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STUDIES ON THE DEVELOPMENT OF TRICHURIS VULPIS (FRÖHLICH, 1789) (NEMATODA: TRICHURIDAE)

By

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INTRODUCTION

The whipworm or trichurid worm is a parasitic nematode which inhabits the cecum and proximal portion of the large intestine of mammals. It has been observed also in the terminal portion of the small intestine of certain hosts. It has been reported from man, from all of the domestic mammals except the horse, and also from numerous wild mammals, particularly rodents. The life cycle is direct and infection occurs by the ingestion of eggs in which larvae have developed. This worm has a distinctive shape in that the anterior, longer part of the body is slender and hair-like and the posterior, shorter part, considerably thicker. This whip-like appearance is responsible for the common name of the parasite. The worm lives in the host with part or all of the slender anterior end embedded within the mucosa, while the posterior, thick end is free in the lumen of the cecum or large intestine.

Although trichurid worms were described from man and certain of the domestic animals late in the 18th century, no extensive studies of the life cycle were made until about the middle of the 20th century. Even this work, which was with the species in the dog, was incomplete since it dealt almost exclusively with the early development of the worm in the host. Very little about later development was included.

Only sketchy life cycle data have been reported for the species in the sheep, the ox, and the pig, and the accuracy of some information in the literature regarding these forms is indeed questionable. No

information is available on the species in the rabbit. The presence of trichurids in the cat and mouse has been taken for granted. Recent work (Enzie, 1951) seems to indicate that there is no trichurid in the cat, in spite of the numerous reports in the literature. The species peculiar to the mouse has never been reported officially in the United States.

The human trichurid has been studied sparingly but has been written about many times, and the majority of the articles relate either to egg development or pathology based on clinical cases. The papers on egg development studies are for the most part scientific, but those on pathology contain much conflicting information, and results are often inconclusive.

Because this parasite is present in man and most of his domestic animals, and because the biology of this worm is incompletely known, further research is necessary. A more complete understanding of the biology will better enable us to understand the pathology associated with the worm. Furthermore, it will enable us to devise more critical measures of control both from the standpoint of husbandry and anthelmintics.

Being aware of the impressive lack of information with regard to this common parasite, the writer explored various phases of the different life cycle stages of Trichuris vulpis, the dog form. Certain problems which presented themselves during the course of the investigation could not be followed to a conclusion because of the limited amount of time and money available. It has been possible, however, to obtain data on the incidence and abundance of T. vulpis in the dog for the immediate locality, on the development of ova into infective larvae, on the growth process of the immature trichurid worm, on the prepatent and patent period of T. vulpis, and on the histopathology associated with trichurid infections.

REVIEW OF THE LITERATURE

The following is a general account of the available information relative to the genus Trichuris:

There are many data on egg structure and development. Dinnik and Dinnik (1941) described the layers of the shell of the egg of T. trichiura, and they ascribed functions for different layers. Miller (1939a) reported the period of time necessary for the eggs of T. vulpis to embryonate and mentioned how embryonation was speeded up or retarded by different normalities of sodium chloride. Spindler (1929a) presented similar data but the time requirements for embryonation are somewhat different from those given by Miller. Spindler (1929b), Brown (1927), and others gave data on the egg development of T. trichiura. The rate of development of eggs, as well as some excellent drawings of developmental stages of the eggs of T. suis, was presented by Alicata (1935). Aerated distilled water was reported by Deo (1946) as the best medium in which to develop eggs of T. ovis. Deo (1946) also reported that the newly formed larvae within the eggs were at first motile; and, according to him, they retained this motility for a definite period of time, after which they became quiescent. The writer observed a period of motility for the larvae within the eggs of T. vulpis, and such data for this species are not to be found in the existing literature.

Artificial hatching of embryonated T. vulpis eggs was accomplished by Miller (1939c) The structure of the fully developed first-stage larva was described by Fülleborn (1923a), Alicata (1935), and Miller

(1947).

Some early workers suspected that there was a larval migration outside of the alimentary tract, but detailed work, especially that of Fülleborn (1923b) and Miller (1947), indicated that no such larval migration occurs. But among those writers who agree that there was no larval migration, there was disagreement as to the location of development of the early stages in the intestinal tract. Fülleborn (1923b) and Whitney (1950) disagreed with Miller's finding concerning this phase of development. Miller and Fülleborn related experimental data to support their viewpoints, whereas Whitney did not.

No one has reported on the changes that occur between the first-stage larva and the adult.

Chitwood (1932, 1935) described some details of the histological structure of the esophagus of the mature trichurid worm.

The ratio of adult males to females, the length of the prepatent period, and the number of eggs laid per female per day are known for T. vulpis, and Miller (1939b) was responsible for these data. Similar information for T. trichiura was reported by Burrows (1950).

Whitney (1938) reported on the longevity of T. vulpis.

Specific characteristics for certain worms in the genus Trichuris were given by Chandler (1930) and were helpful in separating the species. Until Chandler's paper was published, it was difficult even to distinguish the various species with certainty.

The intimate relationship of the adult worms to the cecal and intestinal mucosa, and the manner in which this association is achieved lack satisfactory explanations. Efremov and Shikhobalova (1939) offered a possible explanation as to how the worms penetrate the mucosa.

A review of the literature on the pathology and symptomatology leaves one confused and discouraged because of the inconsistency of reports. The writer suspects that some investigators assume that every morbid symptom shown by a host can be attributed directly to the trichurid worm. Other investigators are more cautious in their claims, while still a third group admits that confusion and uncertainty exist in regard to the effects of the trichurid worm on the host.

Whitney (1950), writing unscientifically for the lay reader, claimed that T. vulpis is the most debilitating parasite harbored by the dog. The writer immediately calls to mind the astounding debilitating effects of hookworms in dogs and wonders what basis Whitney had for his claim. Emmerson (1941) believed that the whipworm is responsible for a specific barking hysteria in dogs five months to two years of age. Wright (1930) reported that inflammation, echymoses, and necrosis were associated with T. vulpis. Hung (1926) described pathological changes in the ceca of dogs with trichurid infections. He reported such changes as follicular enlargement, hyaline degeneration, and hyperemia in cases where few worms were present. His opinion regarding the mechanism of follicular enlargement was interesting but, according to the writer, incorrect from a histological viewpoint.

Jacob (1947) reported a heavy infection of T. myocastoris in the nutria, Myocastor coypus, that caused hemorrhagic inflammation of the entire intestine and cecum. Maenhout (1947) stated that heavy infections of T. ovis were severely pathogenic for eight-month-old heifers and caused emaciation, weakness, restlessness, sunken eyes, edema, and diarrhea. He reported also one death from peritonitis caused by the worm. Deo (1946) attributed the death of a lamb to an experimental infection of T. ovis.

He found immature worms in the small intestine and stomach 50 days after infection. It is difficult to correlate Deo's findings with other known life cycle data. Chandler (1930) attributed the death of a camel to a heavy infection of trichurid worms and estimated the number to be between 20,000 and 50,000. The worm involved was Trichuris tenuis, a new species described by Chandler.

Reports of T. trichiura as a pathogen in man are numerous. Faust (1949) stated that much has been written about the pathogenicity of the human whipworm but very few facts are known. Craig and Faust (1949) admitted that the exact mechanism by which the worm affects the host is not known, and they believed that both traumatic and toxic processes were involved. Plessen (1945) stated that he has observed clinical symptoms associated with the trichurid worm in man which led him to suspect that it is a cause of serious pathology. Burrows (1950) indicated that the intensity of infection did not always show a positive correlation with the worm burden. Miller (1947) believed that symptoms in trichurid-infected individuals involve the alimentary tract, the blood system, and the nervous system. Swartzwelder (1938) reported that T. trichiura was no mere commensal, but that it definitely produced pathology.

The writers who reported that the trichurid worm, whether in man or beast, is more or less harmless are few in number. Mönnig (1949) stated that these parasites are not very pathogenic in mild infections. Efremov and Shikhobalova (1939), who studied T. muris in mice, stated that the parasites crawl around in the tissue and produce neither hemorrhage nor inflammatory reaction. Belding (1952) reported that "although the whip-like anterior portion is embedded in the mucosa and surrounded by mucus, the parasite usually causes no pathological reaction."

Many pathologists and parasitologists have become aware of the controversy that exists with regard to the pathology of the trichurid worm and state it in their writing. Miller (1939b) admitted that the pathogenicity of whipworms is controversial and he writes: "Some authors consider this group of worms to be entirely innocuous and believe them to live within their host as commensals. Others believe them capable of causing mild digestive disturbances when present in great numbers, while still others believe that they can cause a very severe disease and even death." Swartzwelder (1938) stated that there is a wide divergence of opinion among authorities as to the pathogenicity of T. trichiura. Morgan and Hawkins (1949) wrote that the pathogenicity of T. vulpis in the dog is still a very controversial subject and one which cannot be decided with the present available evidence. Furthermore, they stated that there have been no careful studies to determine the symptomatology of this infection in the absence of other disease-producing agents.

The fact that the dog trichurid occurs in a significant percentage of dogs in certain locations emphasizes the importance of this parasite. Wright (1930) found T. vulpis in 81.0 percent of 150 dogs in a survey in Washington, D. C. Mann and Fratta (1952) examined 55 dogs in northern New Jersey and reported an incidence of 50.9 percent. Underwood (1933) reported a 60.0 percent incidence in 20 dogs in Virginia. Hinman and Baker (1936) found a 57.4 percent incidence of T. vulpis in a survey of 1315 dogs in New Orleans, Louisiana. Cross and Allen (1948) reported a 20.0 percent incidence in 100 dogs from Chicago. As far as the writer is aware, very few surveys to determine the incidence of the trichurid worm in the other domestic mammals have been made. In one such survey (Cooperrider, 1948) the incidence of T. ovis was found to be 17.0 percent

in 53 cattle in Oklahoma.

The incidence of human infection with T. trichiura is quite variable (Belding, 1952). In the United States the incidence is low, usually under 1.0 percent. However, in some areas of heavy rainfall and high humidity the incidence is high. In Mauritius it is 91.0 percent; in China, where night soil is used, 80.0 percent; in Puerto Rico, 76.0 percent.

The high incidence of the parasite in certain areas is cause for study. Also, there must be some basis for the reported pathology and symptomatology. Furthermore, it should be stated that the value of the use of anthelmintics in connection with this worm is controversial, and it is reasonable to assume on the basis of known facts that there is no efficacious one. Therefore, the insufficiency of life cycle data, the lack of agreement relative to pathology and symptomatology, and the need for suitable anthelmintics suggested to the writer both the need for research and the opportunities available to the person who could produce scientific data to help clear up the existing confusion.

METHODS AND MATERIALS

When an investigation of the trichurid worms was decided upon, it was necessary that the writer be able to reproduce the life cycle under laboratory conditions. Both our facilities and the available knowledge concerning the various species were carefully considered, and Trichuris vulpis, the one in the dog, was chosen to initiate the investigation.

Eggs of T. vulpis were secured in order to establish infections in experimental dogs. Two methods of collecting eggs were available. One was to maintain animals infected with T. vulpis and to collect the ova from the feces by either flotation or sedimentation. The other method was to obtain ceca from dead dogs and remove any trichurids that might be present. The latter method was chosen because it was more convenient and more economical.

Ceca were obtained from various sources. During the summer of 1950 the writer conducted a survey on 100 dogs from Oklahoma County, and the ceca of these dogs were used as a source of worms and eggs. Later the writer was able to make use of ceca from dogs that were autopsied by the Pathology Department and those destroyed following surgical and physiological exercises at the Veterinary School of Oklahoma Agricultural and Mechanical College. In addition, several trips were made to the Oklahoma City Animal Shelter, and ceca were collected from dogs destroyed there. Worms were obtained also from laboratory-infected dogs after the prepatent period was determined and the dogs were of no further value. Plate I,

figure 1 shows a cecum, containing numerous adult trichurids, that was removed from an experimentally infected dog.

