Their relationship indicates a typical bifurcation. This tetracotyle solenocyte pattern is therefore logically a development of that of *Cercaria neotropicalis.*

In view of the epidemiologic and morphologic evidence suggesting the identity of this cercaria and this tetracotyle, it is desirable to inquire into their collateral relationships and probable life cycle. First of all, the cercaria bears marked resemblance to *C. douglasi* Cort, 1917 (from Douglas Lake, Michigan), which Van Haitsma[39] found to develop *via* an encysted tetracotyle stage (*T. flabelliformis* Faust, 1917) into a cotylurid, *Cotylurus flabelliformis,* parasitic in the gut of ducks. The general shape of the two cercariae is similar, although *Cercaria neotropicalis* is considerably the larger. The suckers, digestive tract and penetration glands are almost identical. Moreover, the excretory system is comparable, although not identical, since the formula for *C. douglasi* is $2\ [(2 + 2) + (2 + 2 + 2)]$. The life cycle of this species involves (1) a molluscan host for the phase between the miracidium and the cercaria; (2) the same or a different species of mollusc for the penetration and encystment of the cercaria and development of the tetracotyle, and (3) a snail-eating water bird, in the intestine of which the adult worm develops. Since Van Haitsma[39a] has shown that a cercaria (*C. michiganensis,* La Rue), which bears less close relationship to *C. flabelliformis* than does *C. neotropicalis,* and which encysts in the viscera of fresh-water fishes, also develops into a species of *Cotylurus,* the homologous evidence supports the view that *C. neotropicalis,* with a tetracotyle stage in a mollusc, is the adolescaria of a species of *Cotylurus* or close relative, completing its development in the intestine of a snail-eating bird.

Closely related tetrocotyles found encysted in snails include *Tetracotyle cornuta* (Rud.) Hughes 1929[40], which develops into *Strigea cornuta* (Rud.); *T. molluscipeta* (Lutz) Hughes, 1929[40], which probably develops into a species of *Strigea; T. orientalis*[41], the larva of *Cyathocotyle orientalis* Faust, 1922, and *T. iturbei* Faust, 1918. The last named species was described by one of us (E.C.F.)[42] from *Australorbis glabratus,* collected by Iturbe in Venezuela and containing an infection of *Schistosoma mansoni* parthenitae and cercariae.

These forms, like *T. flabelliformis,* may be readily separated from the Guayama tetracotyle since they all have a well-developed hold-fast organ which we have not been able to identify in the Guayama specimens. It seems evident, therefore, that *C. neotropicalis* is a species of strigeoid larva which has hitherto not been described except from the identical locality and in the same species of snail from which we have recovered it (*i. e.* Marín[23]).

Cercaria marini n. sp. (Figs. 23–25)
(Marín's Cercaria III)

This large cercaria was recovered from a few specimens of *Australorbis glabratus* obtained from Sabana Llana. It is a large distomate species (Fig. 23), tapering anteriorly and broadly truncated posteriorly, with a tail which is somewhat longer than the body. At rest, the cercaria is characteristically curved ventrad (Fig. 24). The body measures 650μ in length by 340μ in greatest width and 120μ in thickness. (Marín's figures of 310μ for length and 150μ for breadth appear to be based on erroneous calibration). The tail is about 700μ long and 110μ in diameter near its proximal end. The entire worm is aspinose. The oral sucker is broadly pyriform and measures approximately 100μ in both longitudinal and transverse diameters. In the midline of its anterior margin it is characterized by having a grooved indentation. The ventral sucker, which is situated an appreciable distance behind the middle of the body, measures, when relaxed, about 130μ in diameter. It is provided with a deep fluted rim (Fig. 24*a*), which is capable of marked constriction, or of relaxation to a flat collar-like extension. This rim is completely lacking in nuclear elements and is regulated by circular and radial muscle elements in the acetabulum proper.

The oral cavity opens into a short, delicate prepharynx, 34μ in length. Behind this region is the spherical pharynx, which measures 35μ in diameter. From this level posteriad the digestive tract consists of solid tubules composed of cells filled with granules. About one-third way from the pharynx to the bifurcation of the gut there is a transverse diverticulum on either side of the esophagus. Bifurcation occurs approximately in the middle of the body. The ceca extend to the level of the excretory bladder. There is a clump of minute paraphyngeal (penetration?) glands, the ducts of which join on each side to form a pair of delicate common ducts which pass through the dorsal wall of the oral sucker and open through minute pores on the antero-dorsal aspect on the head. Because of their minute size it is doubtful if these glands are of any great assistance to the larva in gaining entrance to the next host. The entire body of the cercaria is filled with large polygonal cells crowded with cystogenous granules.

