used in both direct and indirect transmission experiments were not refrigerated. These eggs were incubated at room temperature immediately after dissection from gapeworm uteri. When active juveniles were noted within them (after approximately 10 days) they were either fed to chickens or were mixed with an earthworm-rearing

medium prior to exposure of intermediate hosts (earthworms).

In all studies involving juveniles, earthworms were exposed to embryonated eggs (uterine or fecal) for 10 days and were then fed to hosts (see Materials and Methods).

Results and Discussion

No previous studies on the susceptibility of chickens to the grackle gapeworm have been conducted. My studies (Table 1) indicate that 1-day-old male chickens are suitable hosts for S. trachea recovered from grackles and that the source of infective material affects the susceptibility of these hosts. Infections can be transmitted using either intrauterine eggs or juveniles developed from intrauterine and fecal eggs. In contrast, attempts to transmit infections using eggs recovered from host feces were wholly unsuccessful. Other investigators (Walker, 1886; Morgan and Clapham, 1934; Gräfner et al., 1964) have assumed a direct cycle to account for infections transmitted from chicken to chicken, but experimental data to support this view have been based on the use of intrauterine, not fecal eggs. My data indicate that a direct cycle (using fecal eggs) does not occur when one attempts to transmit S. trachea infections from grackles to chickens. Studies using eggs recovered from the feces of naturally infected chickens should be undertaken to completely explore the problem of the likelihood of a direct life cycle of S. trachea in chickens.

Table 1. S. trachea recovered from male chicks exposed when one day old as related to: 1) egg source; 2) exposure method; 3) serial passage of infection; and 4) dosage size

Egg source	Exposure method[b]	Passage[c]	No. hosts Exposed	No. hosts Infected	Avg no. pairs recovered[a] Approx. dosage size 151-250	251-350	351-450
fecal	eggs	1st	42	0	-	0.0(21-0)	0.0(21-0)
intrauterine	eggs	1st	24	24	5.5(12-12)	6.6(6-6)	6.8(6-6)
		2nd	24	11	5.3(16-3)	-	7.0(8-8)
		3rd	24	0	-	0.0(8-0)	0.0(16-0)
fecal	juveniles	1st	10	10	5.5(7-7)	10.8(3-3)	-
		2nd	15	15	12.2(8-8)	20.0(5-5)	15.0(2-2)
		3rd	15	15	10.6(7-7)	18.8(6-6)	15.0(2-2)
		4th	20	20	18.8(8-8)	14.0(8-8)	18.0(4-4)
		5th	12	12	12.8(8-8)	15.5(4-4)	-
intrauterine	juveniles	1st	20	20	5.6(10-10)	9.0(10-10)	-
		2nd	24	24	12.8(9-9)	19.6(6-6)	13.2(9-9)
		3th	20	16	5.0(7-3)	5.9(6-6)	6.5(7-7)
		4th	17	3	0.0(10-0)	2.0(7-3)	-

[a]In parentheses, no. hosts exposed - no. hosts infected.

[b]Eggs = direct cycle; juveniles = indirect cycle (in earthworm intermediate host).

[c]1st passage = infection passed from grackles to chickens; 2nd and subsequent passages = infection passed from chicken to chicken.

Exposure method, serial passage of infections, and dosage size were also found to have an effect on the susceptibility of 1-day-old male chicks (Table 1). Significantly fewer worms were recovered from hosts fed intrauterine eggs as compared to those hosts fed juveniles in earthworm pieces.[1] Wehr (1937), Clapham (1934), and Baruš (1965) reported comparable results when they transmitted chicken gapeworm infections either by feeding intrauterine eggs to chickens or by feeding juveniles developed from intrauterine eggs (in earthworms) to chickens. My investigations indicate that no significant difference in worm burden was noted in infections transmitted from grackles to chickens (first passage) by juveniles developed from either intrauterine eggs or fecal eggs.[2]

Pronounced differences in susceptibility were noted when infections involving either intrauterine eggs or juveniles were serially transmitted from host to host (Table 1). All 24 chicks having ingested intrauterine eggs developed infections in first-passage experiments, whereas the number infected on the second passage declined with only 11 of 24 infected; and on the third passage none of 24 was positive. In the laboratory, although transmission of

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[1] "t" test of equal means could not be accepted at 5% level of significance.

