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## Development of Sporocysts of the Turtle Lung Fluke, *Heronimus chelydrae* MacCallum (Trematoda: Heronimidae)

By MARTIN J. ULMER AND S. CHRIS SOMMER

### INTRODUCTION AND HISTORICAL REVIEW

Although the turtle lung fluke, *Heronimus chelydrae*, has been known for more than half a century, its life cycle has remained enigmatic. MacCallum (1902) was the first to describe this trematode, examples of which he recovered from the lungs and bronchi of a snapping turtle, *Chelydra serpentina*, collected in Ontario, Canada. Barker and Parsons (1914) in a preliminary report described the same worm under the name *Aorchis extensus*. Their specimens were from the lungs of a painted turtle, *Chrysemys marginata*, from lakes in Minnesota and from the Mississippi River at Fairport, Iowa. A fuller description of the parasite by these authors was published in 1917. Ward (1917) established the family Heronimidae including therein the genera *Heronimus* and *Aorchis*, but suggested that *Heronimus chelydrae* and *Aorchis extensus* might prove to be identical, or at least might be congeneric. In Ward and Whipple's "Fresh Water Biology" (1918), Ward, however, differentiated between the two genera on the basis of extent of the vitellaria and the presence or absence of the seminal receptacle. It remained for Stunkard (1919) who compared MacCallum's and Barker and Parsons' specimens with additional worms he had collected, to demonstrate that *Heronimus chelydrae* and *Aorchis extensus* are identical, and that the correct name for the parasite should remain *Heronimus chelydrae* MacCallum 1902. Stunkard, who found the adult worms in six different species of turtles, provided additional details of morphology, supplementing the observations of MacCallum. No information, however, was presented relative to the life cycle.

In 1921, MacCallum described as new species, *Heronimum geomydae* and *H. maternum*, using the structure of the testes as a criterion for distinguishing them from *H. chelydrae*. Caballero (1940), however, showed that MacCallum's *geomydae* and *maternum* are in reality identical to the type species of the genus, and that any apparent differences are merely the result of regressive changes in the specimens themselves. The morphology of the miracidium of *H. chelydrae* was presented in detail by Lynch (1933). Sizemore (1935) examined several hundred adult *H. chelydrae* collected from snapping turtles and concluded that smaller turtles harbor more lung flukes, but that these are correspondingly smaller than worms from larger

turtles. Gametogenesis in the adult was reported on by Guilford in 1955, who used adult worms from turtles collected in Wisconsin.

Our interest in problems concerned with the life cycle of this interesting digenetic trematode was stimulated in the early summer of 1956 when we recovered adult worms from snapping and painted turtles collected from various regions in northwest Iowa. The comparative lack of difficulty in observing penetration of miracidia into physid snails and their subsequent development into mature sporocysts enabled us to follow this portion of the life cycle during the summer months. Late in the summer we learned that investigations on the life cycle of *H. chelydrae* were being carried on by Cable and Crandall at Purdue. A short preliminary paper on their findings was published late in 1956. It is the purpose of the studies here presented to record only the development of the sporocyst in the molluscan host. Elucidation of the complete cycle still awaits further investigation.

#### MATERIALS AND METHODS

During the summer of 1956, turtles were collected from the following areas in the vicinity of the Lakeside Laboratory at Lake Okoboji, Iowa: West Lake Okoboji (Miller's Bay), Diamond Lake, Welch Lake and Silver Lake, all in Dickinson County. Two species of turtles were found in these localities, namely, the snapping turtle (*Chelydra serpentina*) and the painted turtle (*Chrysemys picta belli*). Table 1 summarizes the findings relative to natural infections of *H. chelydrae* in these turtles. Some of the adult worms, after removal from the lungs, were teased apart to obtain eggs, while from others miracidia emerged from the genital pore when the worms were placed in distilled water.

