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Article VII.—STUDIES ON NORTH AMERICAN BLOOD FLUKES[1]

By Horace W. Stunkard

Plates II to XIII

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INTRODUCTION

The group of blood-infesting trematodes as at present constituted comprises three families, the Schistosomidæ, the Spirorchidæ and the Aporocotylidæ. The first of these families is the best known and con-

[1]Contribution from the Biological Laboratory, New York University, and the Department of Lower Invertebrates, The American Musum of Natural History.

tains the diecious forms parasitic in the vascular system of birds, cattle, and man. The Spirorchidæ and Aporocotylidæ are hermaphroditic forms, the former occurring in the blood vessels of turtles and the latter in those of fishes. Certain morphological characters are common throughout the group of blood flukes, but within the families and even within some of the genera great morphological disparities are present. The fish parasites are without organs of adhesion; one group of turtle parasites has only an oral sucker, while the other has both oral sucker and acetabulum; and in the family Schistosomidæ there are genera without suckers and others with both oral and ventral adhesive organs. In the Aporocotylidæ the genital pore is dorsal; in the Spirorchidæ it is either dorsal or ventral and somewhat lateral; and in the Schistosomidæ it is ventral, either in the median line or at the right or left of it. Among the blood flukes there are genera with a long coiled uterus containing many eggs and others with a short uterine portion of the female genital duct containing a single egg. These major points of distinction are associated with minor differences and constitute a large and unusual list of anomalies in the group of blood-infesting trematodes. Probably no other trematode group manifests such unusual morphological diversity and no satisfactory explanation has as yet been offered for the presence of the structural dissimilarity that exists in the group of blood-inhabiting trematodes. The discovery of new blood flukes in North America and a study of their distinctive features will, I believe, afford evidence of considerable value in the interpretation of data accumulated in the study of the previously known forms. The addition of such information should aid materially in an understanding of the morphological and biological characters of other blood flukes.

For the sake of completeness and also to facilitate comparison of previously described forms with new ones described in this paper, a brief outline and description of the families and their genera is given.

SCHISTOSOMIDÆ Looss, 1899

Elongate forms parasitic in the vascular system of birds and mammals; sexes separate; pharynx absent; intestinal ceca unite to form a single intestine. Suckers present or absent; acetabulum when present anterior to genital pore. Male with four or more testes; may be widened posterior to acetabulum and have sides curved ventrally to form a gynecophoric canal. Female more slender than male; ovary elongate; vitellaria extensive, extend far posteriad.

The family Schistosomidæ as characterized by Odhner 1912 contains the genera *Schistosoma*, *Bilharziella*, *Gigantobilharzia*, *Ornithobilharzia*, and *Austrobilharzia*[1].

[1]While this paper was in press, Tanabe, in the Journal of Parasitology, June 1923, IX, pp. 183-199, described the structure and life history of a new schistosome, *Schistosomatium pathlocopticum*.

SCHISTOSOMA Wienland, 1858

SYNONYMS.—*Gynæcophorus* Diesing, 1858; *Bilharzia* Cobbold, 1859; *Thecosoma* Moquin-Tandon, 1860.

Schistosomidæ with long filiform females and shorter males. Male with gynecophoric canal in which the female is enclosed. No cirrus sac; no Laurer's canal; eggs with spines and no lids. Miricidia ciliated, with large glandular cells discharging anteriorly beside the gastric sac. Development in various snails. Cercariæ with forked tails and no eye spots; develop in sporocysts; enter mammalian hosts through skin or mucosa and pass into blood vessels.

The type species, *S. hæmatobium*, was discovered in 1851 by Bilharz in Cairo, Egypt. Its structure has been known since the classical description of Looss (1895). In 1915, Leiper discovered its life cycle, the miricidia entering snails of the genus *Bullinus*. The sporocysts give rise to daughter sporocysts and these to cercariæ. Adults live in the pelvic veins. The eggs have a terminal spine and are voided in the urine.

Two other species, *S. japonicum* Katsurada, 1904, and *S. mansoni* Sambon, 1907, occur in man, and several species have been reported from various species of cattle.

The splendid account of this genus by Castellani and Chalmers (1919), dealing with the literature, classification, anatomy, life history and pathology of the human schistosomes, renders further summary here unnecessary.

BILHARZIELLA Looss, 1899

Female shorter than male, both much flattened; integument spined; intestine unpaired; genital pore lateral, usually on the left side. Cirrus sac present, well developed, seminal vesicle largely outside of cirrus sac. Prostate large, longer than the cirrus. Female less elongated than in other schistosomes; ovary short, weakly spiral; vitellaria less than one-half length of body; uterus short, contains only a single egg.

Type species: *B. polonica.*

Genus proposed by Looss to include *B. polonica* Kowalewski, 1895, and *B. kowalewski* Parona, 1896, parasites in the vascular system of various species of birds. Braun (1902) added *B. pulverulenta*, a form in which suckers are entirely lacking, and transferred *Distomum canaliculatum* Rudolphi to this genus.

GIGANTOBILHARZIA Odhner, 1910

Sexes separate but worms not paired as in *Schistosoma;* no suckers or spines; esophagus as in other schistosomes; excretory pore at posterior end; short bladder, which divides almost immediately; vitellaria extend to posterior end of body; single egg in uterus. Parasitic in *Larus fuscus.*

Single species: *G. acotylea.*

ORNITHOBILHARZIA Odhner, 1912

Female shorter than male; suckers present with small spines. Male with gynecophoric canal; copulatory apparatus small, on posterior wall of acetabulum. Seminal vesicle entirely outside a rudimentary cirrus sac; no prostate; genital pore slightly left. Female long, threadlike, flattened; ovary long, strongly spiral; vitellaria extend over two-thirds of body length; single egg present in uterus.

Type species: *O. intermedia* Odhner, 1912.

Odhner (1912) removed the species *Bilharziella canaliculata* and *B. kowalewski* to this genus.

AUSTROBILHARZIA Johnston, 1917

Male shorter than female; gynecophoric canal present; cirrus sac well developed, encloses vesicula seminalis; prostate present; two suckers, without spines. Female has anterior filiform and posterior flattened regions; acetabulum stalked as in the male, oral sucker absent; ovary, long, spiral; vitellaria in posterior third of body; single egg present in uterus. Parasitic in *Larus novæ hollandiæ*.

Single species: *A. terrigalensis*.

APOROCOTYLIDÆ Odhner, 1912

Hermaphroditic blood flukes, parasitic in the heart and arterial system of various species of fishes. Suckers absent; only adhesive structures are cuticular spines. Pharynx absent; esophagus long; ceca H-shaped; two anterior and two posterior crura; excretory pore terminal, slightly dorsal; unpaired excretory bladder with two long vesicles which extend forward below the ceca; genital pore dorsal near posterior end of body, median or lateral; testes numerous, anterior to ovary; cirrus small; vitellaria well developed, duct single.

The family Aporocotylidæ was proposed by Odhner to contain the genera *Aporocotyle* and *Sanguinicola*. In the original description Odhner (1900) reported *Aporocotyle* as an ectoparasite from the gills of the flounder. Plehn (1905) described *Sanguinicola* as a turbellarian and three years later (1908) decided it was a monozoic cestode. Odhner reinvestigated these forms and discovered their true nature. In his paper (1911) announcing them as blood parasites, he discussed the fundamental agreement between their structure and that of *Deontacylix ovalis*. The latter form had been described by Linton (1910) from the intestine of *Kyphosus sectatrix*, and, unable to recognize any near resemblance between it and any then known group, he proposed a new suborder to contain it. It is an interesting and noteworthy fact that in the original descriptions the true character of not one of these forms was recognized and only *Sanguinicola* was originally reported from the blood vessels.

Communicating with Dr. Linton, I learned that his material of *Deontacylix* consisted of specimens mounted *in toto* on two slides. One

of these was sent to Dr. Odhner in December 1911 and, failing to reach its destination, the other was sent in March 1912. The latter slide with all the available material of the species was kindly loaned to me for examination. It is difficult to identify and trace structures with certainty in the mounted specimens and I am unable to add anything to Linton's description of the form. His figure is an accurate representation of the specimen and his description as complete as possible from the material at hand. In the letter accompanying the slide he expresses the belief that the form is a blood parasite. I think there is a strong probability that the specimens came originally from the mesenteric blood vessels and on the basis of morphological similarity I assign the form to the family Aporocotylidæ.

In a postscript to his article announcing *Sanguinicola* as a blood fluke, Odhner (1911) reported experiments and published a series of drawings done by Looss on the life history of this form. Because of morphological similarity, Odhner had suspected that *Cercaria cristata*, a forked tailed cercaria present in several species of European snails, was the larval stage of *Sanguinicola*. The work of Looss confirmed and established this suspicion. Looss demonstrated that this cercaria develops into *Sanguinicola* in goldfish and carp. Infected snails were placed in aquaria with these fishes and heavy infection followed, resulting in the death of the fish. All stages in the transformation of the cercariæ to the adult worms in the heart were obtained.

SPIRORCHIDÆ Stunkard, 1921

Slender, blood-inhabiting trematodes with slightly developed musculature and one or two weak suckers. Pharynx absent. Testes lobed, multiple, anterior and sometimes also posterior to the ovarian complex. Ovary lobed; Laurer's canal present; uterus short. Eggs large, thick shelled, discharged singly.

The name Spirorchidæ was proposed by the writer (1921) for the family outlined by Ward (1921) to contain the blood flukes of turtles when the name Proparorchidæ Ward became invalidated through the synonymy of the genera *Spirorchis* and *Proparorchis*. As originally erected, the family contained only the genera *Spirorchis* and *Hapalotrema*. Because of unique differences these genera were referred to separate subfamilies, Spirorchinæ and Hapalotreminæ. The following year the discovery of two new genera, one of which belongs to each of the subfamilies, made it possible for the writer (1922) to characterize these groups with more definiteness. The discovery of another new genus, which is described in the present paper, further confirms the arrangement.

Spirorchinæ Stunkard, 1921

Hermaphroditic, blood-inhabiting monostomes with weak oral sucker. Esophagus without pharynx and surrounded by secretive cells which are more numerous near its posterior end. Ceca end blindly near posterior end of body; excretory vesicle small, dividing almost immediately into lateral collecting ducts. Testes numerous, arranged in a linear series in the intercecal area anterior to the ovary; cirrus sac small; ovary dextral in position between the testes and the genital pore; seminal receptacle and Laurer's canal present; vitellaria both extra and intercecal; genital pore ventral, sinistral, near the posterior end of the body; uterus short, containing a single oval egg.

The type genus, *Spirorchis*, was described by MacCallum (1918) but this author unfortunately omitted the specific name intended for the species. MacCallum reported the form from the intestine of *Clemmys insculpta*. This paper appeared while I was in the U. S. army in France. On my return to New York University after release from military service, I noticed the description of the form and was struck by the likeness of the parasite described by MacCallum to certain trematodes I had collected from the vascular system of several species of turtles during the years 1913 to 1916, while a graduate student in the department of zoölogy of the University of Illinois. The blood flukes I had collected and the form described by MacCallum are monostomes of similar size and shape; they agree in position and character of oral sucker, position and extent of intestinal ceca, position and extent of vitellaria, vitelline ducts and receptacle, position and shape of ovary, oviduct and uterus, position and extent of testes, shape and location of seminal vesicle and vas deferens, as well as position of the excretory pore. They are alike in the character of intestinal content, which led MacCallum to describe the form as a hæmatophagic trematode. The only points of difference are to be found in the statement of MacCallum that in *Spirorchis* a pharynx is present and that the genital pore is median near the posterior end of the body, while in my material a pharynx is absent and the genital pore is lateral, slightly posterior to the level of the ovary. Conferring with Dr. MacCallum, I learned that the description was made from specimens mounted *in toto*, but unfortunately at that time his slide could not be found. Dr. MacCallum examined several of my specimens and noted the similarity between them and the form he had described, but was not certain whether they were the same.

Ward (1921) described a new trematode from the heart and arteries of various species of North American fresh-water turtles, giving to the parasite the name *Proparorchis artericola*. In the introduction of his paper he stated that the parasite had been under observation in the zoölogical laboratory of the University of Illinois for several years, and added:

Since the material is easily obtained, it will afford perhaps the best opportunity available in this country for the laboratory study of forms adapted to this particular environment, so that, despite the incompleteness of the observations, the publication of this note is justified. It is further called for by the fact that several others, who had their attention called to this species, plan to give it more detailed study than I can make at the present time, and will be glad to have a record of the facts thus far determined in order to utilize them as a basis for further study.

He described the blood flukes of North American turtles as belonging to a single species, and says: "according to records of collection here, it has been met with in *Pseudemys elegans* from Havana, Illinois, in *Malacoclemmys leseurii* in Newton, Texas, in *Pseudemys scripta* from Raleigh, N. C., and in *Chrysemys marginata* from Fairport, Iowa."

Although he described *Proparorchis artericola* as the type and only species present in fresh-water turtles, he says:

The data in my possession are not all referable to the single species which has just been described. In details of structure, in the location in the host in which they have been observed, and in some other details, certain specimens differ so distinctly from the account above that I can not at present include them under the same heading. It is possible that they represent phases in the life cycle of a single species. I am inclined to think the structure of this worm too delicate for one to consider it probable that any part of its life history could be passed in the intestine. But such a transfer must still be kept in mind as a possibility. In my opinion it is much more likely that further study will disclose the presence of several species parasitic in the blood of reptiles and amphibia.

Discussing the form described by MacCallum, Ward pointed out that "MacCallum's description is brief and in some details confused, since the dimensions given are clearly wrong and the text does not agree in full with the illustration." Comparing the structures described in MacCallum's text and shown in the figure accompanying it with the form he had described, Ward was "impressed by the general likeness," and regarded the form as "undoubtedly closely related" to the blood flukes. However, the differences were too great to warrant a final conclusion, and Ward accepted MacCallum's diagnosis, assigned to the worm the specific name *innominata*, and included the genera *Spirorchis* and *Proparorchis* in a new subfamily, Proparorchinæ. He removed the genus *Hapalotrema* Looss from the subfamily Liolopinæ Odhner, and included it with the Proparorchinæ in a new family, Proparorchidæ.

Publication of the results of my studies had been delayed because of uncertainty regarding the relation of the blood flukes to the genus *Spirorchis*, and also because of difficulty in specific determination of the material at hand. Both of these problems were recognized and discussed by Ward, although his work did little toward an adequate or final disposition of them. Shortly after the appearance of Ward's paper, Mac-

Callum found and sent me the type specimens of *Spirorchis*. Examination of this material afforded a ready solution for the first of the problems involved. The structure described as a pharynx in *Spirorchis* is in reality the esophageal commissure, and no pharynx is present. The genital pore is ventral, below the cecum of the left side, a short distance posterior to the level of the ovary. Consequently, I published (1921) a further description of the form and corrected the original statements regarding the presence of a pharynx and the location of the genital pore. In this paper also I gave a record of my dissections, pointed out that I had first collected blood flukes from turtles in 1913 while a graduate student at the University of Illinois, and that the distribution and list of hosts as given by Ward agree almost exactly with my records of collection while at the University of Illinois. There can be no question that the specimens I had collected are the same as those described by Ward. On the basis of morphological similarity and the strong suspicion that the specimens of *Spirorchis* came originally from the vascular system, I announced the identity of *Spirorchis* and *Proparorchis*. With the disappearance of the generic name *Proparorchis*, the subfamily and family names Proparorchinæ and Proparorchidæ also disappear. At that time *Spirorchis* was the only known genus of the subfamily to which it belongs and I designated it as type, proposing the subfamily name Spirorchinæ. For the family outlined by Ward under the invalidated name Proparorchidæ, I proposed the name Spirorchidæ, and designated *Hapalotrema* as type of a new subfamily Hapalotreminæ in the family Spirorchidæ.

In a paper dated August, 1921, MacCallum accepted the names Spirorchinæ and Spirorchidæ but objected to the name *innominata* proposed by Ward for the species described by him from the intestine of *Clemmys insculpta*, and for which the name originally intended was omitted in the published account. He says, "Unfortunately, through an error the specific name *eustreptos*, which was intended, was omitted. Ward in his paper of March 1921 (Journal of Parasitology), without consulting me, and without studying the form, suggests the specific name *innominata*. But the name is not acceptable and I maintain the name *Spirorchis eustreptos*." The disagreement between these two investigators is regrettable, but since *innominata* was the first specific name to be published after the generic name *Spirorchis*, the rules of priority sustain its validity.

Referring to the species described by him as *Spirorchis* (specific name omitted), MacCallum reported that he had found the same worm in 1912 in the lung of *Chrysemys picta*. He reported also the discovery in

the lung of *Emys blandingii* of a single specimen which he stated evidently belongs to that genus. In his description of the worm there is the following significant statement: "It is quite possible that this worm may have been lying in the blood vessels of the lung, since Ward has clearly shown that his entirely similar *Proparorchis* is to be found in the blood stream." Later in the paper, discussing the question of a pharynx in the genus, he says: "In the case of *Spirorchis eustreptos* I am now satisfied that the worm should not be credited with a pharynx although in one of the three specimens the outline of a pharynx may be distinctly seen in the position given it in the plate by the artist. None of THESE BLOOD FLUKES apparently are possessed of the usual pharynx." The discovery of *Spirorchis innominata* in the lung would signify that it is not normally a parasite of the intestine and the later statement of MacCallum indicates that he now regards it as a blood fluke. This recognition of the vascular system as the normal habitat of the form and the further agreement that a pharynx is absent confirm the position taken by me in declaring the synonymy of *Spirorchis* and *Proparorchis*.

MacCallum considered the specimen found in the lung of *Emys blandingii* as a new species and for it he proposed the name *Spirorchis emydis*. The description in many respects is indefinite and incomplete, especially as regards the reproductive organs. The testes and seminal receptacle of the specimen are crushed, and neither the cirrus, metraterm, Laurer's canal or genital pore were observed. No definite specific characters are given, nor any evidence to sustain the specific identity of the form. It is impossible to recognize the species from either the description or the figure, and consequently, I believe, to recognize the validity of the specific name. I see no good reason for not regarding it as a synonym of *Spirorchis innominata*.

