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TABLE OF CONTENTS

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COMPARATIVE STUDIES ON FURCOCERCOUS CERCARIAE

WITH 8 PLATES AND 2 TEXTFIGURES

BY

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under the direction of Henry B. Ward
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TABLE OF CONTENTS

INTRODUCTION

Early in the study of larval trematodes, begun in 1920 at the suggestion of Professor Henry B. Ward, the author's interest became centered on the furcocercous cercariae, and exclusive attention was devoted to these forms. In this work all larvae which possess a tail with a bifurcated distal end have been considered, although the heterogeneity of the group is recognized and was, indeed, a reason for the present study; these forms are also of interest because of the relation of some of them to schistosomiasis.

Collections of the common pulmonate snails, Planorbis and Physa, from the Drainage Ditch, Urbana, Illinois, as well as from small streams running into it, yielded furcocercous cercariae. Species of branchiate snails of the genera Goniobasis and Campeloma from several localities were also examined, but no furcocercous infections were found. During the summer of 1921 the investigations were carried on at the University of Michigan Biological Station at Douglas Lake, Michigan; various species of pulmonate and branchiate snails were collected from the waters of this region. Complete collection and infection records are given in another part of this paper.

As a result of this study seven new species of furcocercous cercariae are added to the fauna of North America; and the author is able, from a personal knowledge of some partly described forms, and with the advantage of access to recent literature, to present a survey of this group of larval trematodes.

To Professor Henry B. Ward, under whose direction the investigations have been carried out, the author acknowledges indebtedness for suggestions and helpful criticisms, and for the use of his extensive private library. Thanks are also due to Dr. G. R. LaRue, Director of the Michigan Biological Station, for courtesies extended during the summer of 1921, and to Professor Frank Smith and Curator Frank C. Baker of the University of Illinois for the identification of snail hosts.

HISTORICAL REVIEW

Probably the first furcocercous cercaria to be described is included by O. F. Müller (1773) in the Vermium Terrestrium et Fluviatilium; he placed it in the genus Vibrio, as *Vibrio malleus*. There is no figure, and the description is short, containing the following significant words: "motu literam Y, quiete T simulat." This form was accepted by subsequent workers as a cercaria. In 1794 Abildgaard described a larval trematode from Denmark with a tail distally bifurcated to its middle, to which he gave the name *Cercaria varicans*. This is the first record of a larva, recognized as a trematode, having this sort of tail. The original description is very scanty, and as no details of structure were added by the few subsequent workers who discussed this form, it could not now be identified with certainty. No internal structures are either described or figured, which leaves in doubt the presence or absence of a pharynx; no ventral sucker is shown. In the figures the furcae are about equal in length to the tail-stem.

Nitzsch (1817) very briefly described *C. furcata*, a distome larva with relatively long furcae sharply delimited from the tail-stem; this form has been mentioned by a number of authors but no significant details have been added. Diesing (1850), in his Systema Helminthum, included *Malleolus furcatus* Ehrenberg (1838) as the only known species of distome furcocercous larva, and listed the following as synonyms: *Vibrio malleus* Müller (1773), Zirkelthier of Eichhorn (1781), *Histrionella fissa* Bory (1825), *Cercaria furcata* Nitzsch (1817), and *Cercaria* VI von Baer (1826). This synonymy, with the exception of *Histrionella fissa*, was accepted by Moulinié (1856), who did not recognize the genus Malleolus, but listed the synonyms under *Cercaria furcata* Nitzsch. The present author finds no evidence in the literature which would set aside the disposition of Moulinié; in every case the accounts are so meager, with an almost complete lack of description of internal structure, that the species could not be identified with certainty. Diesing, in the Systema Helminthum, placed *Cercaria varicans* Abildgaard in a new genus Cheilostomum, as *Cheilostomum varicans*, the type and sole species; Moulinié returned this species also to the genus Cercaria.

La Valette St. George (1855) included in his monograph on larval trematodes brief descriptions of four new furcocercous forms, a brevifurcate monostome, *Cercaria cristata*, and three distomes, *C. fissicauda*, *C. gracilis*, and *C. ocellata*. He also figured *C. dichotoma* Joh. Müller, said to have been found by Müller in 1850 in the Mediterranean at Nice. This paper by Müller does not contain any definite reference to a furcocercous larva, and the figure included by La Valette St. George has been accepted by subsequent workers. *C. dichotoma* is the first of the few marine furcocercous cercariae which have been described. Filippi (1857) questioned the validity of *C. cristata*, as being distinct from *C. varicans*. The present author is of the opinion that they are distinct, because the dorsal body crest, prominent in *C. cristata*, was not mentioned or figured by Abildgaard for *C. varicans*; furthermore the latter species is a longifurcate larva, while the former is brevifurcate.

Diesing (1858), in a further systematic treatise on cercariae, made a new genus Lophocercaria to contain only *Lophocercaria fissicauda*, under which he put as a synonym *Cercaria cristata* La Val. St. George; there is no reason, stated or apparent, for such a change of specific name. Two other species of La Valette St. George were placed in a new subgenus, *Cercaria* (*Schizocerca*) *gracilis* and *C.* (*Schizocerca*) *fissicauda*, as well as *C.* (*Schizocerca*) *dichotoma* Joh. Müller. He also established the genus Histrionellina to contain only *Cercaria ocellata* La Val. St. George, which was designated *Histrionellina fissicauda*. No significant details of structure were added to previously described forms by the investigations of Pagenstecher (1857), Wagener (1866), or Villot (1875). Ercolani (1882) briefly described three new species, a brevifurcate monostome, *Cercaria microcristata*, and two longifurcate distomes, *C. aculeata* and *C. minuta*. Morgan (1891) reported the finding of one individual, which he decided was a new species of marine larval trematode, taken in a tow at Jamaica; while his single sketch shows a bifurcated tail, very small in proportion to the body, it is not known whether this cercaria is too aberrant to be included with other furcocercous forms.

Sonsino (1892) briefly described the first fresh water furcocercous larva to be reported outside of Europe, *Cercaria vivax* sp. inq. from Egypt. In a short note (1894) he indicated that there were three pairs of flame cells in the tail-stem of this cercaria; this is the first record of the tail flame cells, which are unique for the furcocercous larvae. The work of Looss (1896) made this the first furcocercous larva to be described with respect to the excretory system pattern in the sporocyst and its development in the cercaria. By his studies was established the bilateral embryonic character of the caudal excretory tube, which is unpaired in the mature cercaria; he figured the presence of an island in the excretory tube at the juncture of body and tail-stem. The branches of the caudal excretory tube which pass through the bifid portions of the tail were described as opening near the tips. A subterminal birth-pore was described and figured at the anterior end of the sporocyst. The differences between the much modified oral sucker of *C. vivax* and the typical sucker of larvae without forked tails were clearly recognized by Looss, who also noted and described about eight gland cells within this modified sucker. Thus *C. vivax* is the first furcocercous cercaria for which there is a careful and complete description. Sonsino (1897) briefly reported a furcocercous distome, *C. bipartita*, from Italy; in contrast to all previously described forms, it was said to develop in rediae.

Haswell (1902) described a marine larva, which, although it apparently belongs to the echinostomes, has a distally bifurcated tail and an excretory system in the body more like the furcocercous than the echinostome cercariae; no flame cells or tubules were seen in the tail. Pelseneer (1906) described *C. syndosmyae* from *Syndosma alba*, a marine mollusc. Lebour (1908) studied *C. dichotoma* Müller, and figured both sporocyst and cercaria.

In his treatment of the trematodes of the fresh waters of Germany and surrounding countries Lühe (1909) briefly summarized the descriptions of the furcocercous larvae; of the ten fresh water species of Europe one, *C. varicans* Abildgaard, was not included. In the scheme of classification the monostome furcocercous larvae, which are characterized by a median dorsal crest, were grouped as the Lophocercariae, and the distomes as the Furcocercous Cercariae. In the key these last were subdivided on the basis of presence or absence of eye-spots, the degree to which the furcae were delimited from the tail-stem and whether development took place in rediae or in sporocysts. Brief notations of two incompletely described forms, which were not named, were also included. The brevity of the descriptions in Lühe's work shows how incompletely these early species are known, a condition in contrast with the work of Looss on *C. vivax*.

Ssinitzin (1909) studied *C. ocellata* and described its morphology and behavior in detail. Two differentiated sets of large unicellular gland cells, occupying the greater part of the body, were reported for the first time in a furcocercous larva, an anterior group from which the contents had been largely dissolved out and a posterior group containing coarse granules. These glands, later designated salivary glands by Ssinitzin (1911), and cephalic, poison, mucus, mucin, salivary-mucin by other authors, are in the present paper termed penetration glands. Although seven pairs of flame cells were noted as being present in the body of *C. ocellata*, they were unfortunately omitted from the two drawings referred to, and the pattern of the excretory system is therefore unknown. The presence of a greatly modified organ in place of an oral sucker, divided into an anterior thin-walled and a posterior muscular portion as subsequently described for schistosome larvae was noted; within, gland cells were seen, later designated as the head gland by Narabayashi. The type of alimentary canal which opens on the antero-ventral surface by a capillary tube was also figured. Blochmann (1910), in a paper which seems to have escaped general notice, called attention to the fact that death resulted to several species of fish and to axolotyl and salamander larvae from the penetration of great numbers of *C. fissicauda*. Their further development was not studied. The results of comprehensive studies on the stages of digenetic trematodes infesting molluscs of the Black Sea were published (in Russian) by Ssinitzin (1911); one furcocercous larva, *C. discursata*, was described. He proposed the term parthenita for the mature sporocyst or redia; and salivary glands for the very large gland cells (penetration glands) frequently occupying the greater part of the body, as in *C. ocellata*, and discharging through heavy ducts opening at the anterior tip of the body.

Odhner (1911) published a brief account of some investigations which Looss had made on the life history of *C. cristata*, and included two sketches of that larva; the excretory tube in the tail-stem bifurcates and passes through each furca, but it is not shown where these branches open to the exterior. A marine cercaria was briefly described by Odhner (1911a) and believed to be the larva of *Haplocladus minor*; no figures of the cercaria were published. Lebour (1912), in a review of British marine cercariae, objected to Lühe's (1909) use of tail form in the classification of larval trematodes, and proposed to divide all cercariae into two primary groups, on the basis of development in sporocyst or in redia. Division of the British marine larval forms was made on this basis; *C. dichotoma* was the only furcocercous form considered.

In 1912 da Silva reported a brevifurcate distome larva, *C. blanchardi*, from Brazil; this is the first record of a furcocercous cercaria from South America. In the brief description and microphotograph it resembles the human schistosome larvae, and is considered by Lutz and others to be probably the cercaria of *Schistosoma mansoni.* Miyairi and Suzuki (1913; in Japanese) determined the infective stage of *Schistosoma japonicum* to be a brevifurcate distome larva. The same authors (1914) published descriptions of the parthenita and cercaria, together with two plates. The cercaria was described as possessing three pairs of large penetration gland cells, and the locations of five pairs of flame cells, four pairs in the body and the fifth in the tail-stem, were indicated. A granular mass in the modified oral sucker was described, and is undoubtedly the structure later designated as the head gland. Ogata (1914) also described the cercaria of *S. japonicum.* His report of the number of flame cells agrees with that of Miyairi and Suzuki. The three pairs of penetration glands were designated poison glands, and the alimentary canal posterior to the modified oral sucker was correctly figured but not recognized as esophagus and cecum.

Cort (1914), in a preliminary report of studies on North American larval trematodes, described one furcocercous form, *C. douthitti*; the presence of "eight large unicellular glands, which seem to be analogous to the stylet glands in certain other forms" was noted. In the complete publication (1915) he gave a more detailed structural analysis of *C. douthitti*, in which the term cephalic glands was used for the penetration gland cells. Both Lühe's (1909) and Lebour's (1912) classifications of cercariae were discussed and that of the former followed; Cort adopted the term furcocercous from Lühe for larvae with distally bifurcated tails, of which *C. douthitti* was the first North American form to be described. Concerning the group Cort stated (1915:51): "The furcocercous or forked-tailed cercariae are very imperfectly known. The anatomy of only a few of the known forms is at all well worked out and the life-history of no one of them has been determined. At least a dozen species have been reported as distinct, some of which, however, have been described very briefly in the older accounts. Sufficient evidence is not available to justify any conclusions as to the natural or artificial character of this group."

Leiper and Atkinson (1915) briefly described the primary and secondary sporocysts and the cercaria of *Schistosoma japonicum*, and also included a record of the presence of a larva (see figure 6 of Leiper and Atkinson) closely resembling *C. vivax* Sonsino. Their account of the cercaria of *S. japonicum* differs from those of Miyairi and Suzuki (1914) and Ogata (1914), in that instead of three pairs of penetration gland cells they reported five or more pairs. Leiper (1915), in the reports of the Bilharzia Mission to Egypt, presented the results of extensive investigations of the causative agents of schistosomiasis. Three distome cercariae were figured, one from *Planorbis boissyi* which upon experiment proved to be the larva of *S. mansoni*, another from Bullinus which was experimentally determined to be the infective stage of *S. haematobium*, and a third very large form from *Planorbis boissyi* (see figure 46 of Leiper); no attempt was made to describe these larvae in detail. All have relatively short furcae without cuticular keels, and are further similar in the lack of pharynges and eye-spots; the figures indicate that in the equipment of the penetration glands the three forms differ. Another form, said to be very similar to *C. ocellata*, was found in three different snails; the possession of a cuticular keel along each side of the furcae, and of pigmented eye-spots anterior to the ventral sucker distinctly set it off from the schistosomes. The provisional name *C. bilharziella* was used. Two other forms were found, *C. vivax* Sonsino and *C. fissicauda* La Val. St. George; both were reported as possessing a muscular pharynx. As a result of Leiper's studies, the schistosome cercariae were differentiated from other furcocercous forms by the lack of pharynx, of pigmented eye-spots, and of cuticular keels on the furcae, which are less than one-half as long as the tail-stem. *C. bilharziella* was thought to belong to a genus closely allied to Schistosoma.

Cawston (1915), in the first of a long series of short papers in which South African furcocercous cercariae are meagerly described and incompletely figured, reported a new species, *C. secobii*, from *Physopsis africana*. Linton (1915) briefly described a brevifurcate monostome from *Hydroides dianthus*, and noted its resemblance to *C. cristata* La Val. St. George; it is the first marine furcocercous larva reported from North America. In a second paper (1915a) he recorded another larva, from *Pecten irradians*, which he found to be much like that from Hydroides; the outline sketches do not make it possible to arrive at any conclusion as to their identity. Leiper (1916), in the fourth section of the report of the Bilharzia Mission, gave a table of Egyptian molluscs in which the various trematode larvae, including the furcocercous forms, were found. Narabayashi (1916), according to Cort's (1919) translation of Miyagawa (1916), designated the gland cells within the modified oral sucker of the cercaria of *Schistosma japonicum* as the head gland (Kopfdrüse).

Fuhrmann (1916) described a longifurcate distome, *C. letifera*, which possesses fine bristle-like hairs on the tail-stem, structures reported for the first time on a furcocercous larva. Yoshida (1917; in Japanese) described a brevifurcate distome, *Cercaria* G, which is figured as having a distinct pharyngeal bulb, a structure previously reported only for the longifurcate forms; development was said to take place in rediae. Iturbe (1917, 1917a) published a brief description, with one diagrammatic figure, of the cercaria of *Schistosoma mansoni* in South America. He reported five pairs of flame cells in the body, and three pairs of large gland cells; subsequent work on this species by other authors is not in agreement with these findings. O'Roke (1917) briefly described three new furcocercous distome larvae from Kansas, an apharyngeal form, *C. echinocauda*, and two longifurcate larvae, *C. inversa* and *C. quieta*. LaRue (1917), from a study of two agamodistomes,* which he called *C. marcianae* and *C. vergrandis*, concluded, on the basis of staining tests with thionin and toluidin blue, that the large penetration gland cells secrete mucus (mucin). Faust (1917), in a preliminary paper, described *C. gracillima* and *C. tuberistoma*, longifurcate forms from the pulmonate gastropods of Montana. He considered the apharyngeal furcocercous cercariae to be "undoubtedly larval schistosomes as demonstrated by the experimental work of Leiper (1916) and by a close comparative study which the writer has made on larvae and adults" (p. 121).

Cort (1917), in a discussion of the homologies of the excretory system, added the exact pattern of that system to the description of *C. douthitti*, and noted for the first time areas in the walls of the bladder arms which were ciliated, organellae which in other larvae had unquestionably been mistaken for flame cells. In the excretory tube of *C. douthitti* he described the small island previously figured by Looss (1896) for *C. vivax*, and later designated by Faust (1919c) as the island of Cort. For *C. douthitti* Cort reported the number of penetration glands to be ten, instead of eight as originally found. Three new species, *C. douglasi* and *C. emarginatae*, longifurcate larvae, and one brevifurcate form, *C. elephantis*, were described,

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* One of these, more properly designated *Agamodistomum marcianae*, has been held by Cort (1918:130) to be the agamodistome stage of a furcocercous cercaria.

together with the excretory system pattern of the cercaria of *Schistosoma japonicum.* The six furcocercous cercariae discussed were divided into three groups, of which the first two were assigned to the family Schistosomatidae. Members of Groups I and II are characterized by the absence of a pharynx and by furcae definitely delimited from the tail-stem and less than half its length; members of Group I possess eye-spots which distinguish them from the larvae of Group II. The third group was created to contain the cercariae possessing distinct pharynges and with furcae which are almost as long as the tail-stem and not delimited from it. The homologies of the excretory systems in the furcocercous cercariae were discussed and the importance of this system as an indicator of relationship was emphasized.

Cawston (1917) suggested the name *C. oculata* for an apharyngeal, brevifurcate distome with eye-spots, and *C. secobiana* for a longifurcate larva. In a subsequent paper (1917a) he again briefly described *C. oculata* and *C. secobii*; later still the synonymy of *C. secobiana* 1917 with *C. secobii* 1915 was acknowledged (1917b). Faust (1918) described *C. gracillima* and *C. tuberistoma* in greater detail than in the first report (1917); both larvae were referred to the Schistosomatidae. A number of parts of the adult reproductive system were recognized in cell masses present in the body of *C. gracillima*; the nervous system was also described in greater detail than had formerly been done for a furcocercous form. The penetration glands in these two larvae were designated salivary-mucin glands. In discussing the morphology of the different systems of larval trematodes he said (p. 44) of the genital system: "This system of organs has been the most constant basis of classification of adult trematodes. It is also the best specific criterion for the larvae, although a more delicate technic is required for differentiation of the genital organs in the cercaria than in the adult worm." And for the nervous system, he stated (p. 55): "this study has shown that the nervous system of the cercaria is constant for the group to which it belongs, and is a definite basis for the natural classification of the groups." Faust (1918a) described two new forms, *C. gigas* and *C. minor*; the former is peculiarly interesting in its type of excretory system. Cort's (1917) three groups of the furcocercous cercariae were discussed; Faust (p. 108) held that "with the broadening knowledge of schistosome larvae, it seems more reasonable to recognize a complete series of larval forms from those with a pharynx sphincter (*C. douglasi*, *C. emarginatae*, and perhaps *C. vivax* Sonsino), thru those with a degenerate pharynx, with or without intestinal ceca (*C. gracillima*, *C. minor*), thru those without any pharynx, but with well-developed mucin glands (*C. gigas*, *C. tuberistoma*, *C. douthitti*), to the human schistosome cercariae." *C. echinocauda* O'Roke (1917) was also studied and compared with *C. gigas.* In a discussion of the eye-spots in Digenea, Faut (1918b) described those of *C. gigas* in relation to the nervous system.

Cort (1918a) described the excretory system of *Agamodistomum marcianae,* which he held to be the agamodistome stage of a furcocercous cercaria; the development and conservativeness of the excretory system were discussed. Later (1918b) he submitted data to support his thesis that the furcocercous cercariae readily adapt themselves to new molluscan intermediate hosts. Cawston (1918) described *C. secobii* as developing in rediae, although he expressed some doubt as to identification of the species; in previous publications the parthenitae had been reported to be sporocysts. In a later paper (1918a) he recorded a cercaria from the Transvaal with furcae much longer than the tail-stem, for which the name *C. gladii* was proposed. Liston and Soparkar (1918) reported the experimental determination of a furcocercous cercaria as the larva of *Schistosoma spindale* of domestic cattle. Southwell and Prashad (1918) briefly criticized Lühe's (1909) classification of cercariae, because it was based on purely larval structures.

Kobayashi (1918; in Japanese) described a brevifurcate pharyngeal larva with eye-spots, *Cercaria* F, the parthenitae of which were rediae. Cort (1919) described in detail and carefully figured the cercaria of *Schistosoma japonicum.* The most striking difference between this and the previous accounts (Miyairi and Suzuki, 1914; Ogata, 1914) is that three, instead of four, pairs of flame cells were reported for the body; Cort also found two ciliated areas in the distal portion of each bladder arm; all authors have concurred on a single pair of flame cells in the proximal region of the tail-stem. He adopted from Narabayashi the term head gland for the gland contained within the modified oral sucker, and again used cephalic glands to designate the penetration glands. Of these latter glands five pairs were described, in contrast to three pairs reported by Miyairi and Suzuki and by Ogata, and the five or more pairs of Leiper and Atkinson. Cort also included a valuable review of previous publications in the Japanese language. Cawston (1919) briefly described *C. spinosa* from South Africa. In another publication (1919a) he reported finding a small eye-spotted larva for which the name *C. parvoculata* was proposed.

Faust (1919), in a survey of the described cercariae of the United States, recorded the change of name of *C. minor* Faust 1918, preoccupied by Lebour (1912), to *C. minima.* The conservativeness of the excretory and genital systems was discussed, and emphasis laid upon the probable greater value of the latter in the determination of relationships. In a discussion of the excretory system in several groups of the Digenea he proposed (1919c) formulae for the flame cell patterns as found in the cercariae. Brief descriptions of four new species of pharyngeal longifurcate larvae were also included in this paper: three distomes, *C. furcicauda, C. quattuor-solenata* and *C. robusticauda*; and one monostome, *C. rhabdocaeca..* The basic groups of flame cells were taken to consist of either a single flame cell and its capillary, or two or more whose capillaries united and emptied into a larger excretory tubule. The different groups were represented in the general formula by Greek letters, $\alpha+\beta+\gamma+\delta+\epsilon$, five being the largest number of groups present among the ten furcocercous larvae discussed. The simplest condition is in the cercaria of *Schistosoma japonicum*, in which there is a definite division into an anterior group of two, α, and a posterior group of two, β; the distinction between anterior and posterior flame cells rests on whether their capillaries empty into anterior or posterior lateral collecting tubules. In the formulae for *C. douthitti* and *C. elephantis* there is the same distinction of α for anterior and β for posterior groups; while in the Brachycoeliidae, with two anterior and two posterior groups, the primed letters $\alpha'$and β' are used for the former and the double-primed letters α'' and β'' for the latter, when it would seem clearer from a comparative standpoint to use α' and α'', and β' and β'', respectively. Where there is no evident division into anterior and posterior groups, as in the excretory system patterns of the four new species described, Faust used three, four, or five letters to represent the basic groups. *C. emarginatae* and *C. douglasi* (Cort, 1917) were included under the general formula $\alpha+\beta+\gamma$, although there is a clear division into anterior and posterior groups.

Faust (1919a) studied Cawston's preserved material of three partly known furcocercous larvae and of the cercaria of *Schistosoma haematobium*; additions were made to the previous descriptions of *C. gladii*, *C. secobii*, and *C. parvoculata*. The description of the cercaria of *S. haematobium* was more complete than any previous one. Three pairs of penetration glands were found, and their ducts, as well as those of *C. gladii*, were described as being capped with hollow piercing spines, structures noted for the first time in connection with glands of cercariae. Material of the cercaria of *S. mansoni* from Venezuela was also studied and the presence of two pairs of granular and four pairs of non-granular penetration gland cells noted; each of the ducts was found to be capped with a hollow piercing spine. The first detailed table for the diagnosis of the human schistosome cercariae was included. Lagrange (1919) very briefly reported a furcocercous cercaria in *Bithynia tentaculata* from France. Iturbe and Gonzalez (1919) published the results of further studies on the cercaria of *S. mansoni* in Venezuela. Four pairs of flame cells were found in the body and one pair in the tail-stem, whereas previously (Iturbe, 1917) five pairs had been reported for the body. Two differentiated sets of penetration gland cells were found and designated as venom and salivary glands; these correspond to Faust's (1919a) granular and non-granular glands.

Sewell (1919) described in detail an apharyngeal larva from India, *C. indica* XXX, which corresponded so closely to the cercaria of *Schistosoma japonicum* that he was not sure of the specific identity of the new form. Instead of the term oral sucker, Sewell employed anterior penetrating organ; the structural modifications from the typical oral sucker of other larval trematodes had previously been observed in certain furcocercous larvae by a number of workers, notably Looss (1896) and Ssinitzin (1909), but no new term had been used. Lutz (1919), in a paper largely of medical character, used the names *Dicranocercaria ocellifera* and *D. valdefissa* for two larvae; microphotographs were included but no descriptions were given in the text. Porter (1920) studied the cercaria of *Schistosoma haematobium* and noted the presence of three pairs of penetration glands with hollow spines capping their ducts, thus confirming Faust's (1919a) previous observation. She reported finding these cercariae in both *Physopsis africana* and *Lymnaea natalensis*; the latter host genus is new for this larva. The larva of *S. mansoni* was found in three specimens of *Physopsis africana*; this is the first record of this cercaria from a mollusc other than of the genus Planorbis. Manson-Bahr and Fairley (1920), in a study of schistosomiasis in Egypt, briefly described the cercariae of *S. haematobium* and *S. mansoni*. They reported the excretory systems to be identical with that described by Cort (1919) for the larva of *S. japonicum*, but also make the conflicting statement that there are "six pairs of flame cells arranged along the margins of the body." Two pairs of large clear penetration gland cells and four pairs of small granular ones were described for the cercaria of *S. mansoni*, and three pairs of large cells with acidophilic protoplasm for the cercaria of *S. haematobium*. Two other furcocercous forms were briefly described and figured, one longifurcate pharyngeal larva (see Manson-Bahr and Fairley 1920, Pl. III, Fig. 7) which appeared to them to be identical with *C. gladii* Cawston, and a brevifurcate form (see Manson-Bahr and Fairley, 1920, Fig. 5), which, although pigmented eye-spots were lacking, they held to be probably *C. bilharziella* Lieper.

Faust (1920), in a consideration of the pathological changes in the snail liver resulting from infestations with larval trematodes, noted the effects of several furcocercous forms, *C. quattuor-solenata*, *C. gigas*, and the cercaria of *Schistosoma mansoni*; the last two species were described as having two kinds of penetration glands, those which are basophilic and those which are eosinophilic. Cawston (1920) reported the presence of a schistosome larva for which he proposed the name *C. crispa*; no detailed description was given. The morphology and bionomics of *C. parvoculata*, *C. gladii* and *C. secobii* were briefly touched upon. Faust (1920a) discussed the criteria for the differentiation of schistosome larvae, recapitulating the most important morphological features and stressing the absence of those characters which had not yet been found in this group. The emphasis earlier placed by him (1918, 1919) on the parts of the developing genital system for the determination of relationships of cercariae was, for the human schistosome larvae, now placed on the number and character of the penetration glands. The distinction was made between the acidophilic or basophilic reactions of the protoplasm, its finely or coarsely granular nature, and the character of the nuclei. These glands were described and figured for the cercariae of *S. haematobium* and *S. mansoni.* The absence of the head-gland in these two species was also noted.