Snails employed in experiments to determine the first intermediate host of the parasite included laboratory reared *Physa gyrina* (Say), *Physa sayii* (Tappan), *Lymnaea reflexa* (Say), *Menetus exacuon* (Say), *Gyraulus parvus* (Say), *Valvata tricarinata* (Say) and *Helisoma trivolvis* (Say). Sporocysts, when obtained from experimentally infected snails were fixed in 10% formalin, AFA or Bouin's fixatives. Some were sectioned *in situ*, others removed from the snail before fixation. Whole mounts were prepared using a variety of carmine stains with fast green counterstain. Serial sections cut from 6 to 10 microns, were stained in Heidenhain's iron haematoxylin, Harris' haematoxylin, and Mayer's haemalum, with erythrosin or eosin employed as contrast stains.

#### ADULTS AND MIRACIDIA

##### *Notes on Adult Flukes*

Considerable variation exists regarding the number of adult worms in the turtle lung. Lynch (1933) recorded from one to 16 in infected

Table 1  
Summary of Turtles Examined

Collecting Area	Turtles Examined				Turtles Infected			
	<i>C. serpentina</i> (snapping turtle)		<i>C. picta</i> (painted turtle)		<i>C. serpentina</i>		<i>C. picta</i>	
	♂	♀	♂	♀	♂	♀	♂	♀
Diamond Lake ....	2	0	10	13	0	0	2	3
Silver Lake .....	2	0	3	2	1	0	1	1
Welch Lake .....	2	0	4	11	2	0	0	6
West Lake Okoboji (Miller's Bay)	0	0	2	1	0	0	0	0
Totals .....	6	1	19	27	3	0	3	10

individuals. The largest number recovered from our naturally-infected turtles was 31, 26 of these situated in one lung. The host, a female painted turtle from Diamond Lake, was examined in August and very few miracidia were recovered from the adult worms. In other infected turtles, the number of gravid worms varied from one to 21. Contrary to Barker and Parsons' observations (1914), we found no heavier infections in female turtles than in males. Sizemore (1935) and Stunkard (1919), similarly found no differences in degrees of infection between sexes of turtles.

### Hatching of Miracidia

The adult flukes are either oviparous or viviparous, but in either case, miracidia are well developed when they leave the body. When gravid worms are torn apart in saline solution, large numbers of fully developed miracidia may be obtained, many of which emerge from the egg capsule. Transfer of eggs from saline to distilled water facilitates hatching. Viviparous emergence of miracidia from the genital pore occurs readily if recently recovered adults are placed in distilled water. Adult worms, if first refrigerated in distilled water, then transferred to warmer water for several hours, produce miracidia in quantity. Longevity of the emerged miracidia has been observed for as long as 25 hours. Lynch (1933) stated that the life of the miracidium is very short in either tap water or distilled water, and that the organisms died within an hour after hatching. He suggested, however, that this was probably an abnormally short time resulting from the high temperatures prevailing during the time of his studies.

### Snail Hosts

With large numbers of miracidia available, exposure to laboratory-reared snails was undertaken. Numerous aquatic snails\* were employed to determine the course of development of sporocysts. These included: *Gyraulus parvus* (Say), *Helisoma trivolvis* (Say), *Lym-*

\*Grateful acknowledgment is expressed to Dr. Henry van der Schalie of the University of Michigan, for aid in the identification of the molluscs employed in these studies.

*naea reflexa* (Say), *Physa gyrina* (Say), *Physa sayii* (Tappan), *Menetus exacuous* (Say) and *Valvata tricarinata* (Say). A series of 25 experiments involving 114 snails was carried on from late June through September, 1956. These experiments involved both single and multiple exposures of miracidia to snails. Although penetration of miracidia was observed occasionally in all the snail hosts listed above, development of sporocysts occurred only in *Physa gyrina*.