The following year (1922) I announced the discovery of two new genera of North American blood flukes, *Henotosoma* belonging to the subfamily Spirorchinæ, and *Hapalorhynchus* belonging to the subfamily Hapalotreminæ. A single species of each of these genera was described, *Henotosoma hæmatobium* and *Hapalorhynchus gracilis*.

For several years I have made a wide and careful search for blood flukes of North American turtles and have carried on experimental work, so far unsuccessfully, in an attempt to trace the complete life cycle of these forms. I have found these parasites in many different species of turtles ranging in distribution over the entire eastern half of the United States. Blood fluke infections have been observed in *Chrysemys marginata* from Iowa, Illinois, Indiana and Ohio; *Chrysemys picta* from

North Carolina, New Jersey and New York; *Clemmys guttata* (syn. *Chelopus guttatus*), *Terrapene carolina* (syn. *Cistudo carolina*), and *Chelydra serpentina* from the middle Atlantic states; *Pseudemys scripta* from Raleigh, North Carolina; and *Pseudemys elegans*, *Graptemys geographica* (syn. *Malacoclemmys geographicus*) and *Graptemys pseudogeographica* (syn. *Malacoclemmys leseurii*) from the Mississippi valley. In not all of these species were adult forms of the parasite secured, but the characteristic appearance of the tissue filled with eggs of the parasite gives positive proof of infection. Since the eggs are deposited in the blood vessels and must work their way through the tissues to be voided with the fecal and urinary wastes of the host, a procedure which involves a very considerable extent of time, it is possible to find eggs in the tissues and feces long after the adults have disappeared from the vessels.

The present paper contains the results of these researches to date. Additions are made to the descriptions of *Henotosoma hæmatobium* and *Hapalorhynchus gracilis*, and a new genus, *Hæmatotrema* belonging to the subfamily Spirorchinæ is described. A study of the original specimens of *Spirorchis innominata* has made possible a more complete description of that form and five species in that genus are described. The types and figured specimens of the species here described as new are in the collection of The American Museum of Natural History.

Spirorchis

This genus contains several species and produces a widely distributed and prevalent infection in many species of North American freshwater turtles. Adults live in the heart and arteries and have been found with greatest frequency in the heart, the pulmonary, carotid, and mesenteric arteries. The infection is often very heavy and as many as 90 per cent of the turtles from certain districts are parasitized. In one group of fourteen *Chrysemys picta* collected in the fall of 1920 from a single pond near Cold Spring on the Hudson, New York, every turtle harbored the parasite. Usually the number of worms obtained from a given host is not large, sixteen specimens from a painted turtle, *C. picta*, constituting the heaviest single infection found. Often only one or two specimens have been recovered, although there is always the possibility that some have been overlooked. Usually there are from four to eight flukes in each infected turtle.

The length of life of the worm after it enters the blood stream is unknown, but it must extend over a considerable period of time. Living specimens have been removed from the arteries of turtles kept over a

year in the laboratory. During this time there had been no opportunity for subsequent infection or reinfection and the parasites must have been acquired previous to the capture of the hosts.

The eggs are deposited in the blood vessels and distributed throughout the body of the host, especially in the tissue of the visceral organs. The eggs rupture the capillaries and pass into the tissue in enormous numbers, and the presence of eggs in the tissue is the first and best means of recognizing the infection. The eggs then work their way through the tissues of the host and are voided with the fecal and excretory material. All the tissues of the host become involved if the infection is heavy or of long standing. Eggs have been observed in the cerebral lobes of the brain and abound in the lungs, liver, spleen, kidneys, mesenteries and wall of the intestine. In the mesenteries and omenta and on the surface of the intestine and kindeys the arteries frequently appear as dark lines, due to the presence of tremendous numbers of eggs in these vessels. In the wall of the intestine the eggs are most prevalent between the peritoneal investment and the circular muscles and in the submucosa.

The worm is very fragile and delicate. Its presence in the smaller arteries can usually be detected by the dark lines of the intestinal ceca which are visible through the wall of the vessel, although in the larger arteries the wall is too thick to observe the parasite and it can be found only by dissection. These flukes are usually inactive in the arteries and it often requires extreme care to remove a specimen from the vessel without injuring it. In other cases, however, when freed in normal salt solution, the parasite manifests the most violent muscular reactions, exertions entirely unexpected from its delicate structure. These may involve the entire musculature, the contractions and elongations of the body alternating with such rapidity and force that it is almost impossible to follow them, or the lateral edges of the body may show a rapid undulatory movement. After a short time movement ceases and in many, if not in most, cases the parasite displays no motility at all. Sometimes the worm bends very slowly in the form of a loop, bringing anterior and posterior ends together. They straighten out on shaking and contract only slightly on the application of killing and fixing fluids.

Members of this genus are hermaphroditic monostomes, elongated and flattened in form. They are widest near the middle of the body and taper toward either end. Frequently the posterior end is slightly wider and less pointed than the anterior. The body is thin, especially at the edges, and very transparent. These forms are small. The largest observed, a specimen of *S. innominata*, measures 4 mm. in length and

0. 66 mm. in width; the smallest, a specimen of *S. scripta*, is 1.18 mm. in length and 0.24 mm. in width. The length relative to width varies considerably in living specimens due to the contraction or elongation of the specimen.

The body is covered by a very thin cuticula without hooks or spines. The cuticula is easily shed or disintegrated, and a sticky substance is given off which tends to collect and hold bits of débris. The cuticular covering of the body is inturned at the oral sucker and forms the lining of the esophagus. In this region it is very thin, and the gland cells which encircle the esophagus open through it into the lumen of the canal. It is also reflexed at the genital and excretory pores, forming the lining of these ducts for a short distance.

The musculature of the body is very slight and consists of the dermo-muscular sac enclosing the entire worm, the muscles of the sucker, and weak muscular fibers in the walls of the ceca and the genital and excretory ducts. The body wall contains circular, longitudinal, and oblique fibers, but they are not separated into discrete layers; rather there is a reticulum of intermingled fibers. In sections it is possible to determine the relation of the fibers with considerable definiteness, and the circular fibers are external, with the longitudinal fibers between the outer circular and inner oblique fibrils. A loose network of branching and anastomosing parenchymatous fibers fills the body and extends across it, chiefly in a dorso-ventral direction. The muscles of the oral sucker consist of branched fibers, which pass from the external limiting membrane to the lining of the passage. The nuclei of this region are grouped concentrically near the limiting membrane (Fig. 13).

The digestive system is of the triclad type, without a pharyngeal sucker, the ceca extending almost to the posterior end of the body.

The oral sucker is protrusible and retractile; it may be extended until it is almost wholly outside of the body and retracted until it lies entirely within the body. In this retracted condition it is pyriform, the broader end is anterior and flush with the adjacent surface of the body. Ordinarily the sucker is oval, and about one-half protrudes from the anterior end of the body. The organ is usually a more elongated oval in smaller specimens and relatively broader in larger ones, but it is almost as large in small individuals as in the largest worms.

The oral sucker opens into the long esophagus, which extends posteriad to the bifurcation of the alimentary tract, about one-fourth to one-fifth of the length of the worm from the anterior end. In a fully extended specimen the esophagus is a straight tube, but on contraction

of the anterior end it manifests a sinuous or spiral course with three or four bends in the anterior two-thirds of its length, while the posterior third or fourth is expanded and straight. Immediately behind the oral sucker the wall of the esophagus is frequently covered with minute spherical evaginations, which communicate with the lumen of the canal and often contain decomposing bits of blood. In cross-section (Figs. 14, 15, and 16) there are usually six or more of these at a given level, but they are arranged in somewhat irregular alternate series, and the esophagus is studded with these little papilla-like protrusions which give it a beaded appearance. This peculiarly modified condition of the wall of the esophagus may extend throughout the length of the organ. The anterior portion of the esophagus is surrounded by a layer of gland cells and the dilated posterior fourth or third is enclosed in a large gland formed by increased numbers of these secretive cells. The cells are ovate, the narrower end pointed toward the esophagus, into which their product is discharged. At the posterior end of the esophagus the cells are very numerous, stain deeply, and occupy practically all the space between the esophagus and the dorsal and ventral body walls (Fig. 16). Where the alimentary canal bifurcates there is a small median pocket (Fig. 17), which extends posteriorly and ventrally. An examination of this region gives the impression that the ceca do not arise from the end of the esophagus, but branch from the side walls a short distance in front of the posterior end. The ceca pass laterally for a short distance after their origin from the esophagus, and then rather abruptly turn backward, extending almost to the posterior end of the body. They are unbranched, slightly sinuous tubes, circular in outline or flattened laterally. They are lined with the usual digestive epithelium, the nuclei situated near the basement membrane and with lobed processes extending into the lumen of the canal. Near the posterior end of the body the crura approach each other and lie parallel for a short distance just before their ends. In two specimens in my collection the crura have fused near the posterior end of the body, a condition recalling that in the schistosomes.

The nervous system in this genus is especially prominent, and the principal features are conspicuous in living specimens and whole mounts. The esophageal commissure (Figs. 14 and 15) is large and situated about one-fourth of the distance from the oral sucker to the bifurcation of the alimentary tract. On the commissure, especially at either side of the median line, there are large ganglion cells. The subesophageal commissure is small. From the commissure one larger and two smaller nerves pass forward, and three extend backward. The posterior ventralis is the

largest and extends on the ventral side just lateral to the ceca. In favorably stained whole mounts these branches can be traced almost to the posterior end of the body.

The excretory system has presented unusual difficulties. The pore is terminal or slightly dorsal in position and opens from a small median vesicle. This divides almost immediately into two small elongated flask-shaped vesicles (Fig. 11), which pass forward and laterad almost half the distance to the ends of the intestinal ceca. From these vesicles two collecting ducts pass anteriad, one on either side of the body dorsal to the intestinal crura. They are so small that they can not be followed with certainty in sections, and in the living specimen the dark contents of the ceca prevent observation, so that this fruitful method of tracing the system has been unavailing. The main collecting ducts have been followed in sections about two-thirds of the distance from the posterior end of the body.

At the posterior end of the body, extending from the region of the oötype almost to the posterior end, there is a large coiled vesicle. The contents are fluid, and stain like a secretion, but the significance of the structure is not clear. I have not been able to find an outlet or connecting tubules, but I am inclined to think it is not associated with the excretory system. It may prove to be a lymph receptacle.

The male reproductive system is unique and characteristic. The testes in mature specimens are usually ten in number, arranged in a linear series in the intercecal area. Often they seem to be contiguous and grown together and it is then difficult in specimens mounted *in toto* to distinguish their limits and to determine their number with certainty. In *S. innominata* this is especially true. The testes are roughly oval but more often are irregularly lobed. The shape varies from spherical to ovate, though the testes usually are flattened antero-posteriorly and broader than long. In the same individual there may be great variation (Figs. 2 and 8), the testes manifesting different shapes. In certain species, *S. innominata* and *S. scripta*, they fill the area between the ceca throughout the testicular zone, in others they are much smaller, occupying not more than half the space between the crura. In *S. scripta* they extend forward almost to the bifurcation of the alimentary tract, and in other species there is considerable space between the end of the esophagus and the testes. The posterior testis is usually the largest, and they decrease slightly in size anteriorly.

There is no vas deferens, the posterior testis communicating directly with the large seminal vesicle. This structure is pyriform, widest an-

teriorly; the anterior wall of the vesicle is usually about the width of the posterior testis. It may expand to a width exceeding that of the posterior testis or, in case the vesicle is not distended with spermatozoa gradually diminishes in width. The dorso-ventral measurement usually slightly exceeds the lateral. Anteriorly then the vesicle occupies practically all the space between the ceca and as it passes caudad to the ovarian level turns toward the left. The ovary is situated between the ceca, about the length of the posterior testis intervening between it and the ovary. The seminal vesicle is often marked by a sharp constriction slightly anterior to the middle of the ovary and then is continued as a narrow canal. At the ovarian level the seminal vesicle enters the cirrus sac. This structure is about one-half as long as the seminal vesicle; is oval in shape, about twice as long as broad, with weakly developed musculature. The prostate is reduced or absent. The genital pore is situated beneath the cecum of the left side at about the level of the caudal margin of the ovary. The cirrus opens anterior and median to the opening of the metraterm.

The female reproductive system is relatively simple. The ovary is a spherical, oval or lobed structure situated on the right side of the body a short distance behind the posterior testis. It is usually about the size of the posterior testis, although smaller in *S. innominata* and larger in *S. picta*. The oviduct arises at the posterior median margin of the ovary and passes posteriorly and dorsally. It then turns toward the right and increases in size to form a vesicle, the receptaculum seminis uterinum, which is often filled with spermatozoa. It then contracts to approximately its earlier diameter and passes posteriad, ventrad, and mediad. From this point there branches a large oval seminal receptacle which passes dorsally and near the dorsal wall of the body contracts to form a short Laurer's canal which opens to the dorsal surface (Fig. 19). After the seminal receptacle the oötype passes dorsally and receives the short large duct from the vitelline receptacle. Mehlis' gland is absent or represented by a few cells in the parenchyma around the oötype. The uterine duct continues its course anteriorly and laterally for a short distance and then turns ventrad expanding into the uterine portion. This dilated portion is present even though empty and is followed by the muscular walled metraterm which opens to the surface just below the cecum of the left side (Fig. 12). In certain descriptions of blood flukes in which a single egg is present in the body the statement is made that a uterus is lacking. The histological character of this section of the female reproductive duct in *Spirorchis* is similar to that of the uterus of other

trematodes, and I am inclined to regard the structure as a short but characteristic uterus. Such a condition is present in many polystomes and was described for these forms by the writer (1917, p. 30). The opening of the metraterm is posterior and lateral to that of the cirrus sac.

The vitellaria are voluminous and well developed. They consist of a continuous mass of follicles, which extend from the level of the bifurcation of the alimentary tract almost to the posterior end of the body and lie chiefly in the extracecal areas but enter the intercecal area dorsally and ventrally. At the posterior end of the body and extending forward to the vitelline receptacle, the follicles of the two sides meet in the intercecal region. Just behind the level of the genital pore, ducts from the vitellaria of either side pass mediad ventral to the ceca and unite to form the vitelline receptacle. This structure extends dorsally and anteriorly and discharges into the oötype.

The uterus contains a single egg, oval in shape, without filaments or spines, and provided with an operculum. Usually the egg is voided when the worm is removed from the blood vessel. Normally the eggs are passed into the blood vessels and by means of these channels are distributed to all parts of the body. They are particularly abundant in the lungs, liver, spleen, kidneys and wall of the intestine. On rupturing the capillaries they pass into the tissues and through them, the majority ultimately arriving at the alimentary canal or one of its evaginations, from whence they reach the exterior. The passage of the eggs through the tissue appears to be passive, and in this respect they act as any hard foreign body. Apparently either end of the egg may precede and the undeveloped condition of the embryo inside the shell would in my opinion preclude the idea that the egg exerts an influence determining the direction of its migration. The eggs produce lesions in the tissue, weakening its texture and are slowly pushed through, as the result of the natural movement of the tissue concerned. This procedure certainly involves a long period of time in the case of certain eggs and probably large numbers never reach the outside world, the death of the embryo and disintegration of the egg occurring before elimination can take place. Fragments of shells are often encountered in the tissue and probably are the remnants of eggs that have broken up after the death of the embryo. In other cases undoubtedly many of the embryos die before the egg reaches a channel of communication with the exterior. Such an explanation may account for the relatively large number of eggs that fail to hatch.

Eggs in the uterus or recently voided have a golden-yellow color, almost exactly like the vitelline material. As the egg grows older the shell

becomes darker in color, and the time which elapses between the deposition of the eggs and their passage from the body must vary greatly with different eggs, which undoubtedly accounts for the color differences which exist in any group of eggs recovered from the feces. Some of the eggs are semi-transparent and the embryo can be distinctly seen, while others are so opaque that little can be distinguished. The eggs vary greatly in size and in a single species there is considerable variation. Eggs embedded in the tissues of the host and those voided in the ejecta of the turtles are larger than those in the uterus of the worm, and this condition agrees with that of other blood flukes where the eggs increase in size during their passage through the tissue of the host. How this increase in size is accomplished after the deposition of the shell is not clear to me, although the shell is permeable, permitting exchange of gases during embryonic development and an aqueous solution of methylen blue used in an attempt to differentiate structure in the miricidium penetrated the shell. The increase is probably brought about by the absorption of water and in my opinion the tension produced by the pressure inside the egg is the determining factor in opening the cap. I do not believe that the activity of the embryo is of itself sufficient to open the shell, as I have observed actively moving embryos in eggs which for ten days failed to hatch.

Eggs recovered from the feces have been kept under observation for long periods of time. In order to simulate natural conditions, the eggs were kept in tap water and examined at frequent intervals. That eggs normally hatch in decomposing material at the bottom of ponds or aquaria is evidenced by the fact that most of the eggs at the bottom of jars in which infected turtles have been kept for long periods of time are merely empty shells; the caps are open and the embryos have emerged. This requires in the case of most eggs a considerable period of time. During migration through the tissue development proceeds slowly, probably due to a low oxygen supply and the fact that the tissue, with as high or higher salt content than the egg, prevents the absorption of water. On reaching fresh water a much larger amount of oxygen is available and the absorption of water increases the water content, raising the rate of metabolism and greatly accelerating development.

When the egg leaves the uterus of the worm the embryo consists of a small group of cells surrounded on all sides by droplets of vitelline material (Fig. 27). At this stage the droplets are approximately the same size. Development proceeds and the embryo grows by the decomposition of the vitelline droplets and the utilization of the yolk material.

During this process vitelline fragments are aggregated to form a few large droplets, so that the yolk globules become different in size (Fig. 29). The cells of the larva become differentiated into those forming the body wall and the various internal structures. The anterior end is early distinguishable by the shape of the larva, the development of the anterior papilla, and the appearance of the larger germ cells at the posterior end. By the time the miricidium is half grown, pigment begins to form in the eye spots, and soon afterward the cephalic glands, nervous mass, and flame cells are discernible. Soon the embryo begins to move, due to the contraction of muscle cells differentiating in the body wall. This muscular movement should not be confused with the ciliary movement which is manifested later. The miricidium is capable of considerable movement before the cilia are formed, and after the cilia appear the muscular movements are separate and distinct. The cilia are not developed till late, and then their formation often requires several days.

