STUDIES ON TREMATODE CERCARIAE AT REELFOOT LAKE, TENNESSEE, II.[1]

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INTRODUCTION

This is the second portion of a report on the cercariae found at Reelfoot Lake during the summers of 1948 and 1949, and deals primarily with the morphology and systematic position of certain species. It is hoped that in subsequent summers further studies can be completed dealing with the ecology and life history of certain selected species. Grateful acknowledgement is made of the grant from the Tennessee Academy of Science and of the use of the biological station laboratory, made possible through the Director, Dr. C. L. Baker, and to Dr. George R. LaRue, who rendered assistance in the preparation of this report, and to Dr. Henry van der Schalie and Mr. Bruce Lee of the University of Michigan, Museum of Zoology who kindly identified some of the mollusks.

METHODS

The technique followed was similar to that used by previous workers in that both living and preserved materials were studied. Examinations of both emerged cercariae and those from snail dissections were made. All cercariae were first examined alive and unstained, single cercariae being pipetted to a slide and covered with a No. 1 coverglass. Virtually all of the structures could be studied in this manner, but where details were obscure intravitam stains were employed. Aqueous solutions of neutral red, nile blue sulfate, and methylene blue were all used at some time during the study. A very satisfactory temporary mount was made by fixing the cercariae in hot fluid made up as follows; 5 cc. glycerin, 5 cc. 37 percent formaldehyde, 90 cc. 0.001 percent KOH. To this aqueous solution methylene blue was added beneath the coverglass. Staining took place very gradually, often for several hours, while the glycerin prevented drying and crushing of the material on the slide. Such preparations are often suitable for study for two or three days, and for much longer periods if rimmed with vaseline. Measurements can be taken of such cercariae with considerable ease. In some instances measurements were also taken of cercariae which had been relaxed and fixed over a hot microscope lamp for several seconds.

SNAIL COLLECTIONS

Collected snails were examined from several points around the lake and outlying basins. Good collecting areas are extremely abundant at Reelfoot Lake. One of the most profitable areas is

[1]A contribution from the Reelfoot Lake Biological Station and the University of Michigan, Department of Zoology.

"Cranetown," on the west side of the lake. "Cranetown" can be approached either by boat from its lake side or by wading eastward from the west margin of the lake. It is the annual nesting site of hundreds of birds, the bulk of them being American egrets, *Casmerodius albus egretta,* Ward's herons, *Ardea herodias wardi,* and cormorants, *Phalacrocorax a. auritus.* Also nesting in some numbers are black-crowned night herons, *Nycticorax nycticorax hoactli,* and formerly anhinga, *Anhinga anhinga leucogaster,* although I observed no anhinga nesting here in either summer of this study. The entire nesting colony has been estimated at 2,000 birds in some years, and is approximately a quarter of a mile long. The nests are all in tall cypress (*Taxodium distichum*) trees, many of which have their bases submerged in water most of the summer, and it is in fact necessary to wade nearly a mile at times to get to the colony. It is to be expected that the snails in such an environment would be heavily infected with larval trematodes. The most striking impression upon entering the colony (beside the noise) is the continuous rain of droppings and regurgitated food onto the ground and water from the nests sixty or more feet above. Several trips were made to "Cranetown" in 1948 and 1949 for the purpose of observing the birds and making snail collections. Over 50 percent of the snails were infected with larval trematodes. Most of the snails were found by breaking open rotten stumps and half-submerged logs. Sometimes several hundred snails were collected in this manner from a single log. They were scooped out with the hands, placed in minnow pails and brought back to the laboratory for examination. The same technique was followed in other areas, but with less success than at "Cranetown." Host examinations were made on young American egrets and cormorants which had fallen from the nests and been abandoned. They proved to be heavily infected with adult helminths of several species.

Snails were brought into the laboratory and placed in finger bowls, three to five snails per bowl. The snails from bowls containing released cercariae were isolated individually to determine which were the infected snails and to determine percentage of infection. Eventually all of the collected snails were crushed to determine the total percentage of infection, including those not sufficiently mature to be producing released cercariae. Such an examination also yielded information on the presence of metacercarial cysts and evidences of mixed infections.

Cercarial Groups

Altogether twenty-one species of cercariae were observed in the course of the investigation. Several species were encountered repeatedly, others but once. Echinostome cercariae were most often encountered, while fork-tailed Strigeid cercariae were second in abundance. Finally, somewhat less common were the Xiphidiocercariae. Yet, in total number of species they ranked highest with

ten species being found in the two summers of investigation. Following is a list of the species and the groups within which each is located.

I. Longifurcous pharyngeal distomate cercariae
'Strigea' group (Wesenberg-Lund, 1934)
1. *C. obioni* sp. n., host *Physa gyrina* Say.
2. *C. byrdi* sp. n., host *Physa gyrina* Say.
3. *C. fimbriata* sp. n., host *Physa gyrina* Say.
4. *C. paralinearis* sp.n., host *Physa gyrina* Say.
5. *C. samburgi* sp. n., host *Physa gyrina* Say.

II. Longifurcous apharyngeal monostomate cercariae
'Multicellulata' group (Mihi)
6. *C. paramulticellulata* sp. n., host *Physa gyrina* Say.
7. *C. isomi* sp. n., host *Physa gyrina* Say.

III. Longifurcous pharyngeal monostomate cercariae
'Tetis' group (Sewell, 1922)
8. *C. yankapinensis* sp. n., host *Viviparus intertextus* Say.

IV. Echinostome cercariae
'Agilis' group (Sewell, 1922)
9. *C. palegae* sp. n., host *Viviparus intertextus* Say.
'Echinata' Group (Sewell, 1922)
(Two species, not described in the present paper).

V. Xiphidiocercariae (Ten species, not described in this paper)
A. 'Ornatae' group (Luhe, 1909). Three species.
B. 'Armatae' group (Luhe, 1909). Two species.
C. 'Brevicaeca' group (Mihi). Five Species.

Naming of Cercariae

It is realized that the naming of new cercariae places an additional burden on the already extensive list of described species. Many have not yet been related to any known adult, nor can some be assigned to a family. This is necessarily so until more knowledge is accumulated about both adult and larval stages and their relationships, and this knowledge can come only through many more life history studies than have now been completed. In the meantime each new cercaria must be placed as nearly as possible into its correct group. In presenting new names I have largely avoided those which are morphologically descriptive of the new species. Most new names in this paper refer to specific locations in the Reelfoot Lake vicinity, characteristic vegetation reminiscent of the lake or of the snails' habitat, or to the names of parasitologists who have carried on investigations at Reelfoot Lake in previous summers. By this method of nomenclature it is believed incongruity is avoided when the adult form of the parasite becomes known.

Species Descriptions

Longifurcous Pharyngeal Distomate Strigeid Cercariae. 'Strigea' Group

1. **Cercaria obioni** sp. n.

Host: Physa gyrina Say.