### *Penetration of Miracidia*

Frequent observations of miracidial penetration indicated that the process is effected with little difficulty and requires from two to five minutes. Miracidia seem to prefer the mantle region and the proximal end of the tentacles as sites for penetration. Occasionally, miracidia were seen to penetrate at the anterior edge of the rostrum. Reaction to penetration is generally a rather violent one on the part of the molluscan host, and not infrequently active bodily movements of the snail are sufficient to dislodge some of the attached miracidia. Especially violent reaction may be observed when penetration takes place near the tentacles. Miracidia which penetrated tentacles were seen moving slowly down towards the mantle. During the process of penetration miracidia exhibit characteristic burrowing movements, contracting and expanding periodically, then remaining rigidly extended until the integument is pierced. As has been observed among numerous other trematode species, miracidial penetration seems in large measure to be the result of trial and error. Snails employed in our feeding experiments varied in length from 3-9 mm., but miracidia showed no preference for either smaller or larger individuals, since both were readily infected.

### DEVELOPMENT OF SPOROCYSTS

#### *Experimental Infections*

Following the exposure of miracidia to laboratory-reared snails, the latter were examined periodically for developing sporocysts. When it was found that development was limited to *Physa gyrina* and that these snails could be infected with little difficulty, numerous infection experiments (summarized in Table 2) were initiated, using only this species of mollusc as experimental host. All snails were maintained at room temperature. Since sporocyst development takes place in the mantle, it is frequently possible to observe sporocysts simply by removing the shell of the snail, without disturbing the soft body parts. The yellowish color of older sporocysts is visible through the thin mantle lining. A series of developmental stages ranging in age from 8 hours to 56 days was obtained, using both single and multiple exposures of miracidia to snails. Measurements indicated below were made from unflattened living specimens or from unflat-

tened specimen fixed in warm 10% formalin, in Bouin's or in AFA.

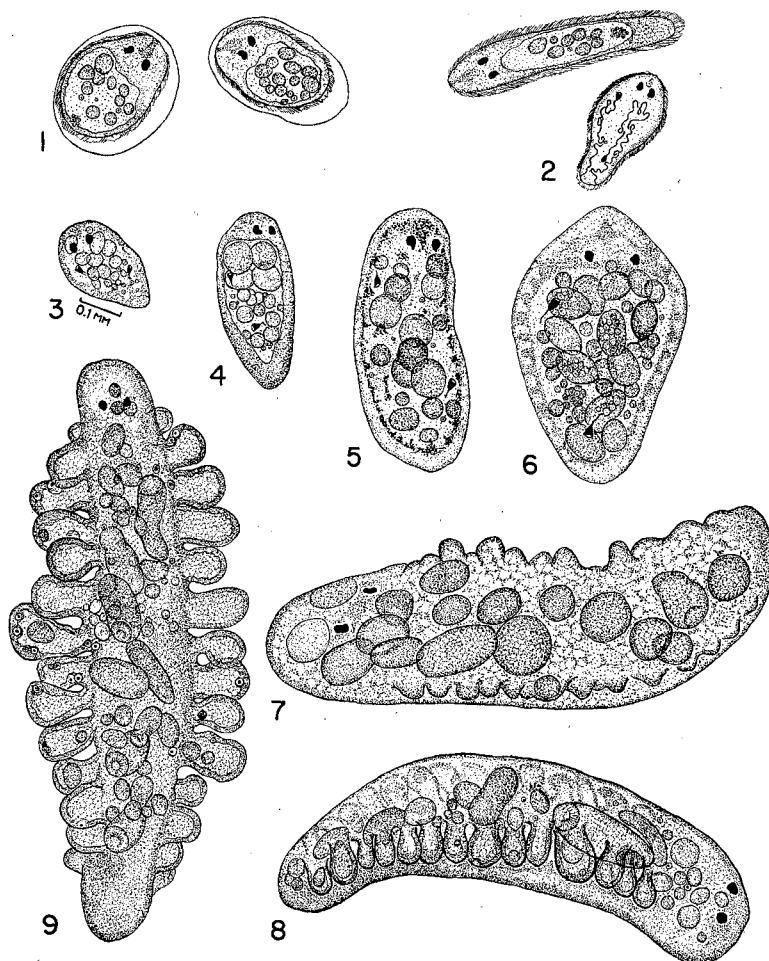
Eight hours after penetration, a single miracidium from a multiple exposure was found unattached in the mantle chamber. It showed little increase in size over that of free-swimming miracidia and measured approximately 0.353 mm. in length. Its shape was more rounded than that of free-swimming miracidia and little movement was apparent. No evidence of cilia could be discerned. Larger germinal masses appeared in the central portion of the body cavity, and smaller masses were seen posteriorly.