Due to differences in shape caused by the muscular contraction, it is difficult to give precise measurements of the miricidium. It may elongate until it is as long as the shell or contract until it is almost spherical. In general, a well-developed larva occupies about one-half of the space within the shell. In shape it is ovate, slightly wider anteriorly than posteriorly, but the anterior end narrows sharply and bears a cone-like prominence that is protrusible and retractile. Frequently the circular muscles will contract at two or three different levels giving the embryo a segmented appearance. With the exception of the anterior papilla, the body of the miricidium is covered with long stiff cilia, uniform in size and distribution but not closely set. In general structure, the larva closely resembles that of the schistosomes.

Discussing the miricidia of the human blood flukes, Cort (1919) says:

> Functionally the schistosome miricidium appears to have no dorso-ventral or lateral differentiation, since it is round in cross section and revolves on its long axis in locomotion. Structurally, however, this differentiation is very striking. The arrangement of the excretory system and cephalic glands gives a very clear bilateral symmetry. The cephalic glands lie nearer one surface of the body, and the central nervous body and rudimentary digestive sac lie nearer the other. Since the use of the terms dorsal and ventral are meaningless for such a type as this miricidium, I propose that these surfaces be designated respectively the glandular and neural surfaces.

While the statement of Cort regarding these miricidia is entirely correct, it seems that his proposal of new terms to designate the surfaces is unnecessary. In forms with such definite bilateral symmetry, and particularly in the turbellarian flatworms, the side containing the prin-

cipal nervous mass is dorsal, and the desirability of introducing a new terminology appears somewhat doubtful. I see no especial objection to it, however, and it is used in the description of this form.

The anterior papilla has a cap-like tip and the two cephalic glands and rudimentary digestive sac open through it. The cephalic glands are large, filled with a granular material and, as a result of the amount and character of muscular contraction in the embryo, extend posteriorly one-third to one-half the length of the body. Between them there is the rudimentary digestive sac. The cephalic glands extend almost to the body wall on the glandular side and about half-way to the body wall of the neural side. The rudimentary digestive sac is almost in the middle of the body and extends back about one-third of the total length from the anterior end. At about the center of the body on the neural side there is a large ganglionic mass. It is irregular in shape, broader than long; the lateral measurement is about two-thirds the width of the body at that level. It is situated just behind the digestive sac. On its anterior and neural face it bears a pair of eye spots. These structures are cup-shaped, so situated that they open toward the latero-neural surfaces, and their bases are close together on the central nervous mass. They are conspicuously pigmented, especially the rim of the cup, and this gives the peculiar X-shaped appearance. The eye spots are frequently irregular in form, but vary from the shape and pattern just described. At the posterior end of the body, and extending forward almost to the nervous mass, there are a number of large germ cells. On either side of the body, a short distance in front of the eye spots, there is a pore through which I frequently observed the extrusion of droplets of an oily material. These pores are the openings of the anterior ducts, but the course and relation of the ducts and the character of these organs I have been unable to determine. Near the posterior end on either side of the body there is an excretory pore. The course of the excretory tubules I have not been able to trace with certainty, but the flame cells are conspicuous. One pair of flame cells is anterior in position, situated between the eye spots and the lateral wall of the body. The flame cell leads ventrally and the duct passes posteriad on the ventro-lateral margin of the cephalic gland of that side. Behind the cephalic gland cell it turns mediad and dorsad and there unites with the duct from the posterior flame cell of the same side. The posterior flame cells are situated just in front of the excretory pores, and the cilia beat dorsad and forward. As just described, the duct from either cell leads forward to unite with that from the anterior flame cell of the same side. I have been unable to trace the

course of the common duct from the union of the primary tubules to the excretory pore but I do not believe there is a connection between the excretory tubules of the two sides.

With the development of the cilia the embryo becomes increasingly active within the shell; and living, moving embryos have been kept under observation for as long as four weeks without hatching. The larva first moves forward and backward and later rotates on its long axis. This movement increases in rapidity and is accompanied by contractions of the muscles of the body wall so that the embryo assumes various shapes and swims round and round inside the egg. I have been unable to confirm the observation of Ward that "eggs placed in hanging drop cultures hatch out in from 4 to 24 hours after being mounted." Such early emergence from the shell would only occur in eggs that were far advanced in development, and that it is not usual is evidenced by the fact that Ward did not observe the escape of the miricidium from the shell. Only in a few instances have I been successful in breaking open the eggs and securing normal miricidia, although tap water and various salt solutions were tried. The embryos are almost always distorted and soon disintegrate. Such a specimen is shown in Ward's figure of a miricidium just out of the shell.

I have observed the normal emergence of miricidia in watch glasses and one such egg was transferred by a capillary pipette to a slide as the cap started to open. It was drawn and the embryo after escaping was drawn (Figs. 32, 33 and 34). Comparison of these figures with that of Ward will show the difference between normally hatched embryos and those experimentally removed from the shell. The egg figured in hatching had been removed from the feces and kept three weeks in tap water at room temperature. As the cap was forced open the larva slowly emerged from the shell. The opercular opening is small and escape is not easy. The miricidium came out little by little in a jerky manner. This required about ten minutes and, when free from the shell, the larva was surrounded by a viscous material, the former contents of the egg. Although the cilia beat regularly, the miricidium remained beside the shell for at least five minutes. During this time the only motion was that produced by the contraction of the muscles. Then, suddenly the action of the cilia became more powerful and the miricidium began to move forward, rotating on its long axis as it progressed. It swam rapidly, and whenever active swimming was interrupted or it encountered bits of débris the anterior papilla was extended and retracted in a peculiar exploring and penetrating motion. The vigorous ciliary and muscular

activity of the larva and the protrusive movement of the anterior papilla made it easy for the larva to work its way through débris on the slide. In swimming, the body becomes more elongate and occasionally the posterior part is contracted in such a way that a small caudal appendage is formed. Such normally hatched, free-swimming embryos have been observed for four hours without appreciable abatement of their activity.

The life histories of *Sanguinicola* and the human schistosomes have been worked out and their larval stages described. The miricidia enter different species of snails and the cercariæ have forked tails. Consequently, it would seem probable that the miricidia of *Spirorchis* enter snails and that the cercariæ also are forked-tailed. The activity of the miricidia should enable them to travel considerable distance in search of the suitable intermediate host and the motility of the anterior papilla would facilitate penetration into the tissue of the snail. A very real difficulty is encountered however in predicting the type of parthenita. According to Faust (1918), the Furcocercariæ develop in sporocysts and monostome cercariæ develop in rediæ. If the cercaria of *Spirorchis* is a monostome and if it is a forked-tailed form, both of which seem likely, we would have a condition at variance with the general type of development in trematode larvæ. During the past two years I have made repeated collections of snails from a pond near New York in which practically every specimen of *C. picta* is infested with *Spirorchis*. Three species of snails, *Planorbis trivolvis*, *Physa ancillaria* and *Lymnæa columella* are common but I have been unable to find any cercaria whose structure would associate it with these blood flukes.

Since the life history and developmental stages of these forms are unknown, specific determination of material collected has presented many difficulties. The specimens of this genus that I have examined may, however, be placed in five different groups, which do not seem to intergrade and which I regard as distinct species. *Spirorchis innominata* becomes the type of the genus. Although the description of Ward in my opinion includes more than one species, his figure and the majority of his data agree with one of my groups and for that form I would retain the specific name *artericola*. For the other three species I propose the names *S. elegans*, *S. scripta* and *S. picta*. Comparison of the figures will give the best idea of the likenesses and differences between the species. *S. innominata* is larger than the others; the testes are larger and less distinct from one another; the oral sucker is relatively smaller; the esophagus is shorter; and the genital pore is near the posterior end of the body. The other species are slightly smaller and differ in many structural features.

In *S. artericola* the testes are smaller, more distinct, and occupy the posterior two-thirds to three-fourths of the region between the bifurcation of the alimentary tract and the ovary; and the genital pore is much nearer the posterior end of the worm. In *S. elegans* the similarity to *S. artericola* is pronounced but the oral sucker is larger; the testes are less distinctly separated from one another; and the genital pore is considerably farther forward than in *S. artericola*. *Spirorchis scripta* is usually more pointed at either end; the oral sucker is larger; the testes are very large and extend forward almost to the bifurcation of the alimentary tract; the genital pore is relatively far forward; and the large vesicle at the posterior end of the body is especially prominent. In *S. picta* the testes and ovary are almost spherical; the lobulations characteristic of other species are reduced or absent; the testes are small, much smaller than the ovary, often distinctly separated; and the ovary is larger than in any of the other species.

Due to the variation in size of eggs and their increase in size during their passage through the tissues, I have not used the size of eggs as a distinguishing character. If eggs *in utero* only are considered, it might prove a valuable characteristic, but the egg in the uterus may not be completely developed and, if ready for oviposition, is usually voided when the fluke is removed from the vessels. Consequently, egg measurements might easily prove confusing. The vitellaria are not divided into discrete lobes; the follicles form a continuous mass and, while there are slight differences in these structures, they do not seem well adapted to serve as a means of specific distinction.

Spirorchis innominata Ward, 1921

Plate II, Figure 1

This species at present is known by three specimens mounted *in toto*, the most characteristic of which I have shown in Fig. 1. This is the specimen designated by MacCallum as type, and the measurements of the specimen are, I believe, representative. The other specimens are about the same size and, although bent and slightly distorted, agree in diagnostic features. The type specimen manifests those features described as characteristic of the genus. This worm is 4 mm. long and 0.66 mm. in width near the middle of the body.

The oral sucker is oval, longer than broad, and measures 77 by 54 microns. The esophagus passes posteriad in spiral fashion, the coils elongating and enlarging posteriorly. There are five of these turns, the hinder one much straightened. The esophagus is narrow at its origin

from the oral sucker and gradually widens through the first third of its course. Here it is crossed by the commissure of the nervous system. The region posterior to the commissure is broader, measuring 60 microns in width. In total length the esophagus measures 0.64 mm. Its anterior portion is surrounded by a layer of gland cells, giving it a beaded appearance, and at the posterior end for a distance of 0.26 mm. there is a deeply staining mass of these cells around the esophagus. The origin of the intestinal diverticula is well shown in the figure. The ceca slightly exceed the esophagus in width, have lobed or crenated walls, and extend almost to the posterior end of the body. They are filled with decomposing blood, which gives them a black color, and the ends of the ceca approach each other but do not fuse.

The ovary is situated a little to the right of the median line, about one-third of the distance from the posterior testis to the end of the body. It is lobed, about 0.17 mm. in diameter, and the oviduct arises at its median posterior margin. After about 0.09 mm. it expands into the receptaculum seminis uterinum, which passes posteriad on the right side of the body. The seminal receptacle is about as long as the narrow portion of the oviduct and then it is obscured by the large transverse duct from the vitellaria. The vitellaria extend as a mass of follicles from the level of the posterior part of the esophagus to the posterior end of the body. They are principally extracecal in position, but extend into the intercecal areas anterior and also posterior to the other reproductive organs. About 0.42 mm. from the posterior end of the body vitelline ducts pass mediad from either side to form a common reservoir. The connection of the vitelline duct with the oötype can not be distinguished, but from this region the uterus passes forward ventrally and laterally to the genital pore. In the uterus there is an egg which measures 77 by 48 microns. I have examined many individuals of *Clemmys insculpta* in the attempt to find worms of this species in the blood vessels. Although I have not been successful in securing adults, I have found eggs in the tissue and in the feces which I believe belong to this species. In the tissue they are slightly larger than the one present in the specimen here described, and eggs in the feces containing living miricidia have an average measurement of 108 by 85 microns.

The testes were described by MacCallum as a rough spiral column almost filling the whole cavity between the ceca. He distinguished an anterior conical mass and nine other irregularly shaped masses. They begin 0.38 mm. behind the bifurcation of the alimentary tract and extend to within 0.95 mm. from the caudal end of the body. The seminal

vesicle as described by MacCallum is conical in shape, its base flush with the posterior face of the last testis, and its apex directed posteriad, ventrad and sinistrad. It passes underneath and at the left of the anterior median margin of the ovary. The cirrus sac in this specimen is rather small and opens at the genital pore located beneath the cecum of the left side 0.47 mm. from the posterior end of the body.

Type host, *Clemmys insculpta* (syn. *Chelopus insculptus*).

This species resembles *S. artericola* in the position of the genital pore and *S. scripta* in the massive character of the testes. It differs from *S. elegans* and *S. picta* in both of these features.

Spirorchis artericola (Ward), 1921

Plates IV to VIII, Figures 7–36

This form was described by Ward as the only species parasitic in the vascular system of various fresh-water turtles. He was unable, however, to make his description cover all his material and clearly was not satisfied with his conclusion. I have restricted the specific description to a group of specimens collected from the heart and arteries of *Chrysemys marginata, C. picta,* and *Pseudemys scripta* which have uniform and common characters.

Adult worms (Figs. 7 and 8) vary in size from 1.4 by 0.24 to 2.84 by 0.67 mm. As described by Ward, the body is an elongated oval, with the anterior end more nearly pointed and much more mobile than the posterior, and it is often slightly concave on the ventral side. It is relatively thin, but I find the dorso-ventral measurement considerably greater than stated by Ward. He gave the thickness as varying from 70 to 80 microns and, while I have specimens equally thin, others measure as much as 170 microns in thickness. The oral sucker is oval, longer than broad, and measures from 60 to 78 microns in length and from 42 to 60 microns in width. The esophagus is on the average about one-fifth as long as the body and has the usual gland cells around it. The ceca have no peculiar features and vary in diameter depending on the amount of material they contain.

The testes are usually ten in number. They are irregular in shape, oval or lobed, and form a regular consecutive series just behind the center of the body. The testicular area occupies about one-fourth of the width of the body, and from one-third to one-half of the length of this area intervenes between the anterior testis and the bifurcation of the alimentary tract. The two or three anterior testes are situated in the anterior half of the body and the seven or eight are located in the posterior

half. The distance between the caudal testis and the posterior end of the body is about two-thirds of the distance between the cephalic testis and the anterior end of the body. The seminal vesicle is conical or pyriform, situated immediately behind the caudal testis. The wider end is anterior, and posteriorly it passes underneath the anterior median part of the ovary. This posterior part narrows to a small duct which communicates directly with the cirrus. The cirrus sac is small, the muscles of the sac weakly developed. As pointed out by Ward, the vesicle and duct form a nearly straight passageway from the posterior testis to the genital pore.

The ovary is a many-lobed organ, situated slightly at the right of the median line a short distance behind the testes. It is somewhat dorsal in position and about one-sixth to one-seventh of the body length from the posterior end. It varies considerably in size. In the smallest sexually mature specimen it measures only 67 to 78 microns and in the largest 190 by 190 microns. The character and extent of the vitellaria are well described by Ward:

> The yolk glands are exceedingly voluminous. They begin at about the end of the esophagus and extend just a little beyond the posterior ends of the intestinal crura. The cells though not crowded form an almost continuous strip or band which lies below, and to some extent, on both sides of the crura but only in the immediate proximity to those structures, for the central area of the body is entirely without yolk cells. At the end of the esophagus and behind the crura, the cells from the two sides approach and become confluent in the median line. Behind the ovary on the ventral side of the body, the transverse yolk duct joins the two yolk glands and on it in the median line is formed a prominent yolk reservoir.

The ducts of the female system show no marked variation from type usual in the genus. The genital pore is situated below the cecum of the left side about one-seventh of the body length from the posterior end. The eggs vary considerably in size. One present in the uterus of the smallest sexually mature specimen measures 50 by 35 microns and eggs in the uteri of larger worms measure as much as 75 by 60 microns. The average size of a large number of eggs taken from the feces and containing living miricidia was 86 by 74 microns, although there was considerable variation from these figures.

This species has been found in *Chrysemys marginata*, *C. picta* and *Pseudemys scripta*.

It resembles *S. innominata* in the relative position of the reproductive organs and genital pore, but the oral sucker is larger, the ovary is larger, and the testes are smaller.

Spirorchis scripta, new species

Plate III, Figures 4, 5

The material of this species consists of one specimen from *Graptemys pseudogeographica* (syn. *Malacoclemmys leseurii*) collected near Newton, Texas, and several others from *Pseudemys scripta* collected near Raleigh, North Carolina. The first specimen was taken December 15, 1913, from the trachea of *G. pseudogeographica.* At that time the true character of the worm was unknown, but the card recording the dissection bears the following note: "This worm moves rapidly by a peculiar flapping or wriggling movement of the lateral edges and also by rapid contractions and elongations. It contracts till very short and then extends a long slender anterior portion. The movements are very rapid and violent, although graceful. Monostome; rather long esophagus with nerve commissure and two trunks running forward and two backward extending laterally almost to the posterior end of body. Ceca with dark contents. Genital organs between ceca, single egg in body." This worm was then stained and cut in serial sections. The next specimen was found November 10, 1914, in the washings of the dissected intestine of a specimen of *Pseudemys scripta* collected near Raleigh, North Carolina. This worm undoubtedly came from the mesenteric vessels. It was stained and mounted *in toto.* Later dissections revealed the true nature of these worms, and on October 21, 1916, twelve additional specimens were removed from the heart and arteries of another specimen of *P. scripta* from Raleigh, N. C.

These worms are almost fusiform in outline; the reproductive organs are large, situated nearly in the middle of the body; and the anterior and posterior ends taper uniformly to rather pointed tips. They vary in length from 1.15 to 1.66 mm. and in width from 0.23 to 0.35 mm. The body is very thin, in one specimen cut in cross-sections it measures only 54 microns in greatest thickness.

The digestive system is of the usual type but marked by the large size of the oral sucker and the small caliber of the intestinal crura. The oral sucker is oval, longer than broad, and measures from 64 by 46 microns to 77 by 54 microns. The esophagus is narrow where it joins the oral sucker and increases in width in the anterior half. The posterior half is of an almost uniform diameter. It is slightly sinuous in preserved specimens and surrounded by the characteristic glandular cells. The enlarged portion of the gland encloses the posterior third of the esophagus. The median pocket, which extends posteriad and ventrad from the bifurcation of the alimentary tract, is large and conspicuous, reaching almost

to the anterior testis. In all the specimens the ceca are small and almost uniform in diameter. These blind tubes undoubtedly vary in size and may be distended by the presence of large amounts of blood, but in this species they seem to be appreciably more slender than in others.