The excretory system is characterized posteriorly by a transversely compressed bladder, with a median ventral pore. There is a short blind caudal reservoir. The collecting tubules from the body enter the bladder from the median anterior aspect. Each main lateral canal can be traced through a tortuous course to the pharyngeal plane, where it bends backward and runs an unbranched course to the lateral margins of the bladder. It then bends forward again, giving off 4 secondary tubules *en route*. Each secondary tubule trifurcates and each branch terminates in two capillaries, with a terminal flame-cell each. Thus the formula for this pattern consists of: $2\ [(3 \times 2) + (3 \times 2) + (3 \times 2) + (3 \times 2)]$. (See Fig. 23*a*). The primary collecting tubule is considerably enlarged between the ventral sucker and the level of the pharynx; in this region it is packed with excretory granules. On its return posteriad the middle length of the primary collecting tubule is alternately ciliated and non-ciliated.

The cercariae develop in rediae which are stained a burnt-orange hue, have a long sepia-colored rhabdocele gut, a distinct collar prominence and a pair of short "feet" (Fig. 25*a*). Both cercariae and rediae of the third generation are found in these rediae (Fig. 25*b*). On emerging into the water the cercariae are capable of very rapid movement, but soon settle down to the bottom of the container and assume a pose with the body and tail curved strongly ventrad (Fig. 24). No encystment has been observed by us, although this step is the next logical one in the life cycle. However, Marín's observations (p. 400)[38] indicate that both under laboratory and natural conditions (at Guayama) these cercariae, when free in water swarmed around and attacked the mouth and gills of minnows and were later found encysted in "the body portions of the gills and in the abdominal cavity". The further history of the fluke is unknown, but it seems most probable that some piscivorous animal (probably a bird) serves as the definitive host.

The taxonomic relationships of this larva deserve consideration. Although the cercaria is free of collar spines, there is intrinsic evidence that the organism has affinities with the echinostomes. The "wish-bone" type of intestine with the solid esophagus and ceca suggest this relationship. However, the most direct evidence is found in the excretory system. The shape of the bladder and the openings into it of the collecting tubules in the body and caudal trunk, likewise the collecting tubules themselves and the character, amount and disposition of the excretory granules are all echinostomatoid in type. The most convincing homology, however, is found in the flame-cell pattern, which is built upon the three-forked type, on to which has been superimposed a terminal bifurcation. The entire excretory system conforms to that of the ''Cristacantha'' group of Faust (1924) of which *Cercaria cristacantha* Faust, 1922, was designated as type. It has been suggested by Faust[43] that this group possibly shows kinship to the genus *Echinoparyphium* Dietz, which belongs to the subfamily Echinostomatinae. In view of this intrinsic evidence of echinostomatoid relationship it is interesting to note the confirmatory information furnished by Marín (l. c.)[38]. The metacercariae encysted in the fish ''exhibited a double collar of spines, thirty-four in the anterior ring and thirty-eight in the posterior one''. Since this number of spines, with their stated arrangement in two distinct rows, is far in excess of the number described for any adult species of echinostome, the generic relationship can not be forecast and must await further life-history study.

Cercaria paucispina n. sp. (Figs. 26–28)
(Marín's Cercaria IV)

The body of this echinostomate cercaria, which was obtained from *Australorbis* collected at Guayama, is oval, and our living material in relaxed, slightly compressed condition, measured 200μ long by 100μ in width. (Marín's figures of 90 × 68μ appear to be based on erroneous calibration.) There is a definite, but rather inconspicuous collar constriction (Fig. 27). The oral sucker is broadly oval, with a width of 44μ and a length of 30μ. The ventral sucker, which is situated in the third quarter of the body, is transversely compressed and may be exserted or introverted into the body tissues. It measures 35μ long by 50μ wide. The body is closely beset with minute spines, while the collar is provided with nineteen spines which are blunt at the point of insertion and sharpened at the free end. Within the oral cavity there is a long narrow prepharynx, following which there is a spherical pharynx 13μ in diameter. The esophagus divides almost immediately behind the pharynx. The ceca end just below the anterior plane of the ventral sucker.

The excretory system empties through a slightly compressed subspherical bladder at the posterior end of the body. Primary collecting tubules arise directly from the antero-lateral aspects of the bladder. As they are traced forward they are found to dilate in the region between the ventral sucker and the pharynx and are filled in this portion with several large ovate excretory granules. The tubules become constricted again in the plane of the collar constriction and bend back on themselves to return posteriad. The more delicate portions of the system were masked by the densely packed cystogenous glands. One triad of very small flame cells was found at the anterior reflexion of each collecting tubule. The cystogenous glands extend in paired chains in the fields external to the intestinal tract and dorsally in a broad band from the pharyngeal region to the caudal extremity. The glands are polygonal, with rounded corners and contain rodlets of cyst-forming substance. Penetration glands, if present, are completely obscured by the cytogenous material.