To collect worms, a cecum which had been removed from a dog was opened in a finger bowl containing water. With the aid of thumb forceps the fecal contents were eliminated by shaking the opened cecum in the water-filled container. The mature worms, when present, were of such size that they were readily visible after the feces was removed and the worms were carefully transferred with thumb forceps to physiological salt solution in a small container. This fluid was changed several times in order to cleanse the worms as much as possible. The sexes were separated; the males were preserved in hot 10 percent formalin and the females were used as a source of eggs.

The eggs were removed at once or, if time was not immediately available, the females were placed in the refrigerator until it was convenient to work with them.

Two methods were used to collect eggs from the parasites. The first involved tearing the worms apart in a Petri dish partly filled with water. This was done with teasing needles under a dissecting microscope. The worms were severed at the junction of the thin and thick portions and the former discarded. The remaining thick part was thoroughly teased and all tubular reproductive structures were expressed or opened in order to release the contained eggs. The second method, which was employed on a few occasions, also involved placing the worms in a Petri dish partly filled with water. The nematodes were cut into small pieces with scissors. These pieces were then crushed against the bottom of the dish with a piece of a glass slide to expel the eggs. Although the first-mentioned method was more time consuming, it was considerably more efficient and

was used most frequently.

After the eggs were released, the debris associated with them had to be reduced to a minimum. The less debris with the eggs, the less was the possibility of bacterial and fungus growth in the egg cultures. Separation of the eggs from the worm parts was accomplished by pouring the material through a glass funnel into an Erlenmeyer flask. The funnel was lined with bolting cloth which was of such a mesh as to allow only the eggs and fine detritis to pass through.

A further step to secure the maximum number of eggs was to take the debris retained by the bolting cloth and transfer it to a flask containing several dozen glass beads and some water. The flask was stoppered and was then vigorously shaken. This manipulation freed more eggs, which were collected by again using the bolting cloth sieve.

The eggs were allowed to settle out in the Erlenmeyer flask, and the supernatant fluid was then carefully poured off. More water was added, the container was shaken, and the eggs again were allowed to settle before the supernatant fluid was decanted. This process, which helped cleanse the eggs, required about one-half hour and was repeated three or four times. After the cleaning process the flasks, which were either 125 or 250 milliliters in capacity, were kept about half filled with water for culturing eggs. A cotton plug was inserted into the mouth to reduce evaporation.

If there was an immediate need for embryonated eggs, they were allowed to develop at room temperature or in the incubator. The incubator was a cabinet type, electrically heated, and was regulated to maintain a temperature of about 37.5° C. Eggs kept in the incubator developed faster than those at room temperature. All flasks in which eggs were embryonating

were agitated daily, and every few days some eggs were removed with a pipette, transferred to a slide, and observed under the microscope in order to determine the stage of development.

Following the collection, if eggs were not to be used in the near future, the Erlenmeyer flask with its contents was refrigerated at about 5.0° C. Refrigeration prevented embryonation, yet the eggs would develop at a later date when removed to room or the incubator temperature.

In addition to the regular procedure of allowing eggs to develop in Erlenmeyer flasks, several experiments were conducted in which daily observations were made on the development of the eggs. To do this, a few eggs were isolated in water in Bureau of Plant Industry watch glasses, 28 by 7 millimeters. These watch glasses were in turn placed in large culture dishes, 180 by 62 millimeters. Moistened cotton was put in the bottom of the large container to compensate for evaporation. To further reduce evaporation, the small watch glasses were stacked and an inverted 125 milliliter beaker was placed over them. Finally the covers were placed on the large culture dishes. These experiments were conducted at various temperatures ranging from 4.4° C. to 55.8° C. and were for the purpose of comparing rates of development. Temperatures were recorded with minimum-maximum thermometers and in the data for the various experiments the temperature extremes are given. It would be impossible to give an average temperature in these instances since the duration of any one temperature within the range was not known. The effect of aeration on egg cultures was also studied. For such a study, an Erlenmeyer flask, containing eggs and water, was stoppered with a two-hole rubber stopper. Glass tubes of different lengths were inserted in the holes so that about 3 inches of each tube projected above the stopper. The longer tube, the lower end

of which reached almost to the bottom of the flask, was attached by its upper end to an air outlet. This allowed air to bubble constantly through the egg culture. The shorter tube, the lower end of which was above the surface of the water, allowed the excess air to escape. Data were kept on the length of time required for the eggs to develop larvae and on the length of time these larvae were actively motile within the shell.

Bacteria, protozoa, and molds can all develop in egg cultures. Their influence on the development of eggs is not well known. Consequently, efforts were made to keep them at a minimum in these cultures. At room temperatures all three types of contaminants presented a problem: at incubator temperatures bacteria were the only extraneous organisms encountered, and at refrigerator temperatures only mold growths were present. The bacteria and protozoa in cultures were controlled by the addition of a few drops of 10 percent formalin. Mold could best be removed from the cultures by passing the contents of the cultures through bolting cloth. The writer has recently found a method to culture eggs without the accumulation of foreign material. Such accumulations can be kept at a minimum by daily decanting the supernatant fluid, adding fresh water, and thoroughly shaking the container each time.

Those eggs which embryonated in Erlenmeyer flasks were used, for the most part, to infect experimental definitive hosts. In most of the experiments young, weaned puppies were considered to be the best host to use. Experimental puppies were secured from two sources. Pregnant bitches were obtained from the Oklahoma City Humane Society whenever needed. These bitches were transported to Stillwater and were individually housed in standard dog cages in an animal room shared by the Departments of Physiology and Veterinary Parasitology. The bitches were kept under conditions of

strict sanitation. The floors of the cages were covered by newspaper and this paper was changed twice daily. Once a day the cages were washed with a hose and hot water. The floor in this kennel room was washed and all the excess water removed with a squeegee once a day from both cages and floor. Feed and water containers were kept clean by daily or bi-daily washing.

A well balanced diet was fed. Adult animals were fed once daily. A feeding of checkered dog meal was alternated with a feeding of a mixture of kibbled meal and 100 percent horse meat. To the latter was added a commercial vitamin preparation and mineral supplement. Lactating bitches were fed more horse meat and less meal and given calcium gluconate tablets in addition to the vitamin supplement.

Puppies were weaned on a diet consisting of a mixture of evaporated milk, "Pablum," horsemeat, and dog meal, to which a mineral and vitamin supplement was added. Within two weeks following weaning, this diet was changed by gradually eliminating the milk and "Pablum."

Puppies were protected against distemper with the use of anti-canine distemper serum which was administered at two-week intervals following weaning. None of the laboratory-reared puppies developed distemper, although they were frequently exposed to Physiology Department sub-dogs, clinically sick with the disease, kept in the same kennel room.

Considerable trouble was experienced early in our work with weaned puppies. Almost all of them suffered with painful, sore feet. The foot pads became raw and partly denuded. It was concluded that the urine and feces that accumulated between cleanings were the irritating factors. We initiated the use of raised wire platforms and these were placed on the floors of the cages in which puppies were housed. When these were used,

no more foot trouble occurred.

Daily records were kept on both the bitches and puppies, and such items as temperature, appetite, and bowel movements were recorded, as well as any additional data of importance. Such comments included the time of exposure to infective eggs, the culture of eggs used, and the immunization and worming dates.

The mortality of the puppies born to the bitches from the Oklahoma City Humane Society was high, well over 50 percent. The writer believes that the main cause of this loss was the poor condition of the bitches. Some suffered from malnutrition and all suffered from parasitism to some degree. A few experiments were interrupted and much unavoidable expense was incurred from these losses. Because of these factors it was decided by the Parasitology Department of the Veterinary School to purchase some purebred bitches and to raise our own animals in order to have healthy, uniform experimental dogs available. After communicating with one of the larger pharmaceutical supply houses on the subject of the breed of animal to use, we accepted their recommendation and used the Beagle breed. The department bought three Beagle bitches on March 1, 1951. At this writing the bitches are still in our possession and have collectively provided us with 22 puppies for experimental use.

By profiting from earlier experiences with Humane Society dogs, the writer was able to raise 20 of the 22 puppies. One of the two that died was infected prenatally with ascarids, the other with ascarids and hookworms. The writer chose not to treat these animals because, by the time the infections were discovered, these animals were on experiment, and the use of an anthelmintic possibly would have interfered with the results.

The method used to subject experimental puppies to infection was a

simple, yet apparently effective one. Whether the puppy was infected a few days after birth or after weaning, the same method was used, and the procedure is outlined as follows:

In all instances a sample of the eggs to be used was first examined under the microscope and was considered usable if some eggs contained larvae. The eggs to be used for dosing were concentrated by very gently moving the container with a circular movement. This agitation tended to collect the eggs in a small area in the bottom of the container. The concentrated mass of eggs was picked up in an ordinary "eye-dropper" or pipette and introduced slowly into an animal's mouth. In no instance was any dog observed to regurgitate the egg suspension. The writer was not able to count or calculate the larvae used to infect an animal, because many of the eggs were trapped in masses of foreign material, in spite of the measures taken to clean the eggs following collection.

Some puppies were used specifically for determining the prepatent period of T. vulpis. The prepatent period is the time that elapses from the ingestion of infective larvae until the worms reach maturity. Maturity is evidenced for practical purposes by the recovery of eggs in the feces of the host. This period was accurately established for seven dogs. About 60 days following infection, daily salt flotations were made of the animal's feces and these flotations were examined for the presence of Trichuris eggs. The date on which eggs were first recovered was recorded and the prepatent period determined. Infection was confirmed by autopsy of the host and recovery of adult trichurids.

Other puppies which had been fed infective eggs were sacrificed at dates that would permit recovery of the worms at different stages of development. It was necessary to autopsy these experimental hosts to

recover the partially developed nematodes. The dogs were destroyed either by "Euthanol," a toxic barbiturate, given intravenously, or by ether inhalation. Autopsies were performed using the regular and accepted method, and the organ or organs in which the parasites were suspected were removed. A piece of these organs was preserved immediately in 10 percent formalin for sectioning. The viscera were then opened in a container partially filled with physiological salt solution. Fecal material was removed so that the mucosa could be examined for the presence of worms.

The examination of a piece of opened viscus for immature worms of microscopic size presented a problem. A representative piece, as previously indicated, was placed in a container of 10 percent formalin for sectioning and examination of fixed material. Other representative pieces were placed in Petri dishes in physiological saline solution and the mucosa was removed with a pair of teasing needles. The mucosa and sediment were then carefully examined under a dissecting microscope for the presence of immature trichurids.

Another method used sometimes to examine for early infections was one in which a small piece of mucosa was removed, crushed between two slides, and examined under a microscope.

If both the examination of the sediment in the Petri dish and the examination of the mucosa on the slides were negative, the Baermann apparatus was used as a further procedure to find these small larvae. For the Baermann process all of the mucosa was stripped off of the intestine and placed in a glass funnel lined with bolting cloth. A rubber tube was attached to the end of the funnel and closed with a clamp. Physiological salt solution, heated to body temperature, was added in an amount sufficient to cover the mucosal material. After 18 to 24 hours

the clamp was released enough to collect the fluid and its contents from the bottom of the funnel. This material was examined under a dissecting microscope for the presence of larvae. According to the principle of the Baermann apparatus, some of the larvae, if present, would pass through the bolting cloth by their activity and settle in the funnel.