Table 2

Experimentally-induced Sporocyst Infections with *Heronimus chelydrae*  
in Laboratory-reared *Physa gyrina*

Date of Exposure	Size of Snail (in mm.)	Date of Examination	Age of Sporocyst	No. Sporocysts Recovered	Type of Exposure S—single M—multiple
7-19-56	3 mm.	7-19-56	8 hours	1	M
7-19-56	7 mm.	7-21-56	2 days	2	M
8- 3-56	3 mm.	8- 5-56	2 days	3	M
8- 2-56	6 mm.	8- 6-56	4 days	2	M
7-18-56	9 mm.	7-23-56	5 days	1	S
8- 3-56	6 mm.	8- 9-56	6 days	1	M
7-19-56	6 mm.	7-27-56	8 days	5	M
8- 2-56	6 mm.	8-10-56	8 days	2	M
7-27-56	6 mm.	8- 5-56	9 days	1	M
7-19-56	3 mm.	7-29-56	10 days	2	M
7-19-56	5 mm.	7-29-56	10 days	2	M
7-23-56	6 mm.	8- 4-56	12 days	1	M
7-23-56	5 mm.	8- 4-56	12 days	1	M
7-19-56	4 mm.	8- 2-56	14 days	2	M
7-27-56	5 mm.	8-12-56	16 days	1	M
7-27-56	5 mm.	8-13-56	17 days	1	M
7-27-56	4 mm.	8-14-56	18 days	2	M
7- 3-56	5 mm.	7-21-56	18 days	1	S
7-19-56	3 mm.	8- 6-56	18 days	1	M
6-25-56	6 mm.	7-19-56	24 days	34	M
6-25-56	5 mm.	7-22-56	27 days	1	S
6-25-56	4 mm.	7-22-56	27 days	1	S
6-25-56	5 mm.	7-22-56	27 days	3	M
8- 3-56	6 mm.	9-14-56	42 days	5	M
8- 3-56	6 mm.	9-28-56	56 days	1	M

Two days after penetration of miracidia, sporocysts from a multiple exposure were recovered (Fig. 3). When first removed from the mantle chamber, these were globular and showed little motility. Shortly after removal, however, the sporocysts became oval. The largest of the three sporocysts recovered measured 0.340 mm. in length and 0.215 mm. in width, but when fully extended measured 0.510 mm. x 0.225 mm. Several large developing embryos were clearly visible in the anterior portion of the body cavity. Eye spots were still very prominent. One of the sporocysts from this infection was not free in the mantle, but seemed to be embedded in the softer tissues at the base of the tentacles. This specimen was recovered with



## PLATE I

### Explanation of Plates

(All drawings were made with the aid of the camera lucida, unless otherwise specified.)

#### PLATE I

Figures 1 through 9, all to the same scale as that shown in Figure 3.

- Figure 1. Miracidia within egg capsules.
- Figure 2. Emerged miracidia showing variations in shape.
- Figure 3. Two-day sporocyst.
- Figure 4. Five-day sporocyst.
- Figure 5. Eight-day sporocyst.
- Figure 6. Ten-day sporocyst.
- Figure 7. 14-day sporocyst. (Note beginnings of lateral branches.)
- Figure 8. 24-day sporocyst.
- Figure 9. 24-day sporocyst. Note cercariae within sporocyst.

#### PLATE II

- Figures 10, 11. 27-day sporocysts. Note well-formed cercaria in sporocyst branch (Figure 10), and emerged cercaria (Figure 11). (Both drawings to the scale shown in Figure 10.)
- Figure 12. Sketches of sporocyst from naturally-infected *Physa gyrina*, showing variations in shape. (Free-hand sketches.)