There are ten testes, forming an almost solid column between the ceca from the posterior end of the esophagus to the seminal vesicle. The testes are large, irregularly oval or lobed, and not always distinctly separated from one another. The testicular area is situated almost exactly in the middle of the body and extends about two-fifths of the total body length. The testes are flattened antero-posteriorly and measure from 80 to 100 microns in width and from 40 to 80 microns in length. The seminal vesicle and cirrus sac conform to the regular pattern and show no peculiar variations. The genital pore is situated about one-fourth of the body length from the posterior end, and in this respect is quite different from the condition in *S. innominata* and *S. artericola*. Not only is the genital pore relatively farther forward, but the other reproductive organs, testes, ovary, and oötype are correspondingly more anteriad than in the other two species.

The ovary is deeply lobed, about the size of one of the testes, and separated from the caudal testis by slightly less than its width. It is situated at the caudal end of the penultimate fourth of the body. The oviduct arises at the posterior median margin and passes dorsad and dextrad. It soon expands and the enlarged portion is filled with spermatozoa. This section of the genital duct passes posteriad and the oötype is about the diameter of the ovary behind it. The vitellaria occupy the usual position, extending from the level of the bifurcation of the digestive tract almost to the posterior end of the body. Their ducts pass mediad at the level of the oötype to form a common reservoir, which discharges into the oötype just left of the median plane. Immediately before the opening of the vitelline receptacle and slightly right of the median plane, the seminal receptacle branches from the oötype and following an expanded vesicular portion a short Laurer's canal opens to the dorsal surface in the median line. The opening of this canal is behind the vitelline receptacle. Eggs in the uterus vary in size from 65 by 38 microns to 77 by 46 microns.

This species has been found in *Pseudemys scripta* from Raleigh, N. C. and in *Graptemys pseudogeographica* from Newton, Texas.

It resembles *S. innominata* in the large size and massed arrangement of the testes, but is much smaller and the genital pore is farther forward.

Spirorchis elegans, new species

Plate II, Figures 2 and 3

The material of this species consists of two worms taken from the washings of dissected intestines of *Pseudemys elegans* collected near Havana, Illinois. One was found on November 5, and the other on November 18, 1913. Both were stained and mounted *in toto* (Figs. 2 and 3). These two specimens differ so markedly from all others I have examined that they can not be assigned to any of the other groups and I regard them as representatives of a separate and distinct species. The first one found (Fig. 3) is much contracted and flattened but, on comparing the two specimens, the relative position and relationship of structures are strikingly constant and this agreement shows that features like the position of the genital pore, location and extent of testes, as well as size of the various organs, do not vary greatly with the degree of contraction and may well serve as specific criteria. The longer of the two specimens is designated as type and the species is based on its description. Measurements of the other are included for comparison.

In shape the type specimen is an elongated oval, widest at about the middle of the body. The contracted specimen is oval, slightly wider anteriorly, with somewhat pointed extremities. The longer worm measures 1.71 mm. in length by 0.41 mm. in extreme width, the shorter is 1.15 by 0.62 mm.

The oral sucker of the type specimen is 73 microns in length and 62 microns in breadth; that of the contracted worm is 54 microns in length and 81 microns in breadth. The esophagus extends through about one-sixth of the body length and conforms to the pattern typical for the genus. The large glandular mass surrounds the posterior third of the esophagus. The intestinal crura are comparatively large and their course is very sinuous.

The testes are not distinctly separated from one another and it is difficult to distinguish their limits with certainty. In the contracted specimen they appear to form follicles in a single testis, but in the longer specimen the ten testes may be recognized. The testes are deeply lobed, and consequently it is difficult to give precise measurements of individual testes. The group of testes is situated nearly in the middle of the body and extends through slightly less than one-third of the length of the worm. At the center of the series the testes measure 106 microns in width, while at the anterior and posterior ends the testes are only about 70 microns in width. The distance from the cephalic testis to the bifurcation of the alimentary tract is two-thirds the length of the esophagus.

The seminal vesicle and cirrus sac are clearly visible, as shown in the figures. The genital pore in both specimens is one-fourth of the body length from the posterior end, and this ratio thus appears to be constant.

The ovary is conspicuously lobed, slightly larger than any one of the testes, and situated relatively close to the caudal testis. It is on the right side, immediately in front of the level of the genital pore. The oviduct and vagina are visible in both specimens but the vitelline ducts and receptacle make it difficult to determine the details of the oötype in the whole mounts. There is, however, no indication that there is any variation from the usual form. The vitellaria extend from the level of the bifurcation of the esophagus almost to the posterior end of the body and in front of the testes and behind the vitelline receptacle occupy the region between the ceca. Neither specimen contains an egg.

Type host: *Pseudemys elegans.*

In position of genital pore this species agrees with *S. scripta* and *S. picta* but differs from both in the size and character of the testes. In the confluent form of the testes it resembles *S. innominata*, but the testes are much smaller and the genital pore is farther forward.

Spirorchis picta, new species

Plate III, Figure 6

This species is represented by four worms taken from the arteries of *Chrysemys picta* collected in the vicinity of New York City. While these specimens have definite spirorchid characters and certainly belong to this genus, they manifest marked differences from all other members of the genus and especially from *S. innominata*, the type species.

The first difference noted is in the shape of the body. These worms have rounded posterior and pointed anterior ends, while the sides of the body throughout most of its length are nearly parallel. The region of greatest width is at or slightly anterior to the center of the body. The largest specimen is 2.33 mm. in length and 0.47 mm. in width, the smallest is 1.48 mm. in length and 0.35 mm. in width.

The oral sucker is large, oval in shape and longer than broad. It varies in size from 0.046 by 0.038 mm. in the smallest individual to 0.077 mm. by 0.054 mm. in the largest. The remaining portions of the alimentary tract are similar in essential respects to those of other species, but the ceca are large and comparatively straight.

It is in the reproductive organs that the species differs most markedly from *S. innominata.* The testes are small, distinctly separated, and frequently there is considerable of an interval between them. They

are lobed, but the indentations are very shallow and under low magnification they appear to be round. With the exception of the one or two most anterior testes they do not differ much in size. In one specimen they are all 35 microns in diameter; in the specimen shown in Figure 6 the largest testis is 60 microns in diameter and the cephalic testis is very small, measuring only 30 microns in diameter. The testes are situated almost in the center of the body, the cephalic testis about one-third of the body length from the anterior end, the caudal testis about one-third from the posterior end. There is considerable space between the testes and the ceca, and the vitellaria extend into the intercecal area on both sides of the testes throughout the testicular region. This condition is not present in any other species in the genus. The seminal receptacle is of the usual pyriform shape, larger than any one of the testes, and the genital pore is situated one-fourth of the body length from the posterior end.

The ovary is very large, faintly lobed, but almost spherical. In the smallest specimen it is 0.1 mm. in diameter and in the largest it is 0.2 mm. In the specimen shown in Figure 6 it measures 0.17 mm. The ovary has a diameter about three times that of any of the testes, a prominent feature characterizing this species. The ovary is pressed against the cecum of the right side for a considerable distance and closely approaches the cecum of the left side. The oviduct is short, and the structures of the oötype are compressed into a small area. The genital pore is slightly anterior to the level of the caudal margin of the ovary. The vitellaria are extensively developed and lie on both sides of the ceca throughout their length in front of the ovary and behind the vitelline receptacle. Eggs in the uterus average 77 by 54 microns in size.

Type host: *Chrysemys picta.*

In the position of the genital pore this species agrees with *S. scripta* and *S. elegans*, but it differs from both these species in the relative size of ovary and testes.

Key to the Species of *Spirorchis*

1 (4). Genital pore one-seventh of body length from the posterior end.....2.
2 (3). Testes larger than ovary, not distinctly separated.....*S. innominata.*
3 (2). Testes smaller than ovary, distinctly separated.....*S. artericola.*
4 (1). Genital pore one-fourth of body length from the posterior end.....5.
5 (6). Testes large, extend to bifurcation of alimentary tract.....*S. scripta.*
6 (7). Testes large, do not extend to bifurcation of alimentary tract...*S. elegans.*
7 (6). Testes small, not more than one-half the size of the ovary.....*S. picta.*

HENOTOSOMA Stunkard

A preliminary description of this genus was published by the writer (1922) and *Henotosoma hæmatobium* was described as a new species and the type of the genus. In the genus was included provisionally *Spirorchis chelydræ*, a species reported by MacCallum at the meeting of the American Association for the Advancement of Science held in December, 1921, but not as yet fully described. MacCallum's report (1922) states:

> Only July 17, 1921, I found within the heart of a *Chelydra serpentina* (western form) five Spirorchidæ which were attached to the walls of the ventricle, but all coiled together as if in coition. These worms were the largest of any Spirorchidæ I had seen, being in length 8.50 to 9 mm. × 1 mm. wide, and which I have named *S. chelydræ*. The peculiarity about these worms is the much bent esophagus, also the numerous glands at the junction of the esophagus and ceca and possibly posterior also on the outside of the esophagus to the mouth.

The statement of MacCallum is so brief and indefinite that it is hardly possible to recognize a species from his description. The last sentence would indicate that the mouth is posterior, which certainly is not the case. The only data in his report upon which a specific determination could be based are size and location in the host. All members of the family Spirorchidæ, as far as known, may be found in the heart; the course of the esophagus depends upon the amount of extension or contraction in the anterior part of the body; and the esophageal glands mentioned are characteristic of blood flukes in general. Consequently, these features can not serve as specific criteria. Accordingly, I wrote to Dr. MacCallum asking for a loan of the material which, although his description had not yet been published, he very kindly forwarded for examination and comparison. None of the specimens were in good condition. In the only specimen that had not been cut in two, the posterior half of the body was crushed and the testes shattered. The specimens examined manifested the general features designated as characters of the genus *Henotosoma* but in certain particulars they differed from those I had collected and I was unable to include them in the same species. So I described the worms I had collected as a different species, assigned to them the specific name *hæmatobium*, and included MacCallum's form as a second species in the genus *Henotosoma*. In a letter received from Dr. MacCallum shortly after the appearance of the paper, he stated that in his opinion the two forms are identical. He gave no reason for the belief and has not published a final description of his species. In the specimens sent to me the testes are not distinctly separated and are deeply lobed; the indentations are so prominent that the organs have a dendritic appearance and, in my judgment, at least until further evidence is submitted, the two species should be retained.

This genus is characterized by the small oral sucker and relatively short esophagus; absence of pharynx; terminal excretory pore and excretory vesicle which divides almost immediately to form lateral collecting ducts; testes usually ten in number, irregularly lobate or sinuate, arranged in a linear series anterior to the ovary but situated in the posterior half of the worm; seminal vesicle posterior to the testes with only the terminal part of the ejaculatory duct enclosed in a small cirrus sac; genital pore ventral, sinistral, near the posterior end of the body; vitellaria numerous, extending from the bifurcation of the alimentary tract almost to the posterior end of the body; seminal vesicle and Laurer's canal present; uterus short, eggs discharged singly.

Henotosoma hæmatobium Stunkard, 1922

Plate IX, Figures 37 and 38; Plate X, Figures 39 to 44

The generic characters are based on a study of *H. hæmatobium*, the type species. Infection by this species is widespread, extending from the Mississippi Valley eastward to New York and the southern Atlantic states. As a parasite of *Chelydra serpentina*, its distribution probably corresponds with that of its host. The percentage of infection is also great, at least one-half of these turtles that I have examined have had eggs in the tissue and in a considerable number live worms have been found in the vascular system. The first specimen was found December 1, 1914, in the lung of a large turtle collected near Raleigh, North Carolina. In the fall of 1916, six specimens were removed from the left subclavian artery of another turtle belonging to this species and collected in the same locality. Since that time, other specimens have been removed from the heart and larger arteries of turtles collected in New York and New Jersey. In November, 1921, a shipment of twelve turtles was received from North Judson, Indiana, and nine were infected. Records of dissection in this group show one turtle in which twelve specimens were found in the lungs, four in the pulmonary arteries, two in each auricle, sixteen in the ventricle, eight in the mesenteric arteries, and twenty-eight at the posterior end of the aorta. This is the heaviest infection with blood flukes that I have ever encountered and the presence of such a large number is probably unusual. Usually, the number of these parasites present in a single host is small, the average of dissections is five or six. Where several worms have been found together, they were often entangled and very hard to separate. Those found in the ventricle of the heart frequently were partially embedded in the wall.

The infection persists for a very long period of time. Living worms have been removed from the arteries of turtles kept in the laboratory over a year, during which time there was no opportunity for them to acquire new trematode parasites, and the eggs remain in the tissues for a much longer period. It is difficult to see how eggs from certain parts of the body could ever reach the outside world, and the disintegration and removal of the shell following the death of the embryo is probably only slowly accomplished. Consequently, considering the longevity of the adult parasite, it seems likely that traces of a single infection might remain for several years. As in the genus *Spirorchis*, the eggs are deposited singly in the blood vessels, and I regard it as very unlikely that the flukes visit the heart for oviposition, since the eggs are probably formed continuously and discharged almost immediately. The worms undoubtedly resort to the heart at times and may sometimes remain there, when the eggs might be carried by the circulation to any part of the body. In fact, all the tissue becomes infiltrated with eggs if the infection is heavy, but usually most of the eggs are found in the tissue of the visceral organs.

These worms are elongate, flattened monostomes with almost parallel sides, rounded posterior and pointed anterior ends. The anterior end in extended condition narrows uniformly to the tip and may be exceedingly slender (Fig. 38). On contraction it may form a sharp angle or become broad and blunt with crenated margins (Fig. 37). The esophageal section appears to be much more mobile than the rest of the body. Extended individuals are widest in the region of the testes and have a narrow zone in the central part of the body. In a contracted condition the body anterior to the testes becomes approximately the width at their level. Living worms may extend to a length of 12.5 mm. and contract to less than 6 mm. Although this form is much more massive than *Spirorchis* and probably more powerful, its movements are slow and I have never witnessed the rapid contractions frequently shown by *Spirorchis*. Fixed and mounted specimens measure from 5 to 9 mm. in length and from 0.48 to 0.75 mm. in width. The width is from two to three times the dorso-ventral measurement, and varies with the amount of contraction.

The cuticula is thin and smooth, lacking spines or other modifications. In sections, the surface of the body both dorsally and ventrally is sometimes irregularly studded with small droplets of what appear to be a secretion. These globules do not stain with ordinary methods and their significance is uncertain.

The oral sucker is situated at the anterior tip of the body and is capable of considerable extension and retraction. In extended specimens it slightly protrudes from the body. It is ovoid in shape, wider anteriorly, and measures from 0.077 to 0.1 mm. in length and from 0.071 to 0.084 mm. in width. The mouth opening is subterminal. Depending on the amount of contraction in the anterior region of the body, the esophagus is slightly or exceedingly sinuous, the sinuosity varying with the extent of contraction. In length it measures from 0.39 to 0.77 mm. It increases in diameter posteriorly although the size of the lumen is not uniform; frequently there are one or more dilated portions. In cross-section the wall has a crenated appearance (Fig. 39), the lining is cuticular and throughout its length the esophagus is surrounded by gland cells. At the posterior end, for about one-fifth of its length these secretive cells are larger, more numerous and form a conspicuous, deeply staining gland, (Fig. 37). No pharynx is present. The posterior end of the esophagus forms a sac or pouch which extends caudad and ventrad from the origin of the ceca. Its lining is cuticular like the esophagus, and it is filled with disintegrating food material. The intestinal crura arise just before the posterior end of the esophagus and pass laterad about one-half of the distance to the body wall, where they turn sharply posteriad and extend almost to the posterior end of the body. Their course is notably sinuous, and they are spread farther apart in the region of the testes and ovary, passing lateral to these organs. They have an almost uniform diameter and are usually filled with decomposing blood, which gives them a black appearance. The crura are lined with a single layer of epithelial cells resting on a basement membrane. These cells have broad lobate processes that extend into the lumen of the ceca and their nuclei lie close to the basement membrane. The cytoplasm is filled with dark granules, derived from the decomposition of blood. These granules in the intestinal epithelium clearly demonstrate the nature of their food and show that they live on the blood of the host.

The excretory pore (Fig. 44) is situated at the posterior end of the body and the vesicle divides almost immediately to form two lateral collecting ducts which pass anteriorly. In spite of repeated attempts, I have been unable to trace these vessels in living specimens, and their small size, together with the vacuolated character of the parenchyma, has thus far made it impossible to follow them in sections.

Near the posterior end of the body, extending in the median line from the level of the vitelline receptacle almost to the excretory pore, there is a much coiled vesicle (Fig. 44). A similar structure was described in

Spirorchis. It is filled with a fluid substance that takes a plasma stain, but its connections and relations are uncertain.

The nervous system in essential features resembles that of *Spirorchis*. Due to the greater thickness of the body the main trunks are not so prominent, but may be easily seen in whole mounts. The esophageal commissure is situated about one-fourth of the distance from the oral sucker to the bifurcation of the alimentary tract, and the principal pair of anterior nerves pass forward on either side to the oral sucker. The posterior ventral nerves are the largest and extend backward just lateral to the ceca.