From puppies autopsied within a week after being subjected to infection, pieces of lung and liver as well as pieces of the intestinal tract were preserved in 10 percent formalin and sectioned, with the idea of determining the possibility of the larvae undergoing a migration in the circulatory system, as was reported by some workers.

Examination of the viscera for worms approximately one millimeter or larger was not as difficult and did not require some of the foregoing techniques. Worms of such a size could be readily seen on the epithelial surface with the aid of a dissecting microscope and they were carefully removed with teasing needles or fine forceps.

Some of the worms collected were preserved in 10 percent formalin and others were examined in the living condition in egg albumen as described by Krull (1934). The use of egg albumen as a mounting medium proved outstandingly useful. Living worms were transferred from physiological salt solution to egg albumen which had been placed on a slide. The amount of the medium used was practically the same as the amount of balsam or damar that would be needed to make a permanent mount. A cover slip was applied. The addition of a few minims of an aqueous solution of neutral red to the egg albumen proved advantageous because it stained certain structures and made them more easily observed within the worms. The worms remained alive in the egg albumen-neutral red mixture for 24 to 30 hours. For the first part of this period they were very active

and the normal functioning of the body parts could be observed. Toward the end of the period of motility the parasites became sluggish and eventually ceased to move. Camera lucida drawings were made of various parts of the inactive worms. The cessation of activity could be induced by gently heating the mounted specimens. This was accomplished by placing the slides on the microscope lamp for 5 to 30 seconds. This procedure allowed the writer to make the camera lucida drawings at his convenience and eliminated waiting for the parasites to become inactive. Parasites mounted as described could be observed under oil immersion as well as high dry and low magnifications of the microscope.

Measurements were made of the muscular portion of the esophagus, of the glandular portion of the esophagus, and of the intestine of different aged immature worms. These measurements were made to determine the rates of growth of the various parts. To determine these measurements, camera lucida drawings were made and a piece of string was superimposed over the length of the worm or worm part to be measured. The length of string was then measured with a camera lucida drawing of the ocular micrometer, the latter drawing being made at the same magnification as the specimen. This determined the number of divisions that corresponded to the length of string. The number of divisions was then multiplied by the value in microns of one division of the ocular micrometer. The latter figure was determined by previous calibration of the ocular micrometer. The resulting figure was for the measured worm or worm part and was expressed in microns. Using this method, coiled specimens could be accurately measured.

Worms preserved in 10 percent formalin were studied under the microscope by placing them on a slide and clearing them with a mixture of equal

parts of liquefied phenol and 95 percent ethyl alcohol. This technique showed the worms to good advantage, and structures appeared quite similar to corresponding structures observed in live specimens.

Permanent mounts were made for study of some worms either from the living condition or from formalin-fixed specimens, using polyvinyl alcohol as a mounting medium as described by the writer (1951). Tissues for microscopic examination were prepared as follows:

Tissues were fixed in 10 percent formalin. They were then dehydrated, embedded in paraffin, sectioned at a thickness of 10 microns, and the tissue sections placed on slides. The tissue was hydrated, stained with hematoxylin, counterstained with eosin, and again dehydrated. "Piccolyte," a Turtox product, was used to cement the cover slips in place.

Data on the Incidence and Abundance of Trichuris vulpis

The incidence of T. vulpis from several counties in Oklahoma was determined by an examination of 250 ceca. The findings are presented in Table I.

TABLE I

Showing the Incidence and Abundance of T. vulpis in 250 Oklahoma Dogs

Host	Source	Date	No. of Parasites	Host	Source	Date	No. of Parasites	Host	Source	Date	No. of Parasites	Host	Source	Date	No. of Parasites
										Summer					
1	Path.	3-16-50	85	63	O.C.H.S.	7-17-50	0	125	Survey	1950	0	188	O.C.H.S.	3-10-52	0
2	S.E.	3-28-50	0	64	"	"	0	126	"	"	0	189	"	"	0
3	"	"	0	65	"	"	0	127	"	"	0	190	"	"	0
4	"	"	0	66	"	"	0	128	"	"	0	191	"	"	+
5	"	"	321	67	"	"	0	129	"	"	0	192	"	"	18
						Summer									
6	"	"	0	68	Survey	1950	0	130	"	"	0	193	"	"	0
53	"	"	0	115	"	"	18	177	"	"	+	240	"	"	0
54	"	"	0	116	"	"	0	178	"	"	0	241	"	"	6
55	"	"	0	117	"	"	0	179	"	"	0	242	"	"	0
56	"	7-17-50	0	118	"	"	0	180	"	"	0	243	"	"	0
57	"	"	0	119	"	"	0	181	"	"	0	244	"	"	0
58	"	"	0	120	"	"	0	182	"	"	0	245	"	"	0
59	"	"	0	121	"	"	0	183	"	"	0	246	"	"	0
60	"	"	0	122	"	"	0	184	"	"	0	247	"	"	0
61	"	"	0	123	"	"	0	185	"	"	+	248	"	"	0
62	"	"	0	124	"	"	0	186	"	"	0	249	"	5-8-52	0
								187	"	"	0	250	"	"	0

KEY TO ABBREVIATIONS:

Path. -- Pathology Department
S. E. -- Surgical Exercises
O.C.H.S. -- Oklahoma City Humane Society
Physiol. -- Physiology Department

These data show that 20 of the 250 dogs examined were infected with T. vulpis, which is an incidence of 8.0 percent. Animals 176, 177, 185, and 191 were infected, but no data were obtained as to the numbers in each. Time was not available to count the numerous worms in animal 223, and the number given is an estimation. The range in numbers of parasites in any one host was from one to an estimated 500.

Table I includes 100 dogs examined for internal helminths in a previous survey, and the writer (1952) found only a 2.0 percent incidence. All those dogs were from Oklahoma County and are numbered 68 through 167 in Table I. The rest of the dogs in this study were from Oklahoma County, Payne County, and several counties adjacent to Payne County. The exact origin of all these dogs could not be determined.

Data on Egg Development

The eggs of Trichuris vulpis (Plate I, fig. 2) are unsegmented when laid and are eliminated unchanged in the feces of the host. In a favorable environment, cleavage occurs and development continues until a larva is formed within the shell (Plate I, fig. 3). An egg containing a larva is infective for a suitable host.

Development of eggs for some species of Trichuris is reported in the literature. Alicata (1935) observed that the eggs of T. suis embryonated fully in 16 days in water at 37.5° C. and in 25 days at 33.0° C. He also reported that embryonation would take place at temperatures below 33.0° C. He observed that larvae developed in eggs in a charcoal-feces culture in 54 days at temperatures of 22.0° C. to 24.0° C. Using the same culture media, he found that only 10 percent of the eggs completed development in 210 days at temperatures of 6.1° C. to 24.5° C. Spindler

(1929a) studied the development of T. vulpis and observed that when eggs were cultured in water at 30.0° C. they embryonated in 16 days, whereas those cultured at 37.0° C. required only 12 to 15 days. Onorato (1932) obtained best results for the development of eggs of T. vulpis in water at 30.0° C. and mentioned his disagreement with Spindler's findings. Miller (1939c) observed that 98 percent of the eggs kept on dry soil failed to develop, demonstrating that moisture is necessary for embryonation. Experiments by Miller (1939c) demonstrated that eggs can embryonate in 9 to 11 days in water at 30.0° C. to 36.0° C. He also observed that saline solutions of 0.001N to 0.5N stimulated embryonation but that 1N to 3N were lethal. Nolf (1932) found that exposure of eggs of T. trichiura for a short time to temperatures of 52.0° C. to 54.0° C. was lethal.

In the present study, observations on the embryonation of eggs of T. vulpis were made at various temperatures, ranging from 4.4° C. to 55.8° C. The results are presented in Tables II, III, IV, V, VI, VII, and VIII.

The expression "multicell stage" used in the tables includes all developmental stages from the eight-cell stage to the larva. Thus this term includes the stages described by Alicata (1935) as the early morula, late morula, early tadpole, and late tadpole.

All eggs were cultured in water; consequently the moisture requirements of T. vulpis eggs were not studied. However, since the moisture factor was constant, the effect of various temperatures upon development was determined and compared.

Table II gives data on egg development at a temperature range of 19.3° C. to 26.4° C.

TABLE II

Showing Developmental Reaction of Eggs of T. vulpis at a Temperature Range of 19.3° C. to 26.4° C.

Age of culture in Days	Container 1	Container 2	Container 3	Container 4	Container 5	Container 6
1	No Development	No Development	No Development	No Development	No Development	No Development
2	"	"	"	"	"	"
3	"	"	"	"	"	"
4	Numerous Eggs in 2-Cell Stage	Few Eggs in 2-Cell Stage	One Egg in 2-Cell Stage	Few Eggs in 2-Cell Stage	Few Eggs in 2-Cell Stage	Few Eggs in 2-Cell Stage
5	Eggs in 2-, 3-,4-,8-, Cell Stages	Eggs in 2- to 8-Cell Stages	Eggs in 2- to 8-Cell Stages	Eggs in 2- to 8-Cell Stages	Eggs in 2- to 8-Cell Stages	Eggs in 2- to 8-Cell Stages
Duration of Multicell Stage	20 Days	20 Days	20 Days	19 Days	19 Days	19 Days
Total Time for Embryonation	26 Days	26 Days	26 Days	25 Days	25 Days	25 Days
Duration of Larval Motility	5-6 Days	7-9 Days	7-9 Days	5 Days	6-7 Days	----

These data show that the eggs at this temperature range remain in the unicellular stage for three days, in the two- to eight-cell stage for two days, and in the multicell stage for 19 to 20 days. They require a total of 25 to 26 days for embryonation and the resulting larvae are motile for five to nine days.

Table III presents the observations made on developing eggs at 25.4° C. to 32.2° C.

TABLE III

Showing Developmental Reaction of Eggs of T. yulpis at a Temperature Range of 25.4° C. to 32.2° C.

Age of Culture in Days	Containers 1, 2, and 3
1	No development
2	Several eggs in 2- and 3-cell stages
3	Multicell stage for viable eggs
4	" " " " "
5	" " " " "
6	" " " " "
7	" " " " "
8	" " " " "
10	Motile larvae in some eggs
11	Motile larvae in some eggs
14	No motile larvae

SUMMARY:

Duration of Unicellular Stage	1 Day
Duration of 2- to 8-Cell Stages	1 Day
Duration of Multicell Stage	6-7 Days
Total Time for Embryonation	9-10 Days
Duration of Larval Motility	2-5 Days

These data show that the eggs at this temperature range remain in the unicellular stage for one day, in the two- to eight-cell stage for one day, and in the multicell stage for six to seven days. They require a total of nine to ten days for embryonation and the resulting larvae are motile for two to five days.

Table IV gives data on the effect of temperatures of 35.0° C. to 44.4° C.

TABLE IV

Showing Developmental Reaction of Eggs of T. vulpis at a Temperature Range of 35.0° C. to 44.4° C.

Age of Culture in Days	Containers 1 and 2
1	No development
2	" "
3	" "
4	" "
6	Developing eggs in 2- to 8-cell stages
7	Developing eggs in 2- to 8-cell stages
8	Eggs in multicell stage
9	" " " "
10	" " " "
11	" " " "
13	" " " "
14	" " " "
15	" " " "
17	" " " "
18	" " " "
19	Motile larvae in few eggs

SUMMARY:

Duration of Unicellular Stage	4-5 Days
Duration of 2- to 8-Cell Stages	2-3 Days
Duration of Multicell Stage	11 Days
Total Time for Embryonation	19 Days

These data indicate that the eggs at this range of temperature remain in the unicellular stage for four to five days, in the two- to eight-cell stage for two to three days, and in the multicell stage for 11 days. They require 19 days for embryonation. The duration of larval motility was not determined.

Table V gives data on the effect of temperatures of 48.3° C. to 55.8° C.