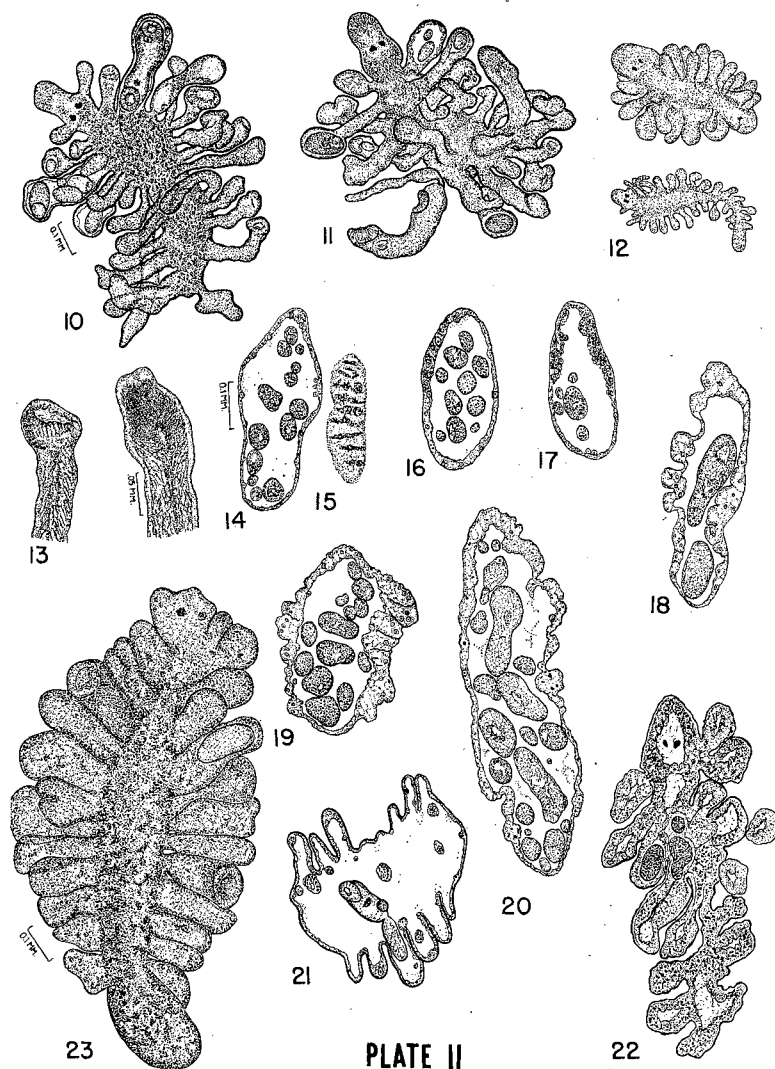


PLATE II

Figure 13. Ends of branches of 27-day sporocyst, showing birth pores.

Figures 14-22. Development of sporocysts as shown in serial sections. (All drawn to same scale as shown in Figure 14.)

Figure 14. Four-day sporocyst, median sagittal section.

Figure 15. Four-day sporocyst, surface view showing accumulation of nuclei at sites of future branches.

Figure 16. 8-day sporocyst.

Figure 17. 12-day sporocyst.

Figure 18. 16-day sporocyst. Note lateral branches and cercarial embryo within sporocyst.

Figure 19. 17-day sporocyst.

Figure 20. 18-day sporocyst.

Figure 21. 27-day sporocyst (Multiple infection).

Figure 22. 42-day sporocyst. Note eye-spots and paucity of cercarial embryos within sporocyst.

Figure 23. 18-day sporocyst (whole mount) from single infection, slightly flattened. Note opacity of the sporocyst and the general absence of cercarial embryos.



difficulty in contrast to those which fell freely from the chamber when the mantle was opened.

Serial sections of the largest sporocyst from a four-day infection (Figs. 14, 15) showed cercarial embryos, the largest of which measured  $0.071 \times 0.051$  mm. Sections which were cut through the surface of the sporocyst (Fig. 15) indicate that at this age there are distinct accumulations of nuclei in the sporocyst wall which mark the site of future branches of the sporocyst.