Scheuring (1920) in a preliminary account reported the experimental determination of the life history of *Sanguinicola inermis* Plehn. This is the first life cycle of a furcocercous cercaria, other than the three human schistosomes and *Schistosoma spindale,* to be worked out in detail. The infective agent was described as a brevifurcate monostome larva which resembled *C. cristata* La Val. St. George. In a survey of Cawston's incompletely described species of cercariae, Faust (1920b) designated *C. spinosa* and *C. crispa* as synonyms of the cercariae of human schistosomes, and *C. bilharziellalunata** as a synonym of *C. oculata.* Porter (1920a) briefly described the cercaria of *Schistosoma mansoni,* confirming Faust's (1919, 1920) findings of two differentiated sets of penetration glands, two pairs of large anterior cells and four pairs of small posterior cells, all opening through hollow spines which cap the ends of the ducts. *Planorbis pfeifferi* was now reported as the usual host, although *Physopsis africana* also harbors this cercaria. Cort (1921) studied the development of the cercaria of *S. japonicum* in mice; although the indications of sexual dimorphism of adult schistosomes have not yet been described in the cercariae, in this publication and in a subsequent discussion (1921a) on sex in the Schistosomatidae references were made to a species of schistosome cercaria with eye-spots, from Michigan, which exhibited size differences such that Cort interpreted them as sexual dimorphism.

In a paper describing a new blood fluke from turtles, Ward (1921) established the family Proparorchiidae and noted that its members are certainly related to the human blood flukes, Schistosomatidae. He also stated that the peculiar blood-inhabiting trematodes belonging to the genera Aporocotyle and Sanguinicola show evident morphological likenesses to the Proparorchiidae. Milton (1921), in a paper chiefly of medical nature, severely criticized the nomenclature which had been used by various workers in describing furcocercous cercariae. Kemp (1921) briefly described, from preserved materials only, *Cercaria* B and *Cercaria* C, two brevifurcate forms from Seistan; he also indicated the presence of a larva with extremely long furcae obtained in *Gyraulus euphraticus* in the Hamun-i-Helmand. Faust (1921) added caudal glands to his previous description of *C. quattuorsolenata.*

In a preliminary report of work dealing exclusively with furcocercous larvae of Brazil, Lutz (1921) stated that three new species were found to develop into members of the genus Strigea; for these larvae he proposed the names *Dicranocercaria mollascipeta, D. gyrinipeta,* and *D. bdellocystis.*

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* A private communication from Cawston makes clear that this species should be designated *C. bilharziellalunata* nom. nud.

Specific descriptions of them were not given. Soparkar (1921) minutely described the cercaria of *Schistosoma spindale* of India; this is the first account of its structure. Four pairs of flame cells were found in the body and one pair in the tail-stem, while the penetration gland equipment was found to consist of four anterior coarsely granular cells with acidophilic protoplasm, and six posterior in which the finely granular protoplasm is basophilic. A detailed table of comparison of the three human schistosome larvae, of the larvae of *S. spindale*, and of *C. indica* XXX was given; the most extensive summary yet made of the common characters of the human and animal schistosome larvae was also included. The term Schistocercaria was proposed for the furcocercous cercariae whose identity with adult schistosomes has been established. Soparkar (1921a) also described in detail four new furcocercous larvae from India. One of these, *C. bombayensis* no. 8, is especially interesting in that it appears to be a connecting link between the monostome and distome groups of the brevifurcate apharyngeal cercariae; development takes place in typical rediae which arise from small sporocysts. Details of the morphology of *C. bombayensis* no. 9, a pharyngeal distome larva, and of *C. bombayensis* no. 13 and no. 19, apharyngeal distomes, were presented, with figures showing the principal systems. Faust (1921d) described *C. octadena*, a brevifurcate pharyngeal distome larva, from preserved material, and added notes on another South African form, *C. secobii* Cawston 1915. In this paper he suggested that cephalic gland (Cort 1919) is a more suitable term than mucin gland (Faust 1918). Porter's (1921) studies on the larvae of *Schistosoma haematobium* and *S. mansoni* confirmed Faust's earlier work (1919a, 1920a) on the morphology of these forms, as well as her own previous findings (1920, 1920a). Yet a third genus of molluscs was said to harbor the cercaria of *S. mansoni*; a single infected specimen of *Isidora tropica* was found.

Khalil (1922) presented a structural analysis of the cercaria of *S. mansoni* based on a study of living material. His report of three pairs of flame cells in the body, together with two pairs of ciliated areas in the lateral excretory ducts, differs from most previous accounts; the larger numbers observed by other authors may be accounted for by the assumption that they have mistaken the ciliated areas for flame cells. Thus the excretory system pattern agreed essentially with that of the only other human schistosome larva for which it was known at that time, the cercaria of *S. japonicum*, according to Cort (1919). Khalil adopted Milton's (1921) designation of peri-acetabular glands for the penetration glands; a posterior set of three pairs was reported, although Faust (1919a, 1920a), confirmed by Manson-Bahr and Fairley (1920) and by Porter (1921), had described four posterior pairs; all agreed on the presence of two anterior pairs. Milton (1922), from an incomplete study of the literature, attempted to show that measurements could be used as the basis of diagnosis of the furcocercous cercariae.

The proposed system is too artificial; furthermore, he incorrectly took measurements from descriptions, assigned confusing specific names, and made misstatements concerning structures the original descriptions of which were clear. Bettencourt and da Silva (1922) described in detail the structure of the cercaria of *S. haematobium*, from snail hosts naturally infested in Portugal. Theirs is the first authentic accound and figure of the excretory system pattern which agrees essentially with that for the cercaria of *S. japonicum* by Cort (1919) and of *S. mansoni* by Khalil (1922).

Cort (1922) studied the escape of cercariae from their snail hosts, using *C. elephantis* emerging from *Planorbis trivolvis* for most of the data. Wide variation was found in the numbers escaping from different molluscs; temperature was shown to be a factor in the regulation of the number from any one snail. Furthermore, the cercariae of this species emerged in regularly recurring waves, once during the twenty-four hours, the time of the wave differing in different hosts.

Sewell (1922), as a result of comprehensive studies of the larval trematode fauna of India, described a large number of new species, of which fourteen were furcocercous forms; he included the first complete survey of all furcocercous cercariae. The lead of Lühe (1909) in considering separately the monostome (Lophocercariae) and the distome (furcocercous) forms was followed, and the composite nature of the latter group was clearly recognized. Practically all of the known furcocercous forms were considered; seven larvae, some of which were incompletely described, could not be included in his groupings. In considering the excretory system pattern he used formulae modified from those devised by Looss (1894:68), and used by Cort (1919b) in the description of a stylet cercaria. Further consideration of Sewell's classification is included in that section in the present paper. He also took up Faust's (1918:108) discussion of the distome larvae, in which a graded series of furcocercous cercariae in the family Schistosomatidae was recognized, from larvae with a muscular pharynx through those with a degenerate pharynx to the apharyngeal forms. This view was strongly contested as being too inclusive, practically making the terms furcocercous and schistosome synonymous. In addition to detailed descriptions of fourteen new furcocercous cercariae, Sewell described the miracidia of *Schistosoma haematobium* and of *C. indica* XV; he found that the sporocysts producing this latter species have in addition the remarkable power of giving rise to miracidia. He discussed the value of the excretory system pattern in the miracidium and in the sporocyst and redia, and used these data in his tables showing relationships between the various subgroups of monostome and distome larvae. In discussing the line of evolution and development of the furcocercous forms, he presented data to show that the Lophocerca and the Lophoides groups of monostomes are closely related to his Groups 1 and 2, respectively, of the distome larvae, and that within each of the distome groups the sub-groups could be arranged in progressive series. Unfortunately, these gradations are in part based on errors, due to incomplete and incorrect details of descriptions of other authors.

Kobayashi (1922) reviewed the accounts of the cercariae from Japan, Formosa and Korea which had been published in the Japanese language; brief descriptions of the furcocercous forms were given, one of them new. No specific names had been ascribed to most of these, although the original authors had designated them by numbers or letters. Kobayashi renamed the ten species by letters from A through J, and gave sketches for three of them. Ruszkowski (1922), in a study of the life history of *Hemistomum alatum*, very briefly described the longifurcate distome cercaria which he obtained from experimentally infested snails. Scheuring's (1922) complete report of the life history of *Sanguinicola inermis* described in greater detail the brevifurcate monostome cercaria, whose identity with *C. cristata* is held by him to be doubtful; the excretory system pattern was not reported. Cawston (1922c), in a note on the differentiation of certain schistosome cercariae, suggested the probable synonomy of *C. crispa* Cawston with the cercaria of *Schistosoma haematobium.* The report of Bettencourt and Borges with de Seabra and da Silva (1922), on the study of schistosomiasis in Portugal, included a description of the cercaria of *S. haematobium* and a discussion of the nomenclature of furcocercous larvae. They found what was thought to be a head gland; Faust (1920a) stated that this organ is present only in the cercaria of *S. japonicum* among the human schistosomes. Brumpt (1922) incidentally mentioned a furcocercous larva, closely allied to *C. fissicauda*, as being the larva of a holostome of the genus Tylodelphis.

Faust (1922a) described in detail *C. leptoderma*, a larva which has the same type of excretory system as has *C. vivax*. This new species is the first furcocercous larva in which the development of this system, including the number of flame cells, has been followed from its first appearance in the germ ball to the stage of development found in the mature cercaria; the observations of Looss (1896) on *C. vivax*, while otherwise complete, did not make clear the numbers and arrangements of the flame cells. On either side of the elongating germ ball of *C. leptoderma* the division of the single flame cell establishes the fundamental anterior and posterior groups, $\alpha+\beta$; then follows a trichotomy of both α and β elements, followed by a trichotomy of each of the resulting cells, which results in eighteen flame cells on either side of the mature cercaria. The complete formula was taken as $(\alpha)^2+(\beta)^2$, with three indicated as the factor to represent two successive trichotomies.

In a preliminary publication on the development of trematodes of Brazil, Lutz (1922) reported having observed a dozen species of furcocercous larvae, many of which he found to belong to the holostomids, with at least one schistosome. Faust and Meleney (1923) published a brief summary of their work on the life history of *Schistosoma japonicum* which later (1924) appeared in an extensive monograph. Tanabe (1923) described a furcocercous cercaria which he found to develop in experimentally infected mice into a new schistosome, to which he assigned the name *Schistosomatium pathlocopticum*. The larva, which is an apharyngeal brevifurcate distome, very closely resembles *C. douthitti* in general appearance and proportions, and agrees with it in the details of the excretory and digestive systems; it has only three pairs of penetration glands, whereas *C. douthitti* has five pairs. Infection of mice was shown to be through penetration of the skin by the cercariae.

Lagrange (1923), in a study of larval trematodes from Indo-China, described two furcocercous cercariae; no specific names were given and there are no figures. One species, Schistosoma?, is a distome and is probably apharyngeal; from the measurements given, it is a longifurcate cercaria, and none of the human schistosomes are longifurcate. The other larva is a brevifurcate distome, but there is no indication whether a pharynx is present; it is one of the few furcocercous larvae which develop in rediae. Miller (1923), in a publication preliminary to the present paper, described seven new species of North American larvae, two apharyngeal brevifurcate distomes, and five longifurcate forms, probably all pharyngeal, of which two were monostomes. A classification of the apharyngeal and pharyngeal brevifurcate distomes was presented; a key, based largely on data obtainable only from living cercariae, was given to separate the groups. Stunkard (1923) described a number of new blood flukes from turtles and discussed the relationships of the Aporocotylidae from fishes, the Spirorchidae from turtles and the Schistosomatidae from birds and mammals. He came to the conclusion that the blood flukes constitute a natural group. The larvae of some, and presumably all, members of the first and last families are furcocercous cercariae, and in view of other similarities it might be expected that the Spirorchidae would also develop from apharyngeal furocercous larvae.

McCormick (1923) studied the larval trematode parasitization of seven species of fresh water snails from Ohio. He reported finding *C. echinocauda* and *C. gracillima*; the present author, from an examination of mounted material, believes that the identification of the latter species is doubtfully correct. Hesse (1923) described in detail a furcocercous cercaria from *Lymnaea peregra* in Scotland. No specific name was given; the larva is a pharyngeal, longifurcate distome, with seven pairs of flame cells in the body and two pairs in the tail-stem; there are four penetration gland cells. Soprakar's (1924) detailed description of a unique furcocercous form from India shows it to be an apharyngeal distome larva in which the genital system is much more highly developed than in any previously reported form; testes and ovary are present and active spermatozoa were found. The excretory system is highly developed, with forty flame cells around the margin of the body; the capillaries were not traced. The tail-stem is unique in the presence of two short cross arms, proximally located; three pairs of flame cells empty directly into the caudal excretory tube. The intestinal ceca are united in the posterior part of the body. Development of this species takes place in rediae.

Szidat (1924) described three pharyngeal longifurcate distomes from Prussia; they were not given specific names, but were designated as *Cercaria* A, *Cercaria* B and *Cercaria* C. The question of the identity of *Cercaria* B and *C. gracilis*, and of *Cercaria* C and *C. letifera*, *C. furcata* and *C. fissicauda* was raised by Szidat, who felt that the incompleteness of the earlier descriptions made a decision impossible. Following penetration of *Cercaria* A into *Lymnaea palustris* and its migration to the hermaphrodite gland, its development into *Tetracotyle typica* Diesing was traced and several stages were figured. This is the first demonstration of the post-larval development of a pharyngeal furcocercous cercaria, although the preliminary report of Lutz (1922) indicated that similar results had been obtained with three South American forms.

Faust and Meleney (1924) published a large monograph on oriental schistosomiasis, in which the results of their extensive studies from both the medical and zoological aspects were presented. They reported the results of much experimental as well as observational work which they had carried out on different phases of the life cycle of *Schistosoma japonicum*, and included a valuable review of the important literature, most of which had hitherto been practically inacessible, since it is in Japanese. Their most important contribution to the knowledge of the cercaria is a study of the excretory system development in five stages, α–ϵ, of the schistosomulum. It was found that the loss of the tail-stem flame cells is compensated by the early division of the other flame cells draining into the posterior collecting tubules. In the γ stage a division of each of the flame cells has taken place, so that there are eight in either lateral half of the body; a further dichotomy has taken place in the ϵ stage, resulting in a total of thirty-two flame cells for the entire body. These stages show the method of systematic elaboration of the flame cell pattern in the cercaria to the excretory system of at least the young worm, and presumably on to the adult schistosome. This is the first record of excretory system development in a number of the post-larval stages of a furcocercous cercaria. Faust (1924), in a further study of larval flukes from China, described three furcocercous forms, *C. pseudovivax*, *C. divaricata** and *C. gigantea*. The first two are pharyngeal longifur-

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* This larva is listed in his Table I, page 296, and in Table II opposite page 298 as *C. divaricauda*; the specific description on page 256 is headed *C divaricata* nov. spec.

cate larvae; although the alimentary canal of *C. gigantea* is unknown, in other respects it rather closely resembles *C. bombayensis* no. 19, and is probably apharyngeal. It is surprising that the three new larvae are included under the family Schistosomatidae, especially the two which have definite pharynges; it would seem that Faust has not taken cognizance of the work of Ruszkowski (1922) and Lutz (1922) on the life histories of holostomes, all of which, so far as known, have furcocercous pharyngeal larvae. Faust also considered all previous descriptions of larval trematodes from the Sino-Japanese regions, and assigned specific names to the cercariae reviewed by Kobayashi (1922). The most important part of the paper deals with the systematic grouping of larval and adult trematodes; this will be discussed in detail in this paper under the heading of Classification.

Miller (1924) studied *C. douthitti* and showed that it has most of the typical characters of the schistosome larvae; Cort's description was emended in certain particulars. Studies on co-type material of *C. echinocauda* showed that a very large posterior cell mass of unknown function is present, as are two differentiated sets of penetration gland cells; a head gland and an alimentary canal similar to that of *C. elvae* were also described. Similarities of *C. echinocauda* with *C. elephantis* were noted. Blacklock and Thompson (1924) described the cercaria of *Schistosoma haematobium* from both living and preserved material obtained from *Physopsis* cf. *globosa* in Sierra Leone. Their account differs strikingly from the descriptions of Faust, of Bettencourt and da Silva, and of Bettencourt, Borges et al in the number and character of the penetration glands. Instead of three pairs of similar glands, they report two pairs of large anterior cells containing coarsely granular protoplasm, and three pairs of smaller posterior cells which are finely granular. Except when overwhelmed with stain, the anterior cells are eosinophilic, and the posterior are basophilic to Ehrlich's hematoxylin; "the results obtained by staining were, however, not constant, even in fully developed cercariae." (p. 218). These authors critically surveyed the descriptions of the three human schistosome cercariae and severely attacked the work of Faust on the cercariae of *S. haematobium* and *S. mansoni;* they have either not seen or have ignored the work of Manson-Bahr and Fairley and of Porter which confirmed Faust's descriptions (in details) with respect to gland numbers in these two species. In support of their view that they are dealing with the cercaria of *S. haematobium* is the epidemiological evidence of the presence of the urinary schistosomiasis of this trematode and the absence in Sierra Leone of the intestinal type caused by *S. mansoni.* Furthermore, they found this cercaria in no other host than Physopsis sp., the genus in which the larva of *S. haematobium* in Africa has usually been found. They also reported the recovery of adult males morphologically identical with *S. haematobium,* from guinea pigs and monkeys experimentally infected with the cercaria described.

Their account of the experimental infection of *Physopsis* cf. *globosa* with miracidia, hatched from terminal-spined eggs from the urine of an infected case, is less conclusive, fifteen days, judging from the life history of *S. japonicum*, is much too short a period for the development of the miracidium through the parthenogenetic generations to mature emerging cercariae. Only nine snails were used, and of these three were later found to be infected; the statement that "controls which were dissected did not show any infections" does not indicate the number used. It seems likely that the three experimental snails harbored natural infections which, in one case, resulted in emerging cercariae on the fifteenth day. These cercariae developed in monkeys into adult males of *S. haematobium*.

In a short paper written after studying Khalil's (1922) description of the cercaria of *S. mansoni* and the account of the cercaria of *S. haematobium* by Bettencourt and da Silva (1922), Blacklock and Thompson (1924a) discussed the close morphological correspondence of their species with that described by Khalil from Egypt as the cercaria of *S. mansoni*. On the contrary, there is variance with the description of the cercaria of *S. haematobium* (Bettencourt and da Silva) from Portugal. Blacklock and Thompson conclude that if the glands of the cercaria of *S. japonicum* are constantly of one type this species may be differentiated from the other schistosome larvae; but that the cercariae of *S. haematobium* (as described by them), of *S. mansoni* (according to Khalil), and *C. indica* XXX are without significant morphological differences. They discuss the possibility of classification by intermediate host; the only well established case of the cercaria of *S. haematobium* in a mollusc genus other than Physopsis (Bullinus), that of Bettencourt et al in which *Planorbis metidjensis* in the sole carrier in Portugal, seems to them to make it impossible to identify the human cercariae by this means. This view is supported by the work of Porter (1920a, 1921), apparently unknown to them, in which the cercaria of *S. haematobium* in South Africa was found in both Physopsis and Lymnaea, and the cercaria of *S. mansoni* was found in Physopsis and in Isidora as well as in the usual host Planorbis.

METHODS OF INVESTIGATION

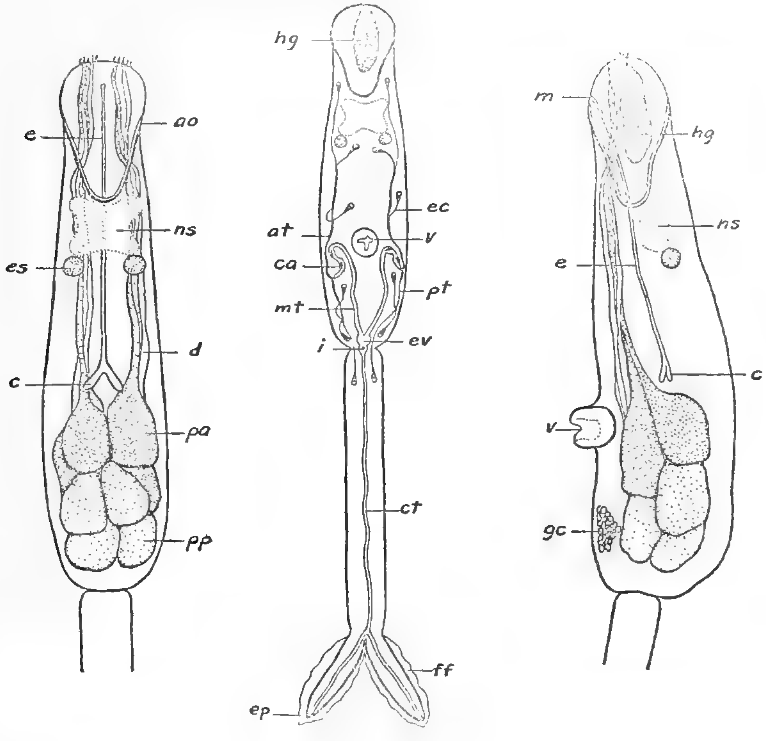
The emphasis laid upon the study of living material by Cort, Faust, Soparkar, Sewell and others is well placed, and the essentials of the method as outlined by Cort (1918c, 1919, 1922) were followed by the author in the study of the structure of all forms. At the beginning of the investigation in 1920 all snails of a collection were crushed to obtain the cercariae and parthenitae. The limitations of this method led to the adoption of the isolation of snails; this was done in suitable glass vials in a small amount of water; if mature cercariae are present they usually emerge from the body of the snail within twenty-four hours and may be detected easily with the naked eye, or with a hand lens. By transference to a small aquarium the infested snail may be kept alive for some time, and a supply of living mature cercariae is made available by periodic confinement to a small amount of water in a vial. The exact percentage of infestation was determined by crushing all snails from which larvae were not emerging after forty-eight hours' isolation. For the preparation of total mounts the mature cercariae were fixed by pouring them into a large amount of warm fixing fluid; Gilson's mercuro-nitric, corrosive-acetic, saturated aqueous corrosive sublimate, and Bouin's fluid were used. Only such material was the basis of the measurements recorded.

When no more living cercariae were needed, the snail was crushed and a portion of the infested tissue was carefully dissected, and the young stages and living parthenitae were studied; permanent mounts of these were also made. The study of immature larvae is an important phase of the work on structure, as certain parts are relatively more easily seen than in mature larvae. A portion of the infested organ, which is usually the digestive gland, was fixed for sectioning. Sections were cut four to five μ in thickness, and stained with various standard stains. The mounting media employed were Canada balsam and, for total mounts, white or green Diaphane. Studies were also made of temporary mounts in various oils, and in glycerine and glycerine-and-water media, in order to secure different refractive indices. Intra-vitam staining with neutral red proved very useful in the definition of certain glands and organs, and in inhibiting the activity of the larvae.

NOMENCLATURE

The lack of agreement in the nomenclature of certain organs in the furcocercous cercariae makes it desirable to establish uniformity for future descriptions. A brief account of structure is presented here, based on an apharyngeal brevifurcate distome larva (Text-fig. 1); the various departures from this type which are found in the different groups are included in the discussion.

The structure here designated as anterior organ (*ao*) is a modified oral sucker, which Sewell (1922) called the anterior protrusible penetrating organ. Its poor powers of attachment, and the difference in the mechanism of ventral sucker (*v*) and anterior organ have been recognized by a number of investigators, although many recent ones retain the term oral sucker. The organ is differentiated into a thin-walled anterior part and a thicker walled posterior part in the brevifurcate larvae; this differentiation is lacking in many of the longifurcate forms. However, the anterior organ seems always to be protrusible and invertible, and represents an oral sucker modified for penetrating tissues. Cort (1919:498) is followed in the use of head gland (*hg*) for the group of cells designated by Narabayashi as Kopfdrüse, which are dorsally located within the anterior organ. As this structure has no connection with the mouth, the term oral gland proposed by Khalil (1922) is not suitable. The head gland is present in most known schistosome larvae, and possibly in all other brevifurcate forms. In several longifurcate larvae two or more cells, similarly located, have been reported; the author suggests no term for these cells; they can not be designated properly until it is known whether they are homologous with the head-gland of apharyngeal brevifurcate cercariae.



Text-fig. 1

The oral cavity is seldom more than a capillary tube through the anterior organ. An esophagus (*e*) and a single cecum, or pair of ceca (*c*), constitute the remainder of the simple alimentary canal. In the majority of longifurcate larvae and in three brevifurcate forms, there is a pharynx at a variable distance behind the anterior organ; in these cases, following the nomenclature for adult trematodes, the portion of the alimentary canal between the pharynx and the anterior organ is called the prepharynx.

A pair of pigmented eye-spots (*es*) may be in connection with the nervous system (*ns*); these are called simple eye-spots when they are composed of a small, but varying, number of pigment granules of different shapes and sizes, and compound eye-spots when there are numerous uniformly fine granules, arranged as a cup within which may often be seen a lens. Unpigmented eye-spots have been reported.

The large unicellular glands, usually in the middle and posterior parts of the body, have been variously designated as salivary, poison, cephalic, digestive, mucus, mucin, salivary-mucin, peri-acetabular and secretory glands. In one group (Vivax) they are located only toward the anterior, and even within the anterior organ. The confusion caused by this multiplicity of terms has been considered by Sewell, who adopted salivary gland, first used by Ssinitzin (1911) for *C. discursata*. The author does not consider this a suitable designation, as the term salivary gland has, in all groups of the animal kingdom, been used in connection with the alimentary canal. Neither is the frequently used term cephalic gland satisfactory, as it would seem to imply an anterior location, and also it is too similar to head gland, which signifies an altogether different structure; mucin gland implies a definite chemical nature, and it is not certain that mucin is present in these cells. All evidence shows that these glands are concerned with the dissolution of host tissue; in the mammalian schistosomes and in certain holostomes a number of authors, including Faust and Meleney, and Szidat, have demonstrated that these glands disappear soon after penetration of the skin of the definitive or intermediate host, and chiefly for this reason the present author has designated them as penetration glands. This term most nearly expresses the known function of the glands, and does not refer them to any definite position within the body; their location varies considerably in the different groups of furcocercous cercariae. In the brevifurcate distome larvae there may be a differentiation of the penetration glands into two sorts: anterior coarsely-granular glands (*pa*) which are oxyphilic in sections, and posterior finely-granular glands (*pp*) which are basophilic.

Various authors have designated as either ovary or testis the mass of germ cells (*gc*); it does not seem safe to venture a prediction as to the adult organ represented, except where the rudiments of all parts have been recognized, as by Faust (1918) in *C. gracillima*.