TABLE V

Showing the Developmental Reaction of Eggs of T. vulpis at a Temperature Range of 48.3° C. to 55.8° C.

Age of Culture in Days	Container 1	Container 2	Container 3	Container 4
1	No cleavage	No cleavage	No cleavage	No cleavage
2	"	"	"	"
3	"	"	"	"
4	"	"	"	"
5	"	"	"	"
6	"	"	"	"
7	"	"	"	"
8	"	"	"	"
9	"	"	"	"
10	"	"	"	"
11	"	"	"	"
12	"	"	"*	"*
13	"	"	"	"
14	"	"	"	"
15	"	"	"	"
16	"	"	"	"
17	"	"	"	"
18	"	"	"	"
19	"	"	"	"
20	Discontinued	"	"	"
21		Discontinued	Discontinued	Discontinued

* Removed to room temperature of 25.5° C. to 35.5° C.

These data show that the eggs at this temperature range did not develop and that eggs exposed to this temperature range for 12 days were destroyed, as indicated by the failure to develop normally when removed to room temperature.

Table VI presents data on the comparison of rates of development of eggs from one culture at temperatures of 4.4° C. to 5.3° C., 23.3° C. to 29.2° C., and 33.3° C. to 38.8° C.

TABLE VI

Showing the Developmental Reaction of Eggs of T. vulpis at Temperature Ranges of 23.3° C. to 29.2° C., 33.3° C. to 38.8° C., and 4.4° C. to 5.3° C.

Age of Culture in Days	Containers 1, 2, & 3 Temp. 23.3° C. to 29.2° C.	Containers 4, 5, & 6 Temp. 33.3° C. to 38.8° C.	Container 7 Temp. 4.4° C. To 5.3° C.	Container 8 Temp. 4.4° C. To 5.3° C.
2	No development	No development	No development	No development
3	"	"	"	"
4	Developing eggs in	Developing eggs in	"	"

These data show that eggs at a temperature range of 23.3° C. to 29.2° C. remain in the unicellular stage for three days, in the two- to eight-cell stage for one day, and in the multicell stage for 12 to 13 days. They require a total of 17 to 18 days for embryonation and the resulting larvae are motile for seven to eight days. Eggs at a temperature range of 33.3° C. to 38.8° C. remain in the unicellular stage for three days, in the two- to eight-cell stage for less than one day, and in the multicell stage for six days. They require a total of 10 days for embryonation and the resulting larvae are motile for six days. Eggs at a temperature range of 4.4° C. to 5.3° C. did not develop but remained viable, as indicated when they embryonated in 10 days after they were transferred to a temperature range of 33.3° C. to 38.8° C.

The three experimental temperatures are grouped together in this table for the reason that eggs from the same collection were used. Separate and different collections of eggs were used in each of the experiments represented in Tables II through V.

Table VII presents a summary of the results in Tables II to VI.

TABLE VII

Summarizing the Results of the Developmental Reaction of Eggs of T. vulpis at Various Temperature Ranges Presented in Tables II Through VI

	4.4°-5.3°C.	19.3°-26.4°C.	23.3°-29.2°C.	25.4°-32.2°C.	33.3°-38.8°C.	35.0°-44.4°C.	43.3°-55.8°C.
Duration of Unicellular Stage		3 Days	3 Days	1 Day	3 Days	4-5 Days	
Duration of 2-to 8-Cell Stages		2 Days	1 Day	1 Day	Less than 1 Day	2-3 Days	
Duration of Multicell Stage		19-20 Days	12-13 Days	6-7 Days	6 Days	11 Days	
Time for Embryonation	No development *	25-26 Days	17-18 Days	9-10 Days	10 Days	19 Days	No development **
Duration of Larval Motility		5-9 Days	7-8 Days	2-5 Days	6 Days	Not Determined	

* Eggs remained viable. ** Eggs did not remain viable.

These data indicate that eggs showed no development at 4.4° C. to 5.3° C.; yet they remained viable, as evidenced when larvae developed in these eggs in 10 days after container 8 (Table VI) was transferred and maintained at a temperature of 33.3° C. to 38.8° C. Eggs kept at 33.3° C. to 38.8° C. and at 25.4° C. to 32.2° C. showed the fastest development and reached the larval stage in nine to ten days. A temperature as high as 44.4° C. was not lethal to eggs of T. vulpis, but this relatively high temperature apparently had some detrimental effect upon embryonation, because it is shown that embryonation required 19 days for completion. Embryonation did not occur at a temperature of 48.3° C. to 55.8° C., and eggs maintained at this temperature for 12 days lost their viability. This was shown by the eggs in containers 3 and 4 (Table V) which after being transferred and maintained at room temperature, failed to develop.

Table VIII presents data on the rate of embryonation in aerated water at a temperature of 25.5° C. to 37.7° C.

TABLE VIII

Showing the Developmental Reaction of Eggs of T. vulpis in Aerated Water at a Temperature range of 25.5° C. to 37.7° C.

Age of Culture in Days	Observation
1	No development
2	Eggs in 2-cell stage
3	Eggs in multicell stage
4	" " " "
7	" " " "
8	" " " "
10	" " " "
11	" " " "
12	" " " "
13	Motile larvae in eggs
14	" " " "
15	" " " "
16	" " " "
19	" " " "
20	" " " "
21	Motile larvae
22	" "
23	" "
24	" "
27	" "
28	" "
29	No motility

SUMMARY:

Duration of Unicellular Stage	1 Day
Duration of 2- to 8-cell Stages	1 Day
Duration of Multicell Stage	10 Days
Total Time for Embryonation	13 Days
Duration of Larval Motility	16 Days

These data indicate that eggs subjected to aeration at this temperature range remain in the unicellular stage for one day, in the two- to eight-cell stage for one day, and in the multicell stage for 10 days. They require a total of 13 days for embryonation and the resulting larvae remain motile for 16 days. The significance of the relatively long period of larval motility in this instance is not clear.

There are no reports in the literature of larval activity for T. vulpis. Miller (1947) determined the viability of larvae of T. vulpis by crushing the eggs and observing movement of the extruded larvae, but he made no mention of their activity in intact eggs. He assumed, apparently, that only active larvae were infective. Deo (1946) observed that larvae of T. ovis are active in eggs for five months, and this is the only report on activity for any of the other trichurids.

Larvae of T. vulpis always have a period of motility in the eggs soon after development. The activity is initiated suddenly and diminishes gradually. At first the motility is constant and energetic, then becomes sluggish, then intermittent and sluggish, and finally ceases. On the basis of data in Tables II, III, VI, and VIII it appears that the duration of activity is correlated, possibly, with the rate of development of the larvae, and it appears that the duration of the period of activity may be shortened with an increased rate of development. Larvae which developed in nine to ten days (Table III and Table VI, containers 4, 5, and 6) were motile for only two to five and six days respectively, whereas larvae that required 26 days to develop retained their motility for five to nine days (Table II).

The relation of motility to infectivity is not known. Eggs containing active and inactive larvae were used in separate experiments, and

it was found that all were infective.

No attempt was made to compare the virulence of active or inactive larvae in eggs. It seems logical to assume that the virulence probably decreases as the length of time the larvae remain in the eggs increases. The writer is of the opinion that infectivity of the larvae decreases with age, that this decrease is gradual rather than abrupt, and that loss of virulence does not coincide with the loss of motility. However, it is not within the scope of this study to prove this point.

During the course of daily observations on the development of eggs, an exceptionally large egg was encountered which measured 105 u by 44 u as compared with the normal eggs which measure 72 to 90 u by 30 to 40 u (Morgan and Hawkins, 1949). The egg failed to develop although it was incubated at 33.3° C. to 38.8° C. with other eggs that developed normally.

Studies of Various Aged Immature Forms of *Trichuris vulpis*

The writer was of the opinion that critical observation of *T. vulpis* during its development would shed some light on the method of tissue penetration by this worm and also on the manner in which the simple, first-stage larva changes into a quite unusual type of adult nematode. For these reasons, specimens of various ages were recovered and examined, and the results of these studies are related. No attempt has been made to give a complete description of the various stages, but significant changes in anatomical features have been described.

Larva expressed from egg. Larvae were expressed by crushing eggs under a coverslip. This manipulation expelled the polar plugs and the larvae usually escaped through the openings. Most larvae were feebly

motile for a short period of time after being forced from the eggs, regardless of whether or not they were motile within the shells at the time of expulsion.

The larvae range in length from 181 u to 318 u and average 261 u (Table IX). The greatest width, 15 u, is at the middle. The worms taper slightly at both ends, but the tapering is more acute at the posterior end. They are covered by a smooth thin cuticle. Internally there is a coarsely granular mass that occupies about the posterior three-fourths of the body (Plate I, fig. 4). In the anterior tip end there is a lancet-shaped hyaline structure, the so-called mouth spear or lancet which varies in length from 7 to 10 u and has a twist of 90 degrees or more at about the middle. The lancet is retractible and in extreme conditions may be seen partially projected beyond the anterior extremity of the body (Plate II, figs. 7 and 9) or retracted in its entirety within the body (Plate II, figs. 6 and 8). The basal end of the lancet is imbedded in a muscular structure, presumably the muscular portion of the esophagus (Plate II, fig. 5), that is capable of movement independent of the body wall of the larva and which causes the lancet to move back and forth. The muscular esophagus extends posteriorly to the anterior level of the granular material which obscures the remaining part of the digestive tract. A narrow lumen traverses the esophagus. There is no indication of a primordium for the reproductive system. The posterior end of the larva has an eccentric indentation (Plate II, fig. 10).

14-day-old-larva. At least 12 puppies were examined in attempts to recover life cycle stages less than 14 days old. Examinations in each case were made both grossly and by tissue sections; in each case the duodenum, jejunum and ileum were involved; and all results were negative.

The 14-day-old larvae were recovered and examined in the living state. They measure 337 u to 512 u in length and average 415 u (Table IX). The width varies at different levels, averaging 12 u anteriorly, 17 u in the middle region, and 10 u near the posterior end. No terminal anal opening can be observed, but the posterior indentation of the cuticle is present. The cuticle at the posterior end appeared loosened, possibly indicating that a molt had occurred or was about to occur. The musculature of the body is thick throughout the length of the worm. The individual measurements for five 14-day-old larvae are recorded in Table IX.

The digestive system is differentiated and distinct segments are evident. The mouth spear in the muscular wall of the anterior extremity of the esophagus projects into a very shallow oral cavity. The mouth spear can be extended by movements of the muscular esophagus through the mouth, which appears to be without lips or papillae. In reality, this is accomplished by the straightening of the serpentine esophagus. In addition to the anterior-posterior movement, the mouth spear exhibits a very rapid, lateral vibratory type of movement, which appears to originate from the area of attachment and not from the entire musculature.

The muscular part of the esophagus immediately behind the mouth is relatively short and uniform in width. The next region, the glandular portion, is relatively long and consists of a series of large cells, intimately associated with a tubular structure, the lumen of which is continuous with that of the muscular part anteriorly and the intestine posteriorly. The cells of the glandular area appear granular and each contains a large spherical body in which there is a smaller spherical one. These structures are assumed to be nucleus and nucleolus,

respectively, and similar structures are shown in Plate II, fig. 15, in a 24-day-old larva. The lumen passing through the glandular area opens and closes repeatedly, and the movements resemble peristaltic action. Measurements presented in Table IX show that the esophagus constitutes approximately three-fourths of the length of the digestive tract.

The intestine is not as wide as is the glandular esophagus and presents no unusual features except an asymmetrical mass of cells projecting from the intestine into the body cavity. This mass could well be the anlage of the genitalia instead of a digestive tract appendage. The entire tract was separated from the body wall by a narrow cavity.