[2] "t" test of equal means could not be rejected at 5% level of significance.

chicken gapeworm infections using intrauterine eggs is commonly employed, apparently no studies to ascertain the effect of serial passage of such infections using intrauterine eggs have been reported. Data from my experiments (Table 1) indicate that infections transmitted from chicken to chicken using intrauterine eggs are gradually lost. Hosts from these passages were reared under similar conditions, and treatment of eggs was similar in all instances, having been pooled after embryonation. No wholly suitable explanation can be offered for the decreased susceptibility noted on serial passage of infections when intrauterine eggs were used. A decrease in susceptibility generally occurred when juveniles developed from intrauterine eggs were used to serially transmit infections. In contrast, when fecal eggs were the source for juveniles, the degree of infection remained fairly constant on passage of the infection and there was no decrease in the number of hosts infected (Table 1). In all infections involving the indirect cycle there was an approximate twofold increase in worm burden between the first- and second-passage infections (Table 1). Taylor (1928) reported comparable results when she transmitted S. trachea (initially recovered from starlings) from chick to chick and suggested that the parasite was physiologically adapting to chickens. My work tends to support her view that gapeworms recovered from wild birds may also physio-

logically adapt to chickens. In many instances, worm burden increased with an increase in the number of eggs or juveniles ingested.

Additional experiments noted below were conducted to investigate effects of host age, sex, and diet on certain Syngamus infections.

14-Day-Old Male Hosts

To determine if 14-day-old chickens differed from 1-day-old chickens in their susceptibility to S. trachea when fecal egg and juveniles (developed from fecal eggs in earthworms) were used, selected experiments were undertaken involving 85 14-day-old hosts (Table 2). Twenty-six such hosts were each fed eggs recovered from the feces of experimentally infected grackles (eggs were stored under refrigeration 40-60 days prior to incubation at room temperature). To investigate the susceptibility of 14-day-old hosts to juveniles developed from fecal eggs in earthworms, 25 chickens were fed juveniles developed from fecal eggs that had been stored in the refrigerator 23-34 days. To ascertain the effect of serial passage on the susceptibility of 14-day-old hosts, 24 additional chickens were fed juveniles in earthworm pieces, the earthworms having been previously exposed to eggs recovered from the feces of the 25 chickens noted previously (these eggs were refrigerated 13 days prior to incubation).

Table 2. *S. trachea* recovered from male chickens exposed when 14 days old to fecal eggs and juveniles developed from fecal eggs in earthworms[a]

Exposure method	Passage	No. hosts Exposed	No. hosts Infected	Avg no. pairs recovered Approx. dosage size 151-250	Avg no. pairs recovered Approx. dosage size 251-350
eggs	1st	26	0	0.0(13-0)	0.0(13-0)
juveniles	1st	25	25	5.2(12-12)	9.6(13-13)
	2nd	34	34	14.3(15-15)	23.2(19-19)

[a]See Table 1 for explanation of column headings.

Attempts to infect 14-day-old male chickens using fecal eggs were unsuccessful (Table 2), as were attempts to infect 1-day-old male chickens using fecal eggs (Table 1). The mean worm burden of first- and second-passage hosts exposed when 14 days old to juveniles in earthworm pieces (Table 2) was compared statistically to the mean worm burden of comparable hosts exposed when one day old (Table 1). This comparison indicated that there was no basis for assuming that the means differed significantly,[1] i.e., it could not be said that the age of these hosts significantly affected worm burden. Worm burdens of second passage 14-day-old hosts were more than twice as heavy as those recovered from first-

[1]"t" tests of equal means could not be rejected at the 5% level of significance.

passage hosts, results approximating those obtained when 1-day-old hosts were used. Results of these experiments using 14-day-old hosts did not differ significantly from results obtained with 1-day-old chicks.