The male reproductive organs are located in the posterior half of the worm. The testes lie, one behind the other, in the intercecal area. In mature specimens there are ten, but as the period of sexual activity declines certain of the testes disintegrate and disappear. In one turtle kept for over a year in the laboratory four of the seven flukes found show this condition. The posterior testis remains but the ones immediately in front of it break up. One specimen has the anterior six testes and the last; another (Fig. 38) has the anterior four and the last. How long before this situation develops can only be surmised, as there is no way of knowing how long these flukes had been in the blood vessels before the hosts were taken. In these specimens the ovary appears to be filled with cells and actively functional, showing no sign of exhaustion. The anterior testes have prominent lobes and are distinctly separated, while in the middle of the group the lobulations are smaller, less conspicuous and the organs closer together. The testes are flattened antero-posteriorly and this is particularly noticeable at the center of the group where the pressure is greatest. Because of their shape it is difficult to make satisfactory measurements of the testes, but they vary in size from 0.12 by 0.27 mm. to 0.27 by 0.43 mm. In the testicular area they occupy practically all the space between the ceca, but do not extend laterally beyond them. The most anterior testis is about three-fifths of the body length from the anterior end and the caudal testis about one-sixth of the body length from the posterior end. The posterior testis opens directly into a large ovoid or pyriform seminal vesicle. The broader end is anterior and the posterior end tapers to a duct which passes on the left side of the body and near the mid-ovarian level enters the cirrus sac. This sac is small and the muscular wall slightly developed. It is pyriform in shape, wider anteriorly, and a prostate is reduced or absent. The cirrus sac varies in length from 0.154 to 0.22 mm. and in width from 0.05 to 0.077 mm. The genital pore is ventral, beneath the

cecum of the left side and about the level of the caudal margin of the ovary. The opening of the cirrus is anterior to that of the uterus and the cirrus is eversible (Fig. 42).

The ovary is a lobed, oval structure situated on the right side of the body between the seminal vesicle and the genital pore. It measures from 0.154 by 0.22 mm. to 0.23 by 0.28 mm. It is oblique in position; its forward end is anterior and at the right; its posterior end caudal and median. The oviduct arises at the median posterior margin and passes dextrad and posteriad. After continuing for a short distance it turns mediad where the seminal receptacle and Laurer's canal are given off and immediately afterward the common vitelline duct is received. The oötype region is short; no Mehlis gland was observed; and there is a distinct uterus (Fig. 44), which shows clearly even though empty. The metraterm passes forward, sinistrad, and ventrad to the genital pore. The vitellaria are enormously developed, and consist of masses of follicles extending from the bifurcation of the alimentary tract almost to the posterior end of the body. They are not separated into lobes but form an almost continuous sheet of cells extending on the lateral side of the crura throughout their length and filling the intercecal area anterior to the testes and posterior to the vitelline receptacle. Wherever there is any space between the testes or the ovary and the intestinal crura, vitelline follicles have grown into the intercecal area. Just behind the level of the genital pore vitelline ducts pass mediad on the ventral side of the body and unite to form the large vitelline receptacle which discharges into the oötype. The uterus is short and contains a single oval egg. The eggs are thick shelled, and golden brown in color. The smallest egg measured in the uterus is 0.077 by 0.06 mm. and the largest 0.086 by 0.065 mm. Eggs in the tissue of the host are larger and those taken from the feces have an average measurement of 0.115 by 0.081 mm. The eggs grow darker with age. They have an operculum (average size 22 microns in diameter) to permit the escape of the embryo. The eggs of this form are longer, more rectangular, and develop more slowly than those of *Spirorchis*. Most of the eggs taken from the feces contain an embryo that is still an oval mass of cells enclosed in vitelline globules. The development of the larva is like that of *Spirorchis* and the miricidia of the two forms are so similar that it would be exceedingly difficult to distinguish them when freed from the shell.

Type host: *Chelydra serpentina.*

HÆMATOTREMA, new genus

A new genus, *Hæmatotrema*, is formed to contain a new species of blood flukes found in the arteries of *Chrysemys picta*. This genus manifests the characteristic features of the subfamily Spirorchinæ and constitutes a third genus in that group. The generic description may be stated as follows.

Exceedingly small and slender monostomes with delicate body which tapers toward both ends. Oral sucker large, elongate, protruding; relatively long esophagus with esophageal glands not strongly developed; intestinal crura sinuous, extending almost to the posterior end of the body. Testes lobed, four or five in number, situated in the anterior part of the posterior half of the body; seminal vesicle between testes and cirrus sac; genital pore below the cecum of the left side, one-fourth of the body length from the posterior end. Ovary lobed, on the right side, at or slightly anterior to the level of the genital pore; vitellaria envelop the ceca throughout their length and fill the intercecal area anterior to the testes and posterior to the oötype; seminal receptacle and Laurer's canal present; uterus short, eggs very large, operculate, discharged singly.

Hæmatotrema parvum, new species

Plate XI, Figures 45 to 49

Twenty five worms of this species have been stained and mounted either entire or in sections and many others have been lost in manipulation. All the material came from the blood vessels of *Chrysemys picta* collected near Cold Spring on the Hudson, New York. Most of the specimens were found in the normal salt solution in which the organs were dissected. They are too small to be readily observed in the tissue or in the arteries and are usually found only when freed in the dissection fluid. In several instances, however, in which the heart and arteries were removed from the body of the host and examined separately, specimens were found in the arteries while teasing these vessels open with needles under a binocular. The largest number obtained from a single turtle was six, although, since they are so small, it is probable that others were present in the tissue and unnoticed. In this species, as in other blood flukes, it appears probable that the infection is light and the number of parasites small.

The specimens vary in size from 2.2 by 0.12 mm. to 0.75 by 0.05 mm. The relative length to width is about ten to one and the thickness is about one-half the width, although these proportions represent a mean about which there is considerable deviation as the body is extended and contracted. The posterior end is not so mobile as the anterior and is usually rounded, while the anterior end is capable of considerable extension and in this condition becomes narrow and tapering. The greatest width is usually in the region of the testes, although some of the specimens have a widened spatulate region near the posterior end of the body.

The cuticula is very thin and the muscular wall of the body extremely delicate.

The oral sucker (Fig. 46) is large and elongate. It is ovoid in shape, wider anteriorly, and varies in size from 0.073 by 0.035 mm. in the largest specimen to 0.052 by 0.027 mm. in the smallest. The sucker protrudes slightly from the body and the mouth is subterminal. The digestive system conforms to the type present in *Spirorchis* and *Henotosoma*. The esophagus is long, extending through one-fifth to one-sixth of the body length and it becomes sinuous with the contraction of the anterior end of the body. It is lined with cuticula; the lumen is relatively large, increasing in size posteriorly although the diameter frequently is not uniform and dilated portions are present. Throughout its length it is enveloped by secretive cells, which are larger and more numerous posteriorly, but these cells are not so numerous or prominent as in *Spirorchis* or *Henotosoma*. The posterior end of the esophagus turns ventrally, forming a small median pocket, and the ceca diverge at right angles from the esophagus immediately in front and above the median diverticulum. The crura extend laterally about half-way to the body wall and then bend sharply backward, passing almost to the posterior end of the body where they end blindly. They are small, their diameter hardly exceeding that of the esophagus.

The excretory pore is terminal, the vesicle is very small and two collecting ducts pass forward. The details of the system have not been worked out, but in general form it agrees with that of *Spirorchis* and *Henotosoma*. The excretory system is probably characteristic for the subfamily.

The esophageal commissure and the anterior and posterior ventralis nerves are the only parts of the nervous system visible in whole mounts, and the others are so small that it is very difficult to trace them in sections. So far as I have been able to determine, the nervous system is similar to that of *Spirorchis*.

The testes are lobed, oval or spherical bodies of almost equal size situated in the intercecal area. They are situated one behind the other and are distinctly separated. In about one-half of the specimens there are five testes, in all the others four. They are usually slightly longer than broad and vary from 46 to 57 microns in length, from 38 to 50 microns in width, and from 32 to 44 microns in thickness. The anterior testis is about midway between anterior and posterior ends of the body, and the caudal testis about one-third of the body length from the posterior end. They extend laterally almost to the ceca filling the

intercecal area at the testicular zone. The caudal testis opens into an ovoid or pyriform seminal vesicle, which is about the size of one of the testes. The broader end of the vesicle is forward and caudally it contracts to form a duct which passes at the left of the ovary and enters the cirrus sac. The cirrus sac turns ventrally and opens at the genital pore. The sac is small and weak; no prostate could be observed; and the genital pore is ventral, at the left of the median line near the level of the posterior margin of the ovary.

At first it seemed possible that the presence of four or five testes represented either a developmental or degenerative phase of the condition in *Spirorchis* and *Henotosoma*, where ten testes are present, and that these small slender forms were young stages of spirorchids. But specimens taken from the vascular system at intervals of a few weeks from the time of capture of the hosts for a period of over a year prevent such a conclusion. The form reaches sexual maturity and continues to live and function without increase in size or in the number of testes.

The ovary is ovoid, lobed, situated on the right side of the body immediately behind the seminal vesicle. The broader end is anterior and pressed against the cecum of the right side, the other end is almost in the median plane. In size the ovary measures from 38 by 48 microns to 46 by 53 microns. The oviduct arises at the posterior end and passes posteriorly on the right side of the body. It has an enlarged portion filled with sperm and then turns toward the median line, where the seminal receptacle branches from the duct. The seminal receptacle narrows to form Laurer's canal, which opens to the dorsal surface near the median line. The common vitelline duct opens into the oötype immediately after the origin of the seminal vesicle and the oötype is followed by the uterus. The vitellaria are well developed and surround the intestinal crura throughout their length, filling the intercrural area anterior to the testes and posterior to the oötype. Median ducts from the lateral masses unite to form the vitelline receptacle that opens into the oötype. Eggs in the uterus measure 54 by 38 microns, a tremendous size for so small a worm. The eggs are oval, golden yellow in color and provided with an operculum.

In general features this genus resembles both *Spirorchis* and *Henotosoma*. It is much smaller and more slender than either and has fewer testes, but the fundamental arrangement of the organ systems is the same. In its slender and elongate form, the location of testes in the posterior half of the body, and in the long interval between the bifurcation of the alimentary tract and the testicular area, it is similar to *Henotosoma;*

but the esophagus is relatively longer and the genital pore farther anteriad. In the large oral sucker and in the position of the genital pore it resembles certain species of *Spirorchis*, but it differs from *Spirorchis* in number and location of the testes.

Type host: *Chrysemys picta.*

Hapalotreminæ Stunkard, 1921

Hermaphroditic, blood inhabiting distomes. Esophagus often with dilated portion or portions, and surrounded by secretive cells. Ceca end blindly near the posterior end of the body. Excretory vesicle branches behind the posterior testis or testes. Ovary and oötype situated near the middle of the body and between the testes; genital pore dorsal and sinistral near the level of the ovary; vitellaria numerous, both lateral and medial to the ceca throughout most of their course; Laurer's canal present; uterus short containing a single egg which bears either filaments or processes.

The type genus, *Hapalotrema*, contains a single species described by Leared (1862) as *Distoma constrictum* from the heart of the edible turtle, *Thalassochelys corticata*. Monticelli (1896) transferred the species to the genus *Mesogonimus* and gave an extended description of its structure. He featured the developmental stages, eggs, and miricidia, and predicted that *Cercaria dichotoma* is the larval form.

Looss (1899) designated this species as type of a new genus, *Hapalotrema*, and later (1902) added to the description of the form. In this latter paper he suggests that *Hapalotrema* is only one of several species of blood flukes parasitic in sea turtles and he described and figured four different trematode eggs in the blood vessels and tissue in addition to those of *Hapalotrema constrictum*. He was, however, unable to find adults of the other species. From the descriptions of Monticelli and Looss the characters of the genus *Hapalotrema* may be formulated as follows.

Hermaphroditic blood inhabiting distomes; posterior end of body spatulate; anteriorly and ventrally the cuticula bears small spines. Pharynx absent, esophagus similar to that of the schistosomes, ceca end blindly near posterior end of body. Testes both anterior and posterior to the ovary, divided into many (8–10) follicles; seminal vesicle outside of cirrus sac; ovary lobed, on right side near the center of the body; seminal vesicle and Laurer's canal present; vitellaria envelop the ceca throughout their course; uterus short; eggs discharged singly. Genital pore dorsal, on the left side at the level of the ovary. Eggs large, with two long polar filaments which are spirally twisted and thickened at the ends. Present in the heart and arteries of various species of marine turtles.

The writer (1921) included *Hapalotrema* in the family Spirorchidæ and designated it as type of a new subfamily in that group. The next year (1922) I reported the discovery of a second distome from the vascular system of turtles and gave a brief description of the parasite. Its morphological similarity to *Hapalotrema* placed it in the same subfamily,

but differences so marked that they must be considered of generic value prevented its inclusion in the genus *Hapalotrema.* Consequently, a new genus, *Hapalorhynchus,* was formed to contain the species which was named *Hapalorhynchus gracilis.* The discovery of a second genus in the subfamily Hapalotreminæ made it possible to outline the group and formulate the subfamily characters.

The genus *Hapalorhynchus* was characterized by the presence of a protruding oral sucker, acetabulum situated near the posterior end of the anterior third of the body; terminal excretory pore and short median excretory vesicle; testes separated by the ovary; large seminal vesicle and prostate gland anterior to the testes; genital pore dorsal, located near the middle of the body and slightly left of the median line; vitellaria extensively developed in front of the acetabulum and behind the ovary; small seminal receptacle and Laurer's canal; and also by the absence of pharynx, cirrus sac and cirrus.

Comparisons.—The genera *Hapalotrema* and *Hapalorhynchus* agree in that both are parasitic in the arterial system of turtles; both are distomes with elongated oval bodies; they agree in the general features of the digestive system; in the lobed form of the ovary and its position between the testes; the extent of the vitellaria; the short form of the uterus; the large size of eggs, which are discharged almost as soon as formed; and in the position of the genital and excretory pores. The two genera differ in many respects and in certain features the disagreement is notable. *Hapalorhynchus* is more slender; the acetabulum is farther posteriad; and the concave spatulate posterior end is lacking. The oral sucker is protrusible; the esophagus is relatively longer; and the ceca do not extend as far posteriad. The greatest differences, however, are found in the reproductive organs. In *Hapalorhynchus* the testes are not divided into separate follicles; the seminal vesicle is anterior to both testes and not between them; a large prostate gland is present; and cirrus sac and cirrus are absent. In this genus, instead of polar filaments, the eggs have three processes, two at one end and one at the other, which gives the egg a tricornuate appearance and probably facilitates its passage through the tissues.

Hapalorhynchus gracilis Stunkard, 1922

Plate XII, Figures 50 to 52; Plate XIII, Figures 53 to 61

This species has been found but once, in the material of *Chelydra serpentina* received November, 1921, from North Judson, Indiana. Of the twelve host specimens, seven were infected with this parasite. Eight

of the twelve turtles have been dissected and furnished the material on which the description of the species was based. Four of them are alive at the time this manuscript is being prepared (September 1922). They have been kept separate in glass aquaria and the feces examined from time to time. Three of the four are infected with *Henotosoma hæmatobium* and many eggs containing living embryos are found in the feces. Two were infected with *Hapalorhynchus gracilis* and, although frequently dark-colored eggs of this form appear in the feces, they are no longer plentiful and do not contain living embryos. These observations would indicate that the adults of *H. gracilis* have died because egg production probably continues throughout the length of life of the parasite; at any rate, I have never seen one in which the ovary was exhausted. *Hapalorhynchus* and *Henotosoma* may both be present in the arteries of the same turtle without apparently affecting each other and it seems that the former is shorter lived. Of course it is impossible to draw conclusions from one or two observations, but the data are worth recording.

Over one hundred specimens of *H. gracilis* were teased from the arteries and collected from the washings of the visceral organs of the five snapping turtles parasitized by this species that have been dissected. Worms were found in the lungs, liver, kidneys, mesenteries, and wall of the alimentary tract. For a short time after they are removed in normal salt solution the worms may show slight movement but I have never witnessed strong or energetic movements and they soon become inactive. The oral sucker is protruded and retracted; the anterior part of the body is extended and contracted; the acetabulum is mobile; but behind the acetabulum the body is less active and often motionless. Living specimens may extend to a length of 2.5 mm. and contract to half this length, the width increasing as the longitudinal muscles contract. The worms (Fig. 50) are fusiform in shape, widest near the center of the body, and taper anteriorly and posteriorly in a similar manner. Before and behind the limits of the vitellaria the body narrows considerably; and cross-sections (Figs. 53, 54) cut at these levels are almost circular. In certain worms (Fig. 54) the body is even compressed laterally at the ends but usually it is slightly flattened dorso-ventrally. The development of the reproductive organs increases its width and cross-sections cut through the middle of the body (Figs. 56–61) are oval, slightly flattened ventrally. Fixed and mounted specimens measure from 1.5 to 1.9 mm. in length, from 0.15 to 0.23 mm. in width, and from 0.092 to 0.12 mm. in thickness.

The cuticula is thin and, unlike that in *Hapalotrema*, is unarmed. The musculature is weak and poorly developed. The suckers are of

moderate size, flexible, but the walls are thin and the muscles not strong. Branching parenchymous fibers pass between the two limiting membranes (Fig. 55). The dermo-muscular sac is exceedingly delicate, weaker even than that of *Spirorchis*, and it is almost impossible to distinguish layers of muscular fibrils. The acetabulum (Figs. 52 and 55) is slightly protrusible but not stalked and is situated near the caudal end of the anterior third of the body. It is cup-shaped, normally circular in outline but sometimes elongated or flattened as a result of pressure or contraction. It measures from 61 to 69 microns in diameter and its depth is approximately equal to its width.

The oral sucker (Fig. 52) is situated at the anterior tip of the body and is capable of considerable extension and retraction. In fixed and mounted specimens, usually about one-half of the sucker protrudes from the body. In shape it is ovate, wider anteriorly, and measures from 0.073 to 0.084 mm. in length and from 0.054 to 0.058 mm. in extreme width. The mouth opening is subterminal (Fig. 52), and the esophagus extends posteriorly from the oral sucker to the bifurcation of the alimentary tract midway between oral and ventral suckers. It is straight in extended specimens, often with two or three dilated portions. The lining is cuticular and it is surrounded by secretive cells. The cells are few in number and do not form an enveloping layer as in *Spirorchis* and *Henotosoma*. Neither do they increase in size and number to constitute the large, deeply staining gland at the posterior end of the esophagus which is so conspicuous in *Spirorchis* and *Henotosoma*. No pharynx is present. The digestive ceca diverge from the esophagus at an angle and end blindly about one-fifth of the body length from the posterior end. They are somewhat dorsal in position (Figs. 55–61) and the left crux is flexed mediad and dorsad near the middle of the body, passing on the median side of the genital pore (Figs. 50 and 59). The intestinal crura are slender, almost straight, and with an almost uniform diameter.