21-day-old larva. The living 21-day-old larva was similar to the 14-day-old one except for size (Table IX). Its average length is 919 u as compared with the average length of 415 u for the 14-day-old one. The widths at the anterior, middle, and posterior ends are 15 u, 35 u, and 20 u respectively, and this was the first indication of the differentiation of the whip-like anterior end from the thick posterior portion, which parts are characteristic of the adult. Plate II, figures 11, 12 and 13, shows this initial differentiation.

The cells comprising the glandular segment of the esophagus are arranged in a linear manner, and they appear to be composed of two types, the already-described granular ones and others lacking these granules. The agranular cells are irregularly interspersed among the others, and occur singularly, or in groups of two, three, or four. It is suggested that these granules may be secretory in nature and that the clear cells are either inactive or have recently discharged their products. A drawing (Plate II, fig. 14) shows the junction of the muscular and glandular esophageal regions. It is shown in Plate II, fig. 16, that a tubular

portion of the esophagus projects into the intestine beyond the glandular cells of the esophagus.

24-day-old larva. Several larvae were formalin-fixed and these ranged in length from 1.8 mm. to 4.7 mm., average 2.6 mm. The very decided increase in length as compared with the 21-day-old larva (average 919 u), as well as with the 17-, 18-, and 19-day larvae, which average 870 u, 628 u, and 803 u long respectively (Table IX), is suggestive of a molt having occurred. Further support for this contention is found in the fact that no loosened cuticle was observed. It is assumed, therefore, that a molt occurs between the 21st and 24th day of development.

A mass of cells similar to the one described for the 14-day-old larva was observed in this stage, and no further information was secured concerning its identity (Plate II, fig. 18).

28-day-old larva. Five living larvae of this age were measured and ranged in length from 1.3 mm. to 3.1 mm. (Table IX), average 1.7 mm. This average is less than the 2.6 mm. average for the 24-day-old larvae and may possibly be explained by some internal factor in the host operating to attenuate the 28-day-old larvae. Also, it is known that the developmental rate varies from host to host.

One of these 28-day-old larvae had a loosened cuticle at the posterior end (Plate II, fig. 17), and this could well indicate that a molt was about to occur. Enough data were not accumulated to determine which molt was in progress in the 28-day-old larvae. However, with a few additional data, which are difficult to secure, the molts in the cycle could be ascertained with certainty. At present such data are not available for any of the species in the genus Trichuris.

32-day-old larva. Four formalin-fixed larvae were measured and

ranged from 4.0 mm. to 5.4 mm., average 4.7 mm. Table IX).

The table shows that the great increase in length of the worms from the 14-day-old larva to the 32-day-old larva has taken place in the glandular area of the esophagus and is the result of both an increase in size and number of the glandular cells. The glandular region of the esophagus has increased an average of more than 26 times while the length of the muscular portion of the esophagus and intestine have increased only three and six times, respectively.

42-day-old larva. Ten living 42-day-old larvae were measured and ranged from 2.4 mm. to 7.2 mm., average 4.0 mm. (Table IX). Again the average is less than that for the 32-day-old larvae which average 4.7 mm. in length. As was the case for the 32-day-old larvae, the 42-day-old ones have increased in length for the most part in the glandular esophageal region. The width of the larva is not uniform. One specimen measured 42 u near the anterior end, 88 u at the junction of the esophagus and intestine, and 68 u near the posterior end (Plate III, figs. 20, 21, and 22). A definite coiled tubular structure, separate from the digestive system, is shown in Plate III, fig. 24, and interpreted as being part of the reproductive system. However, sufficient data are not available to definitely associate this structure with the cellular mass described in the 14 and 24-day-old larvae.

54-day-old larva. Several 54-day-old living larvae were examined and showed a marked resemblance to the adult form. The sex of these larvae could be determined and coiled, tubular reproductive structures were evident in both the male and female. The spicule of the male was well defined (Plate III, fig. 27). The uterus and vagina of the female were evident but a vulvar opening was absent (Plate III, figs. 19 and 26),

and the absence of this opening is a good indication that another molt must occur.

Adult worms. The adults have been described in varying detail by several writers; Yorke and Maplestone (1926), Morgan and Hawkins, (1949), Chandler, (1949), and Mönnig, (1949). Yorke and Maplestone (1926) described the mouth as a simple opening for the genus Trichuris and made no mention of a mouth spear. On the other hand, Chandler (1949) and Miller (1939b) both mentioned the presence of a mouth spear for the genus, but neither figured the structure. A photomicrograph of a mouth spear for T. trichiura was shown by Li (1933). The writer's observations indicate that the mouth spear (Plate III, fig. 23) is present in the adult T. vulpis and, as far as can be determined, there is no illustration of the mouth spear in the literature.

Two problematic gland-like structures were observed near the junction of the esophagus and intestine in both the adult male and female T. vulpis (Plate III, figs. 25 and 28). These structures are freely movable except at an area of attachment, which is either at the terminal part of the glandular esophagus or at the beginning of the intestine, but the exact location of the attachment could not be determined. The shape of these structures is variable; they are, for the most part, oval to egg-shaped, but may be spherical. They are uniformly granular with no nuclei evident, and their function remains obscure. Chandler (1930) illustrated similar structures for T. trichiura, but did not show them in a drawing of T. vulpis included in the paper, and he did not mention them in the text for either.

TABLE IX

Showing Measurements of Immature Specimens of
Trichuris vulpis at Various Ages

Age	Overall Length	Length of Muscular Esophagus	Length of Glandular Esophagus	Length of Intestine
Express from egg	253 u			
" " "	248 u			
" " "	181 u			
" " "	318 u			
" " "	304 u			
14 Days	337 u			
"	398 u			
"	412 u	118 u	207 u	97 u
"		93 u		
"	512 u	117 u	248 u	146 u
17 Days	870 u	220 u	470 u	180 u
18 Days	628 u			
19 Days	803 u			
21 Days	919 u			
24 Days	1.8 mm.			
"	4.7 mm.	440 u	3.6 mm.	670 u
"	2.4 mm.	303 u	1.7 mm.	380 u
"	2.5 mm.	345 u	1.7 mm.	380 u
28 Days	1.4 mm.	190 u	1.0 mm.	175 u
"	1.3 mm.	219 u		
"	3.1 mm.			
"	1.4 mm.			
"	1.3 mm.			
32 Days	5.4 mm.			
"	4.7 mm.	380 u		
"	4.0 mm.	370 u	3.1 mm.	530 u
"	4.8 mm.	423 u	3.5 mm.	873 u
42 Days	2.4 mm.	175 u	1.9 mm.	248 u
"	4.3 mm.			
"	4.3 mm.	277 u	3.4 mm.	540 u
"	3.3 mm.	219 u	2.6 mm.	438 u
"	4.9 mm.	234 u	3.8 mm.	920 u
"	7.2 mm.	263 u	5.9 mm.	1.1 mm.
"	3.3 mm.	204 u	2.6 mm.	409 u
"	2.9 mm.	219 u	2.1 mm.	643 u
"	3.4 mm.	219 u	2.7 mm.	511 u
"	3.9 mm.	244 u	3.2 mm.	481 u
51 Days	16.3 mm.			2.9 mm.

The Length of the Prepatent Period for Trichuris vulpis in Dogs

The prepatent period extends from the time that infective eggs are ingested to the time that eggs of the next generation can be recovered. The prepatent period was determined for this parasite in dogs kept under experimental conditions.

In order to be certain that eggs were detected in the feces on the first day they appeared, daily fecal examinations using sodium chloride flotation were begun well in advance of reported prepatent periods, and examinations were continued until trichurid eggs were recovered.

Data on the prepatent period of T. vulpis were obtained for seven dogs and the results are summarized in Table X.

TABLE X

Prepatent Periods for T. vulpis in Seven Experimental Dogs

Dog	Date Infected	Date Positive	Period
Susie A	9-19-50	12-14-50	86 Days
Susie B	9-19-50	12-15-50	87 Days
Susie C	9-19-50	12-14-50	86 Days
Brownie	3-14-51	6-6 -51	84 Days
Whips Pup	7-24-51	10-17-51	85 Days
Exp. IX	7-19-51	10-2 -51	74 Days
Joshua	8-26-52	11-9 -52	75 Days

The range of the prepatent period extended from 74 to 87 days, with a mean of 82.4 days, which is well within the 70 to 90 days given by Morgan and Hawkins (1949).

Observations on the Longevity of *Trichuris vulpis*

A study of the longevity of *T. vulpis* was not planned, but limited data were collected and considered to be significant. These data are not in agreement with those of Whitney, (1938) who is the only writer to offer information concerning the life span of *T. vulpis*. Fecal examinations of dogs in his kennels in the late fall revealed the presence of eggs of *T. vulpis*, later examinations in the spring were negative, and from these observations he concluded that the life span of *T. vulpis* was five months or less. Certainly his observations proved little or nothing from a scientific viewpoint.

One dog maintained in our laboratory supplied data which indicated that worms may live long. One of the three Beagle bitches purchased by the Parasitology Department on March 11, 1951, was determined to be infected with *T. vulpis*. This dog was treated on three different occasions with an anthelmintic to rid her of these parasites, and each attempt failed. Periodic fecal examinations showed the presence of trichurid eggs, and the last positive findings were made April 15, 1952, but examinations were continued until June 27. In this instance eggs were present for a period of more than 13 months, denoting a patent period of more than a year. It is quite unlikely that this dog picked up new trichurid infections during the period of confinement because no dogs reared under experimental conditions acquired an infection during the entire course of the investigation. Since the average prepatent period is about three months, it can be assumed that the life span of *T. vulpis* is longer than 16 months. However, this limited datum does not show the possible range for the normal life span of this parasite.

Observations of the Histopathology of *Trichuris vulpis* Infections

The pathology caused by the presence of *T. vulpis* is infrequently described in the literature. Wright (1930) concluded an infection of *T. vulpis* was responsible for the death of a dog which at autopsy showed necrosis of the cecum and peritonitis. He stated that in this and other cases the mucosa was thickened and covered by a thick, tenacious exudate. Hung (1926) associated hyaline degeneration and follicular enlargement with infections of these nematodes. Efremov and Shikhobalova (1939), as a result of experiments with *T. muris* in white mice, reported that the adult parasites crawled around in the tissue with great care, causing neither hemorrhage nor inflammatory reaction. According to them, the larvae of *T. muris* invade the mucosa, and the posterior ends of the worms emerge into the lumen as they grow. Furthermore, they reported that this trichurid in mice is not a blood sucker, is not capable of destroying the mucosa in an active manner, and is usually not accompanied by a lymphocytic infiltration. According to these writers, the parasites secrete a proteolytic substance while in the tissue which digests the proximal tissue. Hoeppli (1933), whose work is cited repeatedly, discussed and illustrated his findings in man. The picture as he presents it is essentially that the tunnel walls surrounding the imbedded worms consist of epithelial cells which fuse and form syncytial-like structures with eosinophilic cytoplasm and numerous pyknotic nuclei. The writer cannot concur with these findings, and there is either a difference in man and the dog or the age of the infection alters the picture, since these studies on infections of known ages do not entirely substantiate Hoeppli's work.

Ceca from dogs with long-standing trichurid infections were not studied; the mature infections reported were from experimentally infected dogs in which the worms had been patent for less than two months. Conceivably, additional pathology might occur if the worms are present over a longer period of time. Also all dogs were fed a well balanced, adequate diet, and this may have reduced the harmful effects of the parasites.

The writer has studied both fresh and formalin-fixed tissue from numerous trichurid-infected, as well as normal ceca. The pathological findings associated with the presence of these nematodes, as well as the relationship of the whipworms to the cecal mucosa, will be described.