The nomenclature for the parts of the excretory system has been compiled from that used by Looss, Cort, Faust and Sewell. The posterior median bladder, or excretory vesicle (*ev*), has two lateral arms which may pass anteriorly with gradually diminishing caliber or which may be tubes of uniformly much smaller diameter than is the excretory vesicle itself. Cort considers these lateral arms as parts of the bladder, while Faust, Soparkar and Sewell have desingated them as main collecting tubes, main excretory tubes, and main lateral collecting tubes (*mt*); Sewell's usage of the latter term has been accepted here. Into each main lateral collecting tube there usually pours an anterior collecting tubule (*at*) and a posterior collecting tubule (*pt*). Further subdivisions into capillary tubules (*ec*) lead to the flame cells. The Vivax group, the members of which have a highly developed excretory system, have, in addition to the lateral collecting tubes, a median collecting tube which joins with a branch from each of the laterals at its anterior end, and which divides toward its posterior end before entering the excretory vesicle (see *C. leptoderma* in Faust, 1922a). In some cercariae there are cilia in one or two places in the main lateral collecting tubes; the term ciliated area (*ca*) has been used in describing these (Cort, 1919). Although, as figured by different authors, the cilia may be in a compact tuft or may project independently into the lumen (in the cercaria of *Schistosomum japonicum* only, as figured by Cort, 1919), this term may be used to designate either type of ciliation. It may be noted here that these structures are seen only in the instant before a cercaria goes to pieces due to cover glass pressure. At the junction of body and tail, the excretory vesicle joins the caudal excretory tube (*ct*), usually with a small protoplasmic island at the place of union. The studies of Looss (1896) on the development of *C. vivax* revealed this as a remnant of the embryonic paired condition of the caudal excretory tube; Faust (1917) termed it an eyelet anastomosis, and later (1919c) the island of Cort (*i*), which latter designation the present author has used.

In some species the bifurcations of the tail are less than one-half the stem length, while in others they are equal to and in some cases longer than the tail-stem; both the pharyngeal and the apharyngeal larvae are subdivided partly on this basis into brevifurcate and longifurcate groups. The caudal excretory tube bifurcates with the tail, and in brevifurcate larvae the branches open at the tips of the furcae (*ep*); in other cases the openings are somewhere along the edge, usually midway of the furcae. In some cercariae the furcae may be laterally flattened, and in addition provided with a dorso-ventral extension of the cuticula; this furcal fin-fold (*ff*) may be narrow or wide, and in the latter case it is usually fluted. It has also been called cuticular keel and paddle edge.

DESCRIPTION OF SPECIES AND COMPARISON WITH RELATED FORMS

APHARYNGEAL BREVIFURCATE DISTOME CERCARIAE

CERCARIA ELVAE MILLER 1923

[Figs. 19-28, 38-42]

Host, *Lymnaea stagnalis* var. *appressa*
Locality, Douglas Lake, Michigan (Hook Point and Bessey Creek)
Occasion, twice, in July and August, 1921

This cercaria is similar to those of the family Schistosomatidae in a number of characters. It is most closely like *C. bombayensis* no. 19, which was found once in *Lymnaea acuminata* from Bombay by Soparkar (1921a: 30), who noted that it probably belonged to the "Bilharziella" group of cercariae. The description of *C. ocellata* La Val. St. George which was given by Ssinitzin (1909:314), although incomplete in some important details of the excretory system, indicates close relationship of *C. elvae* to this form also. *C. gigantea*, recently found by Faust (1924) in China, is most closely similar to *C. bombayensis* no. 19.

The behavior is strikingly like that of the larvae of the schistosomes which have been studied in this particular. The emerged cercariae sink slowly through the water with body down and furcae 60° to 80° apart, and with tail-stem generally straight; occasionally the body is somewhat recurved upon the tail. Swimming is effected by a rapid lashing of the tail, with either body or tail in advance; the latter is more frequent. Both beginning and cessation of locomotion are abrupt and the direction is usually erratic; there is probably less locomotion in a straight line than Soparkar (1921) reported for the cercaria of *Schistosoma spindale* and the author found in *C. wardi*. The inchworm locomotion described for the cercariae of *Schistosoma japonicum* by Cort (1919) and of *S. spindale* was observed in numerous specimens of *C. elvae*; under a cover glass it takes place as follows: after extension of the body, the anterior organ takes hold of the substratum, the body is contracted, and the posterior part is rotated through about 80°; the ventral sucker, which therefore protrudes laterally, is placed beside the anterior organ and takes hold of the substratum; the attachment of the latter is now released, and the series of movements is repeated. The intermittent lashing of the tail which occurs is not definitely correlated with either extension or contraction of the body. After decaudation, which takes place easily in this species, the animal is able to progress by the method just described, but not so readily as before. Sewell noted for *C. indica*

XXX, apparently a true schistosome, that there was a marked tendency to shed the tail while under observation. This organ, when detached, continues in erratic locomotion for some time. When the larva is at rest, or practically so, the furcae are often held at right angles to the tail-stem.

There are several additional points of behavior under a cover glass to be noted. The animal takes hold of the substratum with its anterior organ and makes slow, jerky movements of the body; or body and tail are held in a straight line, somewhat rigid, and then rapidly bent in the middle to one side and the other several times. Often there are rapid vibrations of the tail, such that the animal is spun around on the anterior organ as a pivot; less frequently, the ventral sucker is attached and acts as the center of turning through an angle of less than 180°, but, due possibly to the large size of this form and consequent greater pressure of the cover glass, there is no complete spinning about, such as was reported by Cort (1915:50) for *C. douthitti* from *Lymnaea reflexa*, and has been observed by the present author for the same form from *L. stagnalis* var. *appressa* when studied under a cover glass.

Sizes under various conditions are: maximum extension when living, body 368 μ by 80 μ, tail-stem 501 μ, furca 328 μ; well-extended specimens mounted in Canada balsam (average), body 368 μ by 41 μ, tail-stem 382 μ, furca 290 μ. Although both *C. bombayensis* no. 19 and *C. ocellata* are larger than *C. elvae*, the proportions in length of body, tail-stem, and furcae remain practically constant; the tail-stem is somewhat longer than the body, which in turn is longer than the furcae. *C. gigantea* is smaller than any of these three.

C. elvae is very transparent; the deeply pigmented eye-spots stand out in sharp contrast to the hyaline body of the living animal, and the thick ducts of the penetration glands are very prominent structures, especially from the region of the eye-spots forward and through the anterior organ. The spindle-shaped body tapers more gradually from the ventral sucker toward the anterior end than toward the posterior; it is the contraction and extension of the anterior part of the body which cause the great changes in length. Because of the protruding ventral sucker a frontal mount is difficult to obtain, and the cercaria is usually seen lying on its side, in which position practically all observations must be made.

The entire surface is evenly and finely spined; Soparkar showed a like condition for *C. bombayensis* no. 19. For *C. ocellata*, sensory hairs were reported on the body and ends of the furcae; it is possible that Ssinitzin mistook the flutings of the furcal fin-folds for hairs, as O'Roke did later on *C. echinocauda* (1917); the latter error was corrected by Faust (1918a). *C. gigantea* is spined on body, tail-stem and furcae.

The anterior organ is large, and occupies the entire anterior third of the body; the length in mounted specimens averages 96 μ. Its shape is pyriform in the living animal, with the small end posterior (Fig. 22), and elongate-oval or dumb-bell shape in mounted cercariae. The walls of the posterior part are strongly muscular (Fig. 28) as in the known schistosome larvae, and as in *C. ocellata* and in *C. bombayensis* no. 19. The anterior part is thinner (Fig. 26), especially toward the foremost part which is, as Cort reported for the cercaria of *Schistosoma japonicum*, in direct contact with the cuticula (Fig. 27); the same condition is present in *C. ocellata* and *C. bombayensis* no. 19. The head gland is conspicuous in the anterior organ; its size varies, but it never extends far into the posterior muscular part. It appears coarsely granular in the living animal and is strongly eosinophilic in sections. Ssinitzin observed in *C. ocellata* what was probably a head gland; such an organ is present in *C. bombayensis* no. 19 and in *C. gigantea*. Whether it consists of one cell or many has not been definitely determined. Large nuclei are seen in both total mounts and sections; it could not be observed whether they are enveloped by the head gland wall or merely pressed against its surface. Cort noted for the cercaria of *Schistosoma japonicum* that "a layer of large nuclei surround the gland and are evidently a part of it." Soparkar, in his description of the larva of *S. spindale*, was less confident of the relations, and stated that "it is surrounded by several nuclei, but these do not seem to be a part of the gland." The opening is on the extreme anterior end, slightly dorsal.

The ventral sucker is prominent; it has a diameter of about 33 μ in living larvae and averages 23 μ in specimens mounted in Canada balsam. There are at least two sets of muscle fibers: circular ones are especially prominent around the non-nucleated distal part (Fig. 21), while powerful bands radiate from the proximal region to parts of the dorsal side of the body, where they are inserted. These bands are very clearly seen in the living animal and are more striking structures in this cercaria than in any other form observed by the author.

The powerful tail is attached terminally to the body; it is about as wide as the body at its proximal end and diminishes slightly toward the end where the two furcae arise. These are not so sharply delimited as in the larvae which are known to be true schistosomes, but represent an intermediate condition between them and the longifurcate forms. The furcae of *C. ocellata* are shown with constrictions at their bases by both La Valette St. George and Ssinitzin; Soparkar does not so figure them for *C. bombayensis* no. 19. There are four large bands of longitudinal muscles, and two small ones which apparently consist of but one fiber each (Fig. 23). The furcae are somewhat laterally compressed.

The eye-spots of *C. elvae* are compound; each is a cup, composed of fine brownish granules, within which a lens is found (Fig. 39). The average measurements are 8 μ wide and 5 μ deep, and the greatest diameter of the protruding lens is about 5 μ. It is evident that the same type of eye-spot is present in *C. bombayensis* no. 19; Ssinitzin's account for *C. ocellata* is not absolutely clear on this point; Faust described a pair of pigmented eye-spots in *C. gigantea,* as well as pigmentation on the body.

The type of alimentary canal is similar to that found in the schistosomes, with a small ventral mouth, a capillary esophagus through the anterior organ (Fig. 28), penetrating its wall in the posterior median region, and continuing (Fig. 41) to bifurcate into short ceca. In the cercariae of *Schistosoma japonicum* and *S. spindale* the ceca are represented as heart-shaped, somewhat variable; at the most they are short dilated diverticula. In both *C. elvae* and *C. ocellata* they are short and straight (Fig. 20), differing only in length from those of *C. bombayensis* no. 19, in which they are curved partly around the ventral sucker, terminating at about its middle. The difficulty of observing the presence of the mouth and oral tube, especially in preserved material, is considerable, even with a magnification of 1380 diameters; Ssinitzin noted the same difficulty in *C. ocellata.* Faust was unable to find an alimentary canal in *C. gigantea.* No trace of a pharynx is found in any of these forms.

The main part of the nervous system is represented by a bilobed mass which lies just anterior to the eye-spots, in connection with it (Fig. 19). In *C. bombayensis* no. 19 two large lobes lateral to the penetration gland ducts were observed, without a cross-connection; in *C. elvae* the penetration gland ducts of each side pass directly under the ganglionic mass (Fig. 41). These ducts are median to the lobes of the nervous system also in the cercariae of *Schistosoma spindale* and of *S. japonicum.*

The penetration glands occupy a great part of the body, almost the entire posterior half of *C. elvae,* and even a considerably greater portion of *C. ocellata.* Furthermore, there is a definite distinction in each between an anterior and a posterior group of cells. On the contrary, these glands in *C. bombayensis* no. 19 and *C. gigantea* are less prominent structures, and no distinction of two sets is shown. Under low magnification, the body and tail of *C. elvae* are transparent, and slightly yellow in color, with the exception of the greater part of the body posterior to the ventral sucker, which is a clear light gray. Around the ventral sucker there is a yellow, more granular area representing the anterior set of penetration glands (Fig. 25). The number and relation of the cells within each group are not easily determined in the living animal, due to their transparency and contiguity, and it is only under magnification of about a thousand diameters that the outlines are visible. There are three pairs of clear grayish glands in the posterior part of the body and two pairs of circum-acetabular glands with more granular contents; of the latter one is anterior and the other posterior to the ventral sucker. In unstained specimens mounted in Canada balsam the grayish glands become very dark and stand out in marked contrast. The ducts from these five pairs of cells run forward in a bundle on each side, most prominent just anterior to the eye-spots. In lateral view of the living animal there are two yellow granular ducts from the anterior cells, dorsal to an apparently single transparent grayish duct; this latter is composed of three which drain the posterior cells (Fig. 39). Both cells and ducts of the two groups differ in staining reactions; the posterior take a very deep stain with Delafield's hematoxylin and then appear coarsely granular; the anterior are practically chromophobic to both hematoxylin and the eosins, and the greater part of the contents appears to have been discharged, or dissolved out at some stage in the preparation.

C. ocellata and *C. elvae* are not quite identical in their penetration gland equipment; the fact that *C. bombayensis* no. 19 and *C. gigantea* have only one set of four pairs of similar cells does not, in view of other characters, preclude their being placed with these two. For, among the larvae which are known to be schistosomes, the cercariae of *Schistosoma japonicum* and *S. haematobium* were described as having only one group of acidophilic glands, while Faust (1920a) showed that even in the immature larva of *S. mansoni* two sets have been differentiated, the anterior composed of four coarsely granular acidophilic cells, and the posterior of eight, smaller and basophilic. Soparkar definitely described the ends of the penetration gland ducts in *C. bombayensis* no. 19 as being capped with hollow piercing spines; in *C. elvae* spines are present, but whether they are hollow was not definitely determined. Ssinitzin did not record their presence in *C. ocellata*, and Faust made no mention of them in *C. gigantea*.

The details of the excretory system were worked out in the living animal (Fig. 20). There are six pairs of flame cells in the body; three on each side empty into the anterior, and three into the posterior collecting tubule. There is a seventh pair in the proximal region of the tail-stem. There is practical identity with *C. bombayensis* no. 19, with only minor differences such as locations of flame cells and length of tubules. The excretory vesicles are of the same type; and an island of Cort is present at the junction of body and tail. The caudal excretory tube bifurcates at the origin of the furcae, each branch passing to the tip. The bulbous expansions which project beyond the furcal tips in *C. bombayensis* no. 19 are absent in *C. elvae* (Fig. 24). The main collecting tube in the latter is more nearly an arm of the excretory vesicle, and its lateral bending is more anterior; just before giving off the anterior and posterior collecting tubules there are two dilations, in each of which is found a ciliated area. The details of the excretory system n *C. ocellata* were not completely worked out by Ssinitzin; he noted seven pairs of flame cells and a small pear-shaped excretory vesicle. Unfortunately the flame cells were not shown in the figures to which he referred, and the text statement appears to have escaped the notice of Sewell, who assumed an excretory system similar to that of *Cercariae indicae* XXV and XXXVI and established an "Ocellata" group to include the three forms.

The group must be set aside and other disposition made of the members. The excretory system in *C. gigantea* was not completely analyzed.

The principal mass of cells which in part represents the reproductive system of the adult is located posterior to the ventral sucker. A similar mass was shown in *C. ocellata*, *C. bombayensis* no. 19 and *C. gigantea*. It has not been possible to trace definitely other scattered germ cells in *C. elvae*.

The two snail hosts both died and disintegrated during the author's enforced absence from the laboratory, so that the description of the parthenitae of *C. elvae* is lacking. One of eight large specimens of *Lymnaea stagnalis* var. *appressa* collected in Hook Point Cove, Douglas Lake, Michigan, on July 8, 1921, was infected; the second host was in a collection of twenty-three snails of the same species and variety from Bessey Creek on August 4, 1921.

CERCARIA WARDI MILLER 1923

[Figs. 29–37, 43–45, 50–54]

Host, *Planorbis trivolvis*
Locality, Urbana, Illinois (old stream bed and pool)
Occasion, three times in April, 1921

This cercaria is less like the members of the schistosome group than is *C. elvae*. The forms which it resembles most closely are *C. bombayensis* no. 13 and *C. indica* XXV. All three possess a unique posterior gland, which in *C. wardi* reacts in such a way as to make it probable that the contents are of a mucin nature (Mathews, 1920:323; Hawk, 1921:112); the other two have not been examined in this regard.

This larva is readily visible to the naked eye when swimming about in a small glass container; although quite transparent, the rapid vibration makes it seen even in somewhat turbid water. The general type of spasmodic, intermittent locomotion common to most of the furcocercous cercariae is found; however, *C. wardi* has not been observed to swim with the tail forward. While sinking through the water, the tail is usually bent around so that the animal has, with variation, the shape of a horse-shoe. When cercariae have freshly emerged from the snail, the touching of any surface is sufficient to initiate rapid darting movements. Sometimes they creep upon the bottom, attaching alternately the anterior organ and the ventral sucker; this method of locomotion is not frequently employed, although fairly rapid progress can be made. When cercariae are kept in a stender dish for some hours, the periods of quiescence upon the bottom become lengthened; in the great majority of cases the animal is curled about, varying from a wide horse-shoe to a form in which the anterior end of the body lies upon some part of the tail. Often the furcae project upward; when they, or any part, are touched with a needle or by another swimming cercaria, rapid locomotion is resumed. This is effected by rapid vibration of the whole animal, especially of the tail; however, progress does not necessarily accompany vibration; there is a node at the origin of the furcae and another at the junction of body and tail, and when the anterior organ is attached there is a third node at this point.

Some simple experiments on viability were carried out. An infected snail was placed in a small stender dish containing water of the stream in which it had been found; after about twenty cercariae had emerged, the snail was successively placed in stender dishes filled with tap water and with distilled water, and each was covered with a ground glass top. Observations were made several times daily. At the end of nine hours all the cercariae in distilled water were dead, and fifty per cent were decauded. At the end of two days those in stream and in tap water appeared to be normal; dead animals were observed for the first time on the morning of the third day. Some were alive at the end of four days, although none lived much longer. It is quite evident that their viability is very low in distilled water, and it would seem that emerged cercariae may be kept equally well in stream or tap water. It is possible that under more favorable conditions the length of life of some individuals after emergence might be considerably greater than four days. In this connection it may be noted that the human schistosome larvae are generally said to survive about forty-eight hours after emergence.

Sizes under various conditions are: maximum extension of a living cercaria, body 467 μ, tail-stem 730 μ, entire tail 935 μ; well-extended specimens which had been mounted in Canada balsam for two years (average), body 243 μ by 69 μ, tail-stem 564 μ, furca (to extreme tip of fin-fold) 202 μ; unstained cercariae recently mounted in Canada balsam (average), body 265 μ, tail-stem 682 μ by 50 μ, furca 273 μ. Body width is not easily determined, due to the irregular outline presented; in occasional specimens which showed a dorsal view in the freshly mounted material the body averaged 75 μ wide. *C. wardi* is somewhat smaller than either *C. bombayensis* no. 13 or *C. indica* XXV, but in all three the proportions of body to tail-stem to furcal length are practically identical.

There is a prominent ventral sucker, located somewhat posterior to the middle of the body; it almost always protrudes decidedly, and therefore a lateral view is the one usually obtained under a cover glass. Its greatest diameter measures 28 μ; when completely everted, it has a rounded cone-shape (Fig. 34), and a cap of small spines extends about 20 μ back from the tip. *C. bombayensis* no. 13, which Soparkar noted to be often seen lying on its side, and *C. indica* XXV also have prominent ventral suckers.

The entire surface of the animal is covered with fine spines, except that part of the anterior organ which is protrusible; this agrees with the description for *C. indica* XXV. Because of confusion in Soparkar's use of the word *tail,* just what the exact condition is in *C. bombayensis* no. 13 is not clear. In most of his descriptions he distinguishes between *tail* and *furcae,* or *furcal rami*; but in illustrations the parts of the tail are labelled *stem of tail* and *furcal rami.* Another example of the confusion is in the case of *C. bombayensis* no. 19, where the figure shows both tail-stem and furcae to be spined, and the description states that the body and *tail* are covered with spines; here *tail* is evidently meant to include both parts, although in the preceding sentence tail and furcae are used. In the drawing of *C. bombayensis* no. 13 the furcae are shown without spines; the statement is, "both the body and the tail are covered with spines and the furcal rami have a thin membrane attached to them." It is probable that spines are not present on the furcae, both because they are absent in the figure, and because tail has been usually used for tail-stem. The spines on the ventral sucker of *C. wardi* are larger than those on the cuticular surface; those on the anterior organ are small, retrorse, and very closely set together in diagonal rows, so as to give the appearance of the surface of a fine file.

The anterior organ is not distinctly divided into a thin-walled anterior and a muscular posterior part, although it is furnished with circular muscles in the latter region (Fig. 32). The head gland is median and dorsal (Fig. 43), and varies somewhat in size in different individuals; its exact nature has not been determined, but it is apparently more similar to that of *C. bombayensis* no. 13 than of *C. indica* XXV. In the latter two large refractile cells were noted, with clear nuclei, and apparently with ducts opening anteriorly; whether these cells are equivalent to the head gland in schistosome and nearly related larvae is a matter for further investigation.

The tail-stem is more than twice as long as the body; it is firmly attached, as decauded specimens are rarely met with. It has prominent muscles passing spirally around the proximal part, which straighten gradually until in the distal third they are parallel to the longitudinal axis. This condition exactly duplicates that found in *C. indica* XXV. The muscles are distributed in four fields (Fig. 45); there is a central area of large cells in the tail-stem which appear quite clear, and the caudal excretory tube passes through the center. The furcae are delimited from the tail-stem and are furnished with wide and thin dorso-ventral fin-folds (Fig. 51). What appear to be thickenings are seen at irregular intervals and are due to fluting (Fig. 44).

There is a large H-shaped nervous system lying behind the anterior organ and extending forward somewhat on each side of it; the compound eye-spots are posterior to it, about two-fifths of the body length from the anterior end. Each is composed of a number of large brown-black granules arranged to form a cup, with the open side dorso-lateral (Fig. 52). In living cercariae they appear almost spherical, 13 μ by 15 μ, and lie in a clear area 22 μ in diameter. No similar pigment was observed in any other part of the body. Soparkar did not describe the nervous system of *C. bombayensis* no. 13; the eye-spots in this form are composed of dark granules, and there is a refractile lens in the center of the mass. *C. indica* XXV has an irregular mass of nervous tissue anterior to the salivary gland cells and dorsal to their ducts; the eye-spots are in contiguity with its anterior surface, in contrast to their posterior location in *C. wardi*. That the latter condition is more usual is supported by the statement of Faust (1918), "the eye-spots of the binoculate species are usually in direct connection with the posterior dorsal nerve trunks." However, in *C. gigas* (Faust, 1918b) and in *C. douthitti* (Cort, 1915) they are connected with the anterior rami.

The mouth is a small opening on the ventral surface of the anterior organ, about 22 μ from the tip; the esophagus passes through the anterior organ close to the ventral wall, and penetrates the posterior wall. From this point the esophagus passes ventral to the eye-spots, enlarges, and bifurcates into large ceca, the length of which varies somewhat in different individuals. There is no trace of a pharynx.

At least three different kinds of glands are present; the ordinary type of penetration glands encountered in the schistosomes and nearly related larvae will be considered first, after which the posterior mucin gland, so far reported for only the three larvae discussed here, will be described. There are two sets of penetration gland cells, an anterior group of four, and a posterior group of six. It is clearly seen in the living animal, as well as in sections, that the protoplasm of the anterior cells is coarsely granular, while that of the posterior is very fine (Fig. 50). The distinction is further seen in the staining reactions; the former group is eosinophilic, and the latter basophilic to Delafield's hematoxylin; when hematoxylin is used alone, the anterior cells are chromophobic. In general, then, these two sets of glands are similar to those in certain of the schistosomes and allied forms. Faust (1921d) stated that "a comparative study of the effects of these glands on host tissues indicates that basophilic and acidophilic glands are complementary in function and that a larva possessing the two differentiated types can penetrate the host much more effectively than one possessing one type. The schistosome cercariae are notable examples of the dimorphic type of staining reaction." This last sentence seems to the author to be unjustified, in view of the fact that of the five cercariae known to be the larvae of schistosomes, namely those of *Schistosoma japonicum*, *S. haematobium*, *S. mansoni*, and *S. spindale* and *Schistosomatium pathlocopticum*, only the first three were described at the time of Faust's writing;

and of these only the larva of *S. mansoni* had been reported to have two sets of glands (Faust, 1920a). The larva of *S. spindale* (Soparkar, 1921) was subsequently described as having an anterior group of four eosinophilic cells, coarsely granular, and a posterior set of six with slightly larger nuclei and finely granular or almost homogeneous protoplasm; with intra-vitam staining the anterior cells remain unstained and the posterior stain deeply. This reaction was not studied in *C. wardi* or *C. elvae*. The ducts from the two groups of gland cells pass ventral to the alimentary canal, eye-spots, and nervous system (Fig. 52), and enter the anterior organ ventro-laterally just at the junction of its two regions. They then continue through the substance of this organ and open at the anterior tip, probably through spines which cap the duct openings; these are seen only with difficulty in stained specimens.

The posterior mucin gland is of particular interest (Figs. 36, 37). What are probably homologous structures have been reported for *C. indica* XXV and for *C. bombayensis* no. 13. For the former Sewell stated: "Behind these cells is a large and somewhat horse-shoe shaped mass of finely-granular protoplasm in which I was unable to detect any cell outlines, nor could I see any corresponding ducts, but I take it to be the posterior part of the salivary gland." Soparkar described, behind the rudimentary genital system, "a large irregular cell with coarse granules which takes a deep stain when colored by the intra-vitam method. It is difficult to say what function this large gland-like structure performs. No duct arising from it could be made out." In living *C. wardi*, mounted in water and examined by transmitted light, this posterior mass is clearly defined, and seen to be homogeneously granular and somewhat yellow. Definite ducts leading anteriorly from it can not be clearly observed, although up to the region of the eye-spots, where they seem to converge, and less clearly between them, some of this same yellowish granular material is seen. In well-cleared specimens it was possible to trace these granules farther to the anterior than Sewell found them in *C. indica* XXV. Study of sections of immature forms revealed the fact that this posterior mucin gland is composed of many small cells, although the cell outlines are not seen in mature larvae and only an occasional nucleus is observed. In an attempt to determine the nature of this structure some specimens were killed in warm saturated aqueous solution of corrosive sublimate, and after washing for a few hours in distilled water were stained with dilute thionin in one percent phenol. From the fact that this posterior granular gland and the lateral extensions from it stain reddish, while the surrounding tissue is blue, would seem to indicate that this is a typical meta-chromatic reaction, and that the contents of the gland are of a mucin nature (see Lee's Vade Mecum, 1921:133, 391). Simple aqueous solutions of both thionin and toluidin blue were also employed, following the method of LaRue (1915), with equally good results.

There are five pairs of flame cells in the body (Figs. 30, 31), and except for minor details of relative position and length of capillaries the excretory system is identical with that of *C. bombayensis* no. 13; the distal part of the main excretory tube on each side is provided with two ciliated areas. *C. indica* XXV has four pairs of flame cells in the body and no cilia were noted in the excretory tubes. The island of Cort is apparently absent in all three; each has one pair of flame cells in the tail-stem. *C. indica* XXV is quite different also in that the caudal excretory tube is distended to equal one-third of the tail-stem diameter throughout the greater part of its length. In all three, branches pass through the furcae to open at the tips, without bulbous extensions.

A single prominent mass of germ cells is present in each larva, similarly situated and probably representing the same organ of the adult. In spite of Sewell's statement that "the genital organ is represented by a compact mass of small round cells situated ventrally, immediately behind the acetabulum and between the paired salivary-gland cells and the undifferentiated cell mass noted above," it is clear, from a comparison of his figures referred to, that the genital mass appears to be close to the ventral sucker only when seen from the ventral side. This is also the case in *C. wardi*, the lateral view of which clearly shows that the mass of germ cells really lies almost mid-way from the ventral sucker to the posterior end of the body. The apparent inconsistencies are seen to be due in both cases to the body shape of the larva and the positions typically assumed in consequence. Although Sewell assumed that this germ cell mass represented the future ovary of the adult, the author believes that until more is known concerning the development of the reproductive system, and sexual dimorphism in cercariae, the definite naming of the larval fundaments is hazardous.