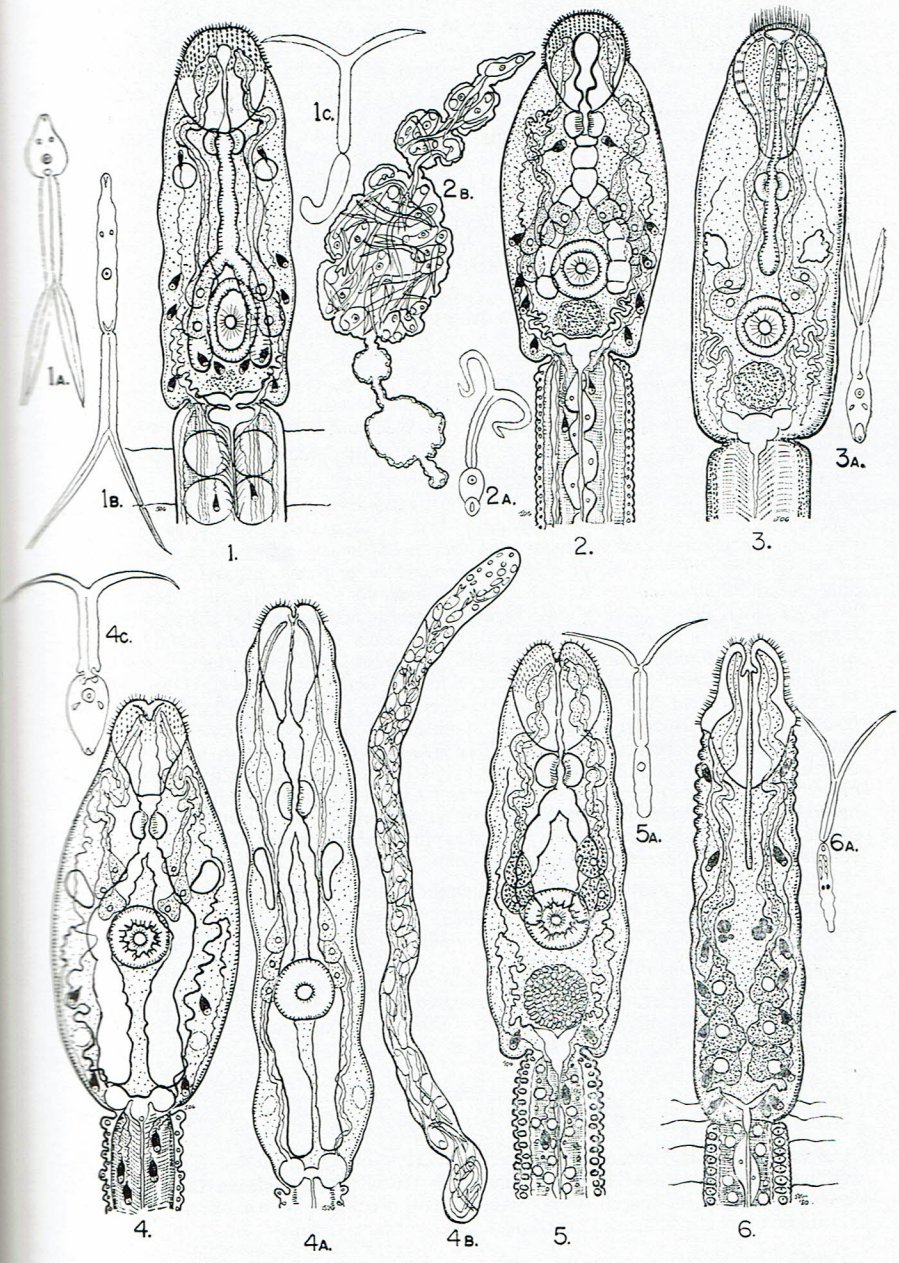
Locality: Isom Lake, July 10, 1949. This cercaria was encountered several times from snails collected at Isom Lake, Lake County, Tennessee. Possession of two pairs of anterior penetration glands place this form with Wesenberg-Lund's 'Strigea' Group of furcocercariae.

Specific diagnosis: Longifurcous, pharyngeal, distomate cercaria. Body elongate oval, flexible, capable of great elongation; unpigmented, eyespots, paired, slightly posterior and lateral to pharynx; oesophagus capable of great contraction and extension; pharynx large with short prepharynx; caeca extending to rear margin of acetabulum or slightly beyond; two pairs of conspicuous penetration glands occupy antero-lateral edge of acetabulum, slightly overlapping that structure; penetration gland cell ducts emptying at sides of oral opening; bladder characteristic for group, with short cornua; main excretory vessels considerably convoluted before receiving larger branches; Island of Cort not observed; genital primordium obscure, anterior to bladder; oral sucker opening surrounded by four rows of enlarged spines; tail strong, muscular, possessing two rows of prominent caudal bodies and four rows of muscle strands running longitudinally down stem; tail flagellets present on margins; furcae lacking fin-folds; body containing seven pairs of flame cells; a single oblique pair in upper portion of tail stem; excretory formula $2[(3+4)+(1)]$; measurements of length; body 132 microns, tail stem 198 microns, furcae 182 microns, oral sucker 36 microns, acetabulum 27 microns, pharynx 15 microns, penetration gland cells 15 microns; development from elongate yellowish sporocysts; cercariae hang in the water with body bent at an acute angle. (Fig. 1c).

Other cercariae, similar in the possession of two pairs of anteriorly placed penetration glands are: *C. indicae* XXII Sewell, 1922; *C. letifera* Fuhrmann, 1929; *C. tenuis* Miller, 1923; *C. marcianae* Cort and Brooks, 1928; *C. indicae* I Sewell, 1922; *C. tropicalis* Faust and Hoffman, 1934; C. of *Neodiplostomum lucidum* LaRue and Bosma, 1927 (West, 1935); C. of *Alaria mustelae* Bosma, 1934; C. of *Alaria intermedia* Odlaug, 1940; C. of *Fibricola texensis* Chandler, 1942; *C. helvetica* XXXIV DuBois, 1934; *C. stonii* Brooks, 1943; C. of *Pharyngostomum cordatum* Wallace, 1939; *C. theta* Brooks, 1948; *C. nolae* Brooks, 1948; *C. septicaeca* Brooks, 1948; *C. helisomensis* Brooks, 1948; *C. eleanori* Brooks, 1948; *C. Xi* Brooks, 1948; *C. kappa* Brooks, 1948; *C. mu* Brooks, 1948; *C. heleni* Brooks, 1948; and *C. tetradena* Johnston and Beckwith, 1945. The adults of these species parasitize mammals (*Alaria, Pharyngostomum,* and *Fibricola*), marsupials (*Neodiplostomum*), and birds (*Neodiplostomum*).

It should be mentioned here that the name *C. tetradena* is preoccupied by *C. tetradena* Faust, 1924, making *C. tetradena* Johnston and Beckwith, 1945, a homonym of *C. tetradena* Faust, 1924. The name *C. tetradena* was also used by E. L. Miller for a species of Xiphidiocercaria which he described in 1935, but later renamed *C. pachycystata* Miller, 1935. According to the rules of zoological nomenclature (Article 36) *C. stonii* Brooks, 1943, is not preoccupied by *C. stonei* Porter, 1938, and will stand as a valid name.