A single sporocyst, five days post-infection (Fig. 4) measured  $0.570 \times 0.195$  mm. Little movement was noted and no evidence of formed branches could be seen. In the living specimen, a peripheral band of opaque granular material was apparent, presumably associated with the formation of future branches.

Sporocysts of six days were very transparent and exceedingly active. One specimen from a multiple exposure was found free in the mantle cavity. The granular opaque areas at the lateral surfaces of the sporocyst were very apparent. Although rounded in shape for the most part, the sporocyst contracted and expanded rhythmically.

Eight days after miracidial penetration, the activity of the sporocyst (Fig. 5) is decidedly more marked. In one experiment, sporocysts which were found in the anterior portion of the mantle chamber were continually contracting and expanding. The peripheral granular band was better developed than in earlier stages, although lateral branches, so characteristic of the older sporocysts, were not yet visible externally. Many of the cercarial embryos within were elongated, although the majority were round. A sectioned sporocyst of this age (Fig. 16) measured  $0.435 \times 0.187$  mm.

The two large distinct flame cells which are conspicuous structures in the miracidium, are still visible in 10-day sporocysts (Fig. 6). The largest sporocyst recovered at this age measured  $0.510 \times 0.247$  mm. Approximately ten large embryos were observed in one sporocyst, the largest one measuring  $0.129 \times 0.078$  mm.

Sections of a sporocyst 12 days post-exposure (Fig. 17) showed no fully-developed cercariae within, the cercarial embryos still rounded in outline. Greatly thickened areas of the sporocyst wall are visible at this stage of development.

In multiple infections of 14 days, developing cercarial embryos may already have left the sporocyst, since the mantle chamber of one snail was full of embryos. No evidence of a broken sporocyst could be found. Within the sporocyst itself, cercarial embryos (Fig. 7) in all stages of development up to and including those with short stubby tails could be seen. Ten to 12 sporocyst branches, 0.05 mm. long, appear at this stage.

A 16-day sporocyst (Fig. 18) showed well developed cercarial embryos exhibiting rudiments of suckers and tail. The lateral branches of the sporocyst were much more distinct, measuring approximately 0.06 mm. in length. No movement of the branches was apparent. In the region anterior to the eyespots, considerable movement of the sporocyst takes place, for rhythmic contractions and expansions of the body are frequent. A greater opacity of the sporocyst is noticeable at this age. The single sporocyst recovered was embedded in the tissues adjacent to the buccal mass of the snail.

A single sporocyst was recovered from a 17-day infection (Fig. 19). Although no evidence of a break in the sporocyst wall could be found, stubby-tailed cercariae were moving about in the mantle chamber. The bluntly rounded sporocyst branches showed little movement and, as in the 16-day infection, movement of the sporocyst itself was limited to the anterior end.

Both single and multiple exposures were represented by sporocysts 18 days old (Fig. 20). These sporocysts recovered from a multiple exposure showed 10-14 branches, all of which exhibited vigorous pulsatile movements. A peculiar condition was observed in one infection resulting from a single exposure, however. In this instance, the sporocyst, measuring 1.5 mm. was extremely dark with mottled surfaces (Fig. 23). Its movements were very sluggish, and the branches lacked the pulsatile activity of sporocysts of the same age developing from multiple exposures. When this snail was opened, the mantle chamber appeared crowded with well-developed cercariae (more than a millimeter in total length), as well as with developing cercarial embryos. The amphistomatous nature of the cercariae was very apparent. It was clear that development in this instance had progressed much further than in the case of multiple infections of the same age. Although rounded in general outline when first removed from the mantle region, the sporocyst under very slight coverslip pressure became elongate. Its general sluggishness and fragility, together with its over-all opacity suggested that it probably had reached the limits of cercarial production. Practically no embryos were seen within this sporocyst and a stained whole mount of the specimen confirmed the absence of cercariae within.