The excretory pore is located at the posterior end of the body, and a large median collecting vesicle (Fig. 50) passes forward, dividing near the caudal limits of the vitellaria to form two lateral collecting ducts. These pass forward on the dorsal side of the body, but whether they continue a dorsal course I am not certain.

The nervous system is not so well developed as in other blood flukes. Even the esophageal commissure is not distinct in whole mounts and the nerves can not be traced in sections without the use of special technique. The esophageal commissure is situated a short distance behind the oral sucker but is much smaller than that of *Hapalotrema* as described and figured by Monticelli.

The testes are situated one behind and the other before the ovary. They are not divided into follicles as in *Hapalotrema* but the organs frequently are faintly lobed. The posterior testis is the larger; it has an elongated oval form and measures 0.18 to 0.21 mm. in length, 0.05 to 0.06 mm. in width, and 0.06 to 0.07 mm. in depth. The anterior testis is situated obliquely, immediately in front and slightly at the right of the ovary. It is ovate to triangular in outline; the widest portion is anterior and median; and the organ narrows laterally and posteriorly. The posterior end occupies the right side of the body at the ovarian level. Its long axis measures from 0.064 to 0.084 mm. and its transverse axis 0.04 to 0.05 mm.

There is a large seminal vesicle (Figs. 50 and 56), which extends from the level of the acetabulum about one-half the distance posteriad to the ovary. On the right side it frequently has one or two indentations and is partially covered by a lobe of the vitellaria. In cross-section it is almost circular and in mature worms is filled with spermatozoa. From the median posterior margin of the vesicle the ejaculatory duct (Figs. 52, 57) emerges as a small tube. It enlarges almost immediately and passes posteriad, dorsad and sinistrad to the genital pore. The anterior part has an epithelial lining and is often filled with spermatozoa, while the terminal part has a cuticular lining and is usually empty. Near the genital pore the duct contracts to a small tube which opens to the dorsal surface just median and anterior to the opening of the uterus. The pore (Fig. 59) is double, the male and female canals opening separately, although the intervening wall is very thin and they appear to discharge through a common orifice. A cirrus sac and cirrus are lacking. The caudal portion of the seminal vesicle and the ejaculatory duct are enclosed in a large, lobed, prostate gland, which occupies most of the body space between the vesicle and the anterior testis.

The female reproductive system is very similar to that of *Hapalotrema*. The ovary in *Hapalorhynchus* is only faintly lobed, while in *Hapalotrema* the indentations are prominent, but otherwise the comparisons are very close. In *Hapalorhynchus* the ovary is ovoid to pyriform in shape, situated obliquely in the body with its long axis almost at right angles to the long axis of the worm. It is slightly at the left of the median line and posterior to the middle of the body. The broader end is anterior and at the left; the smaller end posteriad and right of the median line. Its long axis measures from 0.1 to 0.12 mm. and its shorter axis from 0.06 to 0.08 mm. The oviduct arises at the posterior end and passes posteriad almost to the level of the posterior testis. Here it gives off a seminal

receptacle, often filled with spermatozoa, and Laurer's canal passes dorsally, opening to the surface (Fig. 61) near the median line. Immediately following the seminal receptacle the female duct receives the duct from the vitelline receptacle, and then passes forward on the dorsal side of the body to the genital pore. The vitellaria (Figs. 55–61) consist of masses of follicles extending on either side of the body from the bifurcation of the alimentary tract to the bifurcation of the excretory vesicle. They extend to the median line, forming a continuous mass in front of the acetabulum and behind the ovary, except for a small area where the posterior testis, occupying almost all the space between the dorsal and ventral walls of the body, restricts their presence. Between the acetabulum and the ovary they are limited to narrow tracts at the sides of the body lateral to the intestinal diverticula.

The genital pore (Fig. 59) is dorsal in position, situated near the middle of the body, slightly at the left of the median line. The diverticulum of the intestine and the vitelline duct of that side are bent mediad at the level of the pore and pass median to it. This condition suggests strongly that the genital pore has migrated from a ventro-lateral or lateral to a dorsal position, pushing the intestinal and vitelline structures before it.

The uterus is short and in only two of the many individuals examined has an egg been found in the body. The size of the egg makes it practically certain that not more than a single egg can be present in the uterus at one time. The egg (Fig. 51) is tricornuate; the shell is thick and resistant to pressure, although almost colorless. In the body the egg lies in the uterus with the single horn forward and the forward tip is often bent or slightly coiled. The eggs reach the outside world with the feces of the host and are often present in large numbers. Eggs in the feces measured 0.27 mm. in length, 0.07 mm. in width at the level of the embryo, and 0.2 mm. between the tips of the posterior horns. The miricidium develops slowly and in essential features resembles that of the other blood flukes.

Type host: *Chelydra serpentina.*

Holotype.—No. 125, Dept. Lower Invertebrates, Amer. Mus. Nat. Hist.

DISCUSSION

The question of the relationship and systematic position of the blood flukes has been discussed by previous investigators, although only Odhner (1912) has attempted any definite arrangement of the forms. The addition to our knowledge of the data afforded by the recently dis-

covered North American representatives of the group furnishes a firmer and better basis for comparison of these parasites and should contribute materially to the solution of the problem.

The genera *Hapalotrema* and *Bilharziella* were erected by Looss (1899). With the exception of the human forms belonging to the genus *Schistosoma*, they were at that time the only known blood flukes. The fundamental agreement of *Schistosoma* and *Bilharziella* made their close relationship apparent. Although he observed the similarity between *Hapalotrema* and the schistosomes in structure of suckers, dermomuscular sac, and details of the digestive tract, the important items of difference seemed to preclude a phylogenetic interpretation and Looss concluded that these points of resemblance were merely adaptations produced by existence in a similar and constant environment and by the common food supply. The structures most subject to environmental influences appeared to be the ones involved.

The discovery of the blood flukes of fishes and additional genera of schistosomes extended the field for comparative study and Odhner (1912) advanced the idea that the blood flukes are genetically related. Further evidence for this conclusion was afforded by the discovery of the life cycle of *Sanguinicola* and the results of certain Japanese investigators on the life history of *Schistosoma japonicum*. The group of blood-inhabiting trematodes contains distomes, monostomes, and suckerless forms, but this did not constitute a real difficulty since in his earlier studies on the formulation of a natural system for the digenetic trematodes this author had presented convincing evidence to show that the group of monostomes has no inherent and genetic entity and that the forms included under this heading have descended from different distome families. He contended that these forms manifest merely superficial resemblances and that the absence of an acetabulum, due to the gradual diminution and loss of that organ, is a cenogenetic feature of doubtful taxonomic value. In this paper he erected a new family, Harmostomidæ, with two subfamilies, Harmostominæ and Liolopinæ. In the subfamily Liolopinæ he included the genera *Liolope* Cohn, *Helicotrema* new genus, and *Hapalotrema* Looss. He constructed a type series—*Liolope, Hapalotrema, Bilharziella, Ornithobilharzia, Schistosoma,*—and regarded *Hapalotrema* as the important and connecting form in the series. He derived the *Bilharzia* type from *Hapalotrema* and deferred to a later paper a discussion of the relation of the blood parasites of fishes.

Noting marked differences in the character of the digestive, excretory, and reproductive systems, Ward (1921) asserted that the inclusion

of *Hapalotrema* in the family Harmostomidæ and subfamily Liolopinæ was an unnatural arrangement and necessitated a large series of exceptions in the descriptions of those groups which disturb their morphological basis. He removed this genus from the subfamily Liolopinæ and outlined a new family to contain *Hapalotrema* Looss, *Spirorchis* MacCallum, and *Proparorchis*, a new genus formed to contain a blood fluke from North American turtles that had been studied by him. Ward regarded the blood flukes of turtles as certainly related to the schistosomes and relatively closely associated with the fish parasites *Aporocotyle* and *Sanguinicola*.

The writer (1921) made corrections and additions to the description of *Spirorchis* and showed the identity of *Spirorchis* and *Proparorchis*. The name Spirorchidæ was proposed for the family outlined by Ward and two new subfamilies, Spirorchinæ and Hapalotreminæ were erected in the group. Concerning the blood flukes of North American turtles the statement was made that their discovery establishes a firmer basis for the conception of the unity and evolution of the blood-inhabiting trematodes. The Aporocotylidæ of fishes, the Spirorchidæ of turtles and the Schistosomidæ of birds and mammals were regarded as constituting a well-defined group with inherent natural relationships. The opinion was stated that the Spirorchidæ stand in an intermediate position and that the schistosomes are to be derived through them from the Aporocotylidæ, rather than from the Harmostomidæ as maintained by Odhner.

The discovery of new genera belonging to each of the subfamilies Spirorchinæ and Hapalotreminæ and their description in the present paper confirms the arrangement and conclusions of the earlier paper. Much of the evidence for a monophyletic origin and genetic relationship of the blood flukes has been presented by Odhner and Ward. The similarity of *Sanguinicola* and *Aporocotyle* was discussed by Odhner (1911) and they were included in the same family by him the following year. In an extended comparison Ward (1921) demonstrated the similarity between *Spirorchis* and *Hapalotrema* and included them in the same family. The family Schistosomidæ manifests so many common and unique features that its unity and validity can not be doubted. The three families then appear well outlined, coherent, and firmly established. Proof of the relationship between the spirorchids and schistosomes has been submitted by both Odhner and Ward. Both subfamilies of the Spirorchidæ have been related to the Schistosomidæ, Odhner demonstrating the similarity between *Hapalotrema* and *Schistosoma* and Ward that of *Spirorchis* and *Schistosoma*. In many respects the schistosomes agree

more closely with *Hapalotrema* than with *Spirorchis* and this appears natural since *Spirorchis* shows closer affinities with the fish parasites. With the establishment of the relationship between the Schistosomidæ and Spirorchidæ, there remains only the consideration of the relation between the latter family and the Aporocotylidæ.

Spirorchis and *Aporocotyle* agree in the position of the excretory pore and the general features of the excretory system. They are alike in that the musculature is delicate and an acetabulum is lacking. Both have prominent ventro-lateral nerves. The digestive systems of the two correspond in the absence of a pharynx and the presence of esophageal glands. The relative length of esophagus to ceca and the position of the primary bifurcation of the tract compare closely. The reproductive systems are strikingly similar. The testes are situated in the intercecal area anterior to the ovary and, although in *Aporocotyle* they consist of irregularly massed follicles, in *Sanguinicola* they are arranged in a double linear series. In both *Spirorchis* and *Aporocotyle* the terminal part of the vas deferens is enclosed in a small and poorly developed cirrus sac and the cirrus is eversible. This agreement in character of the copulatory organs is significant. In *Aporocotyle* the genital pore is dorsal, at the left of the median line near the posterior end of the body and, although it is anterior to the ovary in *Aporocotyle*, it is behind the ovary in *Sanguinicola*. In *Spirorchis* the genital pore is sinistral on the ventral side of the body but this disagreement I do not regard as important since in the description of *Hapalorhynchus* the migration of the genital pore from a ventral to dorsal position is explained. Other instances of the same condition are not uncommon. In both genera the ovary is oval, situated on the right side of the body a short distance caudal to the testes. The relations of the oviduct, vitelline duct, and uterus are very similar, although in *Aporocotyle* as in *Schistosoma* the uterus is longer and Laurer's canal is lacking. This latter structure is generally regarded as vestigeal and its absence in *Aporocotyle* is not subversive to the thesis. The vitellaria in both genera are similarly situated, enveloping the ceca throughout most of their length, although they extend farther posteriad in *Spirorchis*. The single vitelline duct in *Aporocotyle* is explained by Odhner by the reduction of the duct of the left side.

In the excretory, nervous, muscular, digestive, and reproductive systems there is substantial agreement and, although there are dissimilarities, the long series of structural likenesses constitutes conclusive evidence of more than fortuitous and convergent adaptation. One is

then justified in regarding these forms as closely related and the blood fluke series may be regarded as proceeding from *Sanguinicola* and *Aporocotyle* through *Spirorchis* and *Hapalotrema* to the schistosomes.

Modern classification is based primarily on anatomical characters but the data afforded by the study of the comparative anatomy of the blood flukes does not comprise all the evidence for their common ancestry and genetic relationships. Certain physiological and developmental features point very clearly to the same conclusion. That these forms have been able to enter the vascular system and become adapted to life in the blood stream suggests common fundamental likenesses in structure and physiology that may indicate a common origin and relationship.

Further, it is a significant fact that the most degenerate blood flukes, the suckerless forms with reduced alimentary tract, are found in the oldest and most primitive vertebrates, the fishes; while the most highly specialized blood flukes, the diecious forms, are present in the most recent and highly specialized vertebrates, the birds and mammals. This correlation of the evolution of the parasites with the evolution of their hosts is most suggestive and indicates that the blood flukes are a very old group. While the time of their entry into the vascular system can not be determined with anything like certainty from the evidence at hand, it seems probable that they have long been parasitic in the vertebrates. Either they were parasitic in vertebrates before the division of the vertebrate stem and have remained with their hosts through the transition periods and the evolution of the modern classes of vertebrates or they have changed their primary hosts from one class of vertebrates to another as these developed, a power of adaptation that seems very unlikely.

The genetic interpretation of the morphological similarity of the blood-inhabiting trematodes necessitates an explanation of certain structural differences that are present in the group: the reduction in length of the uterus, the degeneration of Laurer's canal, the migration of the genital pore, and the origin of the diecious condition. A satisfactory explanation is, I believe, possible. Existence in the blood vessels and the constant pressure exerted on the fluke by the elasticity of the walls of these tubes would tend to produce a narrow elongated body and prevent the development of a spacious uterus. This constant pressure, varying in intensity with the pulsations of the heart, would prevent the accumulation of eggs in the body of the parasite and actually force them out of the uterus. Since the eggs are voided in the blood vessels and must pass through the tissues of the host to reach the outside world, a process that requires a long period of time, they must be provided with hard shells

and contain large amounts of food material to supply the embryo during the period of migration. This requires the production of large eggs and the increased size of the egg would act as a potent factor in hastening its discharge from the uterus. Consequently, the uterus has been reduced in length and in certain genera the eggs are deposited almost as soon as they are formed. The absence of Laurer's canal in the Aporocotylidæ and Schistosomidæ does not constitute a serious difficulty. This structure is regarded as vestigeal by most students of the Trematoda; and Brandes, Goto, Looss, Odhner, Monticelli and others have cited instances to show its gradual reduction and ultimate disappearance. It is entirely lacking in the Monopisthocotylea and certain families of the Digenea, while in others it is represented by a blind sac opening from the oötype. Its absence in the most degenerate and most highly specialized blood flukes is then not surprising. The migration of the genital pore from a ventral to a dorsal position is not unique in the group of blood flukes. A corresponding dorsal migration of the genital pore is seen in *Axine*, *Microcotyle* and *Octobothrium* and its relations were traced by the writer (1917, p. 15). I have met a similar condition in the subfamily Telorchinæ, where the genital pore of *Protenes* is dorsal. The structural conditions in *Hapalorhynchus* as discussed in the present paper show clearly how such migration of the pore has been effected.

The origin of the diecious condition in the Schistosomidæ and an explanation of its appearance present a more serious problem. It is bound up with the whole question of the origin of sex. According to the observations of Cort (1921, 1921*a*) and Tanabe and Yokogawa, cited by him, in the schistosomes sex is determined at fertilization and all the individuals produced by parthenogenetic multiplication from a given miricidium are of the same sex. According to Lindner (1914), there are two different kinds of spermatozoa produced in *Schistosoma* and this heterozygous condition of the male he contends is responsible for the sexual differentiation of these diecious trematodes. The maturation processes in hermaphroditic forms are not well known; the observations reported are insufficient and far from conclusive but from the work of Goldschmidt on *Polystoma integerrimum*, *Dicrocœlium lanceolatum* and *Zoogonus mirus*, of von Dingler on *D. lanceolatum*, of A. and K. E. Schreiner, Grégoire and Wassermann on *Z. mirus*, of Schellenberg on *Fasciola hepatica*, and von Kemnitz on *Brachycœlium salamandræ*, it appears that the spermatozoa as well as the eggs are all alike and that every zygote contains complete sets of factors for the production of both male and female gametes. The work on *Schistosoma* indicates that the

males are heretogametic, and, if these observations are correct, the problem narrows to an explanation of this change in maturation.

Considerable light is thrown on the problem by a study of aphids, rotifers, and the smaller Crustacea, where sexual reproduction normally alternates with a series of parthenogenetically produced generations and corresponding differences occur in the maturation phenomena. It is true that in these species the female is heterozygous for sex, producing two kinds of eggs, but here experimental alteration of the sex ratio has shown the effect of environmental factors in determining the kind of eggs produced. In these forms environmental conditions seem to be the determining factors that control the type of gametogenesis and the sex of the ensuing individual. In daphnids Smith (1912) has shown that the type of egg and therefore the type of maturation can be influenced by temperature and food. In a series of papers Whitney (1914, 1916 and others) has discovered that rotifers, if fed on small amounts of a colorless flagellate, *Polytoma*, continue to produce parthenogenetic females, but when fed abundantly on *Euglena* or *Chlamydomonas*, chlorophyll-containing forms that produce oxygen, male-producing females appeared and sexual reproduction occurred. A most interesting and significant observation, and one that may bear directly on the origin of the diecious condition of the blood flukes, was made by Shull and Ladoff (1916) that in the rotifers the production of males is correlated with the supply of oxygen. The direct effect of oxygen was later discredited by Whitney (1919) but it appears certain, however, that these investigators have succeeded in influencing the type of maturation by modification of environmental conditions. By influencing maturation in aphids and phylloxerans, Morgan (1909) and von Baehr (1909) have made important observations on the determination of sex. Similar results were reported by Malsen (1906) for *Dinophilus*. Here it seems that the type of maturation is controlled by the size and organization of the egg. In experiments on moths Seiler has shown that the relative numbers of the two kinds of eggs produced can be influenced by temperature changes at critical stages in the process of maturation.