Plate I. (Opposite page.) Fig. 1, *Cercaria obioni* sp. n., a, body contracted; b, body extended; c, floating position. Fig. 2, *C. byrdi* sp. n., a, floating position; b, daughter sporocyst containing cercariae. Fig. 3, *C. fimbriata* sp. n., a, floating position. Fig. 4, *C. paralinearis* sp. n., a, extended cercaria; b, daughter sporocyst; c, floating position. Fig. 5, *C. samburgi* sp. n., a, floating position. Fig. 6, *C. paramulticellulata* sp. n., a, floating position.


1A.
1B.
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1.
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4A.
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6A.

C. obioni sp. n. differs from all previously described cercariae by the position of its unpigmented eyespots, these being lateral to the pharynx. They are in a similar position in *C. septicaeca* Brooks, 1948, but different body measurements, lack of caudal bodies in the tail, and type of caeca separate these two species. The cercaria of *Fibricola texensis* Chandler, 1942, has anteriorly placed, unpigmented eyespots, but lacks caudal bodies, flagellets, and has only five pairs of flame cells in the body instead of seven pairs. The cercaria of *Neodiplostomum lucidum* LaRue and Bosma, 1927 (West, 1935) has eight instead of seven pairs of flame cells in the body, the unpigmented eyespots are located posterior to the fork of the intestine, and the tail stem lacks caudal bodies. The long oesophagus and anteriorly placed eyespots in combination with the presence of caudal bodies and tail flagellets serves to distinguish *C. obioni* from all other closely related species.

2. **Cercaria byrdi** sp. n.

Host: Physa gyrina Say.

Locality: Goose Basin and Yankapin Basin, July, 1948, and Yankapin Basin, June 10, 1949. This cercaria was found more often than any other forktailed Strigeid during the two summers at Reelfoot Lake.

Specific diagnosis: Longifurcous, pharyngeal, distomate cercaria. Body oval to elongate, aspinose except on tip of the oral sucker; oral sucker large and conspicuous, projected ventrally, with a prominent slotted opening; pharynx large; prepharynx absent; oesophagus broad, separated by conspicuous constrictions into three compartments; intestinal caeca extending to posterior edge of acetabulum, divided by constrictions into five or six compartments on each side; acetabulum small, muscular, between ends of caeca; eyespots absent; four pairs of small penetration glands located anterior and lateral to the acetabulum; bladder small, bicornuate; main excretory vessels slightly convoluted, branching near acetabulum into anterior and posterior collecting ducts; excretory commissure absent; flame cells along sides of body, anterior pair at level of oesophagus, second pair at level of pre-acetabular penetration gland cells, three more pairs posterior to acetabulum; a single oblique pair located in anterior part of tail; excretory formula $2[(2+3)+(1)]$; tail stem long, without flagellets; caudal bodies present; furcae long, lacking fin-folds; central excretory duct from bladder emptying at tips of furcae; measurements of length; body 98-125 microns, tail stem 173 microns, furcae 165 microns, oral sucker 27 microns, acetabulum 20 microns, pharynx 13.5 microns; development from constricted bag-like sporocysts, 1.3-1.5 mm. in length. (Fig. 2B).

This cercaria is recognized by its prominent oral sucker, constricted nature of the caeca, lack of eyespots, possession of four pairs of anterior penetration glands, and lack of an excretory commissure. The only previously described cercaria with four pairs of anterior penetration glands seems to be *C. stephensi* Brooks, 1943, from *Lymnea stagnalis jugularis* at Rush Lake, Iowa. *C. stephensi* has larger dimensions throughout, possesses unpigmented eyespots, and has flagellets on the tail stem. Furthermore, the description of the daughter sporocysts of *C. stephensi* does not agree with that of *C. byrdi.*

3. **Cercaria fimbriata** sp. n.

Host: Physa gyrina Say.

Locality: Yankapin Basin, Reelfoot Lake, June 14, 1949. This cercaria was found only once in the two summers. It is remarkable in that intestinal caeca are totally lacking in this species. This, combined with other characters, is sufficient to constitute a new species of furcocercaria.

Specific diagnosis: Longifurcous, pharyngeal, distomate cercaria. Body opaque, making finer details of anatomy very difficult to observe; two prominent unpigmented eyespots with ragged edges located in lateral fields near middle of body; oral sucker large, with forward projecting hair-like spines

at tip; shorter spines covering anterior two-thirds of oral sucker; rest of body aspinose; tail stem short, broad; tail furcae long, wide, lacking fin-folds; acetabulum muscular, located posterior to center of body; penetration glands near antero-lateral edge of acetabulum, ducts passing directly forward to edge of oral sucker, then separating and dilating as they enter posterior edge of oral sucker, emptying at the margin of the oral opening; pharynx prominent, globular, with long pre-pharynx present; oesophagus straight, tubular, terminating near middle of body; caeca absent; bladder large and with swollen cornua; flame cells not seen; cercaria capable of rapid swimming movements, and due to vigorous actions tail easily disengaged when transferred to a slide; caudal bodies, tail flagellets, and transverse excretory commissure absent; development from sporocysts in snail liver; measurements of length; body 195 microns, tail 190 microns, furcae 240 microns, oral sucker 45 microns, acetabulum 33 microns, pharynx 8 microns.

Longifurcous Strigeid cercariae lacking intestinal caeca are quite uncommon in the literature, particularly among the distomate forms. Sewell has described *C. indicae* I Sewell, 1922, as lacking caeca, and erected his 'Pahila' Group for its reception. Except for the prominent unpigmented eyespots, *C. fimbriata* resembles *C. indicae* I of Sewell. Both species have forward directed spines around the oral opening, separation of the penetration gland ducts in the oral sucker, and similar configurations of the bladder and excretory vessels. In North America *C. dohema* Cort and Brooks, 1937, shows many resemblances to this cercaria. However, *C. dohema* possesses a post-acetabular transverse excretory commissure and has three pairs of penetration glands located behind the acetabulum. In this respect *C. dohema* shows closer affinities to *C. riponi* Brackett, 1939, than to *C. fimbriata*. *C. fimbriata* can be separated from all previously described species of closely related cercariae by the ragged-edged appearance of the unpigmented eyespots.

4. **Cercaria paralinearis** sp. n.

Host: Physa gyrina Say.

Locality: "Cranetown," June 27, 1949. This cercaria, found only once in the two seasons at Reelfoot Lake, was taken from a single snail at "Cranetown" early in the second summer of study.

Specific diagnosis: Longifurcous, pharyngeal, distomate cercaria. Body long, widest near center; unpigmented eyespots prominent, slanting, just anterior to acetabulum; anterior half of oral sucker spinose; pre-pharynx present; pharynx prominent; oesophagus absent; caeca long, extending to posterior end of body; acetabulum prominent; three pairs of penetration glands located between eyespots and acetabulum; anterior and posterior branches of excretory system joining main collecting vessels at sides of acetabulum; bladder with swollen cornua and thin central portion giving dumb bell-shaped appearance; two pairs of flame cells located in the posterior half of body and two pairs in tail stem, complete excretory formula unknown; caudal bodies and flagellets absent; tail stem annulated, presenting a scalloped-edged appearance; furcae about length of stem; fin-folds absent; body not bent while hanging in water, but furcae held stiffly at right angles to body and tail stem; development in thin, elongate sporocysts with parallel sides, 3 mm. or more in length, and containing 50-75 cercariae in various stages of development.