The liver tissues of the infected snail are found to be filled with masses of sporocysts of varying length and caliber, so tangled that it is difficult to dissect them unbroken. They are very irregularly constricted; the diameter never exceeds 100 μ and is about 15 μ at points of greatest constriction; the longest one dissected free measured 1.4 mm. The cercariae develop in bunches at irregular intervals within the sporocyst (Fig. 53), at the regions of greatest diameter; these are much more transparent than the constricted portions of the tube. Throughout the length are found occasional granules of orange-yellow pigment, and the more opaque narrow regions contain sufficient numbers of minute pigment granules to produce a pale yellow color. Upon all three occasions on which *C. wardi* was found the host was *Planorbis trivolvis*, from a restricted region just north of Urbana, Illinois. On April 6, 1921, thirteen large individuals were collected in a pool north-east of the cemetery; of these one harbored the parasite. From an old stream-bed in Colvin's Field one in thirty-seven, collected April 7, 1921, was found to be infected. Another parasitized snail in a total of twenty-nine was collected April 19, 1921, from a point farther north in the same stream-bed. In the first and last collections the infections with *C. wardi* were the only ones found; in the second, two other individuals were parasitized with immature furcocercous forms, the identification of which was impossible.

PHARYNGEAL LONGIFURCATE DISTOME CERCARIAE

CERCARIAE BURTI MILLER 1923

[Figs. 46–49, 55–58, 62–66]

Host, *Planorbis trivolvis*
Locality, Burt Lake, Michigan (Colonial Point)
Occasion, once in August, 1921.

This cercaria is similar to *C. douglasi* (Cort, 1917:53) which was found in *Physa ancillaria* in the same region. Dr. Cort kindly loaned several slides of this larva. The two are alike and unique in certain features of the excretory system. The general appearance of a number of swimming *C. burti* is similar to that of any other furcocercous form with long furcal rami; locomotion is usually upward, with tail in advance. Under a cover glass there is less activity than is usually seen, and the body is for the most part held contracted into an oval shape. With the ventral sucker attached to the substratum, vibrations of the tail may cause slight rotation on it as a pivot, but never complete turning about. Great changes in body length are possible; the extended body is a blunt-ended cylinder longer than the tail-stem, which is much less contractile.

In permanently mounted material all degrees of contraction and extension are seen; for purposes of determining size, individuals which were moderately extended were chosen, and these give the following measurements (average): body 134 μ by 35 μ, tail-stem 140 μ by 26 μ, furca 157 μ. The tail is often distorted, so freshly-made mounts in Canada balsam were measured, and here the diameter of the tail-stem equals or exceeds that of the body; maximum sizes are: body 157 μ by 34 μ, tail-stem 142 μ, furca 157 μ; minima: body 88 μ by 52 μ, tail-stem 113 μ, furca 139 μ. In the living animal under a cover glass the length of the body at extreme extension is 240 μ, while the usual size is, body 125 μ, tail-stem 165 μ, furca 181 μ. The sizes given for *C. douglasi* are, body 150 μ, tail-stem 180 μ, furca 160 μ. These were presumably made from mounted material; the author has made measurements from type material of this form which practically coincide with Cort's, and which give a body width of 35 μ when the length is 157 μ. The two cercariae agree in that the body, except in extreme extension in *C. burti,* is shorter than the tail-stem; in *C. douglasi* the furcae are shorter than the tail-stem, while in *C. burti* they are consistently longer.

The anterior organ is short, not infrequently almost spherical, or it may be pyriform with either the small or the large end to the anterior. It is not divided into an anterior and a posterior region, nor is there the external constriction which usually accompanies that condition. The entire organ is a thin-walled sac, apparently not muscular. Its length in both cercariae averages 30 μ. There is no trace of a head gland in either. The ventral sucker, situated posterior to the mid-point of the body, is a strong organ of attachment. It extends up into the body and never protrudes prominently, so that a frontal view is the usual one obtained; often it is completely retracted into the body (Figs. 46, 49). Its circular edge is furnished with several rows of small spines, easily visible, which doubtless aid in attaching the organ to a substratum. In mounted material the greatest diameter of the ventral sucker of *C. burti* is about 25 μ, while in *C. douglasi* the average of a number of measurements is 21 μ.

The body and tail spination agrees in general with the brief statement for *C. douglasi*. The anterior organ region is covered with blunt, rather large spines which become more sparse in the region immediately posterior to it and are absent from the rest of the body surface. The tail-stem and furcae are only very sparsely spined. The tail-stem is attached strictly posterior to the body, and the union is evidently a strong one, as decaudation takes place very late when the animal is subjected to increasing pressure under a cover glass. There is a definite annulation of the wall, no doubt due to the contraction of circular muscles lying just under the cuticula. In the living animal the presence of caudal glands and their ducts is readily detected (Fig. 66); they are also seen in many mounted specimens. They are variable in number and arrangement, although the four anterior pairs are usually symmetrically arranged around the central excretory tube. Toward the posterior they may be very irregular in number, shape and location; in some individuals there are eight symmetrical pairs, while in others only a few small pear-shaped cells, irregular as to size and position, are seen in the entire length; this lack of regularity is similar to that recorded for *C. multicellulata*. The tail-stem has exceptionally weak musculature; while there are four muscle fields (Fig. 59), each is apparently composed of a single fiber, which does not stand out conspicuously from the wall. The furcae are laterally flattened, and when not under pressure are held so that their thin edge is seen when looking at a dorsal view of the larva; upon increase of pressure they are turned so that the broad side is seen, which shows a sword-like shape slightly narrowed proximally. As is common with longifurcate forms, there is no constriction between furcae and tail-stem.

The central nerve cell mass is H-shaped, posterior to the pharynx, with the anterior branches lateral to, and extending forward beyond it. No pigmented eye-spots are present, nor any cells which might represent unpigmented eyes. The system in *C. douglasi* presents no striking differences.

The opening of the alimentary canal is terminal; the narrow esophagus passes through the anterior organ (Fig. 55), pierces its posterior wall, and continues as a short prepharynx. The pharynx is readily seen in both living and mounted specimens; in the former its diameter is 13 μ and in the latter 9 μ. Posterior to the pharynx the esophagus continues to the ventral sucker, where it bifurcates into narrow ceca. These are ventral to the penetration gland ducts (Fig. 49) and terminate just in front of the penetration gland cells; the distal part of each is contiguous posteriorly with two disjoined parts (Fig. 65). This condition is doubtless comparable to that which Sewell described for *C. indica* XXII. The ceca are described for *C. douglasi* as extending two-thirds of the distance between the acetabulum and the posterior end of the body. In *C. burti* the walls are relatively thick and are chromophobic to hematoxylin and the eosins; the contents are a granular mass which fills the lumen and stains very deeply with eosin.

In the living animal the penetration gland cells and ducts are seen only with great difficulty, even with high magnification and with oil between the condenser and object slide. The cells are confined to the postero-dorsal part of the body; there are eight of them, containing granular cytoplasm which is eosinophilic and vesicular nuclei which scarcely stain except for a prominent acidophilic plasmosome (Fig. 60). Whether the coarsely granular nature of the cytoplasm is due to fixation is not known, as observations on living cercariae were unsatisfactory because of the presence of many small parenchyme cells. One observation on the ducts of a living animal showed them passing the pharynx laterally, curving to the middle of the body, and entering the anterior organ at its posterior end; in mounted material they seem to enter posterio-laterally. *C. douglasi* has four penetration glands.

The excretory system indicates close relationship to *C. douglasi*; the total number of flame cells is the same in each, but their distribution is different. The feature in which the two cercariae are unique is in the presence, anterior to the ventral sucker in *C. douglasi* and posterior to it in *C. burti*, of a cross-commissure connecting the two main lateral collecting tubes (Fig. 63). The excretory vesicle lies just anterior to the junction of the tail and is small and oval; its long axis is perpendicular to the body length and measures about 12 μ in the living animal. Less frequently it is seen as a crescent, when the lateral arms are swollen. While Cort's diagrammatic representation was probably not intended to show excretory vesicle shape, his figure indicates a somewhat different form for that structure in *C. douglasi*. An island of Cort is present in both larvae. There is a tangled mass of the main lateral collecting tube at either end of the cross-commissure, which finally gives rise to anterior and posterior collecting tubules. The former drains flame cells I and II, which lie anterior to the ventral sucker; the latter subdivides into three tubules at a point about two-thirds of the distance from the ventral sucker to the posterior end of the body. One of these fine tubules drains flame cells III and IV, which are located in and lateral to the complex convolutions; another drains flame cells V and VI in the posterior region of the body; the third comes from the single flame cell in the proximal part of the tail. In comparison, there is an anterior set of three flame cells and a posterior set of two on each side of the body of *C. douglasi*; there are two pairs in the proximal region of the tail, in contrast to the single pair in *C. burti*. Until there are more data on the development of the excretory system from the arrangement found in the cercaria, the closeness of relationship of two such forms cannot be predicted. In both larvae the caudal excretory tube passes through the tail-stem, is attached to the distal end just between the furcae, and divides to continue down one half the length of each ramus to open by a simple pore to the exterior.

The genital system is represented by an irregular mass of small chromophilic cells (Fig. 64) located in the posterior part of the body, just behind and extending slightly forward between the penetration gland cells. Similar scattered cells are found to the anterior, but there are no definite aggregations.

The parthenitae are long thin-walled sporocysts, very much tangled in the liver mass and difficult to dissect entire. The longest piece freed measured more than five millimeters in length, with a range of from 46 μ to 184 μ in diameter (Fig. 47). The cercariae develop in batches, between which the sporocyst is constricted and the walls may be quite thick; the lumen is continuous. Very frequently a large number of larvae, in all stages of development, are present in the same dilated portion. A birth-pore is present near the anterior end (Fig. 48). Cort did not describe the parthenitae of *C. douglasi*; the largest piece found on one of his slides was 1.3 millimeters long and 0.19 millimeters in diameter. It resembled very closely those just described; no unbroken ends were found and therefore it is not known whether a birth-pore is present.

This larva was found once, from a collection of *Planorbis trivolvis* taken in a swamp near Colonial Point, Burt Lake, Michigan on August 9, 1921. Seven out of seventy-three individuals were parasitized with *C. burti*; three other infections with furcocercous cercariae were found, beside two with echinostome and two with stylet cercariae, in the same collection.

CERCARIA TENUIS MILLER 1923

[Figs. 59–61, 67–77]

Host, *Planorbis trivolvis*
Locality, Burt Lake, Michigan (Colonial Point)
Occasion, once in August, 1921.

This is a very slender-bodied pharyngeal larva. It is an interesting fact that it is strikingly similar to an Indian representative of the small group of apharyngeal longifurcate distomes, and not to any of the numerous pharyngeal forms. *C. gladii* Cawston 1918 (according to Faust 1919a: 164) and *C. indica* XXII Sewell are the only two carefully studied longifurcate cercariae which lack any trace of a pharynx, and it is to the latter form that *C. tenuis* is similar in many respects.

There is nothing unique in the locomotion of *C. tenuis*; under a cover glass it progresses by taking hold alternately with anterior organ and ventral sucker, while the tail is rather passive; usually both tail-stem and furcae do not appreciably change their shape or length, but are held straight, with the furcae almost touching or each bent to the side. The sides of the body are usually parallel, with the posterior end square, and the anterior end bluntly rounded. There are no marked changes in body form except those of contraction and extension. The sizes under various conditions are: mounted in Canada balsam, well-extended (average), body 225 μ by 21 μ, tail-stem 216 μ by 21 μ, furca 207 μ; maximum extension of living animal, body 288 μ, tail-stem 240 μ, furca 240 μ.

The anterior organ is oval, or sometimes pyriform with the small end posterior; its average length in mounted material is 45 μ. The wall is thin and non-muscular, not differentiated into anterior and posterior regions. The ventral sucker (Fig. 67) is about three-fourths of the body length from the anterior end, and averages 25 μ in diameter. There is a single row of twenty-two hooked spines (Fig. 71) around its edge; the spines are attached with the hook projecting and pointing toward the center, so that when the sucker takes hold of a substratum, they aid in attachment. On the body surface of *C. tenuis* there is an oral cap of spines which are rather small and sparsely distributed; a slight gradation is exhibited, from large in front to smaller toward the posterior limit of the spined area. The spines are like those of *C. chrysenterica;* the portion from *a* to *c* is embedded (Fig. 80), and *b* projects, pointing toward the posterior. The remainder of the body and the tail is not spined.

The tail is attached terminally to the body, and in the living cercaria it is more narrow; in well-extended specimens mounted in Canada balsam the two diameters are about equal. Fine annulations are present throughout the entire length, and the cuticula is very thin; there are neither spines nor sensory hairs. About five pairs of caudal glands are present, which do not differ from those found in *C. burti*; number, form, and arrangement are not constant. The usual slender outgrowths, which lead to the wall of the tail-stem and evidently may act as ducts, are present. The furcae are broadly lanceolate and terminate in sharp points, and are not delimited from the tail-stem. They are much more transparent than either body or tail-stem.

The nervous system is represented by an irregular H-shaped mass located in the anterior part of the body, generally behind the pharynx; the anterior branches extend lateral to this organ. Eye-spots are lacking. The mouth is subterminal, and the esophagus (Fig. 70) leads back to pierce the posterior wall of the anterior organ. The prepharynx is 8 μ long; the pharynx is clearly outlined and its greatest diameter is 11 μ in living cercariae, 8 μ in mounted material. Just behind this the esophagus is dilated; it bifurcates into long ceca not quite midway of the body, and these pass around the ventral sucker to end in two disjoined but contiguous parts (Fig. 75). These, as in *C. burti*, may be interpreted as sections which have not yet broken through to form a continuous lumen. The esophagus shows regular cross striations. The wider ceca, dorsal to the penetration glands (Fig. 76), contain a homogeneous mass which is eosinophilic in sectioned material.

The penetration glands are located in the region just anterior to the ventral sucker; the details of all structures in this area are obscured by numerous parenchyme cells. In the living animal the penetration glands show as a coarsely granular, grayish and ill-defined area; in a few specimens it is possible to see four definite cells, with rather large refractile nuclei. The confirmation of this comes from the study of sections, in which the number of the glands and their position with reference to the alimentary canal may be determined. The cytoplasm of these cells is chromophobic to Delafield's hematoxylin in toto and in sections, and eosinophilic in sections. The ducts frequently appear empty, but when the contents are present they also are eosinophilic. They are difficult to trace except in sections (Fig. 70). In the region of the openings of the ducts there are about eight prominent spines; they are probably arranged in a semi-circle around the dorsal side of the mouth opening. *Cercaria indica* XXII was said to be crowned with anteriorly-directed spines.

The presence of five pairs of flame cells in the body, in about the positions given them (Fig. 74), can be affirmed, as well as two pairs in the tail-stem. The exact connections of the capillaries with the collecting tubules and of these with the main lateral collecting tubes, are not known beyond all possible question; the arrangement shown is the probable one. The excretory vesicle is a tripartite structure composed of a central vesicle and two large dilations of the proximal ends of the main lateral collecting tubes.

An island of Cort is probably present in *C. tenuis*. The caudal excretory tube passes through the center of the tail-stem and the four flame cells are very close to it; after it bifurcates each branch passes through half the length of the furca, to open to the exterior by a simple pore on the edge.

The genital system is represented by a mass of cells in the posterior part of the body, not so close to the junction of body and tail as in those larvae in which the penetration gland cells are crowded behind the ventral sucker. *C. tenuis* develops in long sporocysts, which do not exhibit the variations in diameter shown by those of *C. wardi* or *C. burti*; the lumen is more evident through the entire length, and the cercariae are not so definitely separated in batches (Figs. 72, 73). The cuticula of the sporocysts, like that of the larva, is very thin. A birth-pore is located near one end, and the opening is in a marked prominence on the surface; the canal through the thick wall is not always seen in total mounts, but the raised lips locate the opening.

Two out of seventy-three specimens of *Planorbis trivolvis* collected in the Colonial Point Swamp, Burt Lake, Michigan, on August 9, 1921 were parasitized with this larva; it was in the same collection with *C. burti*.

CERCARIA CHRYSENTERICA MILLER 1923

[Figs. 78–94]

Host, *Lymnaea megasoma*
Location, Burt Lake, Michigan (Colonial Point)
Occasion, once in August, 1921

This is the first larval trematode to be reported from *Lymnaea megasoma*, which has a restricted distribution in the north central United States and extends far up into Canada (Baker, 1911). *C. chrysenterica* is a longifurcate form, and is quite similar to *C. emarginatae* (Cort, 1917:53); the author received slides of this species through the kindness of Dr. Cort. *C. letifera* (Fuhrmann, 1916:389) will be included in the same group because of general likeness, but descriptions of the penetration glands and of the details of the excretory system are lacking. All three larvae have very long intestinal ceca, which in the first two are dilated distally and filled with a yellow jelly-like substance.

The method of locomotion is not unusual; the body is pulled after the tail in short straight dashes, or longer erratic ones, generally upward through the water. Under a cover glass there may be some progress with the body in advance, for short distances only; the tail lashes actively. The cercaria may move slowly by alternate use of anterior organ and ventral sucker, with accompaning form changes (Figs. 92–94).

Sizes under various conditions are: well-extended specimens mounted in Canada balsam (average), body 260 μ by 48 μ, tail-stem 244 μ, furca

248 μ; maximum body extension of living cercaria, 384 μ. These measurements are slightly larger than those given for *C. letifera,* which is in turn larger than *C. emarginatae*; however, the author's measurement of a large individual of this latter species on one of Cort's slides gave body 254 μ by 37 μ, as against a body length of 160 μ given by Cort.

The body of the living animal is the shape of a spindle with the greatest diameter just behind the ventral sucker, and a gradual tapering from this point to the anterior. The anterior organ is usually pyriform, with the small end posterior, although it may be oval. There are not two regions as distinctly differentiated as in *C. elvae,* although the posterior part is more strongly muscular than the anterior; there are both longitudinal and circular fibers (Fig. 90). In *C. letifera* and in *C. emarginatae* the anterior organ is of the same general shape as that just described. No one of the three cercariae has a head gland. The ventral sucker is about two-thirds of the body length from the anterior end, but its relative position varies with the state of contraction. It is relatively large, especially in comparison with its size in the schistosome cercariae; in living larvae under some pressure of cover glass it is about 45 μ in diameter, while in permanent mounts it shrinks to 31 μ. It does not protrude markedly from the body (Fig. 89). There are small spines around its edge. In *C. letifera* it is smaller, and likewise it is spined; in *C. emarginatae* its diameter is 25 μ in mounted specimens.

There is an oral cap of spines like those described for *C. tenuis.* Behind these there is a small area on which small straight spines are present; this is followed by a short region with no spines. Between this bare region and the ventral sucker are eight or nine irregular bands, each composed of two or three rows of spines. The region around and posterior to the ventral sucker is uniformly covered with spines. For *C. emarginatae* the statement is made, "heaviest spination around acetabulum, with rest of body only sparsely covered." Fuhrmann reported only four or five large spines on the anterior extremity of *C. letifera.*

The tail is attached terminally to the body and is quite transparent; the surface of the tail-stem is finely annulated. The number of caudal glands varies in different individuals, from four to eight or more pairs. They are relatively small and do not take up a great part of the tail-stem cavity (Fig. 78); the usual ducts lead to the outer surface. The furcae are broad and flattened.

The nervous system is represented by an H-shaped mass which extends somewhat to the anterior on each side of the pharynx. This system is not reported for *C. letifera* or for *C. emarginatae.* There are no eye-spots.

The mouth opening is subterminal; the esophagus passes through the anterior organ and penetrates its posterior wall. The prepharynx dilates just in front of the pharynx, and the latter is about 20 μ in diameter in the living animal, shrinking to 15 μ after preservation. The esophagus continues to about midway of the body, passing ventral to the nervous system (Fig. 84), and then bifurcates into ceca which approach the dorsal wall and gradually increase in diameter (Figs. 86, 89). The walls of the ceca are thick, and several nuclei are present in them; the contents within the lumen appear jelly-like and homogeneous, and stain deeply with eosin. From a study of Cort's material of *C. emarginatae*, the author finds an alimentary canal quite similar to the one just described. It is difficult to compare it to that of *C. letifera*, as Fuhrmann's account is incomplete and it is not clear as to the location of the pharynx.

The penetration gland cells are confined to the region median and posterior to the ventral sucker; they are four in number and are readily seen in the living animal. One cell on either side is lateral and ventral to the cecum; the remaining two are median, in tandem position, and so laterally compressed as to be almost in contact with dorsal and ventral body walls (Fig. 86). In a living cercaria the protoplasm of all four cells is coarsely granular; after fixation there is no definite staining reaction to either Delafield's hematoxylin or to eosin, and the greater part of the contents seems dissolved out. The ducts of the lateral cells pass forward ventral to the ceca, and those of the median cells may be contiguous for a little way (Fig. 89). The two of each side come into contact at about the level of esophageal bifurcation, and pass forward together, bending medially to enter the anterior organ. In connection with the duct openings, there are about twenty-two solid piercing spines, arranged in a semicircle around the dorsal edge of the mouth opening; the ten median spines are somewhat larger than the others. In comparison, Cort's account for *C. emarginatae* stated that there were six glands, extending into the post-acetabular region; the author's examination of Cort's material shows the cytoplasm to be coarsely granular and chromophobic to Delafield's hematoxylin in total mounts. Fuhrmann did not include the penetration glands in his description of *C. letifera*.

There are nine pairs of flame cells, three anterior to the ventral sucker, four in the posterior region, and two in the tail-stem (Fig. 79). *C. emarginatae* has the same number anterior to the ventral sucker, but they form one group on each side, with their capillaries emptying into the larger tubule at one point; in *C. chrysenterica* flame cells I and II have apparently arisen from the division of a cell, and are not near III, whose capillary joins separately. Posterior to the ventral sucker *C. emarginatae* has but two pairs of flame cells, the capillaries of which join the posterior collecting tubule at the same point; it has two pairs in the tail-stem, more distally located than in *C. chrysenterica*. Fuhrmann figured none of the excretory system of *C. letifera* except the excretory vesicle outline, so it cannot be included in the comparison.

The genital system is chiefly represented by a somewhat wedge-shaped mass of cells located in the posterior end of the body, just in front of the excretory vesicle and between the ends of the ceca. Anterior to the ventral sucker and extending up toward the origin of the ceca there are two masses of cells which correspond in position to the vagina and cirrus pouch shown by Faust for *C. gracillima* (1918). The relation of these cell groups to the large posterior mass in *C. chrysenterica* is not clear.

The parthenitae are long tubes of varying diameter, which exhibit gradual swellings in several regions, and so are unlike other sporocysts described which have ball-like swellings. The longest entire individual dissected free from host tissue measured more than 8 mm. in length, and was 180 μ and 60 μ in greatest and smallest diameters; in one preparation of sections a maximum diameter of 244 μ was observed. The walls of the narrow regions are thicker, although a prominent lumen extends throughout. The anterior end is distinguished by a solid knob of small cells, behind which the prominent lips of the birth-pore are seen on one side (Fig. 83). Some sporocysts on Cort's slides were studied; they are quite similar to those just described, both in the caliber of the tube and in the presence of a definite birth-pore with prominent lips. Fuhrmann described the sporocysts of *C. letifera* and figured an individual containing immature larvae; a birth-pore was not observed.

C. chrysenterica was found once only, in a collection of *Lymnaea megasoma* from a swamp near Colonial Point, Burt Lake, Michigan on August 9, 1921. One snail out of eighteen was parasitized.

PHARNYGEAL LONGIFURCATE MONOSTOME CERCARIAE

CERCARIAE MULTICELLULATA MILLER 1923

[Figs. 1–8, 17, 18]

Host, *Physa gyrina*
Locality, Urbana, Illinois (Drainage Ditch)
Occasion, twice, in September and November, 1922

Cercaria multicellulata is the second pharyngeal monostome larva with long furcal rami to be described, the first being *C. rhabdocaeca* Faust (1919c: 338); its similarities to this cercaria and to *C. hamata* Miller will be considered in the discussion of the latter elsewhere in this paper. No trace of an alimentary canal has been observed in this larva, but because of its striking similarities to *C. rhabdocaeca* and *C. hamata* the presence of a pharynx, obscured by the small parenchyme cells, is assumed. Another reason for including *C. multicellulata* with the pharyngeal forms is the number of differences between these three larvae and the only apharyngeal longifurcate monostome, *C. indica* XXVII, especially with regard to the excretory system.

C. multicellulata swims sporadically; rapid dashes, generally upward, are effected by lashing of the tail, which is in advance. Between dashes the cercaria sinks body first, the tail-stem is extended in a straight line with the body, and the furcae are spread at an angle of about 100°. It is positively phototactic. A series of movements, probably connected with the entrance of the cercaria into a host, is frequently observed under a cover-glass (Text-fig. 2). From a condition in which the body is somewhat contracted and the anterior end turned in (*A*), the generally rounded contour of the anterior organ is changed to a pyriform shape as it is slowly extended a little (*B*). The anterior part of the body is then quickly thrust forward; the fore part of the anterior organ rapidly everts and presents the large, anteriorly-directed spines (*C*). The whole is then quickly retracted, rounded up, and the anterior-most part in (*A*). This series of movements is frequently alternated with one in which the everted part of the anterior organ (*C*) is rapidly thrust forward again and again, without rolling in and rounding up when withdrawn. The anterior organ has an attaching function also; it is strong enough to hold the cercaria to the under surface of a cover glass which is being pushed along a slide.

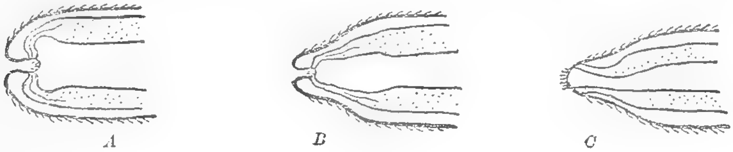


Fig. 2

Sizes under various conditions are: maximum body extension under cover glass but free-moving, 184 μ; almost immobile from neutral red (average), body 170 μ by 37 μ, tail-stem 230 μ, furca 225 μ; fixed in hot Gilson's fluid (average), body 156 μ by 28 μ, tail-stem 198 μ, furca 147 μ; well-extended specimens mounted in Canada balsam (average), body 136 μ by 26 μ, tail-stem 196 μ by 24 μ, furca 147 μ.

When under no compression the sides of the body are parallel up to the region of the anterior organ, where they taper off to a blunt end. With great extension the whole body tapers slightly from the posterior, and the anterior two-thirds may be crenated in the region behind the anterior organ; this crenation is due to the contraction of circular muscles just beneath the surface. The anterior organ varies from an oval to a pyriform shape in changing from a position of rest to extension; infrequently it contracts in the middle, becoming dumb-bell shape. It is approximately one-fourth as long as the body, although this proportion varies, since the anterior half of the body undergoes more extension and contraction than the posterior. The anterior organ is armed with large retrorse spines extending over somewhat less than the anterior half, behind which they are both smaller and more sparse, so that, with the difficulty of observation due to the many small parenchyme cells in the body proper, it cannot be said whether they extend over the entire body; there is indication of sparse spination in somewhat definite bands back to the level of flame cell II. It may be noted here that the parenchyme cells, which are refractile, make difficult all observations on external and internal structure. The anteriorly-directed spines associated with the openings of the penetration gland ducts will be described in connection with those organs. The spination of *C. multicellulata* is on the whole very similar to that of *C. indica* XXVII, except that, in the latter, spines are reported for the anterior end and are shown as extending over only half of the anterior organ.