If the character of the gametes is determined by the type of maturation, and if maturation processes are subject to environmental influences, we have a possible explanation for the origin of the diecious condition in the blood flukes. The schistosomes are the only diecious trematodes known and they are found only in the veins of homothermal vertebrates; consequently, the environmental factors that could have caused the change may be estimated. If, on the advent of vertebrates with a four-

chambered heart, complete separation of arterial and venous circulation and a mechanism for maintaining a constant high temperature, the blood flukes for some reason came to occupy the portal and mesenteric veins they would be located in a medium differing distinctly from their relatives remaining in the arteries of the cold-blooded vertebrates. In this new environmental complex undoubtedly inheres the factor or factors responsible for the development of the diecious state. Temperature alone can not be the determinative factor since birds and mammals are infested by many species of trematodes that retain the hermaphroditic condition. To the question why the blood flukes abandoned the arteries and came to lie in the veins of the higher vertebrates, I have no satisfactory answer. Possibly the oxygen content of the arterial blood in the homothermal vertebrates was too great and they found in the veins about the same amount of oxygen as in the arteries of lower forms. Or it may have been due to food considerations. It is true that the portal and mesenteric veins in these forms (and these are the vessels occupied) contain large amounts of nutrient material received from the small intestine and afford a very rich food supply. But that the amount and character of the food is the decisive factor would, I believe, be difficult to maintain. The blood of the homothermal vertebrates differs from that of cold-blooded forms due to the higher temperature, the increased rate of metabolism, and the greater oxygen content. While other factors may have been operative, it seems probable that the increased oxygen and food supply of the venous blood have been the principal ones concerned with the production of the diecious condition.

Although our knowledge concerning the life histories of the blood infesting trematodes is fragmentary, and for only *Sanguinicola* and the human schistosomes has the complete cycle been demonstrated, considerable evidence to support the hypothesis of genetic relationships among the blood flukes is afforded by developmental data. The miricidia of the various forms are strikingly similar and differ markedly from those of other trematodes. Comparison of the miricidia of *Hapalotrema*, *Spirorchis* and *Schistosoma* as figured by Monticelli, the writer, and Cort will show essential agreement in the structure of these larvæ. The cercariæ so far as known are also very similar and belong to the forked-tailed group. Faust (1919), discussing the group of Furcocercariæ, recognized "a complete series of larval forms from those with a pharyngeal sphincter to the human schistosome cercariæ." Morphological similarity in the larval stages may be considered as of more value in determining relationships than similarity in the adult condition, where parasitic adaptation may have obscured original features.

The cercariæ of all these forms probably penetrate the integument of their hosts. The uniformly general and light infection indicates pretty clearly that the cercariæ are not ingested in mass as would happen if the host ate an infected snail and the cercariæ entered the vascular system from the digestive tract, but that they separately enter the body of the host. A significant observation is that among the blood flukes of turtles the heaviest infections have usually been encountered in the very small turtles. It seems probable that in these young animals the skin is more permeable and not so tough and hard as in older and larger individuals.

If the blood flukes are monophyletic (and present knowledge undoubtedly supports that conclusion), the present system of trematode classification is unnatural, deficient, and defective. Here is a group containing distomes, monostomes and suckerless forms which invalidates the accepted classification of the Digenea. No existing suborder will fairly contain the Aporocotylidæ; the Spirorchinæ would be placed with the monostomes, the Hapalotreminæ with the distomes and the Schistosomidæ, containing forms without suckers and others with one or two suckers, could not be assigned to any suborder as at present characterized. The recognized suborders of the Digenea, Gasterostomata, Monostomata, Amphistomata, Distomata, Holostomata, and possibly also the Aspidocotylea, although only part of these forms are digenetic and *Aspidogaster*, the type genus, is monogenetic, are all based on the character of the adhesive apparatus. As has been argued by many authors and forcefully maintained by Odhner, the adhesive organs of trematodes are adaptive, cenogenetic structures developed with the parasitic habit and consequently of secondary importance in taxonomy. The group of monostomes is rapidly falling apart and increasing knowledge of the digenetic trematodes is certain ultimately to lead to a radical and thorough revision of the classification of these forms. Such a work, however, is outside the scope of the present paper.

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EXPLANATION OF PLATES

All figures except those of reconstructions were drawn with the aid of a camera lucida and, with the exception of those of eggs and embryos, were made from permanent mounts.

Abbreviations used in Plates II to XIII

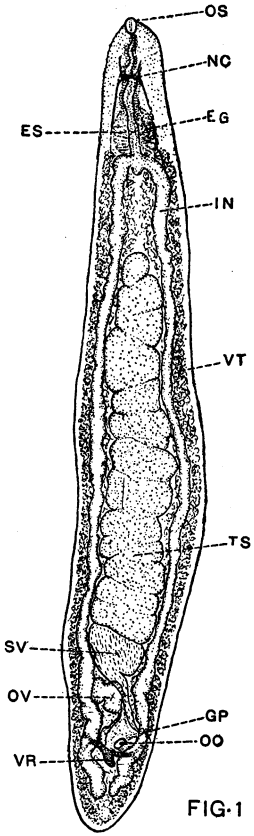
AD, anterior duct.
AP, anterior papilla.
CG, cephalic gland.
CS, cirrus sac.
ED, excretory duct.
EE, esophageal evaginations.
EG, esophageal glands.
FJ, ejaculatory duct.
EP, excretory pore.
ES, esophagus.
EV, excretory vesicle.
FC, flame cell.
GC, germ cell.
GP, genital pore.
IN, intestine.
LC, Laurer's canal.
MT, metraterm.
NC, nerve commissure.
NM, rudimentary nerve mass.
OC, eye spot.
OD, oviduct.
OO, egg.
OS, oral sucker.
OV, ovary.
PR, prostate gland.
PV, posterior ventralis nerve.
RD, rudimentary digestive sac.
SV, seminal vesicle.
UT, uterus.
TS, testis.
VD, vas deferens.
VL, vitelline duct.
VR, vitelline receptacle.
VS, acetabulum.
VT, vitellaria.

Plate II

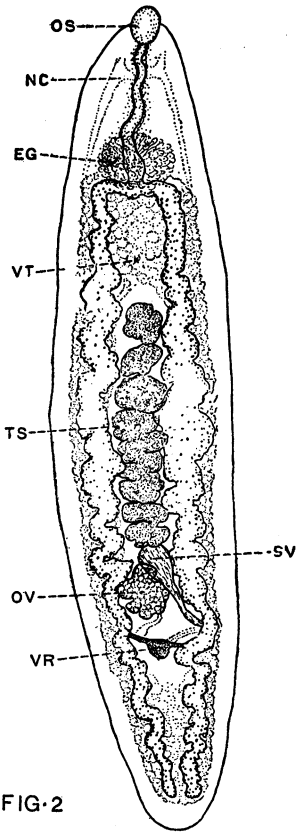
Fig. 1. *Spirorchis innominata*, from whole mount, ventral view, × 27.

Fig. 2. *Spirorchis elegans*, from whole mount, ventral view, × 65.

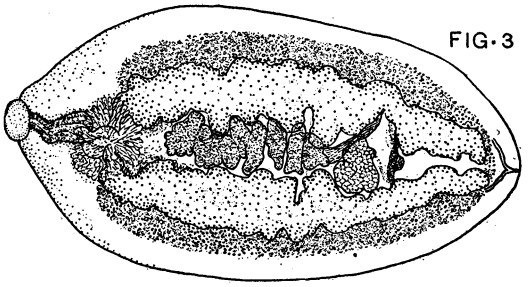
Fig. 3. *Spirorchis elegans*, from whole mount, much flattened, ventral view, × 65.



FIG·1



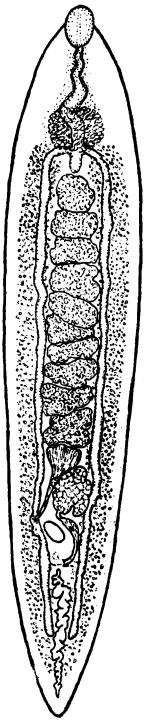
FIG·2



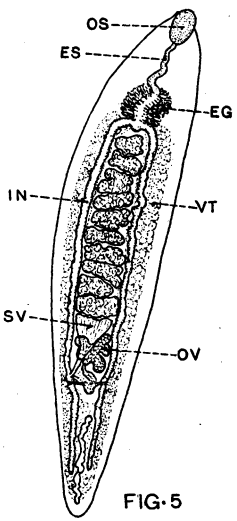
FIG·3

Plate III

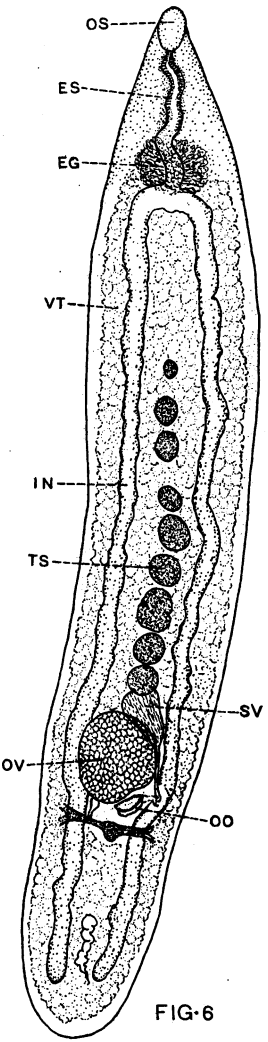
Fig. 4. *Spirorchis scripta*, from whole mount, dorsal view, × 65.
Fig. 5. *Spirorchis scripta*, from whole mount, dorsal view, × 65.
Fig. 6. *Spirorchis picta*, from whole mount, ventral view, × 65.



FIG·4



FIG·5



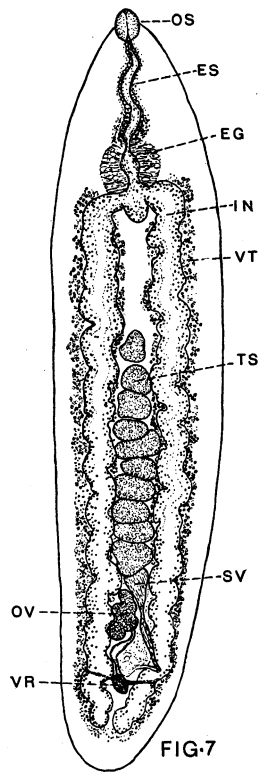
FIG·6

PLATE IV

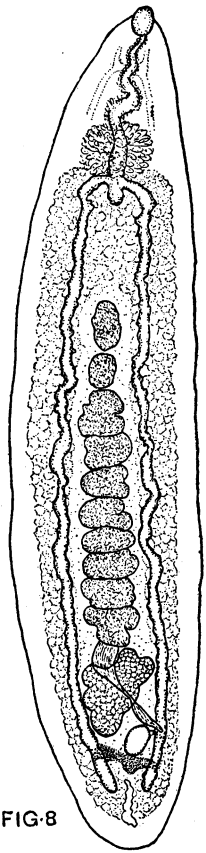
Spirorchis artericola.

Fig. 7. Specimen from mesenteric arteries of *Chrysemys picta*, whole mount, ventral view, × 65.

Fig. 8. Specimen from the mesenteric arteries of *Pseudemys scripta*, whole mount, × 65.



FIG·7



FIG·8

PLATE V

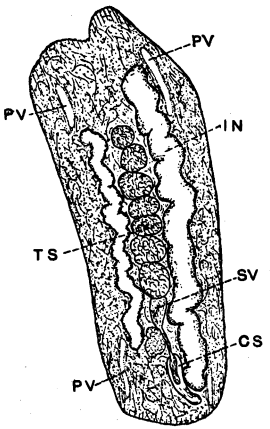
Spirorchis artericola.

Fig. 9. Frontal section near the ventral side of the body showing the posterior ventralis nerves, intestinal crura, testes, seminal vesicle, cirrus sac and ovary, × 60.

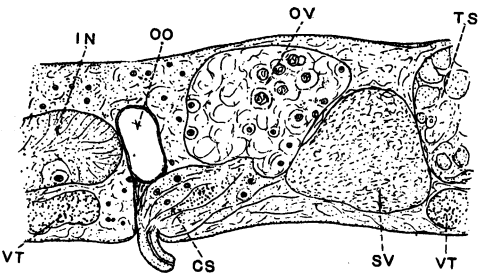
Fig. 10. Sagittal section of the body through the genital pore showing the posterior testis, seminal vesicle, cirrus sac, ovary, uterus, vitellaria and intestine, × 235.

Fig. 11. Reconstruction of the posterior end of the body from frontal sections, showing Laurer's canal, the tips of the intestinal crura, the vesicular structure present in this region, the excretory ducts and pore, × 90.

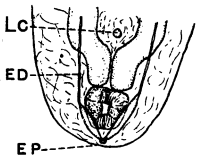
Fig. 12. Cross-section of the body immediately anterior to the genital pore, showing sections of the vitellaria, one excretory duct, intestinal crura, oviduct, uterus, metraterm and cirrus sac. The section is cut through a coil of the ejaculatory duct and it appears twice in the figure, × 145.



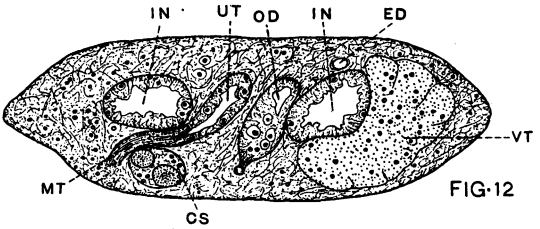
FIG·9



FIG·10



FIG·11



FIG·12

PLATE VI

All figures are cross-sections of *Spirorchis artericola*.

Fig. 13. Section through the oral sucker, × 145.

Fig. 14. Same specimen as Fig. 13; section through the esophageal commissure of the nervous system and showing also the esophageal evaginations and gland cells, ×145.

Fig. 15. Section through another specimen showing the same features as the previous figure. The esophageal evaginations are not so numerous, × 145.

Fig. 16. Same specimen as Fig. 15; section immediately anterior to the bifurcation of the alimentary tract, showing the esophageal evaginations and glands, and sections of the anterior lobes of the vitellaria and posterior ventralis nerves, × 145.

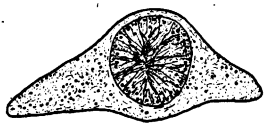
Fig. 17. Section of another specimen, cut through the bifurcation of the alimentary tract and showing the median posterior ventral pocket, × 145.

Fig. 18. Section of another specimen cut through the posterior testis showing testis, intestinal diverticula, excretory ducts and vitellaria, × 105.

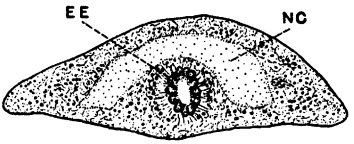
Fig. 19. Same specimen as Fig. 17; section through the opening of Laurer's canal, × 145.

Fig. 20. Same worm as Fig. 16; section behind the intestinal crura, showing the excretory ducts, vitellaria and the peculiar vesicular structure of this region, × 145.

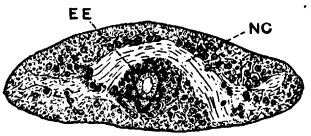
Fig. 21. Same specimen as Fig. 20; section through the excretory pore, × 145.



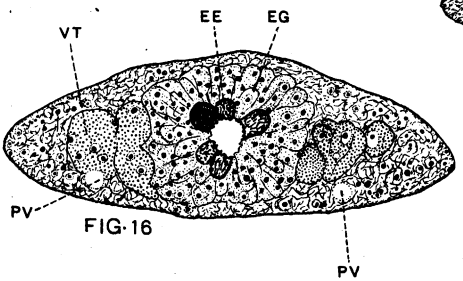
FIG·13



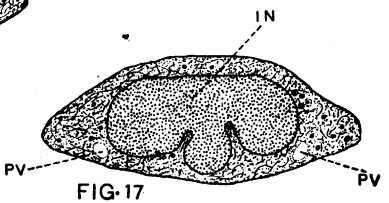
FIG·14



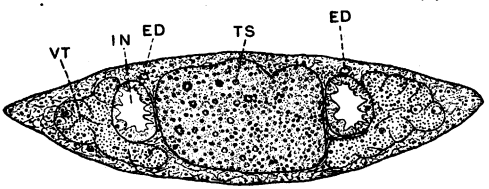
FIG·15



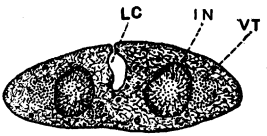
FIG·16



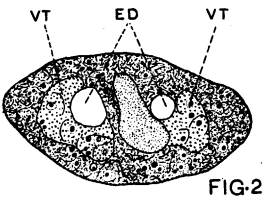
FIG·17



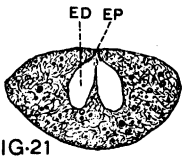
FIG·18



FIG·19



FIG·20



FIG·21

Plate VII

These figures are cross-sections of a mesenteric artery of *Chrysemys picta* containing two specimens of *Spirorchis artericola*. The two worms lie with their anterior ends in the same direction with dorsal sides contiguous, and the figures show cuts at successive levels. Only the media and intima of the artery are reproduced. All are drawn at the same magnification, × 105.

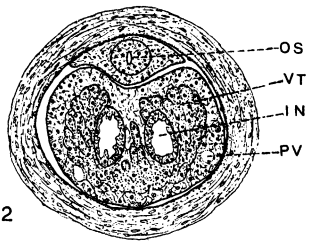
Fig. 22. The worm at the top of the figure is cut through the oral sucker and the one below just in front of the anterior testis.

Fig. 23. The worm in the upper part of the figure is cut through the esophageal gland, the one below through one of the testes.

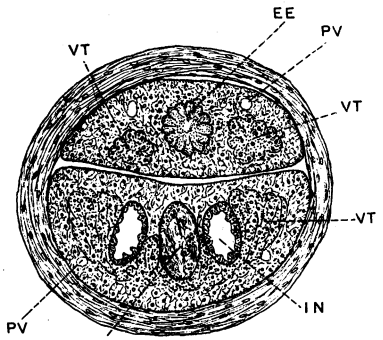
Fig. 24. The specimen in the upper part of the figure is cut through one of the testes, the one below through the anterior part of the ovary and the posterior part of the seminal vesicle.

Fig. 25. The upper specimen is cut through the testis behind the one shown in Fig. 24, and the lower specimen is cut through the posterior part of the ovary and the cirrus sac.