Furcocercaria linearis Wesenberg-Lund, 1934, from *Planorbis corneus,* of the same group, possesses three pairs of penetration glands anterior to the acetabulum, lacks caudal bodies in the tail stem, and in other respects closely resembles the present species. Both have two pairs of flame cells located in the anterior portion of the tail stem and two pairs in the body posterior to the acetabulum, while in *C. linearis* three more pairs are figured anterior to the acetabulum, giving the formula for this cercaria $2[(3+2)+(2)]$. Both *C. linearis* and *C. paralinearis* have similar, very long, slender sporocysts containing large numbers of cercariae. The two species can be separated by the

presence of laterally placed unpigmented eyespots and the lack of an oesophagus in *C. paralinearis*. *C. magaliesia* Porter, 1938, from *Lymnea natalensis* also possesses three pairs of penetration glands placed anteriorly to the acetabulum, lacks unpigmented eyespots, and has a long oesophagus as in *C. linearis*. However, Porter's figure of the excretory system does not agree with *C. linearis* and development is said to take place in rediae rather than in sporocysts.

5. **Cercaria samburgi** sp. n.

Host: Physa gyrina Say.

Locality: Bayou du Chien, Reelfoot Lake, June 9, 1949.

Specific diagnosis: Longifurcous, pharyngeal, distomate cercaria. Body slender, tubular, and possessing distinct annular wrinkles on anterior half when contracted; oral sucker ovoidal in shape, with four rows of spines around oral opening; body aspinose; eyespots absent; tail stem slightly exceeding body in length; caudal bodies and tail flagellets absent; furcae set-off from tail stem by a conspicuous constriction; fin-folds absent; acetabulum round, distinct, slightly post-median; genital fundament prominent, between bladder and acetabulum, and about equal in diameter to the latter; pre-pharynx present; pharynx prominent; oesophagus very short; caeca terminating at middle of acetabulum, their ends turning sharply inward; two pairs of pre-acetabular penetration glands, their ducts running forward to oral sucker in a sinuous course and broading slightly as they enter that structure; bladder small, bicornuate; transverse excretory commissure absent; excretory formula unknown; two flame cells observed near cornua of bladder and one pair along central excretory duct in the tail stem; caudal excretory duct extending to tips of furcae; development in sporocysts in snail tissues.

This cercaria is rather inactive in the water and hangs motionless with body and tail straight much of the time. When movement occurs the action seems to be less vigorous than that of many of the species studied. The body is very opaque, making the study of the finer anatomical details difficult. This species is clearly a member of Wesenberg-Lund's 'Strigea' Group of Furcocercariae, and can be closer identified as one lacking eyespots, caudal bodies, tail flagellets, and a transverse excretory commissure. There are few previously described cercariae with so many negative qualities. The cercaria of *Alavia intermedia* (Olivier and Odlaug), 1938, is one, as is *C. kappa* Brooks, 1948. Other species bearing resemblances to *C. samburgi* are *C. tenuis* Miller, 1923; *C. mu* Brooks, 1948; and *C. heleni* Brooks, 1948. It is believed that *C. kappa* Brooks, 1948, is the closest relative to *C. samburgi*, as both are from *Physa* and have many close anatomical similarities. A comparison of the body measurements in microns is given below.

	C. samburgi	*C. kappa* Brooks, 1948
Body length	140-150	152
Tail stem	165	225
Furcae	150	225
Oral sucker	30-36	32-34
Acetabulum	25.5	32

From the comparison of measurements it can be seen that the slightly longer tail stem and furcae differentiate *C. kappa* from *C. samburgi*.

Longifurcous Apharyngeal Monostomate Cercariae
Multicellulata Group

Cercariae of this group are larvae of the genus *Posthodiplostomum* DuBois, 1936. They are characterized by the total absence of pharynx and acetabulum. Pigmented eyespots are present in the known species at about the midpoint of the body, and three pairs of prominent tandem penetration glands in the posterior end of the body.

Cercariae belonging to this group are *C. multicellulata* Miller, 1923, *C. louisiana* E. L. Miller, 1935, and *C. zeta* Brooks, 1948. This group is distinct from both the 'Dusra' and 'Rhabdocaeca' groups of longifurcous furcocercariae, whose members possess rudimentary digestive tracts but have one or more of the following: a pharynx, acetabulum, or short intestinal caeca. The 'Multicellulata' group has no suggestion of any of these structures in the cercaria. Pigmented eyespots are characteristic of the 'Multicellulata' group but are either colorless or absent in the other groups excepting *C. physae* Cort and Brooks, 1928. The 'Dusra' and 'Rhabdocaeca' groups seem to occupy an intermediate position between the 'Multicellulata' group and the 'Proalaria' group of Wesenberg-Lund. The 'Proalaria' group has more complete development of the caeca, possesses a distinct acetabulum, and the excretory system shows the development of a transverse commissure. Certain members of the 'Strigea' group also possess a transverse excretory commissure, but when it is present in this group it is usually pre- rather than post-acetabular in position. *C. douglasi* Cort, 1917 = (cercaria of *Cotylurus flabelliformis* Faust, 1917) has this type of commissure, as does *C. helvetica* XXXIV Du-Bois, 1934; *C. fissicauda* La Valette (Brown, 1926); the cercaria of *Cotylurus cornutus* Rud. = (*Cercaria* A. Szidat, 1923); *C. Strigeae tardae* Steenstrup (Mathias, 1922); *C. sanjuanensis* Miller, 1927; and *C. leplei* Brooks, 1943. According to Dawes (1946) the 'Strigea' type of cercaria develops into a Tetracotyle in snails, while the 'Proalaria' cercaria penetrates fishes to form a Diplostomulum in the crystalline lens of the eye. Members of both the 'Multicellulata' and the 'Proalaria' groups usually have their adult stages in the digestive tracts of fish-eating birds.

6. **Cercaria paramulticellulata** sp. n.