The tail of *Cercaria paucispina* is a large, delicate, gracefully moving organ, which is four to five times the body-length and from ventral view has the form of a carrot (Fig. 26). At its proximal end it contains an accessory excretory reservoir. Otherwise it is made up of loose parenchymatous tissue. It is attached to the truncated posterior end of the body. By means of this tail the organism moves in graceful undulations through the water.

This cercaria develops in a characteristic echinostome redia.

This larva does not encyst in laboratory containers but swarms about small fishes, on the gills, under the scales or in the flesh of which it readily encysts. For this reason its definitive host may be expected to be a piscivorous animal. While the number of head spines is consistently nineteen (cf. Marín's description, as well as that of our own), there is not sufficient evidence to place this cercaria in a generic group. Such necessary information can probably be obtained only by a complete life history study.

SUMMARY AND CONCLUSIONS

1. While previous investigators in Africa and in the western hemisphere have worked out the life cycle of *Schistosoma mansoni* and have studied certain aspects of the extra-mammalian phase of the organism, the various observations have been disconnected, inadequate and to a considerable degree filled with discrepancies.
2. The present studies were conducted in Puerto Rico and New Orleans, utilizing human cases and experimental monkeys as sources of eggs, and naturally and experimentally infected *Australorbis glabratus* as the material for the molluscan phase of the life cycle.
3. Eggs discharged from the infected mammal in the early stages of acute infection are usually mature and for the most part viable. The period between oviposition and maturity is relatively short, as determined by examination of uterine eggs, those which had just been deposited in the wall of the bowel, those in the mucosa of the bowel and in the lumen at the level of oviposition, and those in feces which had just been evacuated. Non-viable eggs most commonly occur in the evacuations of chronic cases and suggest that they are degenerating fertile eggs which have been retained in the fibrosing wall of the bowel.
4. Five hundred viable eggs from an acute infection in a monkey averaged 152.30μ ± 0.19μ in length by 63.76μ ± 5.27μ in transverse diameter. A similar number from a chronic human infection averaged 142.42μ ± 9.42μ by 60.04μ ± 4.43μ. The minimum measurements are the same (114μ), while the maxima reach 205.2μ for

the monkey and 174.8μ for the human case. Later (more chronic) dejecta from the same monkey contained eggs which had a mean length of 164.1μ and a mean breath of 70.0μ. It is suggested that these differences are due to shrinkage of the eggs after having been placed in the fixative and not to intrinsic differences in the strain or to influences produced by the host.

5. The unhatched larva and the free-swimming miracidium have been carefully studied, and are compared with similar stages of *S. japonicum*. In putrefying feces at room temperature the unhatched larva hardly remains viable for 24 hours; in formed feces at 45–50° F. the majority of eggs remain viable for a week or more. Hatching results from dilution of the fecal medium with a considerable amount of water. It is accelerated by mechanical agitation of the eggs. Hatching of a batch of eggs is not simultaneous, but is spread over a period of 48 hours. During their free-living existence the most active miracidia congregate in the top inch of water. Those which have just hatched, as well as exhausted individuals, accumulate in the half-inch of water above the bottom sediment. Free miracidia, unconfined by débris, have an expectation of life of less than 24 hours. These miracidia have ciliated epithelial plates of the 6–8–4–3 pattern, which is probably the same for all schistosome miracidia.
6. The molluscan host in Puerto Rico is *Australorbis glabratus*. The anatomy of this snail has been studied in order to trace more carefully the path of migration of the miracidium after entering the snail and the multiplication of its progeny within this molluscan host. The orgin of the primary digestive gland pouch from the proximal mid-intestine rather than from the pyloric stomach, and the presence of a transverse septum, separating the proximal from the distal viscera masses, have been demonstrated.
7. Miracidia are attracted to the snail by its specific secretions. The largest number of *S. mansoni* miracidia attack and apparently penetrate the tentacles; a smaller number is attracted to the head-foot organ. In the

laboratory up to 100 per cent infection of *Australorbis glabratus* has frequently been obtained by placing uninfected snails of this species in pans or dishes of hatching miracidia and leaving them over night. In endemic foci, batches of snails collected and tested had infection incidences ranging from 0 to 34.4 per cent. *Helisoma lentum* (subgenus *Pierosoma*), the common planorbid in the New Orleans area, has proved completely refractive to infection in the laboratory, although parallel experiments with *A. glabratus* were successful.