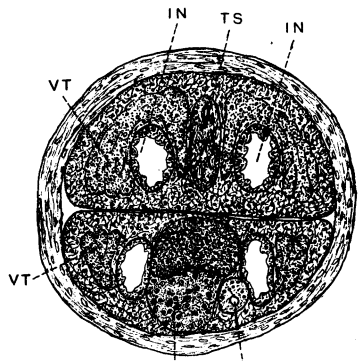
Fig. 26. The specimen in the lower part of the figure is cut through the genital pore, this section showing that these worms did not lie with the genital pores opposed.



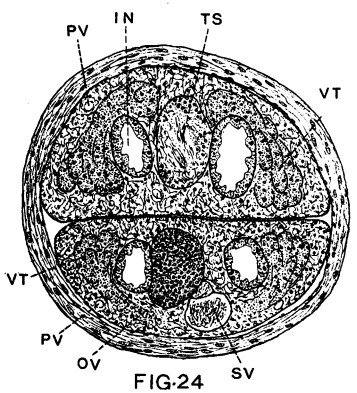
FIG·22



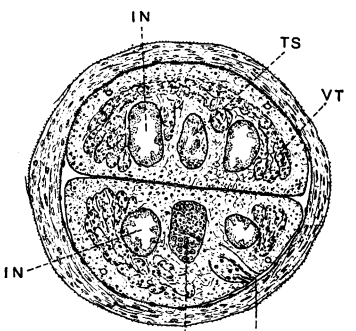
FIG·23



FIG·25



FIG·24



FIG·26

Plate VIII

Series of figures showing developmental stages of *Spirorchis artericola* and structure of the miricidium.

Fig. 27. Egg just voided from the uterus.

Fig. 28. Slightly older egg, showing early embryo.

Fig. 29. Egg containing slightly older embryo with developing eye spots.

Fig. 30. Egg containing older embryo, cilia developing and three constrictions in the circular muscles of the body.

Fig. 31. Egg with embryo almost ready to hatch.

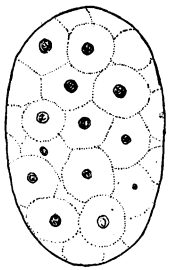
Fig. 32. Egg with operculum just opening.

Fig. 33. Egg shown in Fig. 32 after emergence of embryo.

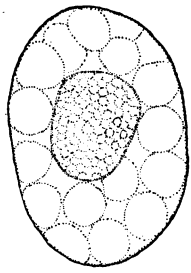
Fig. 34. Embryo from egg shown in Fig. 33.

Fig. 35. Miricidium, view from the neural surface showing anterior papilla, cephalic glands, rudimentary digestive sac, anterior ducts, eye spots, flame cells, rudimentary nervous mass and germ cells.

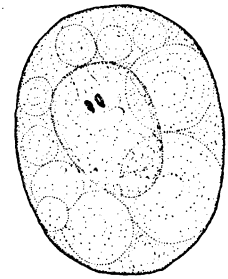
Fig. 36. Miricidium, side view, showing same structures as the previous figure.



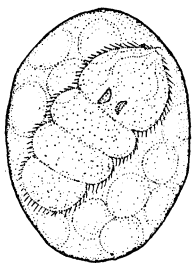
FIG·27



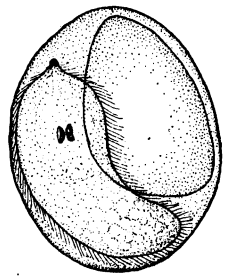
FIG·28



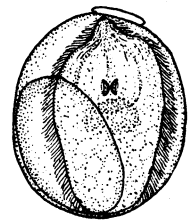
FIG·29



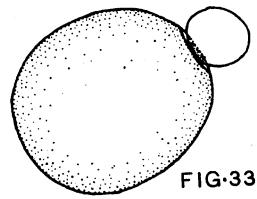
FIG·30



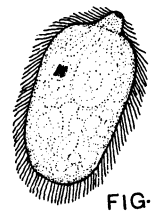
FIG·31



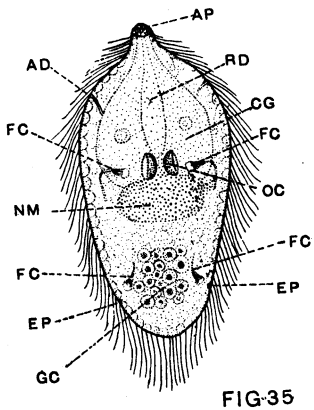
FIG·32



FIG·33



FIG·34



FIG·35

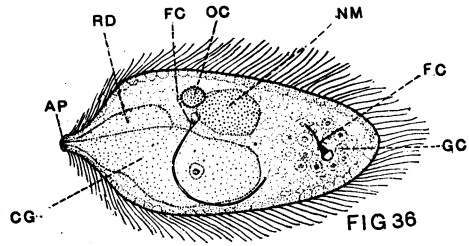
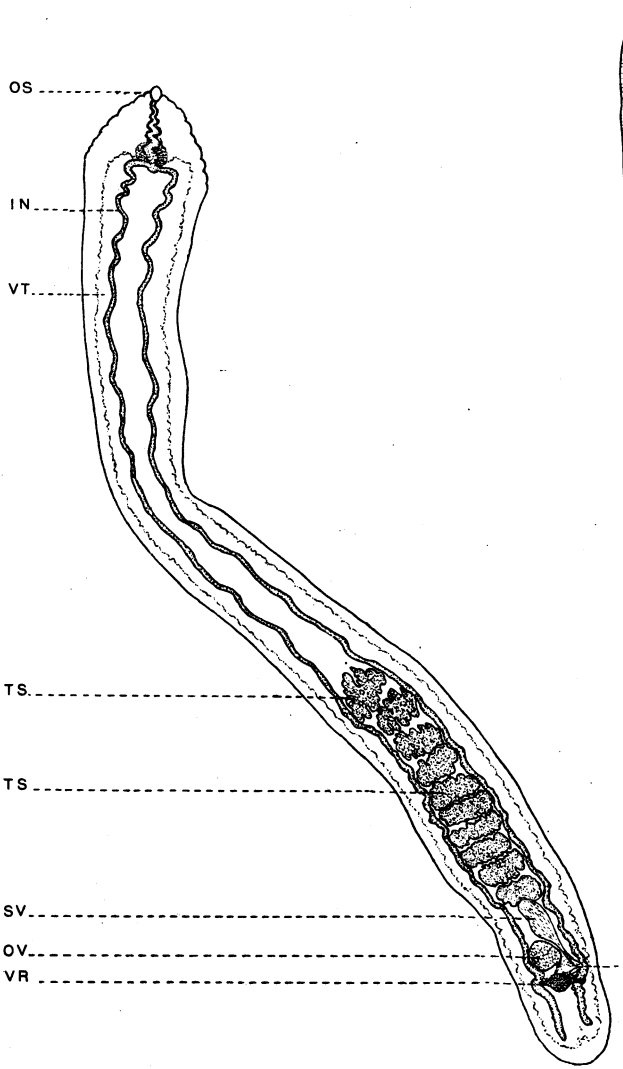


FIG 36

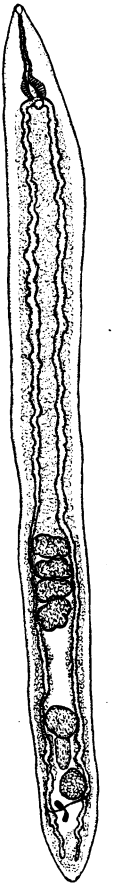
Plate IX

Fig. 37. *Henotosoma hæmatobium*, from whole mount, ventral view, × 19.

Fig. 38. *H. hæmatobium*, dorsal view, from whole mount, showing the disintegration of the testes. The black object just anterior to the vitelline duct and at the left and behind the ovary is an egg, × 14.



FIG·37



FIG·38

Plate X

Henotosoma hæmatobium.

Fig. 39. Cross-section through the esophageal gland, × 65.

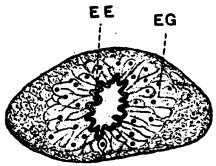
Fig. 40. Cross-section of body anterior to the testes, × 65.

Fig. 41. Cross-section through one of the testes, × 65.

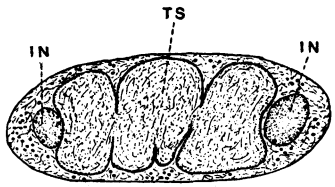
Fig. 42. Cross-section through the genital pore showing the cirrus extruded, × 65.

Fig. 43. Cross-section through the opening of Laurer's canal, × 65.

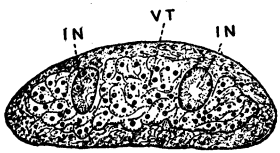
Fig. 44. Longitudinal section of the posterior part of the worm showing seminal vesicle, cirrus sac, ovary, oviduct, origin of Laurer's canal, uterus, intestine, posterior vesicle and excretory pore, × 62.



FIG·39



FIG·41



FIG·40

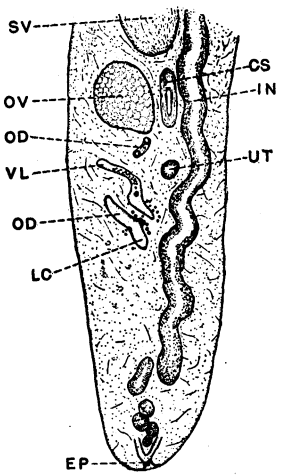


FIG 44

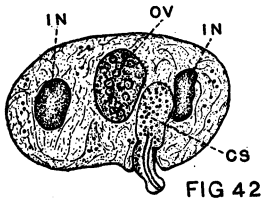


FIG 42

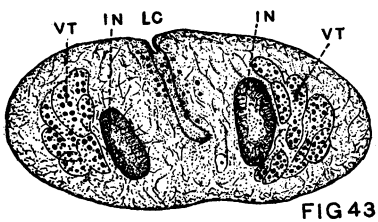


FIG 43

Plate XI

Hæmatotrema parvum.

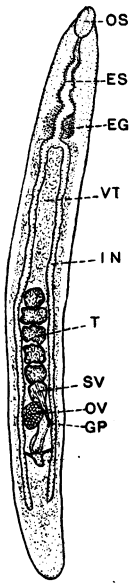
Fig. 45. Whole mount, ventral view, × 65.

Fig. 46. Sagittal section through the oral sucker, × 105.

Fig. 47. Frontal section through the middle of the body showing the bifurcation of the alimentary tract, the testes, seminal vesicle and ovary, × 145.

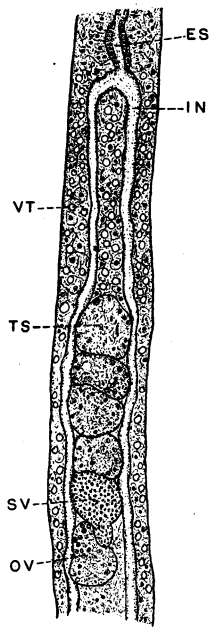
Fig. 48. Reconstruction of the reproductive organs near the genital pore, showing seminal vesicle, cirrus sac, ovary, oviduct, vitelline ducts and receptacle, Laurer's canal, uterus and genital pore, × 260.

Fig. 49. Whole mount, dorsal view, × 105.

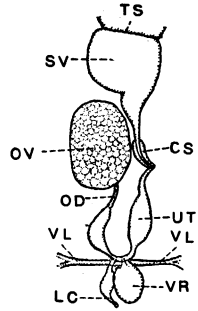


FIG·45

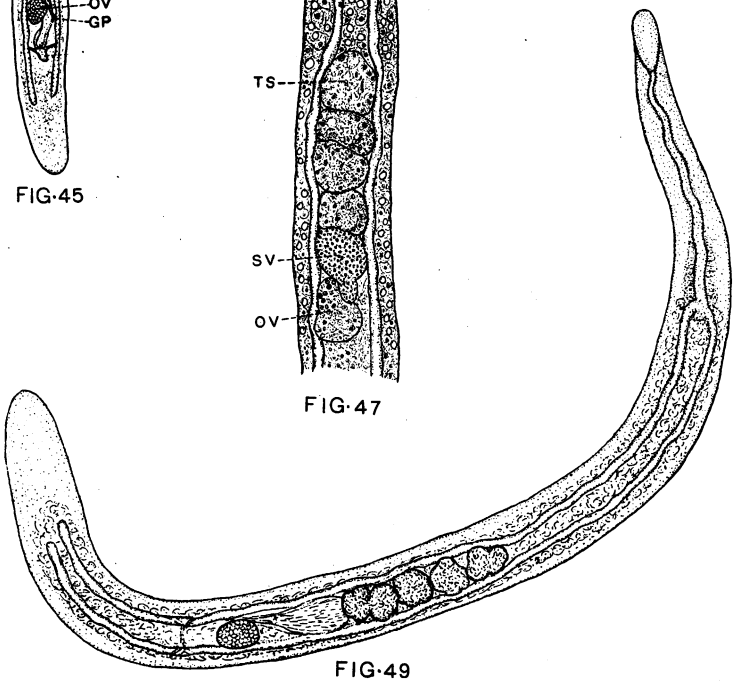
FIG·46



FIG·47



FIG·48



FIG·49

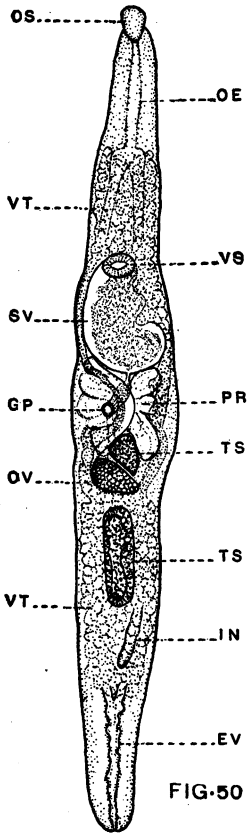
Plate XII

Hapalorhynchus gracilis.

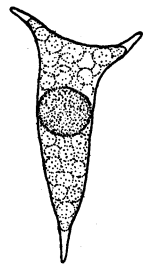
Fig. 50. Whole mount, dorsal view, × 60.

Fig. 51. Egg from the feces of *Chelydra serpentina*, × 125.

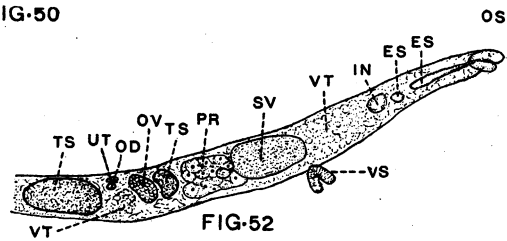
Fig. 52. Sagittal section near the midline of the body, showing oral sucker, esophagus, intestine, acetabulum, seminal vesicle, origin of the ejaculatory duct, prostate gland, anterior and posterior testes, uterus and vitellaria, × 60.



FIG·50



FIG·51



FIG·52

Plate XIII

Hapalorhynchus gracilis, cross-sections from several specimens but all drawn at the same magnification, × 235.

Fig. 53. Section through the esophageal commissure.

Fig. 54. Section at the level of the bifurcation of the alimentary tract.

Fig. 55. Section through the acetabulum showing the relation of structures at that level.

Fig. 56. Section at the level of the seminal vesicle.

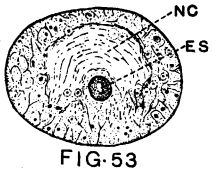
Fig. 57. Section cut through the prostate gland near the seminal vesicle.

Fig. 58. Section just anterior to the genital pore, showing the cuticular lining and enlarged portion of the ejaculatory duct.

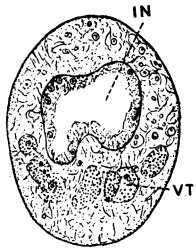
Fig. 59. Section through the genital pore. Note that the intestinal diverticulum of the left side is dorsal in position and median to the pore.

Fig. 60. Section through the posterior part of the cephalic testis and the anterior part of the ovary.

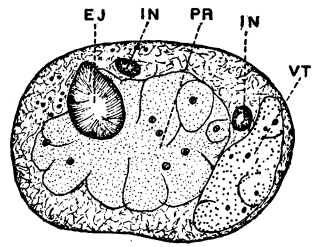
Fig. 61. Section through the opening of Laurer's canal.



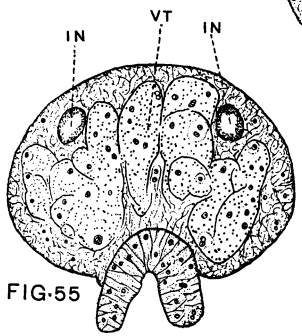
FIG·53



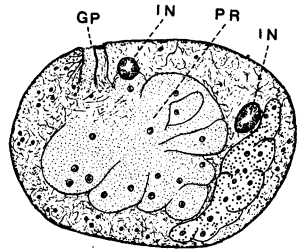
FIG·54



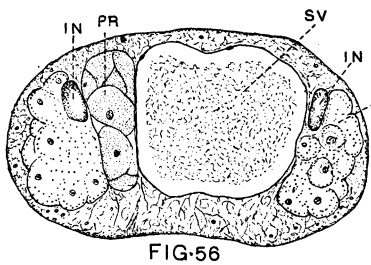
FIG·58



FIG·55



FIG·59



FIG·56

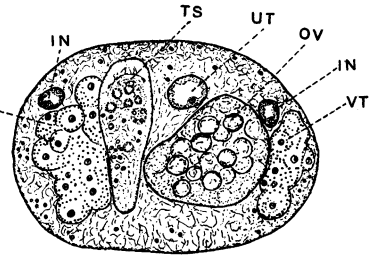
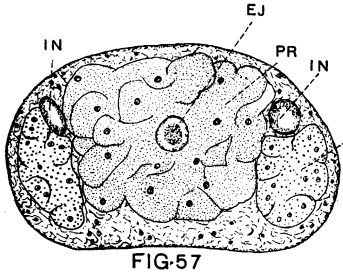
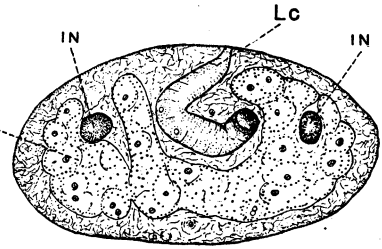


FIG 60



FIG·57



FIG·61