A cercaria similar to, if not identical with, *C. multicellulata* Miller, 1923, was found on three occasions and is believed to be widely distributed in the Reelfoot Lake Region. It was first found June 24, 1948, at "Cranetown," and again on June 28, 1949, at the same location. On July 13, 1949, it was found in snails collected from Upper Blue Basin. In all instances the host was *Physa gyrina* Say. H. M. Miller described *C. multicellulata* Miller, 1923, from *Physa gyrina* at Urbana, Illinois. At that time he placed it with the Pharyngeal group of Longifurcous Monostome Cercariae. In his monograph on comparative studies of furcocercous cercariae (1926) he again placed it with the pharyngeal group, although he admitted that no trace of a pharynx was observed. He believed that it should belong with the pharyngeal group because of its resemblances to *C. rhabdocaeca* Faust, 1917, and *C. hamata* Miller, 1923, both pharyngeal, and which Miller placed in his 'Rhabdocaeca' group of Pharyngeal Longifurcate Monostome Cercariae. Both the 'Rhabdocaeca' and 'Multicellulata' groups have three pairs of large penetration glands with prominent nuclei located in the posterior end of the body. Sewell erected a 'Lophoides' group for his *C. indicae* XXVII Sewell, 1922, which is an apharyngeal longifurcate monostomate cercaria, but which has an entirely different grouping of the penetration glands and lacks pigmented eyespots in the center of the body. E. L. Miller described a cercaria from *Physa gyrina* at Baton Rouge, Louisiana, closely related to *C. multicellulata* which he called *C. louisiana* E. L. Miller, 1935, and which he correctly placed in the apharyngeal group of furcocercariae. However, he retained H. M. Miller's classification of *C. multicellulata* in the 'Rhabdocaeca' group of pharyngeal cercariae in spite of the fact that the two species, *C. multicellulata* and *C. louisiana,* are almost identical.

The experimental life cycle of *C. multicellulata* was reported by M. S. Ferguson, 1938. The adult worm was found to conform to the description by MacCallum of *Posthodiplostomum minimum,* a diplostomatid parasite of the intestine of the Blue Heron, *Ardea herodias.* Ferguson found that the metacercaria encysted in at least twenty different fish, mainly centrarchids, and that these cysts were infective for young chicks as well as young herons.

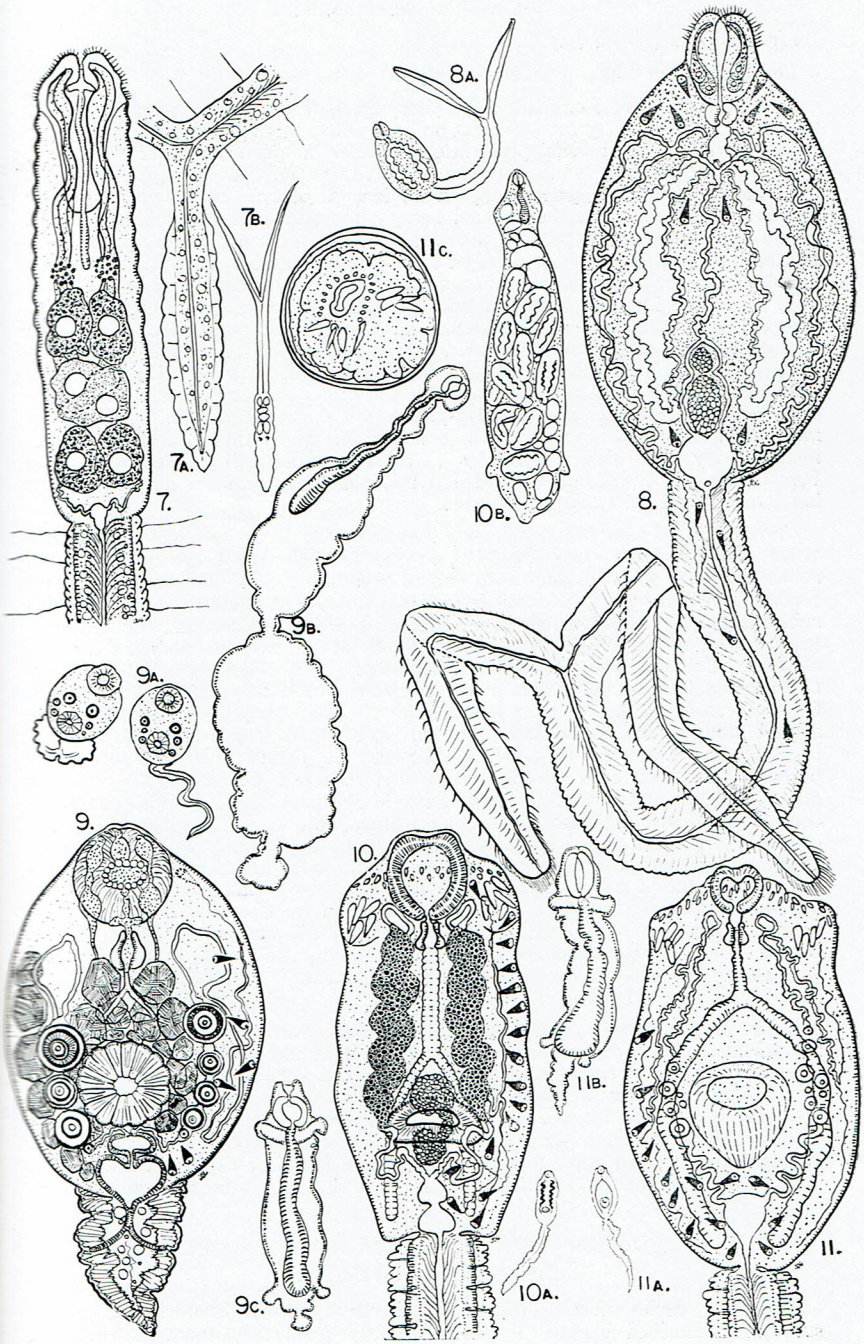
C. paramulticellulata is long and slender, the anterior half of the body being capable of great extension. When partially contracted a series of deep parallel grooves or annulations encircle the anterior portion of the body. The pigmented eyespots are a conspicuous feature. They occur near the center of the body, and each eyespot is usually composed of three masses, one mass being somewhat larger than the other two. The anterior tip of the body has an apical opening which can be inverted or everted. This opening, everted, is surrounded by small, forward-pointing spines. In the Reelfoot Lake specimens spines also cover approximately half of the oral sucker, although Miller has described the spines of *C. multicellulata* as extending completely over the oral sucker and to a short distance posterior to the anterior pair of flame cells in the body. The rest of the body in both species is devoid of spines. The oral opening leads into a straight intestine, which terminates blindly a little behind the oral sucker. No suggestion of a pharynx or paired intestinal caeca is present. The penetration glands are in three pairs in the posterior part of the body. The bladder is quite small and variable in shape. Often it is constricted in its center portion as Miller has figured it for *C. multicellulata,* while at other times it is distinctly Y-shaped. The excretory ducts could not be traced beyond the immediate vicinity of the bladder, but eight pairs of flame cells were noted near the margins of the body. The flame cell formula for *C. multicellulata,* according to Miller's drawing would be $2[(4+4)+(2)]$. In spite of many attempts to locate flame cells in the tail I was completely unable to do so. This is difficult to understand, since in most cercariae the flame cells show up as clearly or more so in the tail than in the body. Therefore, for the time being I must conclude that no flame cells are present in the tail stem of *C. paramulticellulata.* Although Miller found two pairs of flame cells in the tail and I was unable to find any, the number and position of those found in the body exactly agree. The tail stem of both species contains caudal bodies and flagellets. The flagellets on *C. paramulticellulata* were overlooked for two summers, but were immediately evident when a formalin preserved specimen was examined many months later. Two pairs of slightly shorter flagellets were observed attached to the body near its junction with the tail.