Day-Old Female Hosts

To ascertain if host sex was an important factor in certain S. trachea infections, selected experiments were undertaken using 29 one-day-old female chickens (Table 3). Fourteen hosts were fed juveniles developed from eggs recovered from the feces of grackles, and 15 chicks were fed juveniles developed in the uteri of gapeworms infecting grackles. Fecal eggs and intrauterine eggs had been refrigerated 20 and 6 days, respectively.

Table 3. S. trachea recovered from female chickens exposed when one day old to juveniles developed from fecal and intrauterine eggs in earthworms

Egg source (grackle)	No. hosts		Avg no. pairs recovered[a]	
	Exposed	Infected	Approx. dosage size 151-250	251-350
feces	14	14	6.1(7-7)	9.5(7-7)
gapeworm uteri	15	15	5.4(8-8)	8.0(7-7)

[a]In parentheses no. hosts exposed - no. hosts infected.

Statistical comparison of worm burdens harbored by 1-day-old male and 1-day-old female chicks fed juveniles developed from fecal eggs and similar comparison of 1-day-old male and female hosts fed juveniles developed from intrauterine eggs indicated that the "t" test hypothesis of equal means could not be rejected at the 5% level of significance.

Type of Host Diet

All chickens used in the studies noted above were reared on scratch grain. Further experiments were conducted using 24 one-day-old male chicks to determine if diet affected host susceptibility (Table 4). In these experiments, juveniles developed from grackle fecal eggs in earthworms were employed. These eggs had been stored under refrigeration

Table 4. Effect of selected diets on average number *S. trachea* recovered from two groups of chickens exposed to juveniles developed from fecal eggs in earthworms

Host diet	No. hosts		Avg no. pairs recovered[a]	
	Exposed	Infected	Approx. dosage size 151-250	251-350
scratch grain	12	12	5.3(6-6)	8.9(6-6)
egg balancer[b]	12	12	5.6(6-6)	9.3(6-6)

[a]In parentheses no. hosts exposed - no. hosts infected.

[b]Wayne's 26% Egg Balancer (Allied Mills, Chicago, Ill.).

for six months prior to embryonation. Twelve chickens were fed juveniles and were reared entirely on a nutritionally unbalanced diet consisting entirely of scratch grain. Another 12 chicks were fed juveniles and were on a more balanced diet (Wayne's 26% Egg Balancer, Allied Mills Inc., Chicago, Ill.).

All chicks were infected regardless of type of diet, and a "t" test comparison of mean worm burden of these hosts indicated that diet had no effect on host susceptibility.

EXPERIMENTAL STUDIES ON SUSCEPTIBILITY OF CHICKENS TO *SYNGAMUS MERULAE* FROM ROBINS

One hundred-sixteen male chicks were used in two sets of experiments to determine the susceptibility of these hosts to *S. merulae* initially collected from naturally infected robins.

The first set of experiments involved intrauterine eggs, refrigerated 10-132 days after embryonation. Sixteen 1-day-old chicks were each fed approximately 450-500 intrauterine eggs. Six additional 1-day-old chicks were each fed about 500 eggs and four days later an additional dose of 300 eggs. Another 18 chicks were each fed 200-400 eggs on each of six consecutive days commencing when the chicks were 1 day old.

The second set of experiments involved juveniles developed in earthworms, the earthworms having been previously exposed to eggs recovered from the feces of experimentally infected robins. Eggs used to infect earthworms had been stored (10 days to 10 months) in the refrigerator. Fifty-two 1-day-old chicks were each fed 60-1,400 juveniles. Six additional 1-day-old chicks were each fed 300-450 juveniles and were given an additional dose of 300-500 juveniles when they were 5 days old. Another 18 chicks were each fed 75-275 juveniles on each of 4 consecutive days commencing from the time hosts were 1 day old.

Methods used in estimating dosage size and exposing definitive and intermediate hosts have been noted previously (Materials and Methods).