The cylindrical tail-stem is of less diameter than the body; the attachment is strictly posterior. Annulations, much finer than those of the body, are always noted; as Sewell suggests, these are due to the contraction of circular muscles directly beneath the delicate cuticula. The cells composing the wall have relatively large nuclei (Fig. 5) which quickly take a deep neutral red stain from dilute solution. Within the cavity of the tail-stem are ten to fifteen large gland cells, slightly yellowish in color and showing no granulation even under high magnification (1380×); they are arranged in pairs in the proximal portion, the caudal excretory tube passing between them, but farther to the posterior the pairing and size of the glands become irregular and they may lie on but one side of the excretory tube. While alive, the nuclei of these cells are seen to be relatively small and granular. Ducts lead to the wall of the tail-stem, and apparently open between surface cells. With contraction of the tail, the glands move within the lumen and the most posterior may be forced into one of the furcae. There is great diversity among different mature cercariae from the same snail; in some the glands are very clearly seen, while in others the outlines are so irregular that they can scarcely be recognized. As noted by Cort (1915) for *C. douthitti*, they are seen only in living specimens. While not clearly observable as such in the tail-stem of a living cercaria, four principal muscle bands (Fig. 6), strongly acidophilic, are seen in sections stained with Delafield's hematoxylin and eosin. On the surface there are delicate sensory hairs, seen only under high magnification and with proper lighting; their length is about three-fourths of the tail-stem diameter. No relation was observed between them and the openings of the caudal gland ducts. This is the second record of sensory hairs on the tail-stem of a furcocercous cercaria; they were previously reported for the distome, *C. letifera* Fuhrmann (1916). The furcae of a living cercaria are about equal in length to the tail-stem, and are not constricted at the base; they contract more than the tail-stem during fixation, and therefore appear shorter in permanent mounts. There is an irregular lumen. On the surface are small spines in longitudinal rows, and the distal half is furnished with a narrow fin-fold which does not extend around the tip of the furca, nor is it thrown into folds such as are so characteristic of a form like *C. gigas*.

About three-fifths of the length of the body from the anterior end is located a pair of simple eye-spots, composed of from four to thirty black pigment granules of varying shape and size. The diameter of a group of granules composing an eye-spot is about 6 μ, and they are frequently observed, under a magnification of 1380×, to lie in an irregularly-shaped clear area.

Repeated attempts were made to determine whether an alimentary canal is present. Only once or twice was some indication seen of a very narrow tube extending behind the anterior organ to a distance of about one-half its length; the observations were not conclusive.

There are three pairs of penetration gland cells (Figs. 5, 7). The anterior two are separated from the other four by a compact mass of cells, and their ducts are ventral to the others; all six pass dorsal to the eye-spots (Fig. 17) before dipping ventrally in the anterior half of the body; they become small before entering the anterior organ, and expand in that organ. The glands are more easily seen by intra-vitam staining with dilute neutral red; they take a deep red stain, while their ducts do not stain very deeply and are more yellowish, indicating either that they are empty or that the character of the secretion changes after entering them. That such a change from cell to duct may occur has been suggested by Faust (1920a); both cells and ducts appear coarsely granular. The entire penetration gland system is chromophobic to Delafield's hematoxylin in cercariae mounted in toto, but it is strongly eosinophilic when sections are counterstained with eosin. Between the openings of the ducts of the two sides there is a group of about twelve solid piercing spines.

The numerous parenchyme cells in the body make it especially difficult to determine the locations of flame cells and the connections of their ducts. The exact connections of all the small tubules could not be seen, but other details were made out (Fig. 5). The excretory vesicle proper consists of two parts about equal in width, the posterior being longer than the anterior; from the latter, two arms branch off antero-laterally, so large as to give frequently the appearance of a tri-partite vesicle. These arms narrow to become the main lateral collecting tubes, which bend sharply forward around the germ cell mass, extend anteriorly for a third of the body length, and bend on themselves to return a little way before dividing into anterior and posterior collecting tubules. The anterior collecting tubule undoubtedly receives the capillaries from flame cells I, II, III, and IV; the exact connections of I and II were traced, but it is not known whether III and IV join separately or constitute a pair whose capillaries unite in a common tubule (Fig. 1) before joining, as in *C. rhabdocaeca*, with the excretory system of which there are many similarities. The posterior collecting tubule in all probability drains V, VI, VII, and VIII in the body and IX and X in the tail; the fact that V and VI, as well as VII and VIII, lie close together seems to show that their capillaries may unite before entering the posterior collecting tubule. There is a small island of Cort, although it is not easily seen; it is located in a dilated portion of the posterior part of the excretory vesicle, at the junction of body and tail. From this point the caudal excretory tube runs posteriorly through the center of the tail-stem, embedding itself in a mass of cells where the furcae branch off; here it divides and passes down each furca to open on the dorsal edge, midway to the tip. These openings are simple, not having the slight enlargement and protrusion frequent in mid-furcal pores.

Either a rudimentary ventral sucker is present, or the reproductive organs are represented by two cell masses (Fig. 7). A poorly-defined group of cells, lying just behind the posterior pair of penetration gland cells and bounded posteriorly and laterally by the bladder and main lateral collecting tubes, forms the larger mass; the group of cells in this position, usually staining deeply with hematoxylins, has constantly been interpreted as a germ cell mass in furcocercous cercariae. Between the first and second pairs of penetration gland cells is another cell mass, quite different in shape and more definite in outline; the cells composing this mass are apparently identical with those of the posterior mass. Whether this is a proliferating cell mass representing a degenerate ventral sucker, or a germ cell mass, is not entirely clear; no connections between the two masses were observed. The same two cell aggregates were found in *C. hamata.*

The parthenitae are elongate sporocysts of relatively small diameter, so much tangled in the snail liver that it is practically impossible to dissect out one unbroken; the longest obtained measured almost 1 cm. in length, varying in diameter from a few μ to 200 μ (Fig. 18). Both those containing only very young germ balls and those containing mature cercariae are very motile, especially the free ends which project from the liver. The cercariae develop in batches, with constrictions between. The lumen is continuous throughout the entire length, although at the points of constriction it is so narrow that, in spite of rapid surging back and forth, it is likely that the groups remain separate while undergoing development. The free end is tapering and bluntly rounded, the most anterior part being translucent and free from pigment granules. Following this short region there is a considerable amount of yellow and orange pigment, and at a short distance from the anterior end are found the lips of a birth-pore (Fig. 2). The emergence of one cercaria was observed.

Of a collection of ninety-seven *Physa gyrina* on September 18, 1922, from the Drainage Ditch, Urbana, two were infested; on November 4, one-half mile farther up the ditch, twelve in 177 were infested. The sizes of these fourteen snails varied from 11 mm. to 16 mm., greatest length of shell.

CERCARIA HAMATA MILLER 1923

[Figs. 9–16]

Host, *Planorbis trivolvis*
Locality, Urbana, Illinois (Drainage Ditch)
Occasion, three times, September to November, 1922

This cercaria is similar in many respects to *C. multicellulata*, but may easily be distinguished from it by the absence of eye-spots; the figures for the latter may be used to show certain points of structure. *C. hamata* is also strikingly like *C. rhabdocaeca* Faust and may be identical with it, although there are certain differences, and some structures in the former which are not included in the description of the latter. The general form of locomotion in *C. hamata* and *C. multicellulata* is the same, but with a hand lens it is observed that in the case of the former the anterior part of the body is bent toward the ventral surface in a hook-shape when the cercaria is sinking through the water.

Sizes under various conditions are: under a cover glass but free-moving, body, 207 μ by 41 μ, tail-stem, 276 μ, furca 276 μ; mounted in Canada balsam (average), body 179 μ by 28 μ, tail-stem 248 μ, furca 198 μ. It will be noted that in the process of making permanent mounts the furcae shrink more than the tail-stem.

Although body shape is not a reliable criterion for specific differences, *C. hamata* and *C. rhabdocaeca* differ in this regard. The sides of the body of the former are parallel and its diameter is not greater than that of the tail-stem; also a shape is never exhibited such as Faust has shown for the latter cercaria. On the contrary, the body sometimes bulges anteriorly during contraction, and the posterior part never increases much in diameter. All of the measurements of the body are greater than those given for *C. rhabdocaeca*. The two forms differ also in the form of the anterior organ; in Faust's species it is described as "oral sucker pyriform, with larger end directed inward." *C. hamata* has its anterior organ in the shape of a short oval, and while under cover glass pressure or in permanent mounts (Fig. 12) it may be somewhat pyriform, it never appears as Faust figured for *C. rhabdocaeca*. The spination is similar to that of *C. multicellulata*. In both *C. hamata* and *C. multicellulata* the tail-stem is attached terminally and presents the same annulated appearance; it also has a constant diameter throughout; in these characters both species differ from *C. rhabdocaeca*, the tail-stem of which tapers markedly, and shows no annulations.

Practically the entire lumen of the tail-stem of *C. hamata* is filled with caudal gland cells, which are therefore not so clearly defined as in *C. multicellulata*; they have the same clear, homogeneous appearance, slightly yellow, and with transparent nuclei. Sewell's description of short lateral branches of the caudal excretory tube of *C. indica* XXVII, also for *C. indica* II, is thought by the present author to be a misinterpretation of the boundaries of contiguous caudal gland cells; his records are the only ones of such lateral branches. The three longifurcate forms under discussion here are united in the absence of spines on the tail-stem, in contrast to the presence of a number of small, backward-pointing spines with which all four Indian representatives of the brevifurcate monostomes are furnished (*C. indica* IX, XIII, XXXIX, LV). *C. hamata* has four muscle bands in the tail (Fig. 10), and sensory hairs like those reported for *C. multicellulata*, relatively longer, and more numerous, about fifteen on each side; these have not been noted for any brevifurcate cercaria. These two forms have spines on the furcae; they were not reported for *C. rhabdocaeca*. *C. hamata* does not have thin furcal edges; *C. multicellulata* is the only one which has them.

Various degrees of development of the alimentary canal are represented; *C. multicellulata* shows only a trace of a narrow tube posterior to the anterior organ, although it is supposed that a pharynx is present, but is masked by the small parenchyme cells. *C. rhabdocaeca* was shown with a relatively wide prepharynx, slightly muscular pharynx, short inconspicuous esophagus, and single median cecum extending backward almost to the level of the first penetration gland. *C. hamata* has a capillary prepharynx, 10 μ long, and esophagus and cecum are represented by a pyriform vesicle behind the weakly muscular pharynx; the pharynx is 10 μ wide.

The number of penetration glands in the three North American species is the same, although their locations are somewhat different. In both *C. multicellulata* and *C. hamata* the anterior cell mass (rudimentary ventral sucker or germ cell mass) definitely separates the six gland cells into two groups. In the former species two gland cells are constantly anterior and four posterior to it; in the latter the distribution is not so regular, as in some individuals either two or three cells may compose the anterior set, and not infrequently one is also very clearly lateral to the germ cells, leaving only two posterior. In both species the coarsely granular protoplasm of these cells readily stains with neutral red in the living animal and is eosinophilic in sections (Fig. 16). In *C. rhabdocaeca* there is a single group of six contiguous cells. In *C. hamata* the penetration gland ducts from the two sides run through the center of the body, almost contiguous for the greater part of their length; here they are small and difficult to see individually. They diverge just behind the pharynx and enter the anterior organ, where they expand greatly so that their number and location are more readily determined (Fig. 9). Associated with the gland duct openings is a group of about twelve small solid piercing spines which point forward, and which are arranged in a crescent around the dorsal side of the mouth opening. These spines are also solid in *C. multicellulata*, while in *C. rhabdocaeca* they are hollow.

The excretory vesicle is a bipartite structure (Fig. 12), the anterior part being somewhat larger in all dimensions than the posterior. It is about one-fifth as wide as the part of the body in which it is situated. The lateral arms branch off without conspicuous enlargement, bend around the large germ-cell mass, and continue forward as the main lateral collecting tubes. A very small island of Cort is present. The openings of the caudal excretory tube branches are in the mid-furcal region. As in *C. multicellulata*, observation of details is very difficult, and while the locations of all body and tail-stem flame cells were made out, the connections of the capillaries with the larger tubules have not been determined. The figures for *C. multicellulata* serve equally well for the excretory system, except that in *C. hamata* the bending of the main lateral collecting tube is somewhat more anterior. In both species this reflexed tube is very clear; it is not shown in the figure for *C. rhabdocaeca*, in which there is no obvious division of the main lateral collecting tube into anterior and posterior collecting tubules. It is likely that both *C. multicellulata* and *C. hamata* possess ciliated areas in the main lateral collecting tubes near the entrance of the anterior and posterior collecting tubules; several times, at the moment when a cercaria was going to pieces due to cover glass pressure, a flickering was noted lateral to the anterior cell mass in each species. The flame cells in the tail-stem of *C. hamata* are very small and are seen only with difficulty.

There are two large cell masses, consisting of a large number of small, deeply staining cells, similar in size and location to those of *C. multicellulata*. There are some indications of lateral connections between the two groups of cells, and also of lateral extensions forward from the anterior mass which meet in a median plane; thus the whole would form a figure eight. Whether these are both germ cell masses or the anterior one represents a rudimentary sucker has not been decided. These conspicuous cell masses were not described for *C. rhabdocaeca*; Faust mentioned a few large germ cells as lying ventral to the bladder.

The parthenitae are long thread-like sporocysts (Fig. 11), not differing markedly from those of *C. multicellulata*. Bright yellow pigment granules are seen by reflected light, and examination under higher powers, with transmitted light, reveals the presence of other orange-colored spots. Waves of contraction, beginning at one end and passing through the entire length, were observed in sporocysts taken from the digestive gland soon after killing the snail. Puncture of the liver after careful removal of the shell results in a very active waving about on the part of protruding sporocysts, even those containing very young germ balls. A birth-pore is present (Fig. 14).

C. hamata was found in one out of sixty specimens of *Planorbis trivolvis* from the drainage ditch, Crystal Lake Park, Urbana, collected September 25, 1922. On October 26 one *P. trivolvis* in 101 from the same location was infested. On November 4, one-half mile farther up the ditch, a collection of eleven of the same species yielded a single infection.

CLASSIFICATION

There are at present upwards of one hundred furcocercous cercariae more or less fully described. It does not seem possible to devise a scheme of classification, upon either a natural or an artificial basis, which will include all forms; it is especially difficult to dispose of those for which only external characters are known, since they can not be placed except on the basis of general similarities to other completely described cercariae. The classification which the author proposes is preceded by a discussion of other recent ones.

The three groups which Cort (1917) established to contain six furcocercous cercariae were defined in the discussion of his paper in the historical section. He studied the homologies of the excretory systems of these larvae, and stated that his work had convinced him that "a more complete knowledge of this system will do much to clear up relationships and to establish natural families. Also an increased knowledge of the excretory systems of little known types of cercariae will be of great help in solving life-histories by suggesting the groups of adults to which such forms belong. In certain cases the close relationship of two cercariae may be shown by comparisons of their excretory systems, when on account of differing degrees of development of adaptive larval characters they superficially appear to be very different." Because only six fully described larvae were available for classification, Cort's scheme is too limited to allow the inclusion of all forms now known.

Sewell's classification (1922) is the result of a consideration of all well-described furcocercous larvae, including the monostomes. Although he recognized that these last are more closely related to distome furcocercous than to other monostome cercariae, nevertheless he considered them quite apart from the distome forms. No pharyngeal monostomes, other than those in the peculiar Vivax group, were known at the time of publication of his paper; he divided the monostome larvae into the Lophocerca group, with furcae shorter than one-half the length of the tail-stem and with a mid-dorsal body fin-fold, and the Lophoides group, the single member of which has relatively long furcae and no body fin-fold. For the distomes Sewell modified Cort's (1917) grouping to form the basis of his system of classification embracing a much larger number of forms. He united the first two groups of Cort into Group 1, and divided Cort's third into two, Group 2 and Group 3. Group 1 of Sewell, the brevifurcate apharyngeal distomes, was divided into two series mainly on the basis of presence or absence of hollow piercing spines, and of presence or absence of fin-folds on the furcal rami; each series was further divided into subgroups, on the basis of the complexity of the excretory system pattern. The longifurcate distomes, Group 2, were divided into a pharyngeal and an apharyngeal series, the latter based on a single new species, *C. indica* XXII; three subgroups of the pharyngeal larvae were created, chiefly on the basis of the excretory system pattern, each to contain a single well-described larva. Group 3 was formed to contain *C. vivax* and two new species of longifurcate pharyngeal monostomes having the same peculiar type of excretory system. A number of larvae could not be included in his classification, largely because of incomplete descriptions.

Faust (1924) presented a scheme of classification for digenetic trematodes, mostly larvae, in which each ultimate group contains those forms whose excretory system formulae may be elaborated from a basic group formula. The furcocercous cercariae are placed together in the ninth subdivision under Distome Cercariae; furcocercous monostomes are included here also. The importance of the excretory system for the establishment of natural groups has already been stressed by Cort (1917), and discussed in some detail by Faust (1919b, c, d). In the paper now being considered Faust places still greater emphasis upon this system; he states (p. 261):

> A study of the larval characters of the trematodes for some years has brought me to the conclusion that there is only one common system carried over from the cercaria to the adult, which is sufficiently definite and conservative as to be utilizable for purposes of group identification. That system is the excretory system. The more work that is done in this system, the more indicative it is of possessing value as a natural basis of classification, and the more evident is the artificiality of some of Lühe's groupings of larval forms and of the equal artificiality of some of the families of adult trematodes that have been created. While the study of adult correlations with known larval forms is still in its infancy, it is not too much to state that all members of a natural adult group possess the same basic excretory pattern.

This correspondence of close relationship with identical excretory systems has already been pointed out for the larvae of the three human schistosomes; furthermore, Faust and Meleney (1924) have shown that the excretory system in the post-larval stages of *Schistosoma japonicum*, the only species known in this respect, is a regular elaboration from that system in the cercaria.

Among the furcocercous cercariae about half of the groups had been established by Sewell; to some Faust added other larvae, and also set up new groups to contain one or more forms. A fundamental formula, with possible elaborations worked out *a priori*, was used, and it was found that the groups fitted into this formulary scheme, leaving very few gaps. However, the present author finds that certain of these groups are not homogeneous. In the Ocellata group are placed *C. ocellata*, with seven pairs of flame cells, arrangement unknown, *C. indica* XXV with five pairs, *C. indica*

XXXVI with four pairs observed and the possibility of a fifth pair, and *C. bilharziella*, of which nothing is known of the excretory system and practically nothing of the general morphology. Furthermore, identical formulae are given in two instances for widely separated groups; thus, that for the *furcicauda* group is the same as for the *burti* group (although in the latter it does not include the flame cells in the tail-stem); also the Baiswan group in one place, and the *emarginatae* and *tetis* groups in another, are given identical formulae. This raises the question as to where a new species with either of these formulae would be placed; if general structural similarity is to be taken into account in these instances, it is difficult to see why *C. douthitti* and *C. elephantis* are placed together, since they are quite dissimilar in general organization (Miller, 1924). *C. pseudo-vivax* nov. sp. and *C. divaricata* nov. sp. were placed in the same group with *C. vivax*, although a complex excretory system of the Vivax type is not described for either.

Faust states (p. 263) that "the forms included in this table are by no means exhaustive, but no well-described species has been omitted simply because it does not fit into the scheme proposed." The present author sees no reason why *C. indica* IX, *C. indica* XLVII, *C. indica* LV, *C. bombayensis* no. 8, and *C. bombayensis* no. 9 were not included. Although in one of these species, *C. indica* XLVII, the exact connections of the flame cell capillaries are not shown, the same is true for *C. indica* XXXVI, which is included in the *ocellata* group.

The position held throughout as to the significance of the excretory system formulae of larvae must be based on the assumption that the elaboration into the system of the adult will proceed with regular divisions of the flame cells of the larva, otherwise the similarities of larval patterns would be of less value. The post-larval development has been followed in only one species of furcocercous cercariae, the cercaria of *Schistosoma japonicum*; in an early agamodistome stage of this species the posterior flame-cell in the body divided and re-established the condition of two flame cells in both anterior and posterior groups, thus compensating for the loss of the flame-cell in the discarded tail. From this it would seem that some flame-cells of the cercaria might have potentialities for more rapid division such that the pattern of the adult worm could not be predicted. That this may be the case is also indicated by the unequal development in some larvae of the anterior and posterior collecting tubule systems, although presumably each started with a single flame-cell. Furthermore, the fact that certain larvae, including *C. robusticauda* and *C. gigas*, have one or more flame-cells considerably larger than the others may indicate that these cells are about ready to divide; but whether they will dichotomize once or twice in a post-larval stage before the other cells do so cannot be predicted. It is extremely important that the excretory system pattern be worked out for the early post-larval stages of a number of furcocercous cercariae; unhappily only a few life histories are known and so the materials for such studies are limited.

A fact which makes the use of the excretory system not very feasible, at least for practical purposes, is the great difficulty with which the pattern is determined. Cort, Faust and others have called attention to the tediousness of the study involved, and their experiences are born out by the studies of the present author on more than forty larval species. It is reasonably certain that the patterns described for a number of cercariae will have to be revised when these species are restudied; a mistake in locating the point at which any flame-cell capillary empties into the lateral collecting tubule will change the formula. Where the figure does not clearly show the connections, it may be impossible to decide what formula would represent the actual conditions.

In the scheme to be presented below the presence or absence of a pharynx is the first consideration for the division of the furcocercous larvae into two main groups; it is held that this character is of more significance than the presence or absence of a ventral sucker. This view is supported by Stunkard's (1923) studies on adult blood-inhabiting trematodes from reptiles, and his discussion of the relationships of these forms in fishes, reptiles, birds and mammals, a discussion in part previously taken up by Odhner (1912) and Ward (1921). These studies indicate that the blood flukes constitute a natural group. Two of the three families, the Schistosomatidae and the Spirorchidae, include forms which in the older classification would have been placed in the widely separate groups of Monostomes and Distomes. As all of these adults lack muscular pharynges, it would seem that the presence or absence of a pharynx is of great significance, while the possession or lack of a ventral sucker is relatively unimportant. Numerous other studies have shown that the monostomes were probably derived from the distomes by a gradual loss of the ventral sucker. Furthermore, some pharyngeal furcocercous larvae are now known to develop into members of the Holostomata, all of which possess pharynges. Accordingly, in the classification in this paper a division is first made between the pharyngeal and the apharyngeal forms, thus giving much more emphasis to this character than Sewell did; each of these groups is then further divided into brevifurcate and longifurcate larvae; and the monostome and distome members of each of the four resulting groups are separately considered.

An attempt has been made to include all furcocercous larvae for which there are adequate descriptions. As relatively few are described with respect to the exact pattern of the excretory system, all other points of morphology have been taken into consideration; even then it has been necessary to place many cercariae in a separate list of unclassified forms. If Faust's emphasis on the excretory system as the best criterion for the formation of natural groups were strictly followed, a number of larvae would be otherwise allocated in the scheme. To express the degree of development of the excretory system, which is taken into account in the formation of the final groups, the formula used by Sewell has been employed with a slight modification; for example, the formula for the cercaria of *Schistosoma japonicum* is $2\times 3(+1)$, where two represents the two sides of the body, three, the number of flame-cells in one lateral half of the body, and, $(+1)$, the flame cell in one lateral half of the tail.

By far the greater number of the apharyngeal larvae have furcae which are shorter than one-half the tail-stem length; and the opposite is true of the pharyngeal forms, in which thirty-eight out of forty-one are longifurcate, with furcae approximately equal to, or in some cases longer than the tail-stem. The brevifurcate and longifurcate larvae differ in other characters than the relative lengths of furcae and tail-stem, although the terms are retained as convenient designations for the groups. They are compared below.

Brevifurcate Larvae	Longifurcate Larvae
Furcae usually less than one-half the tail-stem length; frequently sharply delimited from the tail-stem.	Furcae longer than one-half the tail-stem, sometimes exceeding it; usually not sharply delimited.
Tail-stem diameter less than that of body; usually attached somewhat ventrally, sometimes decidedly so, such that a dorso-ventral mount is rare.	Tail-stem diameter approximately equal to that of body when fully extended; attached terminally, dorso-ventral mount the usual one.
Furcal fin-folds sometimes present.	Furcal fin-folds absent.
Body frequently very hyaline.	Body usually crowded with small parenchyme cells.
Eye-spots may be present.	Eye-spots usually absent.
Anterior organ a very highly modified oral sucker, with anterior thin-walled and posterior muscular portions; head gland usually present.	Anterior organ less highly modified; cells which possibly represent a head gland present in but a few larvae.
Ventral sucker usually much smaller in diameter than anterior organ; very protrusible and often held protruded.	Ventral sucker frequently large, in some cases of greater diameter than anterior organ.
Penetration glands very large; frequently divided into anterior coarsely granular and posterior finely granular cells.	Penetration glands small in proportion to body; no differentiation into anterior and posterior sets. Usually coarsely granular, and acidophilic in sections.
Penetration gland duct openings frequently capped by hollow piercing spines.	Solid piercing spines more frequent than hollow ones.
Excretory openings at tips of furcae. Never more than one pair of flame cells in proximal part of tail-stem.	Excretory openings typically mid-furcal. Usually two pairs of tail-stem flame cells, seldom confined to a strictly proximal location.

Tail-stem wall usually provided with powerful longitudinal muscles. Caudal glands not conspicuous; when present, are not arranged in pairs along caudal excretory tube.	Tail-stem wall frequently annulated; tail less powerful and more transparent. Conspicuous, more or less regularly paired caudal glands in a number of species.
Tail-stem and furcae usually spined; no sensory hairs. Furcae almost cylindrical in some larvae.	Tail-stem usually devoid of spines; furcae may be spined; sensory hairs on the tail-stems of several larvae. Furcae never cylindrical, usually much flattened.
Alimentary canal opens more or less ventrally as a capillary tube; ceca absent or at most very short.	Alimentary canal usually opens terminally or subterminally; esophagus a fair-sized tube; ceca usually well-developed, frequently reaching almost to posterior end of body.

APHARYNGEAL CERCARIAE

It is quite probable that some of the larvae included under this heading will be found, upon more careful study, to possess pharynges. Certain few larvae have been placed in sub-groups of the pharyngeal forms, in cases where other morphological characters strongly justify it, and point to the possible incompleteness of the description with respect to the pharynx.

APHARYNGEAL BREVIFURCATE CERCARIAE

This group has been most intensively studied, due to the fact that the larval forms of the human schistosomes are included here; accordingly the data for these cercariae permit the formation of a number of groups, on the basis of morphology in general, and in particular the pattern of the excretory system. The first division is into distomes and monostomes. These two groups are rather sharply divided from each other on the basis of several characters which will be discussed later.