Specific diagnosis: Longifurcous, apharyngeal, monostomate cercaria. Body long, slender, capable of great contraction and elongation; tail stem long, with caudal bodies and flagellets; furcae long, slender, without fin-folds; a pair of prominent pigmented eyespots near center of body, usually tri-partite in nature; three pairs of large, tandem penetration glands in posterior end of body; digestive system rudimentary, lacking a pharynx and intestinal caeca; excretory formula $2[(4+4)+(0)]$; development in sporocysts. Comparative measurements in microns are as follows:

	C. multicellulata	*C. paramulticellulata*
Body length (moderately extended)	170	170
Tail length	230	182
Furcal length	225	170

The activity of this cercaria resembles that described for *C. multicellulata.* It hangs motionless in the water, furcae well extended until disturbed, then it moves in a rapid, darting fashion straight across the container. It must be handled with extreme delicacy when being transferred to the slide, for the tail is very easily disengaged during the transfer. The cercaria develops in thin sporocysts which are quite difficult to extract from the snail tissues.

Plate II. (Opposite page.) Fig. 7, *Cercaria isomi* sp. n., a, furca showing fin-fold; b, floating position. Fig. 8, *C. yankapinensis* sp. n., a, floating position. Fig. 9, *C. palegae* sp. n., a, two positions—floating (left) and actively swimming (right); b, mature daughter redia; c, younger daughter redia. Fig. 10, Echinostome Cercaria (a) from Reelfoot Lake, host *Physa gyrina,* a, floating position; b, daughter redia. Fig. 11, Echinostome Cercaria (b) from Reelfoot Lake, host *Viviparus intertextus,* a, floating position; b, redia; c, encysted echinostome metacercaria from *Viviparus.*


8A.
7B.
11C.
7A.
7.
10B.
8.
9B.
9A.
9.
10.
11B.
11.
9C.
10A.
11A.

7. **Cercaria isomi** sp. n.

Host: Physa gyrina Say.

Locality: Isom Lake, Tennessee, July 10, 1949.

Specific diagnosis: Longifurcous, apharyngeal, monostomate cercaria. Body tubular, capable of great contraction and elongation; acetabulum absent; three pairs of prominent penetration glands in posterior half of body; cytoplasm of anterior and posterior pairs of glands coarsely granular, that of middle pair finely granular; penetration glands of central pair greatly overlap on the mid-line, their nuclei being almost tandem rather than parallel in position; pigmented eyespots present, multipartite, being made up of 15-18 granular bodies, and situated close in front of the anterior pairs of penetration glands; oral sucker large, its anterior third covered by coarse spines; rest of body aspinose; intestine a simple tube extending from oral opening nearly to eyespots; pharynx and caecal branches absent; bladder rounded or Y-shaped; tail stem long and muscular; caudal bodies absent; tail flagellets present on margins, length more than half the breadth of tail; furcae with prominent fin-folds which extend around tips and within 65 microns of tail stem; development of cercariae in brownish-yellow sporocysts 0.38 mm. long by 0.09 mm. wide, and possessing numerous constrictions along their length; measurements; body 180 microns long by 43 microns wide, tail 265 microns long, furcae 230 microns long, fin-fold 165 microns long, oral sucker 56 microns long, bladder 11 microns in diameter.

Cercaria isomi was found infecting *Physa gyrina* from a collection of snails taken at Isom Lake, July 10, 1949, in the flooded area below the spillway, about six miles south of the south end of Reelfoot Lake. This cercaria bears certain resemblances to *C. multicellulata* Miller, 1923, and to *C. paramulticellulata* sp. n. However, the spination of the oral sucker and the tendency toward overlapping of the penetration glands at the mid-line indicate a much closer relationship to *C. louisiana* E. L. Miller, 1935. Also, both *C. isomi* and *C. louisiana* lack caudal bodies in the tail stem, while they are present in both *C. multicellulata* and *C. paramulticellulata.* The eyespots of *C. isomi* are always multipartite, being composed of more than a dozen small, discreet bodies, while those of *C. multicellulata* and *C. paramulticellulata* are composed of three or four larger bodies, and those of *C. louisiana* are single bodies. Miller stated that the paired single eyespots of *C. louisiana* may become multipartite at times because of crushing with the cover glass, but if not crushed are always single bodies. In the case of *C. isomi,* and *C. zeta* Brooks, 1948, the eyespots are always in this granular, multipartite condition, regardless of the extent of cover glass pressure. *C. isomi* can also be told from *C. louisiana* by the presence of tail flagellets on its lateral surfaces. In the present study *C. isomi* was distinguished from *C. paramulticellulata* by the nature of the eyespots, the lack of caudal bodies, and longer oral sucker, as well as the deviation from the strictly parallel nature of the penetration glands in the back of the body.

C. isomi is actively positive toward light and swims with direct, darting movements. The body is not excessively bent at any time while hanging in the water. An extreme flexion of the body into a hook shape was described by H. M. Miller for *C. multicellulata* when hanging in the water. A similar position was described by E. L. Miller (1935) for *C. louisiana* and later (1936) he stated that the hook shape is not characteristic, although Plate VIII, fig. 108 shows something approaching a hook shape for *C. louisiana.* At any rate, both *C. louisiana* and *C. multicellulata* seem to do more bending than was seen with *C. isomi.*

Longifurcous Pharyngeal Monostomate Cercariae 'Tetis' group (Sewell, 1922)

The third species of monostomate longifurcous cercaria found in the present survey is described below. It differs greatly from the others, however, in

several respects. The most noticeable differences are found in the greater development of the reserve excretory system, the anterior position of the penetration gland cells, and the presence of a distinct pharynx and intestinal caeca.

8. **Cercaria yankapinensis** sp. n.

Host: Viviparus intertextus (Say).

Locality: Yankapin Basin, Reelfoot Lake, July 15, 1948.

Specific diagnosis: Longifurcous, pharyngeal, monostomate cercaria. Body oval to pyriform in shape; tail stem long, lacking caudal bodies or flagellets; furcae elongate, lacking fin-folds but covered along lateral edges with minute hair-like spines; oral sucker prominent, provided with numerous bristle-like spines on anterior half, rest of body aspinose; oral sucker containing two small pairs of penetration gland cells; acetabulum absent; prepharynx absent; pharynx round, prominent; oesophagus short, thin; caeca wide, long, with undulating margins and thick walls, slightly converging posteriorly; excretory system complex, many of the reserve excretory vessels precociously developed in cercaria; four main excretory vessels entering bladder, two laterally and two centrally; the paired central vessels bound the genital fundament, located directly anterior to the bladder, then fuse to form a single median trunk which extends forward to meet the paired lateral vessels at the level of the oesophagus and intestinal bifurcation; short branches of the excretory system extending forward to encircle the oesophagus, and another pair doubling backward along the path of the lateral ascending vessels to the posterior end of the body where they enter the tail stem, ending in two pairs of capillary tubules with flame cells; flame cells in the body consisting of three pairs immediately behind the oral sucker and lateral to the pharynx, a fourth pair located immediately behind the bifurcation of the caeca, and a fifth pair located directly posterior to the ends of the caeca; capillary tubules not observed; excretory formula unknown, but five pairs of flame cells in body and two pairs in tail, giving a total of 14 flame cells for the cercaria; development occurring in long muscular sporocysts, 0.9-1.0 mm. in length and containing about twenty cercariae in various stages of development; measurements of cercaria: body 275 microns to 300 microns in length, tail stem 475 microns, furcae 380 microns, oral sucker, 62 microns, pharynx 24 microns, oesphagus 29 microns, caeca 20 microns, bladder 40 microns.