None of the chicks exposed in the above experiments developed S. merulae infections regardless of dosage size, age of host, or method of exposure used. Walker (1886) and Ripple (1941), however, reported limited success in the transmission of robin gapeworm infections to chickens. Reference to their published accounts indicates that they used earthworms obtained from nature as experimental intermediate hosts. Possibly these earthworms were naturally infected with S. trachea juveniles. Furthermore, Ripple's description of adults from robins indicated the presence of a cuticularized buccal rim, suggesting that he probably was dealing with S. trachea. Madsen (1950) made S. merulae synonymous with S. trachea. Madsen's decision to place S. merulae in synonymy with S. trachea was based on finding S. trachea that lacked a cuticularized buccal rim in naturally infected hosts. I have noted that S. trachea recovered from experimentally infected hosts lack a cuticularized buccal rim until they are about 14 days old, after which time this rim develops.

Both morphological and experimental data provide compelling reasons for maintaining S. merulae as a separate species. S. merulae lacks a cuticularized buccal rim

(Figures 5 and 7), whereas it is present in 2-week-old S. trachea (Figures 4, 6, and 8). Rizhikov (1949b) and Lengy (1969) also separated S. merulae from S. trachea on the basis of the absence of this rim in the former. My data show that S. merulae will not infect chickens, supporting the view that it should be maintained as a separate species distinct from S. trachea.

EXPERIMENTAL STUDIES ON ACQUIRED IMMUNITY OF CHICKENS TO *SYNGAMUS TRACHEA* FROM GRACKLES

Experiments on 93 chickens were conducted to determine if exposure of these hosts to either *S. trachea* or *S. merulae* juveniles could provide protection against a challenge dose of *S. trachea* juveniles. One- and 14-day-old male hosts were exposed to juveniles (in earthworms) and 62 days later were given a challenge dose of *S. trachea* juveniles (Table 5). All juveniles were obtained by exposing earthworms to eggs (refrigerated about 3 months prior to embryonation) recovered from the feces of grackles and robins experimentally infected with *S. trachea* and *S. merulae*, respectively.

Chi-square evaluation of the data indicated a significant difference in susceptibility of hosts previously exposed to *S. trachea* and *S. merulae* juveniles and then challenged as compared to the susceptibility of those hosts exposed only once to *S. trachea* juveniles ($P < .01$-$.0005$). As can be seen in Table 5, previous exposure of 14-day-old hosts conferred more protection then did previous exposure of 1-day-old hosts. No significant difference in number of hosts infected was found when hosts previously exposed to *S. trachea* were compared with those previously exposed to *S. merulae* ($P > .40$).

Chickens fed *S. trachea* juveniles develop resistance to a challenge dose of these juveniles. The degree of

Table 5. Effect of challenge infections of S. trachea on chicks previously exposed to either S. trachea (S.t.) or S. merulae (S.m.)

Species used and host age (in days)		Avg no. juveniles ingested (Range in parentheses)		No. hosts	
1st exposure	Challenge exposure	1st exposure	2nd exposure	Exposed	Infected
S.t. - 1	S.t. - 62	220(152-291)	209(132-284)	21	7
S.t. - 14	S.t. - 76	243(214-274)	247(218-287)	9	0
S.m. - 1	S.t. - 62	208(151-285)	212(158-297)	31	14
S.m. - 14	S.t. - 76	215(154-264)	216(148-272)	8	0
Controls					
S.t. - 62	-	188(127-282)	-	12	11
S.t. - 76	-	171(135-267)	-	12	12

resistance appears to be related to the age of the host. Chickens fed S. merulae juveniles develop resistance to challenge with S. trachea juveniles (Table 5). Other investigators have also attempted to protect hosts from nematode parasites by exposing them to related nematode parasites. Shikhobalova (1956) found that the resistance developed against Syngamus skrjabinomorpha was active against S. trachea. Scott and Cross (1959) found that the rice rat strain of Litomosoides carinii does not readily infect cotton rats but that cotton rats given an immunizing dose of the rice rat strain are resistant to challenge by the cotton rat strain.

Immunizing hosts by feeding them S. trachea juveniles is not a practical method of protecting them, since they develop infections. Immunizing hosts by feeding them S. merulae juveniles, however, is practical in that hosts develop resistance without developing infections (see previous section).