Freshly opened ceca that are infected usually show an excessive mucus secretion that covers the epithelial surface. The parts of the small immature larvae, up to and including the 54-day-old stage, that are not imbedded in the mucosa are often completely covered by mucus. The free parts of adult worms, however, are only partially covered by mucus, since the posterior ends project through it into the lumen. The thin anterior end of both the immature and mature worms is buried in the mucosa. In spite of the numerous sections and fresh tissue studied, it has been impossible to determine whether the anterior end is completely in tissue or whether it is alternately above and below the surface.

Occasionally an infected cecum grossly shows areas that indicate the presence of petechiation, but sections fail to show any hemorrhage, even though the tissue frequently appears hyperemic. It is to be noted, however, that certain trichurid-free ceca also exhibit grossly petechiation comparable to that observed in trichurid infections. Therefore, it appears that the infection is not necessarily responsible for the condition.

No other macroscopic lesions are evident in the cecal mucosa.

Microscopically, the cecal mucosa shows surprisingly little response to an invasion by trichurid worms. There seems to be an increase of lymphocytes in some instances and this may be accompanied, apparently, by an increase in the size of the cecal lymph follicles. Critical evaluation of changes in sizes of lymph follicles is difficult, however, because normal ceca contain many lymph follicles of various sizes. According to Habel and Biberstein (1952), some lymph follicles in normal ceca may be situated partly in the submucosa, partly in the tunica propria, and where this occurs, the muscularis mucosae is discontinuous. This fact shows that Hung (1926) is in error in stating that follicular enlargement causes rupture of the muscularis mucosae. Hung most likely mistook a normal histological pattern for a pathological one. A photomicrograph of such a follicle from an infected cecum which interrupts the muscularis mucosae is shown in Plate IV, fig. 30.

Tissue sections of one cecum that contained 54-day-old larvae showed some interesting pathology other than lymphocytic infiltration. Sections of trichurid worms were associated with areas of coagulative necrosis in the center of a lymph follicle (Plate IV, fig. 30). The follicle is situated, as previously described, partially above and partially below the muscularis mucosae, and the muscularis is interrupted in the region of this follicle. The worms were below the level of the muscularis mucosae, although obviously they did not have to penetrate the muscle to attain this depth in the tissue. The majority of writers claim that the trichurid worm is seldom, if ever, found below the level of the muscularis mucosae, but it is evident from the photomicrograph that such a condition can exist.

No reference in the literature adequately describes the mechanism

of tissue penetration and this problem probably resolves itself into a matter of interpretation. If penetration occurs, and it does apparently, the movements of the mouth spear, which has been described, must be instrumental in this activity. Tissue sections of worms in the epithelium, tunica propria, and in lymph follicles support the idea of tissue penetration. The fact that considerable traction must be applied to remove the anterior ends of intermediate and adult stages from the cecal tissue is additional evidence that these parasites are imbedded.

The relation of various stages of development of T. vulpis to the cecal mucosa to support these contentions is illustrated in several photomicrographs (Plates IV and V), and the interpretations are described.

The photomicrograph (Plate IV, fig. 29) shows cecal tissue of a 32-day-old infection. The majority of the worms are located in the epithelium, but the one on the extreme right in figure 29 is located mostly below the surface epithelium. The absence of tissue reaction is surprising; cells adjacent to the parasites appear normal. Apparently from these photomicrographs it can be assumed that the earliest tissue penetration in the cecum is an invasion of the epithelium followed by a deeper penetration into the tunica propria.

The photomicrograph (Plate IV, fig. 30) shows a section of cecum from a 54-day-old infection in which a lymph follicle is penetrated by trichurids. The area in the vicinity of the worms shows considerable necrosis, the exact cause of which cannot be determined. Possibly some secretion from the parasite could cause the reaction, or bacterial contaminants could have been carried in from the surface by the worms and are the causal agents. This is the most severe type of pathology that was observed and was found in several different experiment infections.

The photomicrograph (Plate V, fig. 31) shows an infection in which the worms are mature. In this case the tissue shows a marked response to the presence of the parasites, and this is evidenced by the definite increase of lymphocytes in the tunica propria. The relation of the nematode to the tissue is characteristic, and the worm is surrounded by an apparent condensation of connective tissue fibers, in which an occasional pyknotic nucleus is present. Cells which are immediately adjacent to the concentrated connective tissue fibers are normal and no evidence of lysis is present.

The photomicrograph (Plate V, fig. 32) shows another infection in which the worms are mature. The upper left area of tissue surrounding the nematode shows changes resembling necrosis and is similar to one illustrated by Hoeppli. However, the tissue surrounding the worm in the lower left area is fibrous and contains several pyknotic nuclei.

On the basis of the photomicrograph illustrations, besides the numerous sections studied, the following interpretation concerning tissue invasion seems probable. The trichurid worm in the dog penetrates the cecal tissue by the 32nd day following infection and the penetration is confined to the epithelial cells and the most superficial part of the tunica propria. As the worms grow, a tissue response is initiated and results in a concentration of connective tissue fibers around the worms. In some instances, apparently, these fibers are replaced by a surrounding zone of necrosis. Hyperemia and lymphocytic infiltration occasionally accompany a trichurid infection, and only rarely do the worms invade lymph follicles and cause necrotic changes.

SUMMARY AND CONCLUSIONS

The life cycle of Trichuris vulpis has been completed under laboratory conditions, and the following new contributions have been made:

1. The adult T. vulpis possesses a lancet or mouth spear, which heretofore has not been reported.
2. Newly-formed larvae are actively motile within the eggs, and the duration of motility varies from 3 to 16 days. Comparable motility in the genus Trichuris has been reported only for larvae of T. ovis.
3. Various aged immature larvae were studied, and the progressive development of the digestive and reproductive systems is described and illustrated. No such data have been reported previously.
4. Data on the duration of various developmental stages of embryonating eggs are reported at various temperatures within a range of 4.4° C. to 55.8° C. No such complete data are available.
5. The incidence of T. vulpis in 250 dogs in Oklahoma, examined in this investigation, is 8.0 percent.
6. T. vulpis has been experimentally proven to have a life span of more than 16 months, and this is much longer than has been reported.
7. The histopathology is related and illustrated for experimentally

infected dogs and is remarkable in that surprisingly little tissue response was observed at any stage of development of T. vulpis. Hyperemia and lymphocytic infiltration in the cecum were associated occasionally with a trichurid infection and only rarely was an area of necrosis observed. It should be noted, however, that no infection studied was of long duration and that all dogs used were well nourished.

8. T. vulpis are occasionally found below the muscularis mucosae, and Plate IV, figure 30, substantiates this. No other such photomicrograph is in the literature.
9. Egg albumin is an excellent mounting medium in which to study both immature and mature nematodes. Worms remain alive in the medium for 24 to 30 hours, and internal structures are easily discernable. The addition of small amounts of an aqueous solution of neutral red stained certain structures and made them more easily observed.

In addition to these new contributions, the following substantiate pre-existing data:

1. The developmental rate of eggs of Trichuris vulpis in water varies with the temperature. At 4.4° C., eggs do not develop but remain viable. At 25.4° C. to 32.2° C. and at 33.3° C. to 38.8° C. the developmental rate was most rapid. At 44.4° C. development was retarded, whereas a temperature of 55.8° C. was lethal.
2. Under optimum temperature conditions, eggs fully embryonated in nine days.
3. The prepatent period was determined for T. vulpis in seven experimental dogs, and ranged from 74 to 87 days with the mean

of 82.4 days. These figures are well within ranges that have been reported.

This investigation indicated that life cycle studies of T. vulpis are far from complete, and further investigation along the following lines should be profitable:

1. Additional developmental stages should be studied in order to more fully understand the development and biology of T. vulpis.
2. The effects of long-standing trichurid infections in both well-nourished and under-nourished dogs should be studied experimentally.
3. It should be determined whether or not larval motility influences the degree of infectivity of eggs of T. vulpis.
4. The effects of environmental agents other than temperature upon developing eggs need further study since existing information is meager.
5. A more complete knowledge of the biology of T. vulpis is needed in order to develop much-needed, effective anthelmintics and control measures, both of which are wanting at the present time.

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PLATE I

Figure 1. Cecum with numerous T. vulpis from an experimentally infected dog.

Figure 2. An egg containing an unsegmented zygote recovered from feces by salt flotation.

Figure 3. An egg, removed from the uterus of a worm and cultured in water, showing a fully-developed larva within the shell.

Figure 4. A first-stage, infective larva expressed from an egg. The larva shows the anteriorly-located lancet or mouth spear.