Sewell has placed the cyathocotylid cercariae in his Group 3 of Furcocerous Cercariae, which he further divided into the 'Vivax' and the 'Tetis' groups. The two groups can be distinguished primarily in the presence or absence of furcal fin-folds, the number of flame cells in the body, and the presence or absence of a rudimentary acetabulum. Sewell also mentions that in the 'Vivax' group the flame cells in the tail stem empty into the caudal canal, or appear to, while in the 'Tetis' group they arise from the descending loop of the excretory tube that enters the tail from the body. It is very unlikely that the former condition occurs in either group. Also, the acetabulum is very likely to be absent or rudimentary in members of either group, and cannot be used alone as a separating character.

Faust, 1924, added a third group, the 'Leptoderma' group to include *C. leptoderma* Faust, 1922. Szidat, 1933, described the life cycle of *Monostomum viviparae* von Linstow, 1877, and created the genus *Linstowiella* for this species with *L. viviparae* (Linst., 1877) as type. The cercaria of this form is similar to both the 'Vivax' and the 'Tetis' groups of Sewell, but differs sufficiently for Szidat to feel justified in erecting a fourth group, the 'Vivipara' group. At the same time Szidat also recognized *C. tauiana* Faust, 1930, as different from the other cyathocotylids and erected the 'Tauiana' group for this species.

At the time of its erection by Sewell the 'Vivax' group contained only *C. vivax* Sonsino, 1892; *C. indicae* XV, and *C. indicae* LVIII, Sewell, 1922, and possibly a fourth cercaria described by Leiper and Atkinson in 1915. Since that

time several more species have been added. *C. vivax* Sonsino, 1894, from Tunisia, was further studied by Langeron (1924) and shown to be distinct from *C. vivax* Sonsino, 1892, from Egypt. The researches of Azim (1933) verified this, his work on the life history of *C. vivax* Sonsino, 1892, indicating that the host of the adult in nature is the Egyptian kite, *Milvus migrans aegyptiacus,* and in the laboratory the dog and cat as experimental hosts. The life cycle of *C. vivax* Sonsino, 1894, was begun in 1934 and successfully completed in 1941 by Joyeux and Baer. They found the definitive host to be the watersnake, *Tropidonotus viperinus,* from Tunisia. The adult worms of the two forms then become *Prohemistomum vivax* (Sonsino, 1892) Azim, 1933, and *Szidatia joyeuxi* (Hughes, 1929) Joyeux and Baer, 1941.

Unfortunately not all of the members have been so completely studied as these. Other species of cercariae which probably belong to the 'Vivax' group are: *Furcocercaria vivax?* Wesenberg-Lund, 1934, from *Bithynia tentaculata; Cercaria "R"* McCoy, 1928; and *C. dorsocauda* Tubangi, 1928. The first and only adequate description of a member of this group, from the United States is that of *C. kentuckiensis* Cable, 1938, from *Goniobasis semicarinata.* The most recent member of the 'Vivax' group to be described is *C. tatei* Johnston and Angel, 1940, from Australia.

The 'Tetis' group has been shown to develop into adults of the Subfamily *Cyathocotylinae* Muhling, 1898. Both Cable (1938) and Johnston and Beckwith (1945) agree that *C. indicae* XXXIII Sewell, 1922; *C. balthica* Szidat, 1933; and the cercaria of *Cyathocotyloides curonensis* Szidat, 1933, belong here. Johnston and Beckwith also place the cercaria of *Cyathocotyle gravieri* Mathias, 1935, in this group. Porter (1938) described *C. theodoxa* from *Neritina natalensis* in South Africa, which belongs in the 'Tetis' group. It is my opinion that both *Furcocercaria No. 4* Petersen (of Wesenberg-Lund, from *Bithynia tentaculata* in Denmark) and *Furcocercaria* sp. Wesenberg-Lund, 1934, from *Bithynia tentaculata* also belong with the 'Tetis' group. Both species lack caudal furcae, have small numbers of flame cells in the body, and although a rudimentary acetabulum is figured for both species it is located anterior to the fusion of the paired central excretory vessels, and its presence is not mentioned in the text. In fact for *Furcocercaria No. 4* specific mention was made (page 132) that "no trace of a ventral sucker has been observed." The most recent member of the 'Tetis' group, and the only one described from the United States is *C. yankapinensis* in the present paper. It differs from all previously described species in the peculiar arrangement of the flame cells and the relatively longer unbranched stem of the central excretory vessel, which takes a winding course before fusing with the paired lateral branches at the intestinal bifurcation.

The 'Leptoderma' group of Faust contains only *C. leptoderma* Faust, 1922, and is characterized by the short tail furcae, which are less than one-half the length of the tail stem. There are 36 flame cells in the body and tail, six being in the tail.

The 'Vivipara' group, created by Szidat for the reception of the cercaria of *Linstowiella viviparae* (Linst., 1877) Szidat, 1933, now contains at least three more members. These are the cercaria of *Paracoenogonimus ovatus* (Katsurada, 1914) Komiya, 1939; *C. szidati* Anderson, 1944; and *C. notopalae* Johnston and Beckwith, 1945. In this group all four species have had portions of their life cycles completed.[2] The cercariae of *Linstowiella viviparae* and *C. notopalæ* both use mollusks for their second intermediate hosts, while the cercariae of *Paracoenogonimus ovatus* and *C. szidati* have been shown to use fishes. The 'Vivipara' group was included in the 'Vivax' group by Cable in his 1938 paper, but Johnston and Beckwith retain it (1945) and place *C. notopalæ* in this group. F. G. Brooks (1948) described a cercaria from Carrol Lake, Wisconsin, that is very similar to *C. Linstowiella viviparae.* The snail host is not given.

[2]When the above was written, Anderson's completed cycle of *Linstowiella szidata* Anderson, 1944 (1950), had not been published.

The final group, the 'Tauiana' group, contains only *C. tauiana* Faust, 1930, unless *Furcocercaria No. 4* Petersen, 1931, as described by Wesenberg-Lund, 1934, can be placed here, as suggested by Cable. In the 'Tauiana' group no flame cells are supposed to be present in the tail stem, and as no flame cells are figured by either Petersen or Wesenberg-Lund for the body or tail of *Furcocercaria No. 4* it may be the reason for Cable's placing it in this group. *Dicranocercaria utriculata* Lutz, 1933, from Brazil is so inadequately described that Cable made no attempt to place it even provisionally in any group. It is extremely doubtful if it can be correctly assigned until a more adequate description is provided. This is also true of *Dicranocercaria conchicola* Lutz, 1933, described from a Unionid clam, and stated to be of the 'Vivax' type. However, the figure of this form shows it to be without fin-folds, and therefore it would fall into one of the other groups.