APHARYNGEAL BREVIFURCATE DISTOME CERCARIAE

(Sewell's Group 1)

Group A (*japonicum* of Sewell)
    Cercaria of *Schistosoma japonicum*
    Cercaria of *Schistosoma haematobium*
    Cercaria of *Schistosoma mansoni*
    Cercaria indica XXX
    Cercaria in Blacklock and Thompson 1924

It is now clear that all members of Group A have identical excretory system patterns; this consists of three pairs of flame cells in the body and one pair in the tail-stem, formula $2\times3(+1)$. It has already been noted that the ciliated areas in the excretory vesicle arms were probably mistaken by previous workers for flame cells, thus accounting for the larger numbers reported by Miyairi and Suzuki (1914), Ogata (1914) and Iturbe (1917). The same perfect agreement is not found in the penetration gland equipment. The varying number and character of these gland cells in the members of this group have been reviewed in numerous places in the historical section, as have also the conflicting statements concerning them within what is believed to be a single species. Either the observations have been faulty in some cases or there are more species of schistosomes than has been suspected.

Group B (*spindale* of Sewell, in part)
  Cercaria B of Kemp
  Cercaria of *Schistosoma spindale*
  Cercaria indica XLVII

The last two species have four pairs of flame cells in the body and one pair in the tail-stem, formula $2 \times 4(+1)$. The number of penetration glands is identical in these two also, namely two anterior pairs with coarsely granular protoplasm and three posterior pairs with finely granular protoplasm; in *C. indica* XLVII all five pairs are acidophilic, whereas the three posterior pairs of the cercaria of *S. spindale* are basophilic. *Cercaria* B is included here provisionally, chiefly on the basis of number and character of the penetration glands; the excretory system is unknown. This group has not been modified from Sewell, except by the addition of *Cercaria* B.

Several other forms, which have superficial characters of the schistosomes, but are not sufficiently known to be definitely placed, are included here for the sake of completeness. In the single figure given for it, *C. blanchardi* closely resembles the human schistosome larvae; Lutz (1919: 112) is of the opinion that da Silva studied the cercaria of *S. mansoni*. The cercaria in Leiper (1915, Fig. 46), was considered by him to be a schistosome larva; the figure shows it to have the general characteristics of these larvae. The cercaria in Manson-Bahr and Fairley (1920, Pl. III, Fig. 5), also seems to belong here; as already noted by Sewell, these authors were in error to suppose it to be the same as the form which Leiper provisionally called *C. bilharziella*, which has eye-spots, as these structures appear early in development and the figure given by them is of a mature cercaria, without eyespots. According to Cawston (1922c), *C. crispa* is a synonym of the cercaria of *S. haematobium*, and *C. spinosa* is possibly a synonym of the cercaria of *S. mansoni*.

Group C (*douthitti* of Sewell, in part)
  Cercaria douthitti
  Cercaria C of Kemp
  Cercaria of *Schistosomatium pathlocopticum*

This group was created to contain *C. douthitti* and *C. elephantis*; these two larvae are different in certain respects and have been placed in separate groups (Miller, 1924). They differ in character and location of the penetration gland cells; and almost the entire posterior half of the body of *C. elephantis* is filled with a mass of cells not represented in *C. douthitti*.

C. douthitti, the type of the reconstituted group, has the flame-cell formula $2\times5(+1)$. Its close resemblance to the cercaria of *Schistosomatium pathlocopticum*, except in the number of penetration gland cells, has been pointed out by Tanabe (1923); the excretory systems are identical in the number of flame cells. The knowledge of *Cercaria* C is confined to data from preserved material; it belongs here on the basis of general similarity.

Groups A, B and C differ chiefly in the complexity of the excretory system; the members have from three to five pairs of flame cells in the body. Probably all of these larvae will be included in the family Schistosomatidae.

Group D (*elvae*)
- *Cercaria ocellata*
- *Cercaria bombayensis* no. 19
- *Cercaria elvae*
- *Cercaria gigantea*

The reason for dissolving the Ocellata group of Sewell was stated under the description of *C. elvae*; here also was discussed the similarities of the four larvae placed in this group. These forms are especially interesting in that they possess many characters of the schistosome cercariae, and yet differ in having much more elongate bodies, pigmented eye-spots, and possibly furcal fin-folds in *C. ocellata*; these are the only four brevifurcate larvae which do not fall strictly within the definition, but have furcae somewhat longer than one-half the tail-stem. Soparkar (1921a) suggested that *C. bombayensis* no. 19 "belongs probably to the 'Bilharziella' group of cercariae"; the present author knows of no evidence in support of this statement.

Group E (*bombayensis* no. 13)
- *Cercaria bombayensis* no. 13
- *Cercaria indica* XXV
- *Cercaria wardi*

The morphological basis for grouping these forms together was discussed in detail under the description of *C. wardi*. *C. bombayensis* no. 8, an intermediate between the apharyngeal brevifurcate monostomes and distomes, will be discussed under the group of brevifurcate monostomes; it is somewhat similar to *C. indica* XXV.

Group F (Wynaad)
Cercaria indica XXXVI

Although this larva is in general like the members of Group E, it is here tentatively held as the representative of another group; this is partly because of the lack of the so-called posterior mucin gland, of unknown function and unique to the three members of Group E. Furthermore, it possesses a large number of small penetration gland cells, in two differentiated sets; and lacks a head gland, found in Group E larvae.

Group G (*elephantis*)
Cercaria elephantis
Cercaria echinocauda

C. elephantis was placed by Sewell in the Douthitti group, and *C. echinocauda* in the Gigas group. The excretory formula is known for *C. elephantis* only, $2 \times 5(+1)$. The author studied living material of this species, collected from the same region of Michigan as was Cort's material; it was discovered that in addition to the numerous small gland cells which distend the posterior part of the body, designated as cephalic glands (Cort, 1917:53), there are also two distinct sets of penetration gland cells. Five pairs are centered around the ventral sucker; three pairs of small cells are anterior to two pairs of larger cells. Study of some alcoholic material of *C. echinocauda* (by Miller, 1924) revealed the presence of the same sort of a posterior cell mass as is found in *C. elephantis*; the number, location and relative size of the two sets of penetration glands are also the same.

Group H (*gigas* of Sewell, in part)
Cercaria gigas

The unique type of excretory system reported for this larva shows that it is very different from any other described form. However, it does not depart in other of the important characters as far from the Group F or G types as might be concluded from Faust's original description (1918a). The author's material of *C. gigas*, as well as co-type slides in the collection of Professor Ward, shows that an alimentary canal like that described for *C. wardi* is present, contrary to Faust's statement that pharynx, esophagus and ceca are wanting. There are five pairs of large penetration gland cells anterior to the germ-cell mass, and two pairs posterior to it. Sewell regarded *C. gigas* as the highest stage of development in his Group 1, representing the culmination of alimentary canal retrogression and excretory system development. His conclusion may be justified on the basis of the large number of flame-cells; but the larva is not an example of extreme degeneration of the alimentary canal.

Miscellaneous group
- *Cercaria bilharziella*
- *Cercaria oculata*
- *Cercaria parvoculata*
- *Cercaria patialensis*

These larvae complete the list of those known to be apharyngeal brevifurcate distomes. The exact positions of the first three cannot be determined until more complete descriptions are available. All four have pigmented eye-spots, and the last three are reported to develop in rediae. *C. patialensis* has a unique excretory system and tail-stem, and has the highest degree of development of the genital system found in the furcocercous larvae. It cannot now be placed in relation to any other known form.

A key for the separation of these sub-groups of the apharyngeal brevifurcate distomes has been published (Miller, 1923).

APHARYNGEAL BREVIFURCATE MONOSTOME CERCARIAE

Only two of these forms were known to the earlier workers: *C. cristata* and *C. microcristata*. To these are to be added *C. indica* IX, XIII, XXXIX, and LV, *C. bombayensis* no. 8, and the cercaria of *Sanguinicola inermis*. No members have been reported from the fresh waters of this country; one unnamed marine species has been described by Linton (1915). As the present author has no personal aquaintance with these forms, the attempt to critically consider Sewell's disposition of them will be based entirely on a study of the literature. His analysis took into account all species except the cercaria of *Sanguinicola inermis*, and incorrectly included *C. varicans*, which is clearly figured by Abildgaard as a longifurcate larva, with furcae almost if not quite as long as the tail-stem. Sewell took the group name Lophocerca from Lühe; the most striking features of these larvae are the presence of a body crest and the absence of any trace of pharynx or intestine. The group can not be subdivided, as Sewell's species are the only ones for which the excretory and penetration gland systems are known.

The original account of *C. cristata* has been studied, as have also the numerous subsequent references to it by other workers; it seems probable, as Sewell suggested, that more than one larva has been included under this specific name. Because of its inadequate description Scheuring concluded that the identity of this species with the cercaria of *Sanguinicola inermis* was doubtful. Ercolani described *C. microcristata* as similar to *C. cristata* except for smaller size. Both *C. bombayensis* no. 8 and the cercaria of *Sanguinicola inermis* have been described in sufficient detail so that they could readily be recognized. As Sewell noted, the former of these two is intermediate between the monostomes and distomes, both in the presence of a small body crest and of a group of cells probably representing a rudimentary ventral sucker. The descriptions of the four new Indian species contribute many details of structure not previously known for brevifurcate monostomes; Sewell believes that *C. indica* XIII is only questionably distinct from *C. cristata.*

Lophocerca Group of Sewell, in part
- *Cercaria cristata*
- *Cercaria microcristata*
- Cercaria of *Sanguinicola inermis*
- *Cercaria bombayensis* no. 8
- *Cercaria indica* IX
- *Cercaria indica* XIII
- *Cercaria indica* XXXIX
- *Cercaria indica* LV

Here are briefly recapitulated some of the characters enumerated by Sewell: the body is provided with a dorsal longitudinal crest; a definite oral sucker is absent, and the anterior end forms a conical protrusible and retractile snout; there is no trace of pharynx or intestine; where the excretory system has been worked out, the formula is $2\times3(+0)$; development is in small rounded or oval sporocysts. It is to be noted that there are no flame-cells in the tail-stem of these larvae, which makes them unique among furcocercous forms.

APHARYNGEAL LONGIFURCATE CERCARIAE

In general these larvae resemble the pharyngeal longifurcates more closely than other apharyngeal larvae, either distomes or monostomes. Nevertheless, it is thought that the presence or absence of a pharynx is of more significance than similarity in larval characters. The few cercariae under this heading are not all well-described; they do not seem to form a homogeneous group, and the disposition of them into sub-groups will have to be postponed until more species are described.

Apharyngeal Longifurcate Distome Cercariae
- *Cercaria gracillima*
- *Cercaria tuberistoma*
- *Cercaria gladii*
- *Cercaria minima*
- *Cercaria indica* XXII
- Cercaria in Lagrange 1923:175

Apharyngeal Longifurcate Monostome Cercariae
- *Cercaria indica* XXVII

This is the only unquestionable representative of this group. Repeated studies on *C. multicellulata* failed to show any trace of a pharynx, but observation was hindered by the numerous refractile parenchyme cells crowding the body; and this larva is so strikingly similar in most respects to *C. hamata*, which has a definite pharynx, that it has been classed with the pharyngeal forms. *C. indica* XXVII is not very similar to any of the six apharyngeal longifurcate distomes, from which group it would presumably have been derived by loss of the ventral sucker. Its resemblance to the schistosomes in two characters was pointed out by Sewell, that is, the presence of an anterior protrusible penetrating organ and an exactly similar excretory system.

PHARYNGEAL CERCARIAE

Approximately one-half of the furcocercous cercariae are known to possess pharyngeal sphincters. The first division of these, as with the apharyngeal cercariae, is made between the longifurcate forms, of which there are thirty-eight, and the three brevifurcate forms.

PHARYNGEAL BREVIFURCATE CERCARIAE

Pharyngeal Brevifurcate Distome Cercariae
- *Cercaria scripta*
- *Cercaria parthenicola*
- *Cercaria octadena*

Until more complete accounts of these forms are available, including analyses of the excretory system patterns in living material, little can be said of their relationships; the first two were reported to develop in rediae. It is surprising that Faust believes *C. octadena* to be the larva of *Schistosoma bovis*; he figured it with a small pharynx. This is the only recent account which assigns a pharyngeal larva to the family Schistosomatidae.

Pharyngeal Brevifurcate Monostome Cercariae
- No representatives

PHARYNGEAL LONGIFURCATE CERCARIAE

This is the largest group of furcocercous larvae, and the one concerning the adult affinities of which nothing was known until the work of Ruszkowski, Lutz, and Szidat. Many of the members are very incompletely described, and relatively few are known with respect to the excretory system pattern. This system was not described in the cercaria of *Hemistomum alatum*; it was only partially figured by Szidat in *Cercaria* A, which develops into *Tetracotyle typica*. Hence other cercariae for which the complete excretory patterns are known cannot be placed in relation to these known holostome larvae.

PHARYNGEAL LONGIFURCATE DISTOME CERCARIAE

(Sewell's Group 2, Series 1)

In his consideration of these forms Sewell created three sub-groups, each to contain a single cercaria; five other incompletely described larvae were referred either tentatively to one of these sub-groups, or to the series. At the present time there are thirty-one of these cercariae, and probably other members which are classed among the partially known and unplaced forms. The penetration glands have been described in twenty-one larvae, and the entire excretory system is known for eleven species, with incomplete descriptions for five more. Only sixteen larvae have been described with respect to both systems. In spite of this great increase over the number considered by Sewell, the present author has not been able to establish a satisfactory scheme of relationships, due to the paucity of morphological data. The great diversity, even in the eleven fully described species, of flame cell number and of nature and number of the penetration glands makes it almost impossible to arrange them in any feasible systematic scheme. The author has been unable to find correlation between any two of the following: body, tail-stem and furcal lengths; number and arrangement of flame cells; number, location in body, and character of penetration gland cells; type of alimentary canal; size and location of ventral sucker.

The following belong here; formulae for the excretory system are included.

Cercaria A (Szidat)	
“ *aculeata*	
“ B (Szidat)	
“ *bdellocystis*	
“ *bombayensis* no. 9	2×10(+2)
“ *burti*	2×6(+2)
“ C (Szidat)	
“ *chrysenterica*	2×7(+2)
“ *divaricata*	
“ *douglasi*	2×5(+2)
“ *emarginatae*	2×5(+2)
“ *fissicauda*	
“ *furcicauda*	2×5(+1)
“ *gracilis*	
“ *gyrinipeta*	
Cercaria of *Hemistomum alatum*	
“ in Hesse 1923	2×7(+2)
Cercaria indica I	2×5(+1)
“ *indica* II	2×10(+2)

“ *letifera*
“ *longissima*
Cercaria in Manson-Bahr and Fairley (1920, Pl. III, Fig. 7)
Cercaria minuta
“ *molluscipeta*
“ *pseudo-vivax*
“ *quattuor-solenata* $2\times6(+2)$
“ *redicola*
“ *robusticauda* $2\times6(+1)$
“ *secobii*
“ *tenuis* $2\times5(+2)$

PHARYNGEAL LONGIFURCATE MONOSTOME CERCARIAE

These larvae fall into two closely circumscribed groups. The first is the one which Sewell set up to contain *C. vivax* and two new species which he described. All members have a unique type of excretory system in the body, and three pairs of flame-cells in the tail-stem; in no case do the numerous penetration gland cells extend into the posterior half of the body. Only one larva, *C. leptoderma*, is to be added to this group; neither *C. pseudo-vivax* nor the cercaria in Leiper and Atkinson 1915 have been shown to have the highly developed excretory system, although Faust has included the former in the Vivax group. *C. indica* XXXIII (*tetis* group of Sewell) has the same unique arrangement of collecting tubules in the body, but only five pairs of flame-cells in the body and two pairs in the tail-stem; it probably is the sole known representative of a sub-group. Although *C. vivax* possesses a ventral sucker, this structure is either entirely lacking or represented by a mass of cells in the other members. It would seem that the very unique development of the excretory system, together with the three pairs of flame-cells in the tail-stem, is of more significance than the presence or absence of a ventral sucker.

Vivax group (Sewell's Group 3)
Cercaria vivax
Cercaria indica XV
Cercaria indica LVIII
Cercaria leptoderma

Tetis group of Sewell
Cercaria indica XXXIII

The remaining group contains *C. rhabdocaeca*, *C. hamata*, and *C. multicellulata*. As noted above, a pharynx was not observed in the last-mentioned larva. It is included here because of many striking similarities, which have been discussed under the description of *C. hamata*. All three species have eight pairs of flame cells in the body and two pairs in the tail-stem.

Rhabdocaeca group
- *Cercaria rhabdocaeca*
- *Cercaria hamata*
- *Cercaria multicellulata*

FURCOCERCOUS CERCARIAE OF UNCERTAIN POSITION

The following forms have been incompletely described with respect to the presence of a pharynx, the character of the excretory system, or the penetration glands. In some cases, as where a microphotograph is given without description in the text, it is not clear whether a ventral sucker is present. The probable groupings of all are given, on the basis of all known characters.

Brevifurcate Distomes
- *Cercaria andoi*
- Cercaria in Lagrange (1923:177); probably apharyngeal
- Cercaria in Manson-Bahr and Fairley (1920, Pl. III, Fig. 5); probably apharyngeal

Brevifurcate Monostomes
- *Cercaria senoi*
- Cercaria in Lühe (1909:206)

Longifurcate Distomes
- *Cercaria furcata*
- " *inversa*
- Cercaria in Lühe (1909:204)
- " in Leiper and Atkinson (1915)
- *Cercaria paludinarum*
- " *pseudo-divaricata*
- " *quieta*
- " *shinchikuensis*
- " *valdefissa*

Longifurcate Monostomes
- *Cercaria varicans*

Unknown
- *Cercaria bipartita*
- Cercaria in Lagrange (1919)
- *Cercaria ocellifera*; brevifurcate, probably apharyngeal

CHECK-LIST OF FURCOCERCOUS CERCARIAE

The following list contains the specific names and references to the original descriptions of all furcocercous cercariae, both fresh-water and marine; the latter, included for the sake of completeness, are separately grouped at the end. The synonyms and descriptive modifications of Cercaria are also given. In cases where the original descriptions are very brief or entirely inadequate, and a later study has been comprehensive, this latter reference is also given.

FRESH WATER SPECIES

Cercaria A in Kobayashi 1922:14, for Cercaria of Seno 1903; renamed *C. senoi* in Faust 1924:296
" A in Szidat 1924:301-303; text-fig. 1
" *aculeata* in Ercolani 1882:47; Pl. 1, figs. 42-46
" sp. IX in Ando 1918:616; renamed *Cercaria* C in Kobayashi 1922:14; renamed *C. pseudodivaricata* in Faust 1924:296
" sp. X in Ando 1918:617; renamed *Cercaria* B in Kobayashi 1922:14; renamed *C. andoi* in Faust 1924:296
" *andoi* in Faust 1924:296, for Cercaria sp. X in Ando 1918:617 and *Cercaria* B in Kobayashi 1922:14
" B in Kemp 1921:231-232; text-fig. 1, *d*, *e*
" B in Kobayashi 1922:14, for Cercaria sp. X in Ando 1918:617; renamed *C. andoi* in Faust 1924:296
" B in Szidat 1924:303; text-fig. 2
" VI in von Baer 1827:627; Pl. 31, figs. 6a, 6b; synonym of *Malleolus furcatus* in Diesing 1850:295; synonym of *C. furcata* in Moulinié 1856:168
" *bdellocystis* on page 77, for *Dicranocercaria bdellocystis* in Lutz 1921:126
" *bilharziella* in Leiper 1915:259
" *bilharziellalunata* nom. nud., synonym of *C. oculata* according to Faust 1920b:216
" *bipartita* in Sonsino 1897:253
" in Blacklock and Thompson 1924:212-220; 3 text-figs.
" *blanchardi* in da Silva 1912:398-400; 3 figs.
" *bombayensis* no. 8 in Soparkar 1921a:24-26; Pl. III, 4 figs.
" *bombayensis* no. 9 in Soparkar 1921a:26-28; Pl. IV, 4 figs.
" *bombayensis* no. 13 in Soparkar 1921a:29-30; Pl. V, 4 figs.
" *bombayensis* no. 19 in Soparkar 1921a:30-32; Pl. VI, 3 figs.
" *burti* in Miller 1923; in the present paper, page 41
" C in Kemp 1921:232; text-fig. 1, *f*
" C in Kobayashi 1922:14, for Cercaria sp. IX in Ando 1918:616; renamed *C. pseudodivaricata* in Faust 1924:296
" C in Szidat 1924:303-304; text-figs. 3a, 3b
" *chrysenterica* in Miller 1923; in the present paper, page 47
" *crispa* in Cawston 1920a:439, synonym of the cercaria of *Schistosoma haematobium* according to Cawston 1922c:247
" *cristata* in LaValette St. George 1855:23; Pl. II, K

“ D in Kobayashi 1922:15, for Cercaria sp. XIV in Nakagawa 1915:116; renamed *C. paludinarum* in Faust 1924:296
“ *divaricata* in Faust 1924:256; Pl. II, fig. 12
“ *divaricauda* in Faust 1924:283; Table I, page 296; Table II, opp. page 298; error for *C. divaricata*
“ *douglasi* in Cort 1917:53-54; text-fig. 2, C
“ *douthitti* in Cort 1914:77-78; text-fig. 10; 1915:49-52; Pl. VII, figs. 55-64
“ E in Kobayashi 1922:15, for Cercaria sp. XV in Nakagawa 1915:116; renamed *C. shinchikuensis* in Faust 1924:296
“ *echinocauda* in O'Roke 1917:170-171; Pl. V, figs. 39-45; according to Miller 1924: 146-148; Pl. VI, figs. 4, 6
“ *elephantis* in Cort 1917:52-53
“ *elvae* in Miller 1923; in the present paper, page 30
“ *emarginatae* in Cort 1917:53; text-fig. 2, B
“ F in Kobayashi 1918:61; text-figs. 11, 12; 1922:15; Pl. IV, figs. 1, 2; renamed *C. parthenicola* in Faust 1924:296
“ *fissicauda* in La Valette St. George 1855:21; Pl. II, figs. VI and H
“ *furcata* in Nitzsch 1817:49; Pl. 2, figs. 12-18
“ *furcicauda* in Faust 1919c:336-337; text-fig. 6
“ G in Yoshida 1917:117; Pl. II, figs. 17, 18, text-fig. 11; in Kobayashi 1922:16; renamed *C. scripta* in Faust 1924:296
“ *gigantea* in Faust 1924:257; Pl. II, fig. 13
“ *gigas* in Faust 1918a:105-107; Pl. II, figs. 25-30
“ *gladii* in Cawston 1918a:96; according to Faust 1919a:164-165; Pl. XVIII, fig. 1
“ *gracilis* in La Valette St. George 1855:20; Pl. I, fig. XIII
“ *gracillima* in Faust 1917:122; Faust 1918:80; figs. 142-154, 161
“ *gyrinipeta* in the present paper, page 77, for *Dicranocercaria gyrinipeta* in Lutz 1921:126
“ H in Kobayashi 1922:16, for the cercaria of *Schistosoma japonicum* in Miyairi and Suzuki 1914
“ *hamata* in Miller 1923; in the present paper, page 55
“ of *Hemistomum alatum* in Ruszkowski 1922:237-250; 3 text-figs.
“ in Hesse 1923:227-231; 8 text-figs.
“ I in Kobayashi 1922:17, for Cercaria sp? in Suzuki and Nishio 1914; renamed *C. longissima* in Faust 1924:297
“ *indica* I in Sewell 1922:268-270; Pl. XXIX, figs. 1, 2
“ “ II in Sewell 1922:271-274; Pl. XXIX, figs. 3, 4
“ “ IX in Sewell 1922:47-50; Pl. IV, figs. 1, 3
“ “ XIII in Sewell 1922:50-53; Pl. IV, figs. 3, 4
“ “ XV in Sewell 1922:280-288; Pl. XXXI, figs. 1, 2
“ “ XXII in Sewell 1922:276-278; Pl. XXX, figs. 1, 3
“ “ XXV in Sewell 1922:260-262; Pl. XXVIII, figs. 1-3
“ “ XXVII in Sewell 1922:59-61; Pl. V, fig. 3
“ “ XXX in Sewell 1919:425; Pl. XXV; 1922:251-254; Pl. XXVII, figs. 1-3
“ “ XXXIII in Sewell 1922:292-294; Pl. XXX, figs. 4, 5
“ “ XXXVI in Sewell 1922:263-265; Pl. XXVIII, figs. 4, 5
“ “ XXXIX in Sewell 1922:53-55; Pl. V, fig. 1
“ “ XLVII in Sewell 1922:255-257; Pl. XXVII, figs. 4, 5
“ “ LV in Sewell 1922:55-57; Pl. V, fig. 2
“ “ LVIII in Sewell 1922:290-291; Pl. XXXI, fig. 3
“ *inversa* in O'Roke 1917:169-170; Pl. V. figs. 46-51
“ J in Kobayashi 1922:17; Pl. IV, figs. 3-5; renamed *C. redicola* in Faust 1924:297

“ sp. no. 1 in Lagrange 1919:386
“ in Lagrange 1923:175
“ in Lagrange 1923:177
“ in Leiper 1915, text-fig. 46; 1918:239, 241
“ in Leiper and Atkinson 1915:202; fig. 6
“ *leptoderma* in Faust 1922a:255-257; Pl. XXI, figs. 7-11
“ *letifera* in Fuhrmann 1916:389-393; Pl. I, figs. 1-8, 10
“ *longissima* in Faust 1924:297, for Cercaria sp? in Suzuki and Nishio 1914 and *Cercaria* I in Kobayashi 1922:17
“ in Lühe 1909:204
“ in Lühe 1909:206
“ in Manson-Bahr and Fairley 1920:54; Pl. III, fig. 5
“ in Manson-Bahr and Fairley 1920:54; Pl. III, fig. 7
“ *marcianae* in LaRue 1917:3; Pl. I, figs. 1, 2; synonym of *Agamodistomum marcianae* in Cort 1918a:130
“ *microcristata* in Ercolani 1881:56-57; Pl. I, figs. 23-27
“ *minima* in Faust 1919:92, for *C. minor* Faust 1918a, preoccupied by Lebour 1912:424
“ *minor* in Faust 1918a:107-109; Pl. II, figs. 31-33; synonym of *C. minima* in Faust 1919:92
“ *minuta* in Ercolani 1882:46-47; Pl. I, figs. 1-6
“ *molluscipeta* in the present paper, page 77, for *Dicranocercaria molluscipeta* in Lutz 1921:126
“ *multicellulata* in Miller 1923; in the present paper, page 50
“ sp. XIV in Nakagawa 1915:116; fig. 14; renamed *Cercaria* D in Kobayashi 1922:15; renamed *C. paludinarum* in Faust 1924:296
“ sp. XV in Nakagawa 1915:116; fig. 15; renamed *Cercaria* E in Kobayashi 1922:15; renamed *C. shinchikuensis* in Faust 1924:296
“ *ocellata* in LaValette St. George 1855:22; Pl. II, fig. V
“ *ocellifera* in the present paper, page 73, for *Dicranocercaria ocellifera* in Lutz 1919: Pl. 41, figs. 64-66
“ *octadena* in Faust 1921d:11-12; Pl. III, fig. 1
“ *oculata* in Cawston 1917:132
“ *paludinarum* in Faust 1924:296, for *Cercaria* sp. XIV in Nakagawa 1915:116, and *Cercaria* D in Kobayashi 1918:15
“ *parthenicola* in Faust 1924:296, for *Cercaria* F in Kobayashi 1918:61
“ *parvoculata* in Cawston 1919a:401, according to Faust 1919a:165; Pl. XVIII, fig. 2
“ *patialensis* in Soparkar 1924:933-941; Pl. LXII, figs. 1-12
“ *pseudo-divaricata* in Faust 1924:296, for Cercaria sp. IX in Ando 1918:616, and *Cercaria* C in Kobayashi 1922:14
“ *pseudo-vivax* in Faust 1924:255; Pl. II, fig. 11
“ *quattuor-solenata* in Faust 1919c:337-338; text-fig. 8
“ *quieta* in O'Roke 1917:171-172; Pl. IV, figs. 32, 33, 37
“ *redicola* in Faust 1924:297, for *Cercaria* J in Kobayashi 1922:17
“ *rhabdocaeca* in Faust 1919c:338-339; text-fig. 9
“ *robusticauda* in Faust 1919c:337; text-fig. 7
“ of *Sanguinicola inermis* in Scheuring 1920:227; 1 text-fig.; Scheuring 1922:296-299; Pl. 23; fig. 12; text-fig. C
“ of *Schistosoma haematobium* in Leiper 1915:258; text-fig. 47; according to Faust 1920a:192-193; Pl. XV, figs. 1, 3; according to Bettencourt and da Silva 1922:1050; 1 text-fig.
“ of *Schistosoma japonicum* in Miyairi and Suzuki 1914:187-197; 1 fig.; according to Cort 1919:485-507; text-figs. 1-3