PLATE I

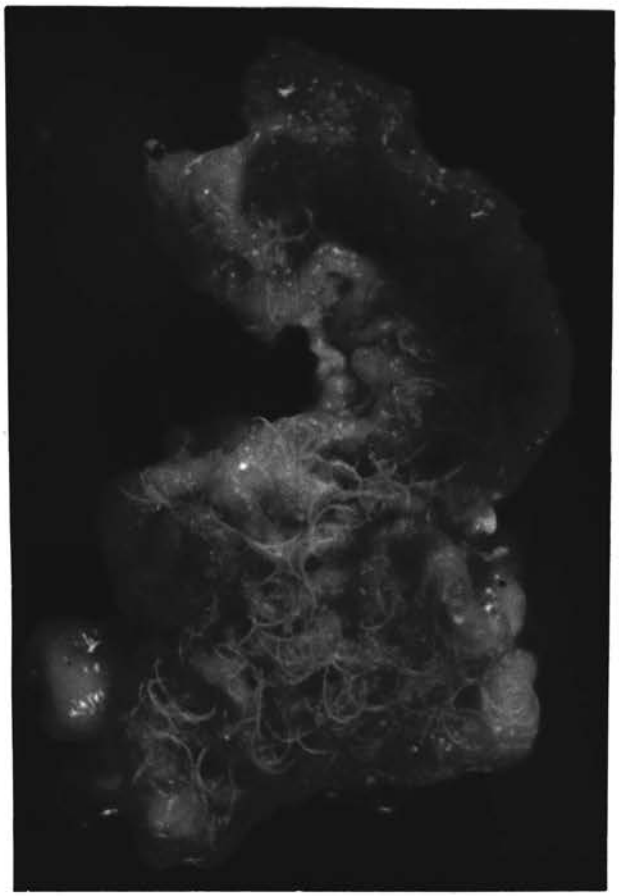


Figure 1

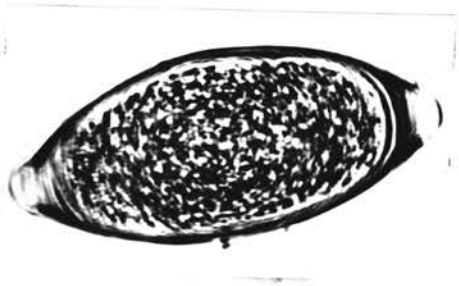


Figure 2

Figure 3

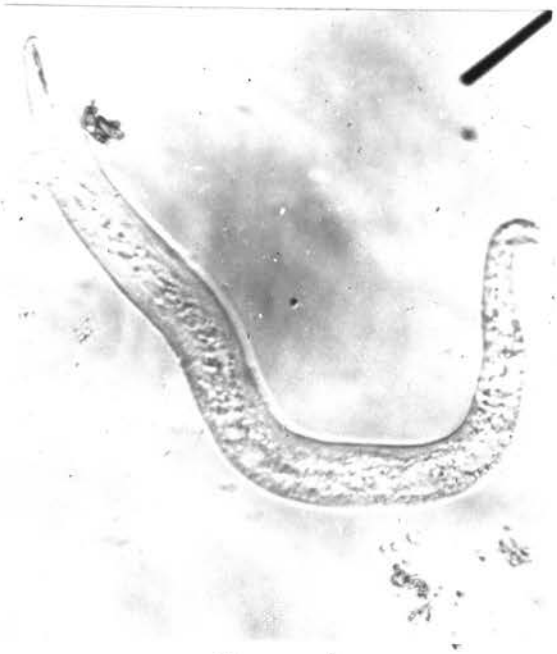
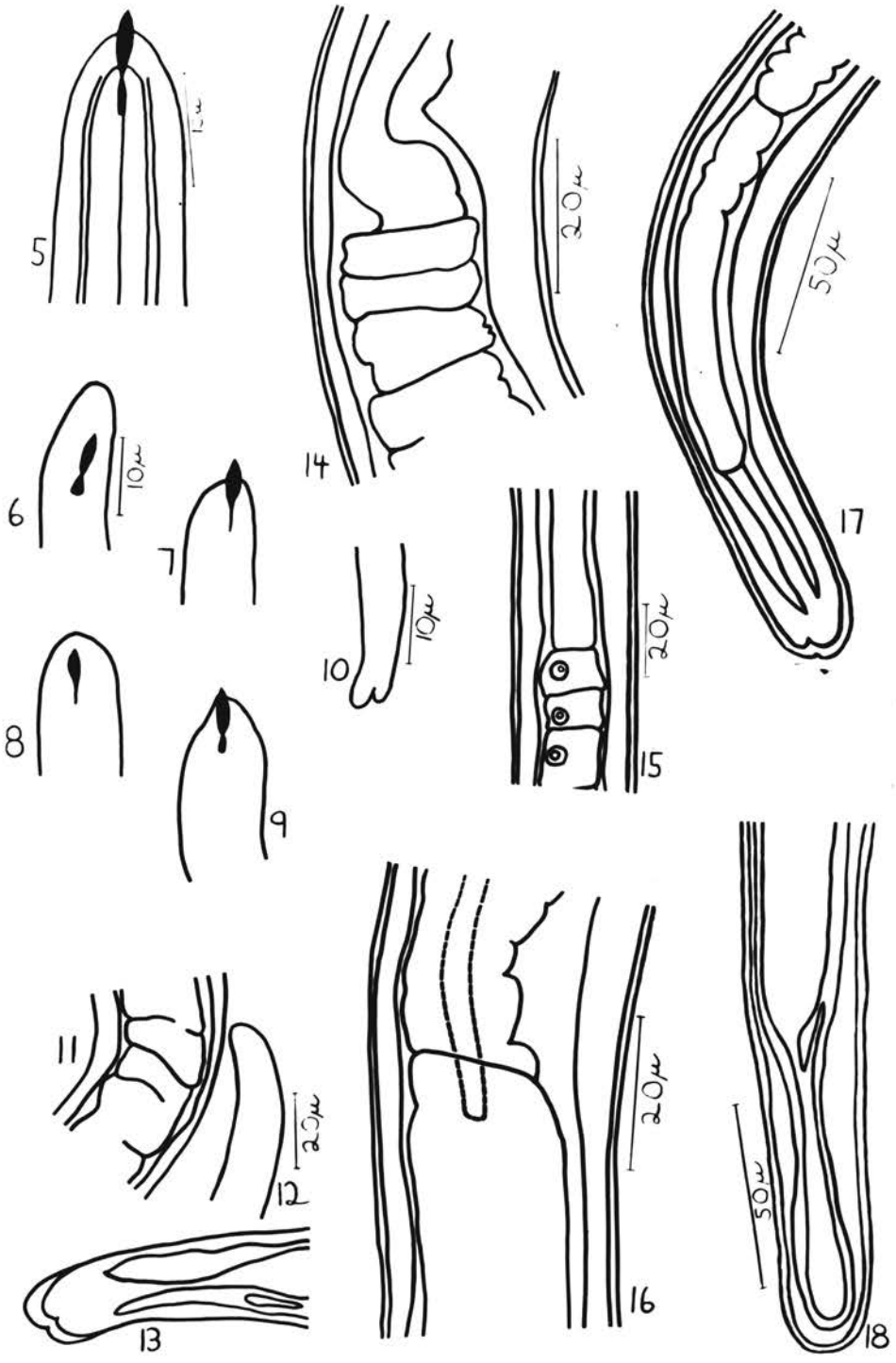


Figure 4

PLATE II



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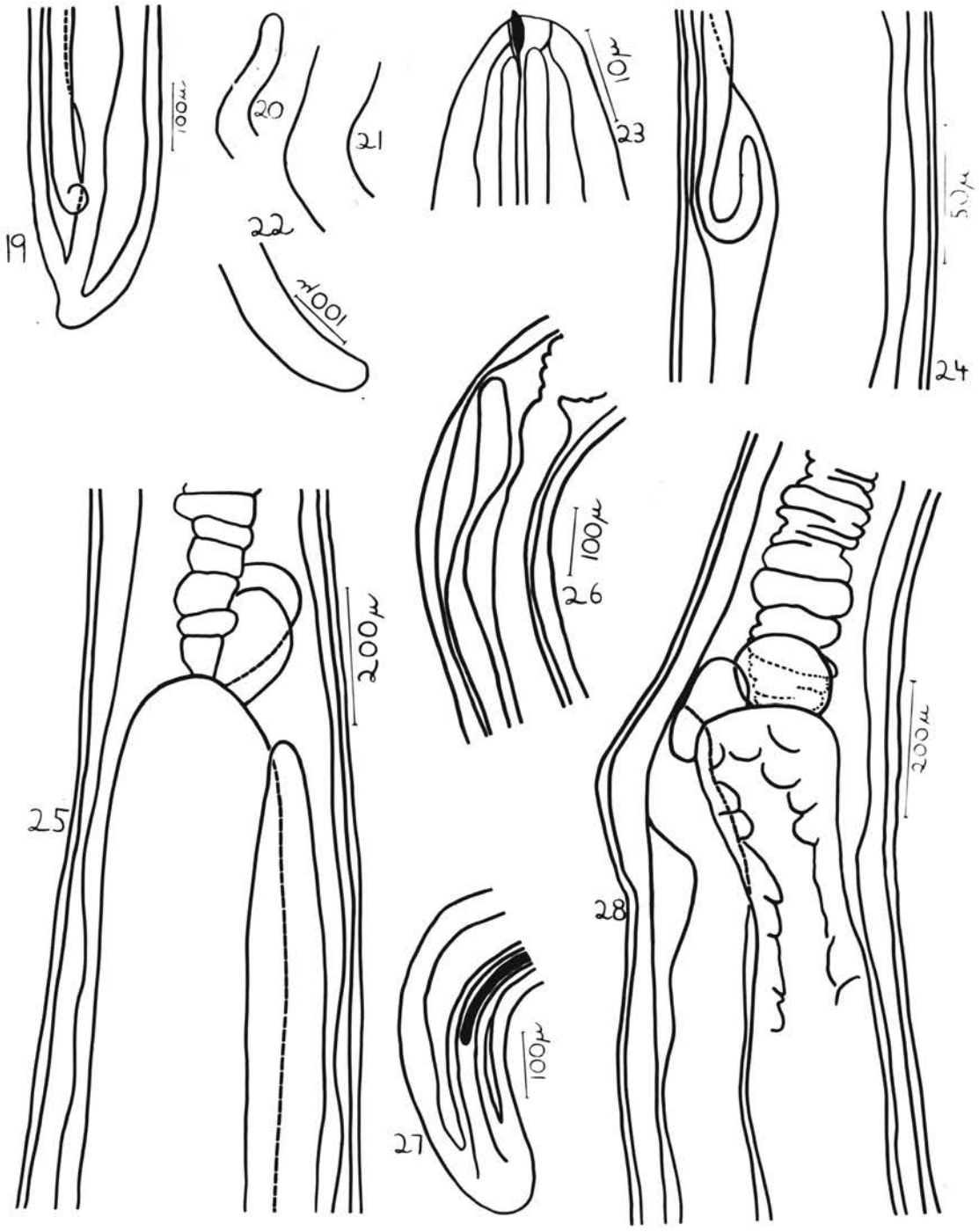
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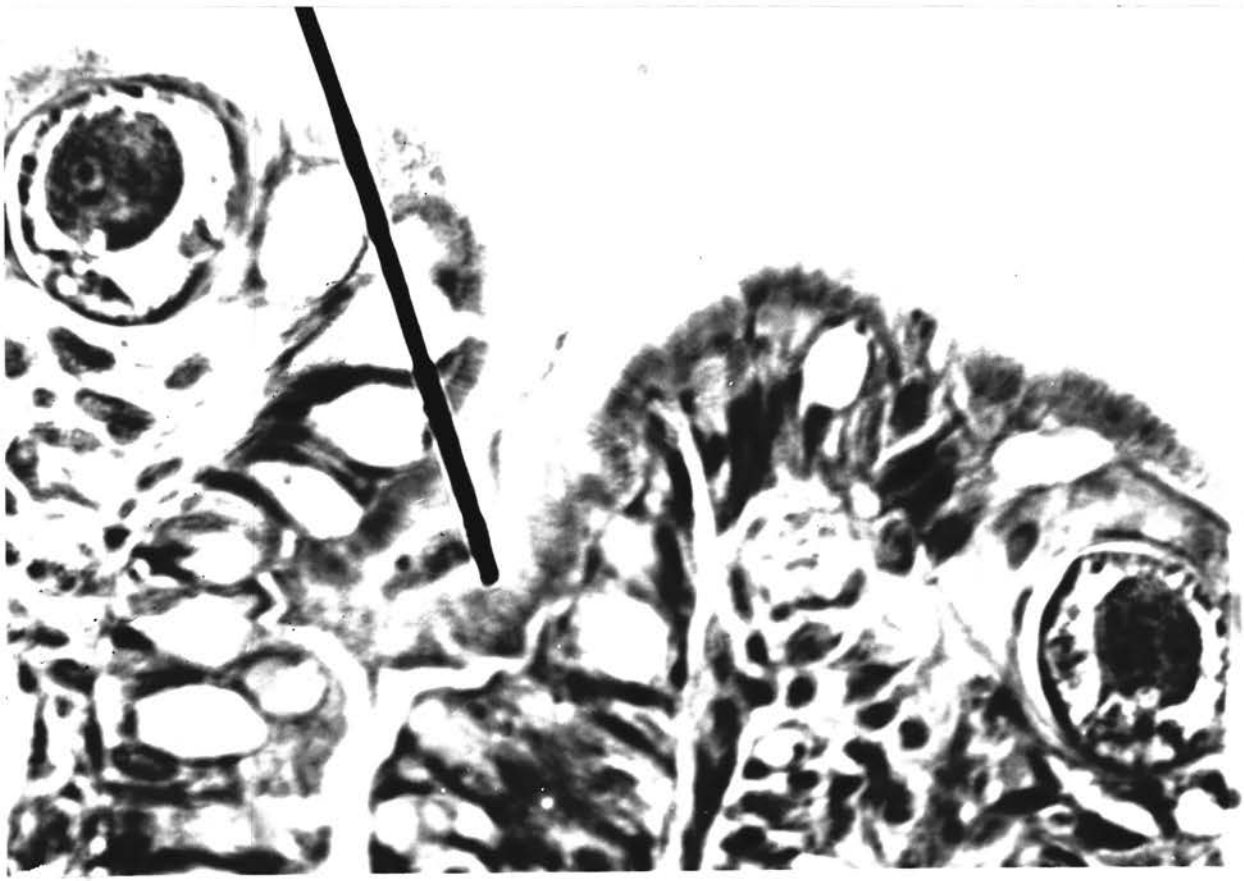