SUMMARY AND CONCLUSIONS

1. Syngamus trachea infections can be transmitted to chickens by feeding them either intrauterine eggs or juveniles developed in earthworms, the earthworms having been exposed to either intrauterine eggs or eggs recovered from the feces of experimentally infected hosts (grackles and chickens).

2. S. trachea infections could not be transmitted to chickens by feeding them eggs recovered from the feces of experimentally infected grackles, suggesting that in nature a direct cycle for the transmission of S. trachea infections from grackles to chickens does not occur.

3. Attempts to continually transmit S. trachea infections from chicken to chicken by feeding them intrauterine eggs were only partially successful; on the third passage none of 24 chickens were infected.

4. Attempts to continually transmit S. trachea infections from chicken to chicken by feeding them juveniles developed from intrauterine eggs (in earthworms) were also only partially successful; on the fourth passage only 3 of 17 chickens were positive and eggs dissected from gapeworms recovered from these hosts failed to embryonate.

5. Attempts to continually transmit S. trachea infections from chicken to chicken by feeding them juveniles developed from fecal eggs (in earthworms) were totally

successful; infections were transmitted for five passages with no decrease in the number of infected hosts.

6. S. trachea infections transmitted indirectly (from grackle to chicken) were approximately twice as heavy on the second passage (chicken to chicken) than on the first, suggesting that there may be a physiological adaptation of this parasite to the chicken host.

7. The age, sex, and diet of chicken hosts did not appear to significantly affect the susceptibility of these hosts to S. trachea infection.

8. The worm burden of infected hosts generally increased with increase in the number of eggs or juveniles ingested.

9. Attempts to infect chickens with gapeworms (S. merulae) recovered from robins were wholly unsuccessful. Morphological study of S. merulae confirmed that it is easily distinguishable from S. trachea by its lack of a cuticularized buccal rim.

10. Acquired resistance of S. trachea infection appears to develop in chickens previously exposed to either S. trachea or S. merulae juveniles. This resistance appears to be greater in hosts immunized when 14 days old than in hosts immunized when 1 day old.

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APPENDIX A

Table 6. Known definitive hosts and geographic distribution of *Syngamus trachea*

Host species	Geographical location	References
Order Anseriformes		
Family Anatidae		
Anser anser (Grey-Legged Goose)	Norway	Madsen, 1950
Order Falconiformes		
Family Falconidae		
Falco tennunculus (Kestrel)	England	Baylis, 1939
Order Galliformes		
Family Cracidae		
Nothoprocta pletandi (Flat-Crested Curassou)	Buenos Aires, Argentina	Grosso *et al.*, 1944
Family Phasianidae		
Alectoris graeca (Chukar Partridge)	Germany England California	Galli-Valerio, 1939 Clapham, 1940 Herman, 1945
Alectoris rufa (Red-Legged Partridge)	England	Clapham, 1940
Chrysolophus pictus (Golden Pheasant)	Germany	Klee, 1903
Colinus virginianus (Bobwhite)	Texas	Webster and Addis, 1945

Table 6. (Continued)

Host species	Geographical location	References
Family Phasianidae (cont)		
Gallus gallus (Red Jungle Fowl)	Netherlands	Madsen, 1950
Lophortyz californicus (California Quail)	California	Herman, 1945
Phasianus colchicus (Ring-Necked Pheasant)	England	Campbell, 1935
	New York State	Goble and Kutz, 1945
	Denmark and Sweden	Madsen, 1950
	Vancouver, Canada	Moynikan and Musfeldt, 1950
	New Zealand	Davenport and Cairns, 1962
	Schwerin, Germany	Gräfner et al., 1964
	Czechoslovakia	Barus, 1964b
Family Tetraonidae		
Bonasa umbellus (Ruffed Grouse)	USA	Wehr, 1940
Lagopus lagopus (Willow Ptarmigan)	England	Clapham, 1940
Lyrurus tetrix (Black Grouse)	Germany	Galli-Valerio, 1939
Tetrao urogallus (Blue Grouse)	Germany	Galli-Valerio, 1939
	England	
	Norway and Sweden	

Table 6. (Continued)