In multiple infections of 24 days duration (Figs. 8, 9), sporocysts were very active, and cercarial embryos present in large number. The lateral branches of each sporocyst numbered 14 per side, a number which apparently remains constant even in older sporocysts. The branches pulsated continually, and cercarial embryos moved back and forth between the branches and the sporocyst lumen. A total of 34 sporocysts, the largest number recovered from any of our infections, were removed from the mantle of the snail. Many tailed cercariae, about half a millimeter in length were found, but these

were noticeably smaller than cercariae from the single exposure of 18 days, indicating that rapidity of development of cercariae is probably closely related to the number of developing sporocysts present within the confines of the mantle chamber.

The results of 27-day infections similarly demonstrated the effect of crowding on development of cercariae, for in experiments involving single exposures, the sluggish sporocysts recovered were very darkly mottled and apparently filled with granular material (Figs. 10, 11). Less than a dozen tailed cercariae were in evidence in the mantle chamber and the lumen of the sporocyst body was devoid of embryos. Branches, however, contained a few well-formed cercariae and cercarial embryos. Study of some of the branches of the sporocysts indicated birth pores (Fig. 13) at the tips of some of them. Variations in the shape of the sporocyst body were apparent at this age, particularly with regard to the individual branches, some of which were distended with cercariae and cercarial embryos moving in accordance with pressure changes of the sporocyst body. Other branches, temporarily contracted and devoid of embryos, resembled the branches of brachylaimatid mother sporocysts described by Ulmer (1951) in the case of *Postharmostomum helicis*. Swaying, undulating movements which characterize the branches of such older sporocysts are in direct contrast to the vigorous pulsating activity of branches from sporocysts of a younger age.

In another infection of 27 days duration (Fig. 21), resulting from multiple exposure of the snail to miracidia, three sporocysts were present near the reproductive ducts in the mantle region. These sporocysts however, were actively pulsatile, although a yellowish opaque central region could be discerned. Eye spots were still clearly seen, and well-developed cercariae fell free when the mantle lining was broken. These cercariae, somewhat smaller than those from the single infection, exhibited little swimming activity, despite their well-developed tails.

Five sporocysts were recovered from a 42-day infection (Fig. 22). These were found free in the mantle chamber. Eyespots were still present, but very few embryos could be seen. The opacity of the body was similar to that noted from a 27-day sporocyst resulting from a single exposure. Careful study of sectioned material indicated the almost complete absence of germinal cells in the sporocyst wall. The few cercarial embryos remaining within the sporocyst were characterized by the presence of large number of intensely staining round bodies, perhaps pyknotic nuclei.

The oldest sporocyst recovered from our series of feeding experiments was removed from the mantle chamber of a *Physa gyrina* 56 days after exposure to miracidia. Although this was a multiple

exposure, only a single sporocyst was recovered. It differed little from those of 42 days of age, except for its greater opacity and sluggishness. No evidence of embryos within the structure could be discerned, nor were cercariae found within the mantle cavity.

*Sporocyst Infections in Nature*

With the recovery of sporocysts resulting from laboratory infections, snails were intensively collected during July and August from areas where turtles were known to harbor the adult fluke. Table 3 summarizes the data concerning the 300 snails examined.

Table 3  
Summary of Snails Examined for Natural Infections of *Heronimus chelydrae* Sporocysts

Snail Host	No. Examined	No. with <i>Heronimus</i> Sporocysts
<i>Gyraulus parvus</i> (Say) .....	22	0
<i>Physa gyrina</i> (Say) .....	51	1
<i>Physa sayii</i> (Tappan) .....	189	0
<i>Valvata tricarinata</i> (Say) .....	38	0

The only infected snail (*Physa gyrina*) found was collected August 3, 1956, from Diamond Lake, and measured 8 mm. in length. Within the mantle chamber was a single fairly active, pulsatile sporocyst (Fig. 12) which apparently represented an infection of considerable duration, for it was quite opaque and filled with yellowish granular material similar to that seen in older experimental infections. Only three mature cercariae were found within the sporocyst lumen and these were extremely sluggish, exhibiting little activity save for occasional tail movements. Developing cercarial embryos were present in limited number, but both the mature and developing cercariae were very fragile, disintegrating under slight cover slip pressure. No cercariae were seen emerging from the snail.