" of *Schistosoma mansoni* in Leiper 1915:258; text-fig. 45; according to Faust 1920a: 192-193; Pl. XV, figs. 2, 5, 6; according to Khalil 1922: 27-34; text-figs. 1, 2
" *of Schistosoma spindale* in Soparkar 1921:1-22; Pl. I, II
" of *Schistosomatium pathlocopticum* in Tanabe 1923:183-186; Pl. XIV
" *scripta* in Faust 1924:296, for *Cercaria* G in Yoshida 1917:117, and *Cercaria* G in Kobayashi 1922:16
" *secobiana* in Cawston 1917:133; synonym of *C. secobii* in Cawston 1917b:91
" *secobii* in Cawston 1915:1427; according to Faust 1921d:12; Pl. III, fig. 2
" in Seno 1903:309; Pl. VII, figs. 2A, B; named *Cercaria* A in Kobayashi 1922:14; renamed *C. senoi* in Faust 1924:296
" *senoi* in Faust 1924:296, for the cercaria in Seno 1903:309, and *Cercaria* A in Kobayashi 1922:14
" *shinchikuensis* in Faust 1924:296, for Cercaria sp. XV in Nakagawa1915:116 and *Cercaria* E in Kobayashi 1918:15
" *spinosa* in Cawston 1919:189, synonym of the cercaria of *Schistosoma mansoni* (?) in Cawston 1922c:247
" in Suzuki and Nishio 1914:587; 3 figs; named *Cercaria* I in Kobayashi 1922:17, renamed *C. longissima* in Faust 1924:297
" *tenuis* in Miller 1923; in the present paper, page 45
" *tuberistoma* in Faust 1917:123; 1918:82-83; Pl. IX, figs. 155-158
" *valdefissa* in the present paper, page 77, for *Dicranocercaria valdefissa* in Lutz 1919:Pl. 41, figs. 67, 68
" *varicans* in Abildgaard 1794:89; Pl. IIIa, figs. 1-4
" *vivax* in Sonsino 1892:137; Pl. XVIII, fig. 3; according to Looss 1896:210-223; Pl. XV, figs. 162-177
" *wardi* in Miller, 1923; in the present paper, page 35

MARINE SPECIES

Cercaria dichotoma in Müller 1850; according to La Valette St. George 1855: Tab. II, fig. 1
" *discursata* in Ssinitzin 1911:67; figs. 45-48
" of *Haplocladus minor*? in Odhner 1911b:105
" in Haswell 1902:497-511; Pls. 19, 20, figs. 1-31
" in Linton 1915:115-118; text-figs. 1-5
" in Linton 1915a:207-208; text-figs. 7, 8
" in Morgan 1891:1137-1139; 1 text-fig.
" *syndosymae* in Pelseneer 1906; 172; Pl. IX, X, figs. 20-22

SYNONYMS

C. (Schizocerca) dichotoma in Diesing 1858:265; synonym of *Cercaria dichotoma*
C. (Schizocerca) fissicauda in Diesing 1858:265; synonym of *Cercaria fissicauda*
C. (Schizocerca) gracilis in Diesing 1858:264; synonym of *Cercaria gracilis*
Cheilostomum varicans in Diesing 1850:293; synonym of *Cercaria varicans*
Dicranocercaria bdellocystis in Lutz 1921:126; synonym of *Cercaria bdellocystis*
Dicranocercaria gyrinipeta in Lutz 1921:126; synonym of *Cercaria gyrinipeta*
Dicranocercaria molluscipeta in Lutz 1921:126; synonym of *Cercaria molluscipeta*
Dicranocercaria ocellifera in Lutz 1919:Pl. 41; synonym of *Cercaria ocellifera*
Dicranocercaria valdefissa in Lutz 1919:Pl. 41; synonym of *Cercaria valdefissa*
Histrionellina fissicauda in Diesing 1858:269; synonym of *Cercaria ocellata*
Lophocercaria fissicauda in Diesing 1858:243; synonym of *Cercaria cristata*
Malleolus furcatus in Ehrenberg 1838:465; synonym of *Cercaria furcata*
Schistocercaria, proposed by Soparkar, 1921, for cercariae known to be the larval stages of schistosomes.

DISCUSSION OF LIFE HISTORIES

Although brief references to the life history studies on furcocercous cercariae are included in the historical review, they are brought together here in order to sum up the present knowledge of the group in this field. Until recently the three species of human schistosome cercariae were practically the only larvae for which the adults were known. *Schistosoma japonicum* was the first which was shown to have as its larval stage a furcocercous cercaria (Miyairi and Suzuki, 1913, 1914). Leiper (1915) subsequently proved that both of the other human schistosomes, *S. haematobium* and *S. mansoni*, also developed directly from such larvae found in certain of the molluscs of Egypt. These findings exploded the theory Looss held persistently for so long, that adult schistosomes developed directly from miracidia without the intervention of an intermediate mollusc host. The life history of another of these forms, *S. spindale*, parasitic in cattle in India, has been experimentally demonstrated (Liston and Soparkar, 1918). Very recently the life cycle of a North American trematode, *Schistosomatium pathlocopticum*, a new genus and species of the family Schistosomatidae, has been worked out (Tanabe, 1923). The larva is a brevifurcate distome very similar to *Cercaria douthitti*; it has been experimentally shown to develop in laboratory rats. Thus five furcocercous cercariae, all brevifurcate distomes, are known to develop into members of the family Schistosomatidae, following direct penetration of epithelial surfaces of the final host.

Previous to this no complete life histories were known; brief notes on a few forms appear in the literature before 1913. In the case of *C. fissicauda* there is an indication of one stage in the life history. Blochmann (1910) noted that this cercaria penetrated and caused the death of several species of fish and of axolotyl and salamander larvae, being found in large numbers in the freshly-examined brain, heart and heart blood. Experiments apparently were not carried on to determine whether the cercariae would develop further in any of these animals. Some unpublished observations of Looss on the life history of *Sanguinicola inermis* were included by Odhner (1911) as an addendum to his discussion of this trematode. Goldfish and carp in aquaria with *Lymnaea auricularia* harboring a furcocercous cercaria became infested in every case with large numbers of young worms, which were found in the mouth cavity and on the gills. In the carp only, these became sexually mature in the blood stream. Only one figure, without an accompaning description, was given for the larva, which is clearly a brevifurcate monostome; although Looss called it *C. cristata*. the information given is not sufficient to establish its identity with this species. Scheuring has raised this question. The adult worms found were *Sanguinicola inermis.* In a parallel case to that of *C. fissicauda* above, *C. letifera* caused the death of five species of fish kept in small aquaria with the mollusc host (Fuhrmann, 1916); death was said to be due to hemorrhages and capillary obstruction caused by migrations of the larvae. Without further experimental proof, Fuhrmann supposed the intermediate host to be one or several species of fish, and the definitive host to be probably a piscivorous fish or bird.

The agamodistome stages of two cercariae were found in *Thamnophis marciana* and *T. eques* by LaRue (1917), who called them *Cercaria marcianae* and *C. vergrandis.* The first, more properly called *Agamodistomum marcianae,* was studied by Cort (1918); on the basis of its excretory and penetration gland systems he concluded that it is the agamodistome stage of a furcocercous cercaria, similar to but not identical with either *C. emarginatae* or *C. douglasi.*

The life history of *Sanguinicola inermis* has been experimentally worked out in detail by Scheuring (1920, 1922); although the larval form is very similar to *C. cristata,* Scheuring concluded that the identity of the two forms is doubtful. The larva reaches the blood stream of its final host, a fish, by direct penetration. The relationship of Sanguinicola, family Aporocotylidae, to the Spirorchidae and Schistosomatidae has been reviewed in the historical section of the present paper.

Several furcocercous cercariae from Brazil have been traced through all stages to tetracotyles, after penetration of an intermediate host; and these, when the proper final host was found by experimental feedings, developed into members of the genus Strigea (Lutz, 1921). In the cases of three new species, *Cercaria molluscipeta, C. gyrinipeta,* and *C. bdellocystis,* the first-named penetrated and continued development in snails, the second in tadpoles, and the third in leeches. One of the most interesting discoveries was that these cercariae do not immediately encyst in the tissues of the intermediate host, but pass a longer precystic stage free in the tissues, during which important structural modifications are undergone. The development of the genital system and the definitive form of the body does not take place until transfer into the final host.

The life history of an European member of the Holostomata *Hemistomum alatum,* has been experimentally determined by Ruszkowski (1922); he cultured the eggs and attempted to infest snails. The miracidia developed in several species of Planorbis, and elongate sporocysts and longifurcate distome cercariae were secured. The description of the latter is not sufficiently detailed to enable them to be placed in a classification scheme. Although the life cycle from cercaria to adult worm has not yet been traced, Ruszkowski's findings supplement those of Lutz on holostomid development. It is now clear that the Holostomata develop from cercariae which have their origin in parthenitae in snails; these, so far as is known, are pharyngeal longifurcate distomes. The mode of development of this group, so long unknown, has now been experimentally determined.

Cercaria vivax may penetrate the skin and perhaps the digestive tube of certain tadpoles so rapidly, under experimental conditions, as to cause death in fifteen minutes (Brumpt, 1922); while the development was not followed out, it was thought that it is the larva of a member of the Holostomata, closely allied to the genus Tylodelphis. The development of another larva, resembling *C. fissicauda*, was followed in tadpoles; this form does not encyst and is said to be a larva of the genus Tylodelphis.

A pharyngeal longifurcate distome cercaria, designated *Cercaria* A, was found by Szidat (1924) to develop into *Tetracotyle typica* in *Lymnaea palustris*. Penetration of the snail host takes place very rapidly, usually in fifteen to twenty seconds, and the larvae rapidly make their way directly to the hermaphrodite gland. There a more or less complete structural reorganization takes place, and only relatively late in development is a cyst secreted. The entire development from cercaria to tetracotyle requires from twenty to twenty-five days; earlier workers have shown that *Tetracotyle typica* develops to a species of Strigea, probably *S. tarda*.

From this survey of the literature it is clear that much light has recently been thrown on the kinship of furcocercous cercariae to certain groups of adult trematodes. The larvae of the Schistosomatidae, and of some, possibly all, of the Holostomata are included among them. *Sanguinicola inermis* of the Aporocotylidae also has a furcocercous larva.

INCIDENCE OF INFECTION OF SNAILS

Collections were made through three years, and the method of handling them changed during this time. At first snails were dissected almost immediately after collection, and only furcocercous infections were recorded; percentages therefore include both mature and immature larvae. During the summer of 1921 the method of isolating to secure emerging cercariae was begun; only mature larvae were found, as the negative snails were not later dissected. However, both furcocercous and other forms were recorded. During 1922-23 a complete infection record was kept, including both furcocercous and other infections, emerging larvae and those found by subsequent dissection of the snails.

MULTIPLE INFECTIONS

As the matter of multiple infections is of some biological interest, the cases found (double infections) are grouped together here.

1. *Planorbis trivolvis* (March 2, 1921) infested with *C. echinocauda* and a redia resembling that of *C. inhabilis.*
2. *Planorbis trivolvis* (March 16, 1921) infested with an unidentified immature furcocercous cercaria and a redia resembling that of *C. inhabilis.*
3. *Physa lordi* (July 8, 1921) infested with an unidentified immature furcocercous larva and the cercaria of *Echinostomum revolutum*?

The third was a single individual given to the author, and so does not appear in the collection records. As all snails were not dissected, it is possible that there were other multiple infections which were not found.

TABLE I

Collection record for 1920-1921; vicinity of Urbana, Illinois.

All snails were crushed; therefore percentages include both mature and immature infections (furcocercous cercariae only).

Species of snail	Place	Date	Number	Infections	Percentages
Planorbis trivolvis........	C	Oct. 12	53	1 (*C. elephantis*)	1.9
Physa gyrina............	C	Oct. 12	17	0	0
Campeloma rufum.......	H	Oct. 30	51	0	0
Planorbis trivolvis........	D	Oct. 30	7	0	0
Planorbis trivolvis........	D	Nov. 27	11	0	0
Planorbis trivolvis........	C	Feb. 16	37	1 (*C. echinocauda*)	2.7
Physa gyrina............	C	Feb. 16	15	0	0
Planorbis trivolvis........	C	Mar. 2	58	1(Double infection No. 1)	1.7
Planorbis trivolvis........	C	Mar. 16	15	1 (Immature Cercaria sp.) 1 (Double infection No. 2)	13.3

Physa gyrina............	C	Mar. 16	10	0	0
Planorbis trivolvis........	C	Mar. 25	18	1 (Immature Cercaria sp.)	5.5
Physa gyrina............	C	Mar. 25	1	0	0
Planorbis trivolvis........	C	Apr. 6	13	1 (*C. wardi*)	7.7
Planorbis trivolvis........	C	Apr. 7	37	2 (Cercaria sp.) 1 (*C. wardi*)	8.1
Planorbis trivolvis........	C	Apr. 19	29	1 (*C. wardi*)	3.4
Physa gyrina............	C	Apr. 19	12	0	0

C, Colvin's Field; D, Drainage Ditch; H, Homer Park.

TABLE II

Collection record, summer of 1921; vicinity of Douglas Lake, Michigan.

Snails were isolated for emerging cercariae and were not later crushed; therefore immature infections were not found.

Species of snail	Place	Date	Number	Infections other than furcocercous	Furcocercous infections	Furcocercous percentage
Campeloma sp..........	D	July 4	37	0	0	0
Lymnaea stagnalis.......	S	July 7	30	0	0	0
Lymnaea emarginata.....	H	July 8	28	0	1 (Cercaria sp.)	3.5
Lymnaea stagnalis....... var. *appressa*	H	July 8	8	1 (Stylet)	1 (*C. elvae*)	12.5
Planorbis bicarinata	H	July 8	9	1 (Stylet)	0	0
Campeloma decisum......	H	July 8	24	0	0	0
Lymnaea stagnalis....... var. *perampla*	M	July 8	5	0	0	0
Lymnaea stagnalis....... var. *appressa*	M	July 8	2	0	0	0
Lymnaea emarginata.....	M	July 8	16	0	0	0
Physa lordi.............	M	July 8	1	0	0	0
Campeloma sp.	M	July 8	1	0	0	0
Planorbis trivolvis........	M	July 8	3	0	0	0
Planorbis trivolvis........	S	July 20	37	0	1 (*C. elephantis*)	2.7
Physa lordi.............	H	July 20	20	0	2 (Cercaria sp.)	10.0
Lymnaea stagnalis....... var. *appressa*	M	July 22	27	0	2 (*C. douthitti*)	7.4
Planorbis bicarinata......	M	July 22	20	0	0	0
Lymnaea megasoma......	T	July 24	35	0	0	0
Lymnaea stagnalis....... var. *appressa*	B	Aug. 4	23	0	1 (*C. elvae*)	4.3
Physa lordi.............	B	Aug. 4	1	0	0	0
Lymnaea megasoma......	C	Aug. 9	18	0	1 (*C. chrysenterica*)	5.5
Lymnaea sp.............	C	Aug. 9	3	0	0	0
Planorbis trivolvis........	C	Aug. 9	73	2 (Echinostome) 2 (Stylet)	2 (*C. tenuis*) 7 (*C. burti*) 1 (*C. rhabdocaeca*?)	2.7 9.6 1.3

B, Bessey Creek; C, Colonial Point, Burt Lake; D, Laboratory Dock; H, Hook Point; M, Maple River; S, Sedge Pond; T, Topinabee Road Pool.

TABLE III

Collection record for 1921-1922; vicinity of Urbana, Illinois.

All snails were isolated for emerging cercariae and subsequently crushed to find immature infections (furcocercous and other).

Species of snail	Place	Date	No.	All infections	Furcocercous Percentage	Other Percentage	Mature Percentage	Immature Percentage	Percentage Total
Physa gyrina......	D	Sept. 18	97	2 (*C. multicellulata*)	2.1	0	2.1	0	2.1
Planorbis trivolvis..	D	Sept. 18	24	0	0	0	0	0	0
Physa gyrina......	D	Sept. 28	71	2 (*C. gigas*)	2.8	0	2.8	0	2.8
Planorbis trivolvis..	D	Sept. 28	103	1 (*C. hamata*)	1.0	0	1.0	0	1.0
Physa gyrina......	D	Oct. 21	15	0	0	0	0	0	0
Planorbis trivolvis..	D	Oct. 21	60	6 (Stylet, mature) 5 (Stylet, immature)	0	18.0	10.0	8.0	18.0
Physa gyrina......	D	Oct. 24	102	2 (*C. gigas*) 3 (Stylet, mature) 4 (Stylet, immature)	2.0	7.0	5.0	4.0	9.0
Planorbis trivolvis..	D	Oct. 24	31	5 (Stylet, mature) 3 (Stylet, immature)	0	25.8	16.1	9.7	25.8
Physa gyrina......	D	Oct. 26	180	1 (Monostome, mature) 2 (Stylet, mature) 1 (Stylet, immature)	0	2.2	1.7	0.5	2.2
Planorbis trivolvis..	D	Oct. 26	101	1 (*C. hamata*) 14 (Stylet, mature) 6 (Stylet, immature) 4 (Cercaria sp. immat.)	1.0	23.8	13.8	10.0	24.8
Physa gyrina......	S	Oct. 31	23	0	0	0	0	0	0
Planorbis trivolvis..	M	Nov. 1	9	0	0	0	0	0	0
Physa gyrina......	C	Nov. 4	81	0	0	0	0	0	0
Physa gyrina......	D	Nov. 4	177	12 (*C. multicellulata*)	6.8	0	6.8	0	6.8
Planorbis trivolvis..	D	Nov. 4	11	1 (*C. hamata*) 1 (Stylet, mature)	0.9	0.9	1.8	0	1.8

D, Drainage Ditch; C, Campus Stream; M, Pond at Muncie, Illinois; S, Spoon River, St. Joseph, Illinois.

Miscellaneous

These snails were isolated for emerging cercariae; they were not subsequently crushed.

Gonionasis sp.	Olentangy River, Ohio	Sept. 1921	200 individuals	Negative
Gonionasis laqueata	Brown's Creek, Nashville, Tenn.	Feb. 1, 1923	378 individuals	Negative

SUMMARY OF RESULTS

1. The furcocercous larval trematode fauna of restricted regions of Illinois and of Michigan has been studied.

2. Seven new species (Miller, 1923) have been here fully described in comparison with morphologically similar cercariae.

3. The literature for one hundred and two fresh-water, and for eight marine species of furcocercous cercariae has been reviewed and summarized; a check list is submitted.

4. Of the new species, the two apharyngeal distomes make clear the establishment of two well-defined groups.

5. The three pharyngeal longifurcate distomes add to the knowledge of this group, in which there are but few complete descriptions.

6. The two longifurcate monostomes, both probably pharyngeal, make possible the formation of a group of these forms.

7. Studies carried on to supplement incomplete descriptions of certain North American larvae have made possible their more exact disposition.

8. It has been possible to make a satisfactory scheme of classification, based largely on the excretory system, for only the apharyngeal brevifurcate distomes.

9. The importance of the excretory system in the determination of relationships is stressed; but due emphasis has also been placed on other features of morphology.

10. From a resume of the literature it is clear that in addition to the Schistosomatidae some members, and probably all, of the Holostomata develop from furcocercous larvae; so also does *Sanguinicola inermis* of the Aporocotylidae.

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EXPLANATION OF PLATES

Unless otherwise stated, all drawings were made with the camera lucida. Abbreviations used:

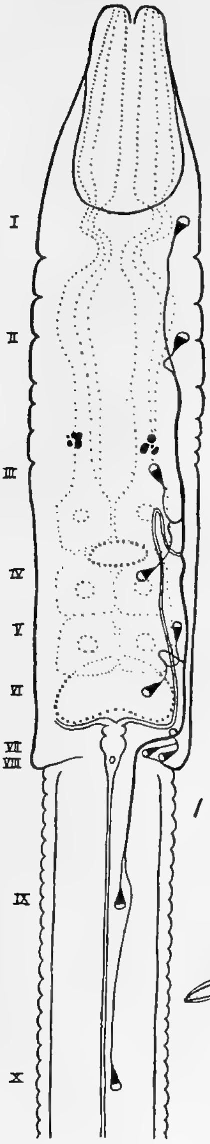
ao	anterior organ	gb	germ ball
bp	birth-pore	gc	germ cells
c	cecum	hg	head gland
ct	caudal excretory tube	mu	muscle band
d	penetration gland duct	ns	nervous system
da	anterior penetration gland duct	pg	penetration gland cell
dp	posterior penetration gland duct	pa	anterior penetration gland cell
e	esophagus	pp	posterior penetration gland cell
es	pigmented eye-spot	v	ventral sucker

PLATE I

DESCRIPTION OF PLATE I

All figures concern *Cercaria multicellulata*

Fig. 1. Diagrammatic view of ventral side, showing probable connections of excretory system. × 760
Fig. 2. End of sporocyst, showing birth-pore. × 760
Fig. 3. Ventral view. ×310
Fig. 4. Diagrammatic outline to show annulations of body. × 365
Fig. 5. Ventral view, showing excretory system in relation to other organs. × 760
Fig. 6. Transverse section of tail-stem, showing four muscle fields, and caudal excretory tube. × 630
Fig. 7. Almost median sagittal section. × 740



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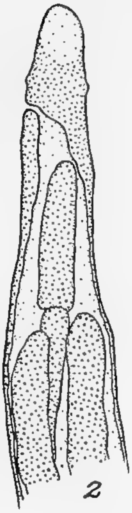

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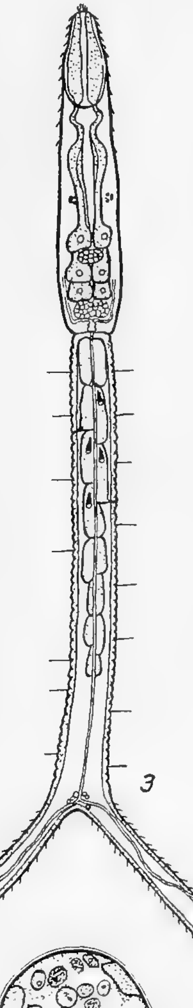

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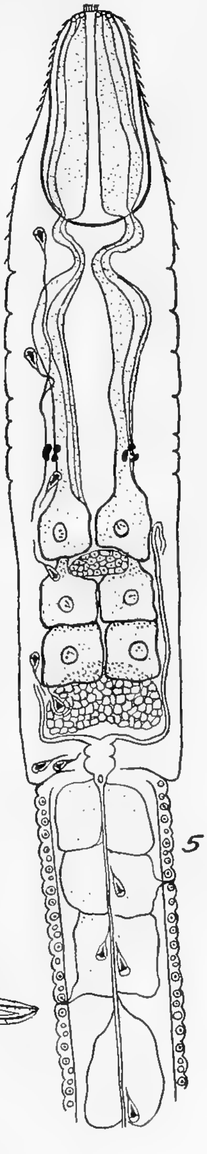

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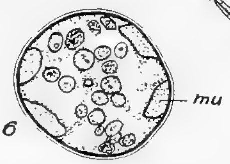

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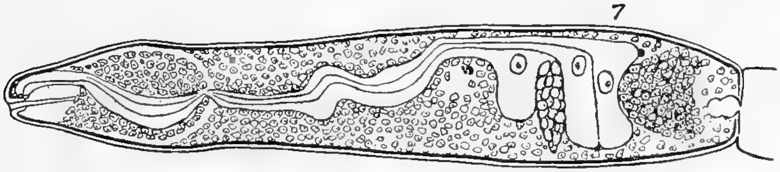


7

PLATE II

DESCRIPTION OF PLATE II

Fig. 8. *Cercaria multicellulata;* transverse section through posterior penetration glands. × 740

Figs. 9 to 16 inclusive concern *Cercaria hamata*

Fig. 9. Transverse section through anterior organ. × 975

Fig. 10. Transverse section through tail-stem. × 775

Fig. 11. Outline of living sporocyst containing early germ balls. × 60

Fig. 12. Semi-diagrammatic ventral view. × 390

Fig. 13. Outline of club-shaped end of living sporocyst. × 75

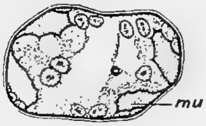
Fig. 14. End of sporocyst showing birth-pore. × 75

Fig. 15. Transverse section through young sporocyst. × 375

Fig. 16. Transverse section through anterior germ cell mass. × 1000

Fig. 17. *C. multicellulata;* transverse section through pigmented eye-spots. × 620

Fig. 18. *C. multicellulata;* outline of living sporocyst. × 42



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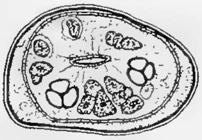

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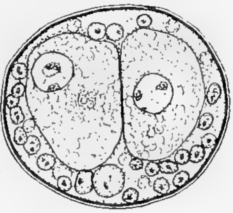

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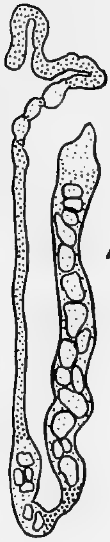

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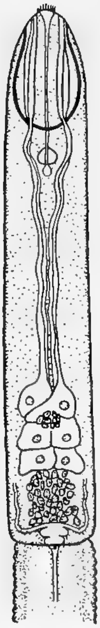

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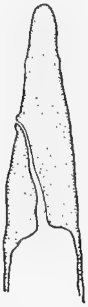

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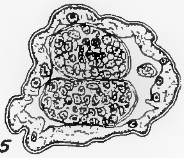

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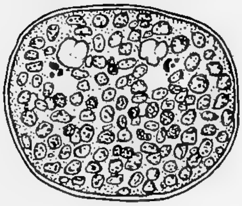

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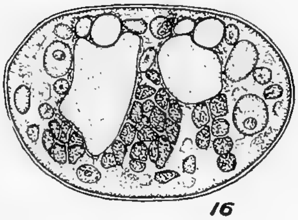