Host species	Geographical location	References
Order Charadriiformes		
Family Scolopacidae		
Calidris maritima (Purple Sandpiper)	England	Campbell, 1935
Tringa nebularia (Greenshark)	Galway, Ireland	Cabot, 1965
Family Laridae		
Larus canus (Mew Gull)	Denmark	Madsen, 1950
Family Rostratulidae		
Rostratula bengalensis (Old World Painted Snipe)	India	Srivastava, 1938
Order Apodiformes		
Family Apodidae		
Apus apus (Common Swift)	Germany	Siebold, 1836
Order Crypturiformes		
Family Crypturidae		
Rhynchotus rufescens (Great Tinamou)	Buenos Aires, Argentina	Grosso *et al.*, 1944

Table 6. (Continued)

Host species	Geographical location	References
Order Piciformes		
Family Picidae		
Picus viridis (Green Woodpecker)	Germany	Siebold, 1836
Order Passeriformes		
Family Alaudidae		
Melanocorpha calandra (Blacklark)	Copenhagen Zoological Gardens	Madsen, 1950
Family Hirundinidae		
Progne subis (Purple Martin)	England	Campbell, 1935
Family Corvidae		
Corvus brachyrhynchus (Common Crow)	England Philadelphia Zoological Gardens	Chapin, 1925 Canavan, 1931
Corvus cornix (Hooded Crow)	Denmark USA Czechoslovakia	Madsen, 1950 Fardell, 1964 Barus and Groschaft, 1965
Corvus corone (Carrion Crow)	England	Mettrick, 1960a

Table 6. (Continued)

Host species	Geographical location	References
Family Corvidae (cont)		
Corvus frugilegus (Rook)	England	Mettrick, 1960b
	Ireland	Rice, 1929
	Denmark	Madsen, 1950
	Czechoslovakia	Baruš and Groschaft, 1965
Corvus monedulae (Jackdaw)	England	Mettrick, 1960b
	Denmark	Madsen, 1950
Cyanocitta cristata (Blue Jay)	Germany	Klee, 1903
Garrulus glandarius (Jay)	Czechoslovakia	Baruš and Groschaft, 1965
Pica pica (Black-Billed Magpie)	Denmark	Madsen, 1950
Family Parulidae		
Seiurus noveboracensis (Northern Waterthrush)	Alaska	Cram, 1930
Family Sturnidae		
Sturnus vulgaris (Starling)	England	Lewis, 1926a
	England	Morgan, 1931
	Denmark	Madsen, 1950
	Czechoslovakia	Baruš and Groschaft, 1965
Heterospar albicapillus (White-Capped Starling of Africa)	South Australian Zoological Gardens	McLennan, 1933

Table 6. (Continued)

Host species	Geographical location	References
Family Ploceidae		
Passer domesticus (House Sparrow)	Czechoslovakia	Baruš and Groschaft, 1965
Passer montanus (European Tree Sparrow)	Czechoslovakia	Baruš and Groschaft, 1965
Family Icteridae		
Molothrus brevirostris (Brown-Headed Cowbird)	Uruguay	Cassamagnaghi, 1948
Quiscalus quiscula (Common Grackle)	Milford, Iowa	Present paper
Quiscalus versicolor (Bronzed Grackle)	New York State	Goble and Kutz, 1945
Sturnella magna (Eastern Meadowlark)	New York State	Goble and Kutz, 1945
Family Fringillidae		
Carduelis cannabina (Linnet)	England	Lewis, 1925
Delichon urbica (House Martin)	England	Lewis, 1925
Donacola pectoralis (Pectorella Finch)	New Zealand	Whitten and Salisbury, 1951

Table 6. (Continued)

Host species	Geographical location	References
Family Fringillidae (Cont)		
Junco hyemalis (Slate-Colored Junco)	Alaska	Cram, 1930
Paroaria coronata (Crested Cardinal)	Buenos Aires, Argentina	Grosso *et al.*, 1944
Poephila cincta (Parson Finch)	New Zealand	Whitten and Salisbury, 1951
Zonotrichia leucophrys (White-Crowned Sparrow)	Alaska	Cram, 1930
Family Zosteropidae		
Zosterops lateralis (Silvereye)	New Zealand	Whitten and Salisbury, 1951