Attempts have been made to unite the various groups of cyathocotylid cercaria. The 'Leptoderma' and 'Vivipara' groups were included in the 'Vivax' group by Cable (1938). More recently attempts have been made to unite the 'Tetis' and 'Vivax' groups (Anderson, 1944, Maxon and Pequegnat, 1949, Anderson, 1950). It is my opinion that until life history studies show that the cercariae of different groups develop into adults of the same genus it is better that the groups be retained. I believe that a study of the few life cycles now completed will warrant the adoption of this procedure. With this in mind I have prepared a simple key to the groups.

A Key to the Cyathocotylid Cercariae

Includes cercariae with furcocerci, reserve excretory vessels entering bladder, lacking (or rudimentary) acetabula, prominent pharynges and digestive tracts, lacking a dorsal body fold, and developing in elongate sporocysts.

(1) Tail furcae lacking fin-folds.....(a)

(2) Tail furcae with fin-folds, acetabulum rudimentary, flame cells 14-30 or more in body and tail (usually 6 in tail).....'Vivax' group

(a) Longifurcate, acetabulum absent .....(s)

(b) Brevifurcate, 30 flame cells in body and tail..'Leptoderma' group

(s) Flame cells present in tail stem.....(x)

(t) Flame cells absent in tail stem, 12 flame cells in the body .....'Tauiana' group

(x) Ten flame cells in body, 2 or 4 in tail stem .....'Tetis' group

(y) Twenty-four to 36 flame cells in body and tail (usually 6 in tail stem).....'Vivipara' group

Echinostome Cercariae
'Agilis' group

This group of cercariae have oval to pyriform bodies, lack the prominent collar of spines, have the body densely crowded with cystogenous cells which contain rod-like granular masses, usually have a rudimentary esophagus and intestinal caeca, have bladders with a conspicuous division into anterior and posterior portions, and develop in rediae with prominent locomotor processes and a long gut. A small cercaria fitting this description in every way was found on three occasions at Reelfoot Lake and is presumed to be well distributed throughout the small basins in the Reelfoot area.

9. **Cercaria palegae** sp. n.

Host: Viviparus intertextus (Say).

Locality: Goose Basin, July 5, 1948, Yankapin Basin, July 10, 1948, and Bayou du Chien, June 8, 1949.

Specific diagnosis: Small collarless echinostome cercaria of the 'Agilis' group. Body round to pyriform in outline, uniformly covered with fine spines; tail capable of great contraction and elongation, often contracted and spread laterally in a cup-shaped manner so that it is broader than long (Fig. 9A); tail lacking a fin-fold; acetabulum prominent, slightly smaller in diameter than oral sucker; a circle of 16 oral papillae on inner edge of oral sucker; three gland cell openings on anterior edge of oral sucker with ducts much dilated; both oral sucker and prepharynx typically are filled with fluid from gland cells; collar and enlarged collar spines absent; pharynx and short oesophagus present; intestinal caeca present but not traceable in dense body tissues; bladder heavy walled and divided by a transverse constriction into two approximately equal portions; entering into anterior portion are a pair of excretory ducts which widen greatly at level of acetabulum; three to five large spherical concretions present in each duct at sides of acetabulum; duct continues anteriorly to sides of pharynx where it loops outward and backward to sides of bladder, turning once more to pass forward and terminate at sides of oral sucker; along this duct are given off the capillary tubules with flame cells; six flame cells were observed, but probably two or three more flame cells are present; excretory formula unknown but believed to be $2[2 + 2 + 2 + 2]$ or $2[3 + 3 + 3]$ giving a total of 8 or 9 flame cells in the body and none in the tail; posterior bladder portion enters tail, continues as a caudal excretory vessel, which forks quickly and either ends blindly or empties at sides of tail; body heavily packed with cystogenous material in the form of large gland cells containing rod-like bodies, forming a cross-hatched pattern within the cells; cells in three somewhat indefinite rows, the first along outer edge of body, the second a middle row at sides of acetabulum, and a third inner row along sides of pharynx and oesophagus; outer row contains 6-8 cells, middle row 5-6 cells, and inner row 3-4 cells per side, giving a total of 30-36 of these cells in body; development in rediae possessing a long intestine and one pair of locomotor processes; twenty or more cercariae in various stages of development in the mature rediae, which are 1.5 mm. in length and broken by narrow transverse constrictions into bag-like portions. (Fig. 9B).

C. palegae is a member of Sewell's 'Agilis' group of Gymnocephalous cercariae. Included in this group are *C. agilis* Filippi, 1859, and *C. indicae* XLI Sewell, 1922. Since the time of its erection several more species have been described. An emended diagnosis of this group was presented by Cable, 1938. He placed nine previously described species in the 'Agilis' group, including *C. ornatostoma* Cable, 1935, and *C. fusiformis* O'Roke, 1917, the only representatives described from the United States at that time. *C. ornatostoma* Cable, 1935, from *Goniobasis semicarinata,* is clearly a member of this group, but it is extremely doubtful if *C. fusiformis* O'Roke, 1917, from *Physa gyrina* can be considered a member. There is no mention made of the prominent rod-like bodies in the body of the cercaria, and the external form, unlike the other members, reveals distinct shoulders. The bladder is totally unlike other members of the group, and finally, the acetabulum is not in the posterior portion of the body. These same objections can be made to Echinostome *Cercaria No. 2* Petersen, 1932, from *Paludina vivipara,* provisionally placed by Cable in the 'Agilis' group. It is much more likely that *C. fusiformis* and Echinostome *Cercaria No. 2* are more closely related to *C. compactisoma* Byrd, 1940, which possesses shoulders and very inconspicuous collar spines and lacks rod-like granules in the cystogenous gland cells. Additional species belonging to the 'Agilis' group, not mentioned by Cable or placed elsewhere are: *C. circumstricta* Faust, 1922, from *Viviparus quadratus* and *V. polyzonatus* in China; [*Amphistome*] *Cercaria No. 2* Petersen, 1931, and *C. obscura* Wesenberg-Lund, 1934, both from *Bithynia tentaculata; C. klarbosiae* Porter, 1938, *C. planorbidis* Porter, 1938, from *Planorbis pfeifferi* in South Africa; and the present species, *C. palegae* sp. n. from *Viviparus intertextus* in Tennessee.

'Echinata' group

Two Echinostome cercariae, both possessing prominent collars bearing spines, were encountered during the survey but have not been specifically identified due to the close similarities between the many species described for this group. It will probably be necessary to complete their life histories before a specific diagnosis can be made of these two species. At present they will be placed on record only as (a) Echinostome Cercaria from *Physa gyrina,* and (b) Echinostome Cercaria from *Viviparus intertextus.*

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