16

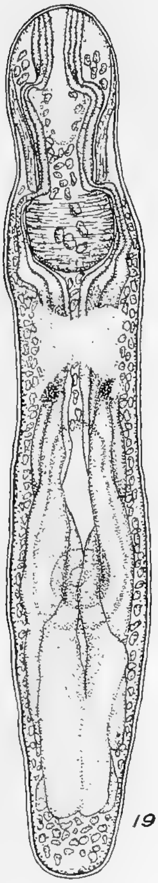
18

PLATE III

DESCRIPTION OF PLATE III

All figures concern *Cercaria elvae*

Fig. 19. Dorsal view of body. × 410
Fig. 20. Ventral view of excretory system. × 410
Fig. 21. Lateral view of body. × 400
Fig. 22. Outline of anterior organ, as frequently seen in living animal. × 135
Fig. 23. Transverse section through tail-stem. × 560
Fig. 24. Furcal tip, dorsal view. × 115
Fig. 25. Semi-lateral view of body characteristic of living larva under cover glass. × 155



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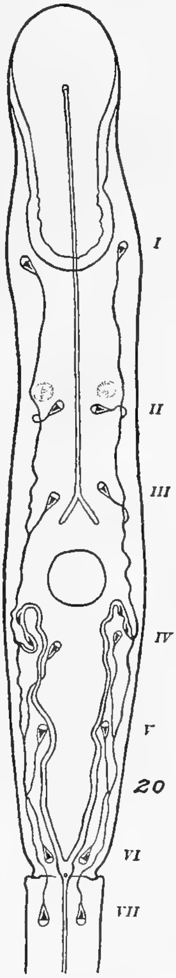

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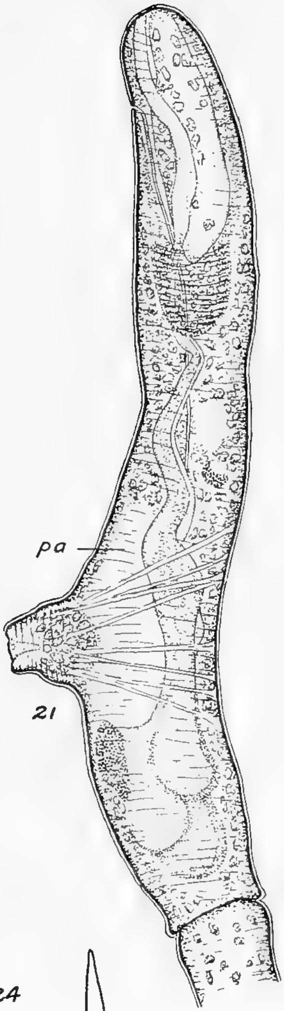

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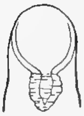

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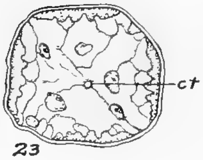

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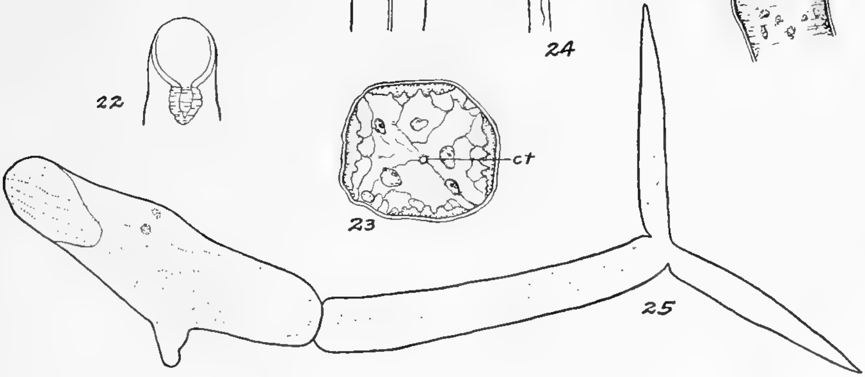
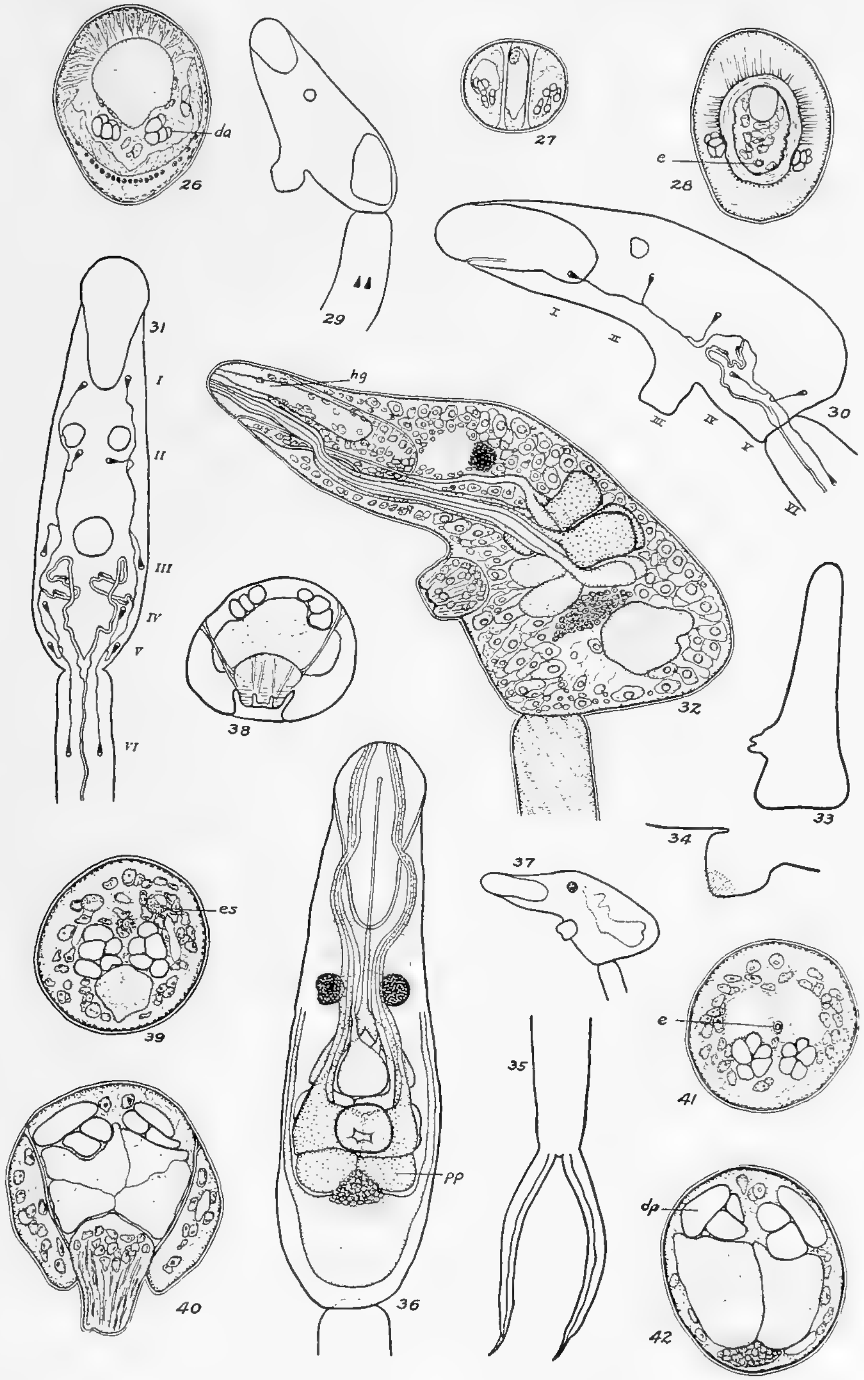


25

PLATE IV

DESCRIPTION OF PLATE IV

Fig. 26. *Cercaria elvae;* transverse section through anterior organ just in front of mouth, showing head gland and penetration gland ducts. × 550
Fig. 27. *C. elvae;* transverse section through tip of anterior organ. × 480
Fig. 28. *C. elvae;* transverse section through posterior end of anterior organ, showing in addition the esophagus. × 450
Fig. 29. *C. wardi;* body outline of living animal frequently observed. × 100
Fig. 30. *C. wardi;* lateral view of excretory system. × 190
Fig. 31. *C. wardi;* ventral view of excretory system. × 180
Fig. 32. *C. wardi;* lateral view of body, with details of structure. × 270
Fig. 33. *C. wardi;* body outline of living animal frequently observed. × 110
Fig. 34. *C. wardi;* outline of everted ventral sucker, showing spination. × 285
Fig. 35. *C. wardi;* outline showing furcal fin-folds from dorsal view. × 145
Fig. 36. *C. wardi;* ventral view of body, with details of structure. × 250
Fig. 37. *C. wardi;* outline showing posterior mucin gland in lateral aspect. × 85
Fig. 38. *C. elvae;* outline of transverse section through ventral sucker region, showing that organ retracted into body. × 315
Fig. 39. *C. elvae;* transverse section through lateral eye-spots, showing also esophagus, an anterior penetration gland, and the five pairs of penetration gland ducts. × 430
Fig. 40. *C. elvae;* transverse section through ventral sucker, showing anterior penetration glands (ventral) and ducts (dorsal) from posterior penetration glands. × 445
Fig. 41. *C. elvae;* transverse section through nervous system, showing esophagus and penetration gland ducts. × 485
Fig. 42. *C. elvae;* transverse section through penetration glands and germ cell mass. × 450



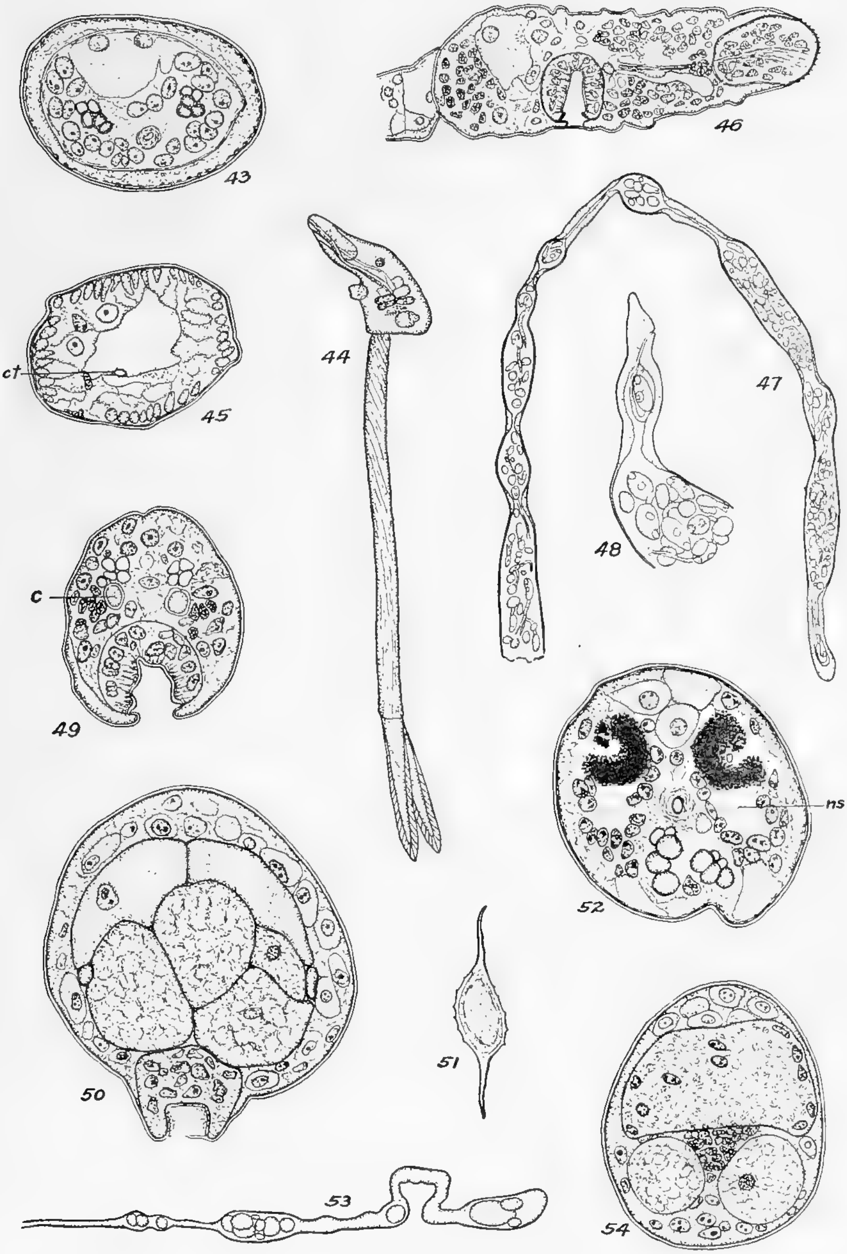
MILLER

PLATE IV

PLATE V

DESCRIPTION OF PLATE V

Fig. 43. *Cercaria wardi;* transverse section through head gland, penetration gland ducts, and esophagus in anterior organ. × 710
Fig. 44. *C. wardi;* lateral view. × 75
Fig. 45. *C. wardi;* transverse section through tail-stem, showing caudal excretory tube and muscles. × 555
Fig. 46. *C. burti;* median sagittal section through immature larva. × 460
Fig. 47. *C. burti;* portion of sporocyst. × 30
Fig. 48. *C. burti;* end of sporocyst, showing birth-pore. × 70
Fig. 49. *C. burti;* transverse section through ventral sucker, showing ceca and penetration gland ducts. × 580
Fig. 50. *C. wardi;* transverse section through ventral sucker, showing both types of penetration gland cells. × 525
Fig. 51. *C. wardi;* transverse section through furca, showing prominent furcal fin-folds. × 750
Fig. 52. *C. wardi;* transverse section through eye-spots of immature specimen, showing esophagus, nerves, and penetration gland ducts. × 770
Fig. 53. *C. wardi;* portion of a sporocyst, drawn from living material. × 60
Fig. 54. *C. wardi;* transverse section through germ cell mass, dorsal posterior mucin gland, and two penetration gland cells. × 430


43
46
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51
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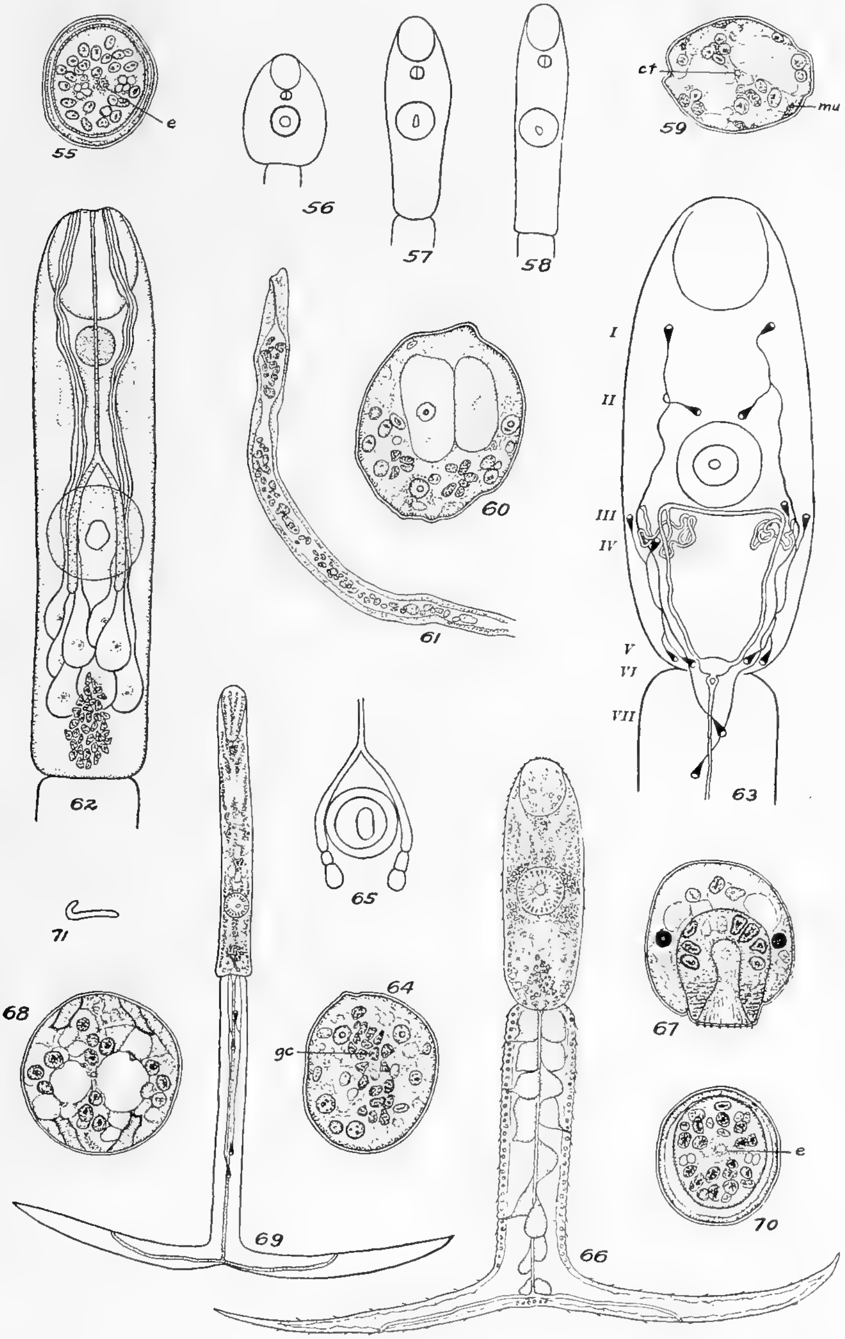
54

PLATE VI

DESCRIPTION OF PLATE VI

Fig. 55. *Cercaria burti;* transverse section through anterior organ. × 600
Figs. 56, 57, 58. *C. burti;* form changes of body of living animal.
Fig. 59. *C. tenuis;* transverse section through tail-stem. × 520
Fig. 60. *C. tenuis;* transverse section through penetration glands. × 560
Fig. 61. *C. tenuis;* portion of sporocyst showing birth-pore. × 45
Fig. 62. *C. burti;* ventral view showing relations of alimentary canal, penetration glands, nervous system, and germ cell mass. × 500
Fig. 63. *C. burti;* ventral view of excretory system. × 480
Fig. 64. *C. burti;* transverse section through germ cell mass. × 525
Fig. 65. *C. burti;* outline sketch showing intestinal ceca. × 375
Fig. 66. *C. burti;* ventral view, showing general appearance. × 245
Fig. 67. *C. tenuis;* transverse section through ventral sucker. × 795
Fig. 68. *C. tenuis;* transverse section through tail-stem. × 865
Fig. 69. *C. tenuis;* general appearance from ventral view. × 160
Fig. 70. *C. tenuis;* transverse section through anterior organ. × 840
Fig. 71. *C. tenuis;* spine from ventral sucker, free-hand drawing. × about 2250



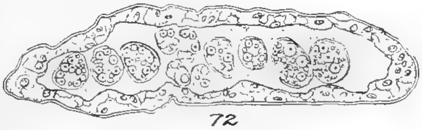
MILLER

PLATE VI

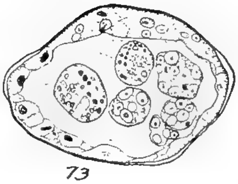
PLATE VII

DESCRIPTION OF PLATE VII

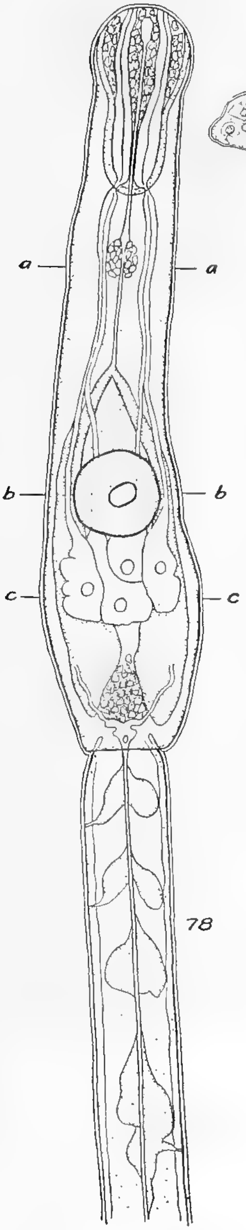
Fig. 72. *Cercaria tenuis;* longitudinal section through sporocyst. × 595
Fig. 73. *C. tenuis;* transverse section through sporocyst. × 280
Fig. 74. *C. tenuis;* ventral view of excretory system in body. × 410
Fig. 75. *C. tenuis;* semi-diagrammatic ventral view. × 410
Fig. 76. *C. tenuis;* transverse section through penetration gland region. × 865
Fig. 77. *C. tenuis;* end of sporocyst showing birth-pore. × 255
Fig. 78. *C. chrysenterica;* ventral view. × 390
Fig. 79. *C. chrysenterica;* ventral view of excretory system. × 220
Fig. 80. *C. chrysenterica;* free-hand drawing of spine from oral cap.
Fig. 81. *C. chrysenterica;* transverse section through furca. × 635



72



73



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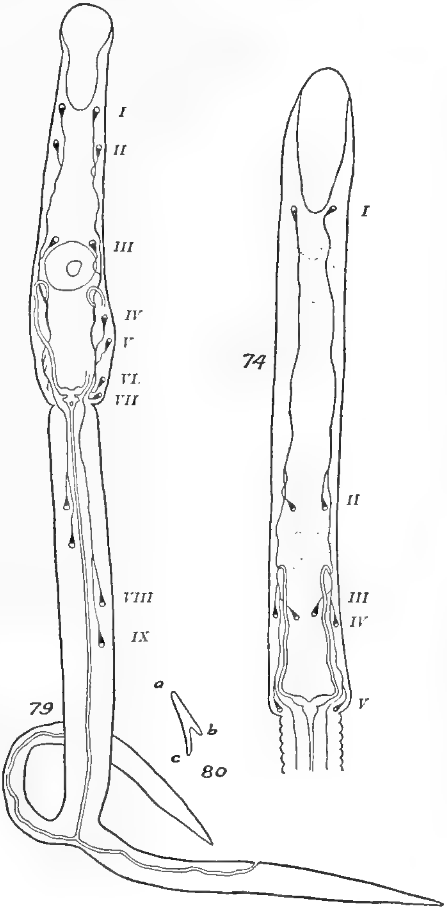
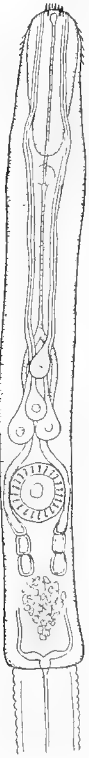


79

80

74



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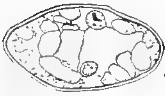

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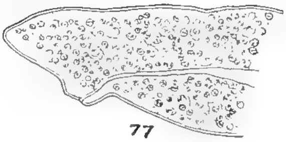
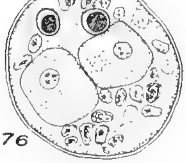


77



76

MILLER

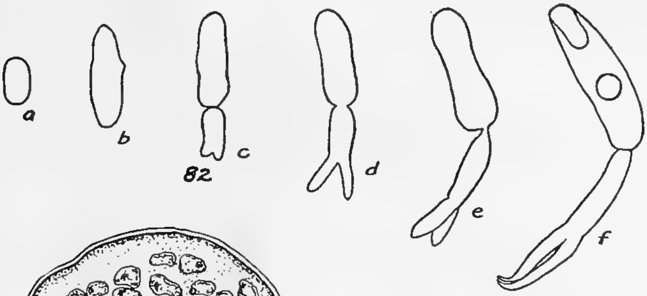
PLATE VII

PLATE VIII

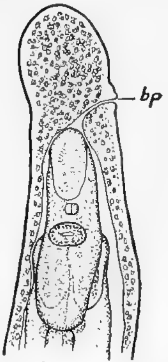
DESCRIPTION OF PLATE VIII

All figures concern *Cercaria chrysenterica*

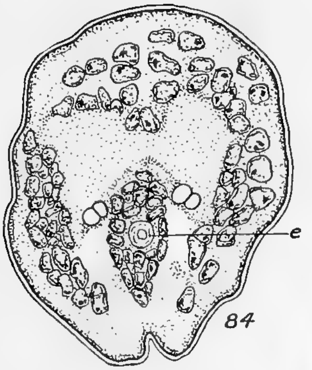
Fig. 82, a-f. Outlines of developmental stages. × 105
Fig. 83. End of sporocyst, showing birth-pore. × 155
Fig. 84. Transverse section through level a—a of Fig. 78. × 915
Fig. 85. General appearance of an entire sporocyst. × 15
Fig. 86. Transverse section through level c—c of Fig. 78. × 730
Fig. 87. Transverse section through sporocyst, showing cercariae in all stages of development. × 220
Fig. 88. Transverse section through distal end of tail-stem, showing caudal excretory tube divided to pass down each furca. × 705
Fig. 89. Transverse section through level b—b of Fig. 78. × 730
Fig. 90. Transverse section through young sporocyst, anterior end of contained cercaria, and germ ball. × 565
Fig. 91. Outline of tail-stem of living larva, as often held when under a cover glass. × 45
Figs. 92, 93, 94. Form changes of body of the living animal under a cover glass.



82



83



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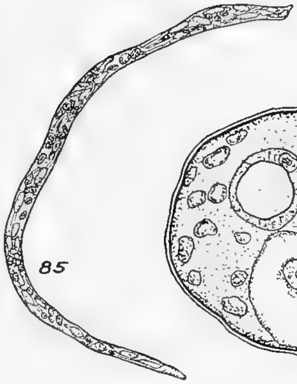

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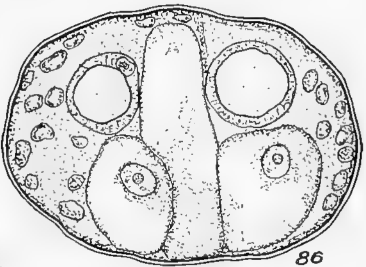
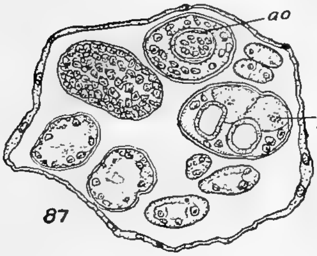


86



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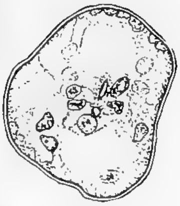

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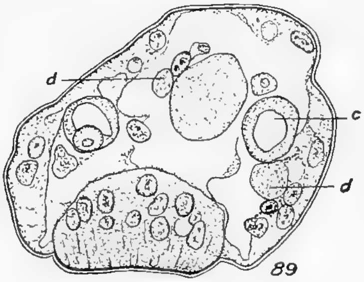
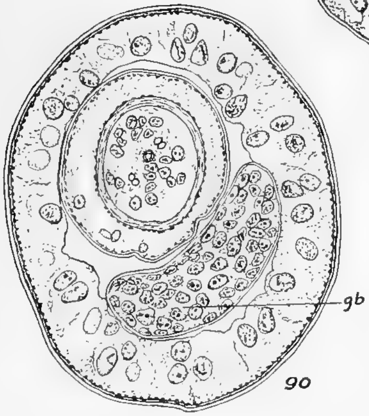


89

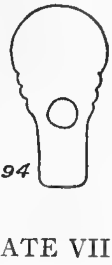


90

91

92

93



94

INDEX OF SCIENTIFIC NAMES