DISCUSSION

Sporocyst development in *Heronimus chelydrae* as described above is markedly different from that in most digenetic trematodes. The presence of branching sporocysts in the family Heronimidae is rather unusual, for only two other families (Brachylaimatidae and Bucephalidae) have been recorded as possessing them.

Our studies indicate that the miracidium-sporocyst of *H. chelydrae* apparently produces cercariae directly without the formation of an intermediate sporocyst generation. There seems to be no evidence, on the basis of our studies at least, to suggest the presence of a second generation retained within the parent sporocyst. Lynch (1933) in his detailed study of the miracidium of *H. chelydrae* observed and

illustrated a thin cellular envelope surrounding the germinal masses of the miracidium. Possibly this represents an abbreviated sporocyst generation. Detailed studies on the germinal development in the intermediate stages of *H. chelydrae* will do much to aid in resolving this matter. The lateral pulsatile branches, too, might be regarded as representing a daughter generation which remains attached to the parent body. Such an interpretation was suggested by Ciordia (1956) in the case of branching sporocysts of the bucephalid, *Rhipidocotyle papillosum*. Yet, in the case of *H. chelydrae*, there seems little reason for the acceptance of such a view, for the branches produced are strikingly similar in structure and in mode of development to those observed in the life cycle of *Postharmostomum helicis* as shown by Ulmer (1951) where mother and daughter sporocyst generations are clearly defined.

This apparent lack of a second generation is unusual, for in general, cercariae of most digenetic trematodes arise from daughter sporocysts or rediae. Study of sectioned sporocysts from our laboratory-infected snails tends to corroborate Cable and Crandall's (1956) report that such a second generation in *H. chelydrae* is lacking.

One consequence of an abbreviated sporocyst generation is a considerable loss of embryos and potential adults. Branching of the sporocyst and the great number of eggs produced by the large adult worm may compensate for this. Nevertheless, cercarial production is somewhat limited in this species as indicated by the small number produced by an individual sporocyst and by the relatively short time required for the completion of this phase of the life cycle. The persistence of the miracidium-sporocyst after cercarial production has been initiated, and its continued presence even later when cercariae are no longer being produced in number, is of interest. In our oldest infections, eye spots were still evident in sporocysts even though cercarial production had apparently ceased.

The adult worm, although a monostome, develops from cercariae possessing two suckers. That distome cercariae are involved in the life cycle of *Heronimus chelydrae* is further evidence that some families of monostomes have been derived from distome ancestry.

Numerous aspects of the life cycle of *Heronimus chelydrae* still await elucidation through experimental methods. Of particular interest is the problem of the mode of infection of the definitive host. How the turtle acquires its infection is not known. Since cercariae apparently do not emerge naturally from the molluscan host, the question of a secondary intermediate host (if one is required) arises. If the cercaria is the infective stage for the turtle, possibly it gains access via the oral or nasal passages, as is the case with cercariae of certain members of the family Spirochiidae. Of interest, too, is the

manner whereby miracidia leave the definitive host and reach the physid snail serving as the intermediate host. Our studies have failed to disclose how miracidia leave the turtle lung and reach the water. Careful examination of scrapings from the lungs, bronchi and pharyngeal regions (including nasal passages) of infected snapping turtles and painted turtles failed to reveal any indication of eggs or miracidia. Furthermore, examination of the entire digestive tract gave no evidence that miracidia might leave the body by way of the intestines. Occasionally, however, it was observed that well-developed worms were frequently situated in or near the larger bronchi, suggesting that such gravid adults may possibly migrate to the pharyngeal region and discharge eggs or miracidia there. Miracidia released in such a manner would encounter little difficulty in leaving the body of the turtle. It is to be hoped that future investigations will enable those now engaged in life cycle studies of this species to resolve some of these problems.

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