APPENDIX B

Table 7. Avian species of *Syngamus* other than *S. trachea*

Species	Host	Location	References
alcyone	*Megaceryle alcyone* (Eastern Belted Kingfisher)	Massachusetts	Boyd, 1966
anterogonimus	*Calidris canutus* (Knot)	Komi, USSR	Rizhikov, 1949b
arcticus	*Gavia stella* (Red-Throated Loon)	White Sea, USSR	Rizhikov, 1949b
gibbocephalus	*Capella sturna* (Common Snipe)	Komi, USSR	Rizhikov, 1949b
gracilis	*Corvus brachynchos* (Common Crow)	Philadelphia New York State	Chapin, 1925 Goble and Kutz, 1945
	Heterospar albicapillus (White-Capped Starling of Africa)	Australia	Johnston and Mawson, 1941
hexodontus	*Phalacrocorax auritus* (Double-Crested Cormorant)	Illinois	Chin, 1950

Table 7. (Continued)

Species	Host	Location	References
merulae	Turdus ericetorum (Song Thrush)	England	Campbell, 1935
	Turdus merula (European Blackbird)	England Czechoslovakia	Baylis, 1926 Baruš, 1965
	Turdus migratorius (Robin)	Nebraska New York State	Ripple, 1941 Goble and Kutz, 1945
	Turdus musicus (Redwing)	England	Campbell, 1935
microspiculum	Phalacrocorax carbo (Great Cormorant)	Turkestan, USSR	Rizhikov, 1949b
palustris	Philomachus pugnax (Ruff)	Komi, USSR	Rizhikov, 1949b
parvus	Nucifraga caryocatacts (Thick-Billed Nutcracker)	Philadelphia	Chapin, 1925
	Turdus pilaris (Fieldfare)	England	Lee, 1958

Table 7. (Continued)

Species	Host	Location	References
skrjabini	Carine noctua (Little Owl)	Garko, USSR	El'perin, 1938
skryabinomorpha	Domestic Geese and Chickens	Komi, USSR	Rizhikov, 1949a
taiga	Nucifraga caryocatacts (Thick-Billed Nutcracker)	Komi, USSR	Rizhikov, 1949a
tenuispiculum	Turdus migratorius (Robin)	Nebraska	Manter and Pinto, 1928

APPENDIX C

Table 8. Experimental intermediate hosts of *Syngamus trachea*

Intermediate host	References
Phylum Annelida	
Lumbricus terrestris - earthworm	Walker, 1886 Clapham, 1934 Taylor, 1938* Baruš, 1965
Eisenia foetida - earthworm	Clapham, 1934
Eulotica fruticum - earthworm	El Refaii, 1960
Helodrilus caliginosus - earthworm	Ripple, 1941
Phylum Arthropoda	
Scolopendra sp. - centipede	Clapham, 1939c
Sminthurus viridis - springtail	Clapham, 1939c
Tipula sp. - leatherjacket	Clapham, 1939c
Musca domestica - house fly	Clapham, 1939b
Phylum Mollusca	
Agriolimax agrestis - slug	Taylor, 1935**
Helix aspersa - snail	Taylor, 1938
Arantia arbustorum - snail	El Refaii, 1960
Planorbis corneus - snail	Baruš, 1964a
Lymnaea stagnalis - snail	Baruš, 1964a

*Earthworms were infective for 4 years 4-1/2 months.

**Snails were infective for 1 year 1-1/2 months.

PLATES

Plate I

Figure 1. Adult *S. trachea*, 27 days old, dissected from the trachea of a chicken fed juveniles when it was 1 day old. Approximately 10X.

Figure 2. *S. merulae* recovered from a naturally infected robin. Approximately 20X.

Figure 3. Chicken, 27 days old, showing typical symptoms of "gapes" disease. Chicken was fed *S. trachea* juveniles when 1 day old.