Figure 29

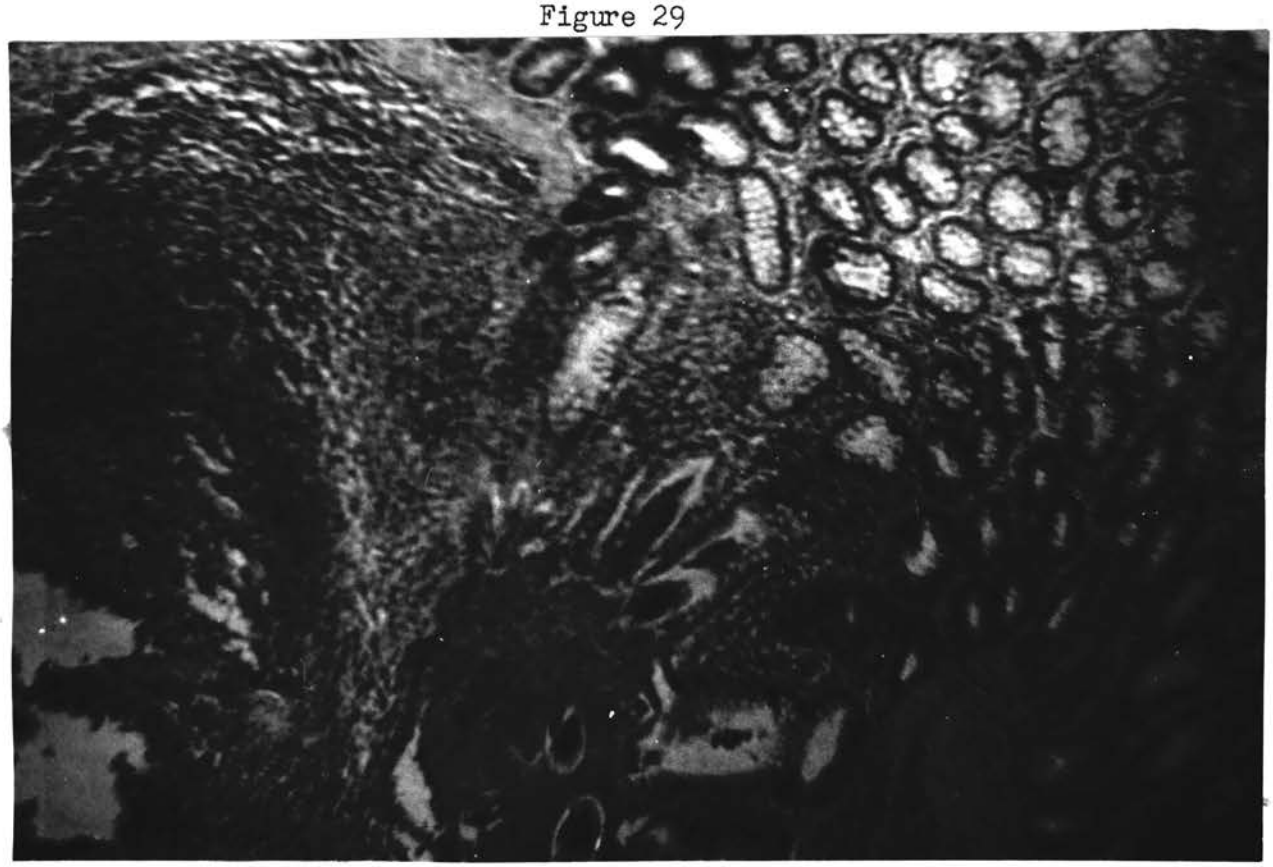

Figure 30

PLATE IV

Figure 29. Photomicrograph of cecal tissue showing cross sections of 32-day-old larvae in the epithelium and superficial tunica propria, greatly enlarged.

Figure 30. Photomicrograph of cecal tissue showing various sections of 54-day-old larvae embedded in a lymph follicle lying below the muscularis mucosae. The area around the parasites is necrotic.

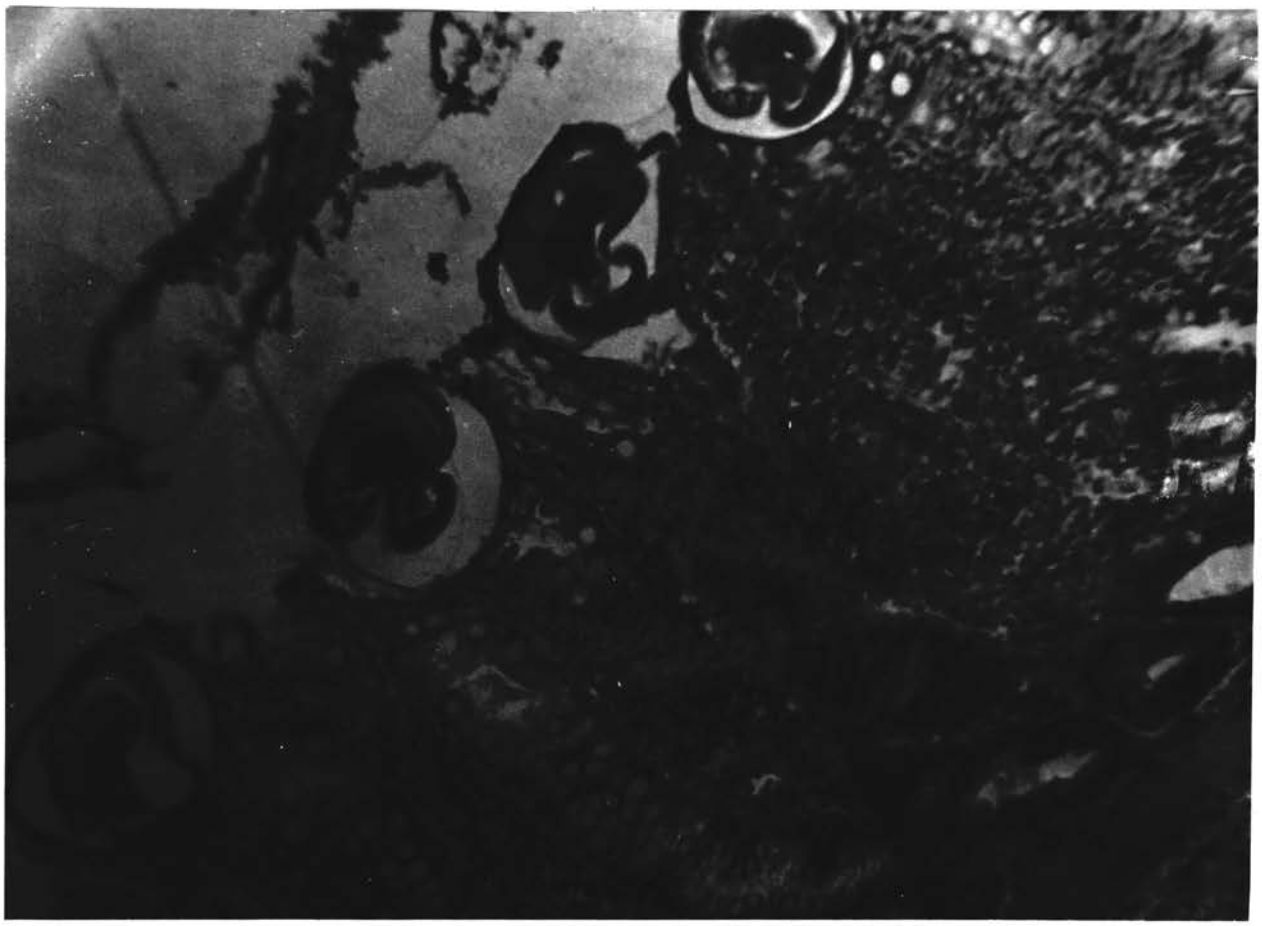

Figure 31

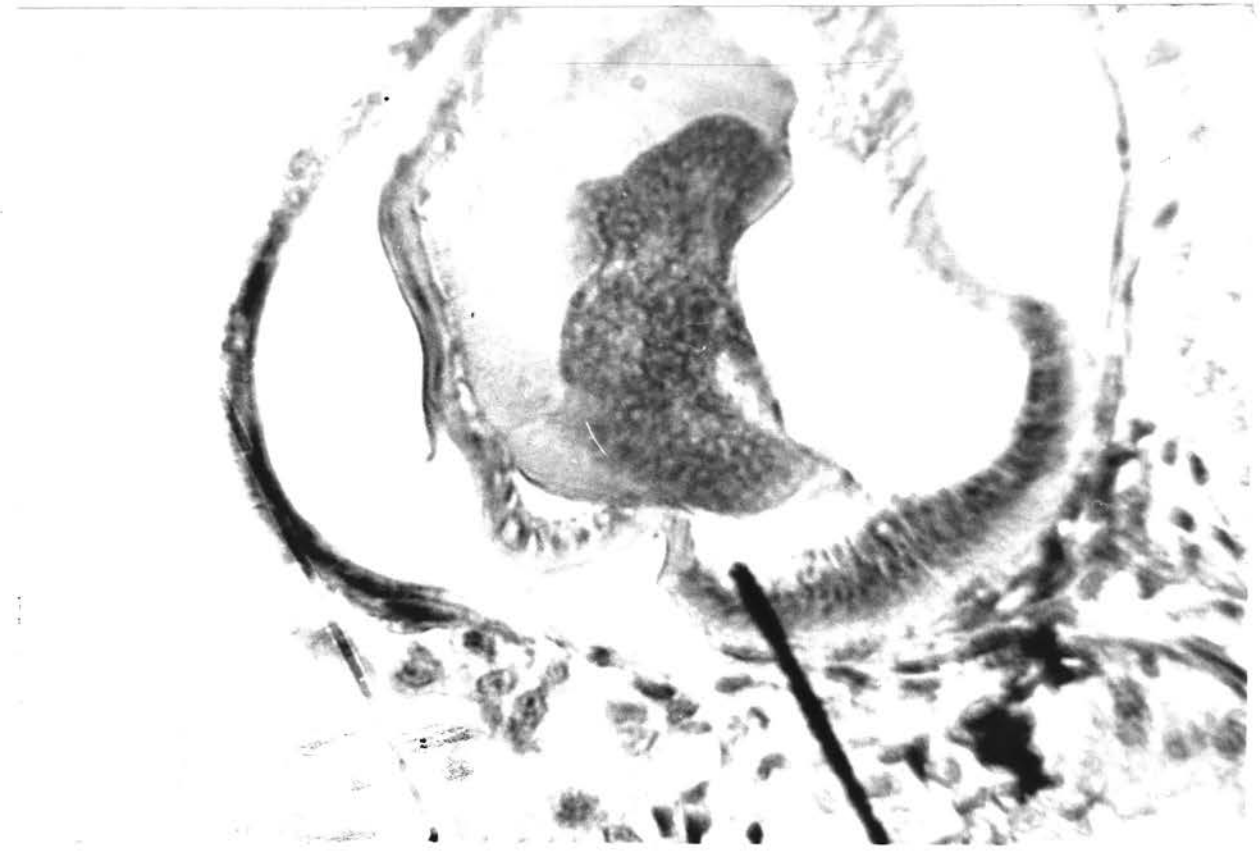

Figure 32

PLATE V

Figure 31. Photomicrograph of cecal tissue showing cross sections of mature worms and a marked increase in lymphocytes in the tunica propria.

Figure 32. Photomicrograph of cecal tissue containing a cross section of a mature worm to show the relationship of the parasite to the host tissue, greatly enlarged.

VITA

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Master of Science

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Date of Final Examination: January 13, 1953.

THESIS TITLE: STUDIES ON THE DEVELOPMENT OF TRICHURIS VULPIS, (FRÖHLICH, 1789) (NEMATODA: TRICHURIDAE)

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