Figure 4. Anterior end of female *S. trachea*, showing cuticularized buccal rim and teeth. Anterior end of male at left. Approximately 90X.


1


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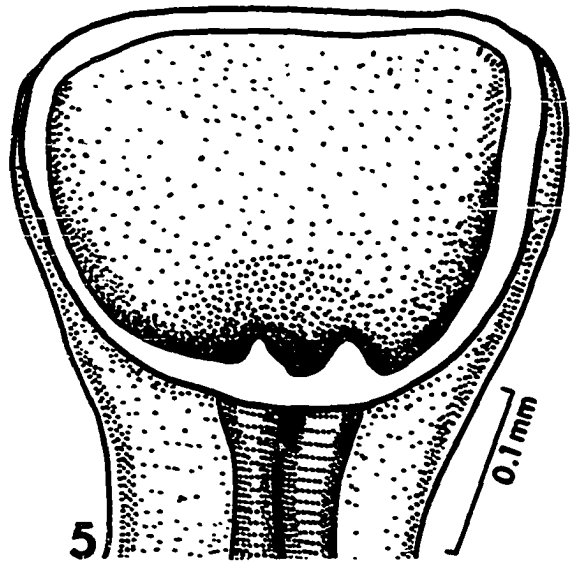
Plate II

Figure 5. S. merulae, buccal capsule, lateral aspect.

Figure 6. S. trachea, buccal capsule, lateral aspect. Note cuticularized buccal rim.

Figure 7. S. merulae, en face view of buccal region.

Figure 8. S. trachea, en face view of buccal region.



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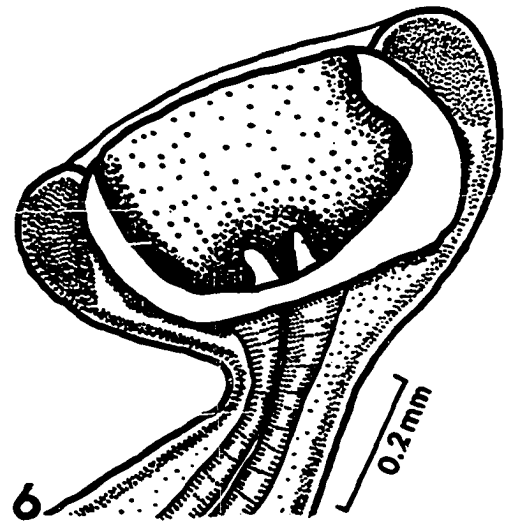

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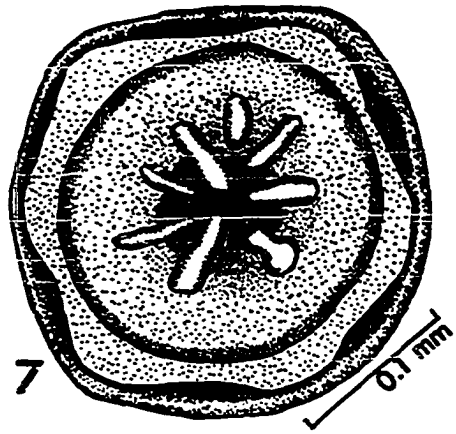

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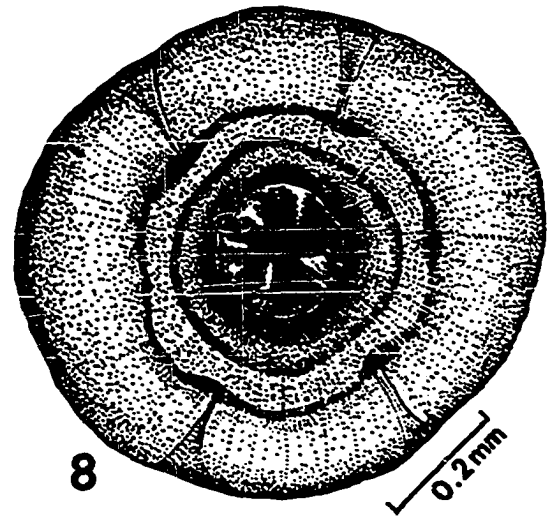

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