8. Over a period of months the cercarial progeny from specimens of *A. glabratus,* infected with a single miracidium of *S. mansoni,* amount to several tens of thousands. Since only a few second generation sporocysts are produced by a single first generation sporocysts (the metamorphosed miracidium), this vast cercarial progeny must be regarded as due primarily to the fecundity of second-generation sporocysts, which continue their production over several months. The critical period for the molluscan host (and likewise for the schistosome infection) occurs between the fifteenth and twenty-fourth days, when rapidly maturing cercariae may erupt from their mother sporocysts *en masse,* with sufficient destruction of the host's tissue to produce its death. The intra-molluscan phase requires 22 to 31 days.

9. Careful examination of immature and mature cercariae, both fresh specimens (stained with brilliant cresyl blue) and fixed specimens (hot formalin and Bouin's fluid), confirms the previous work of Faust (1919, 1926), Manson-Bahr and Fairley (1920) and Mohammed (1932), that these larvae are provided with two anterior pairs of oxyphilic and four posterior pairs of basophilic penetration glands. On one occasion, in living specimens examined with brilliant cresyl blue stain, we found a glandular structure in the head organ corresponding to the head gland of the cercaria of *S. japonicum.* Our mature *S. mansoni* cercaria, fixed with hot formalin after relaxation in the ice-box, had average measurements as follows: body length, 214μ

body breadth, 98μ; length of tail trunk, 225μ; breadth of tail trunk, 68μ, and length of caudal furci, 104μ.

10. The cercariae of *S. mansoni* are definitely phototactic; they emerge from the snail in greatest numbers in direct sunlight between 9 a. m. and 2 p. m. On dark days there may be no emergence whatever. They tend to be equally distributed through the water during the first 16–18 hours after their emergence. With their forked-tails upward in position, the organisms slowly descend and ascend in convection currents. Their free-living existence appears to be limited to 24–30 hours.
11. Three species of non-schistosome cercariae were obtained from *Australorbis glabratus* in endemic foci in Puerto Rico. One of these, *Cercaria neotropicalis* n. sp., is a strigeoid larva, with a flame-cell formula of 2 [(2) + (2 + 2)], and appears to be closely related to the genus *Cotylurus*. The life cycle of *C. neotropicalis* most probably involves (1) a molluscan host for development from the miracidium to the cercaria; (2) a second molluscan host for the encysted adolescercaria (tetracotyle), and (3) a definitive host, probably a snail-eating species of bird. The other two species, *C. marini,* n. sp. and *C. paucispina,* n. sp. are echinostomate forms. Their cercariae attack fresh-water fishes, in which they encyst. Their definite hosts are probably fish-eating vertebrates (most likely birds).

ACKNOWLEDGMENTS

We wish to express our debt of gratitude to Dr. Frank C. Baker, Curator of the Natural History Museum, University of Illinois, for valuable information on the taxonomy and anatomy of members of the planorboid group; to Dr. Elon E. Byrd, for assistance in the study of the anatomy of *Australorbis glabratus* and *Helisoma lentum* and for measurement of *S. mansoni* eggs; to Dr. Charles A. Jones and Mr. José C. Janer, for assistance on the experimental side of our work in Puerto Rico; and to Dr. George W. Bachman, Director of the School of Tropical Medicine, San Juan, and to physicians and other individuals in Puerto Rico who aided us in our project.

A preliminary report on our study of the extra-mammalian phase of the life cycle of *Schistosoma mansoni* has been recently published (Faust and Hoffman, 1934)[44].

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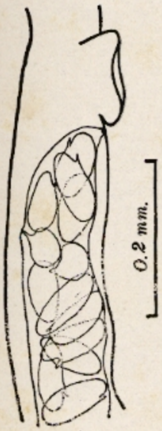
DESCRIPTION OF PLATES

PLATE I

FIGURES 1–7

1. Immature eggs in proximal uterus of *Schistosoma mansoni.*
2. Slightly immature egg of *S. mansoni,* showing four flame cells, primitive gut and secretory glands of miracidium, but before development of the cilia.
3. Mature egg, ready to hatch.
4. Miracidium, in characteristic rotating position inside egg shell with globules of excretory waste at opposite end of shell.
5. Miracidium of *S. mansoni* breaking out through a rent at a weak place in the shell.
6. Detailed structure of the hatched miracidium of *S. mansoni,* showing primitive gut, secretory glands and ducts, excretory system, "nerve center", germ balls and ciliated epithelium, stained supravitally with brilliant cresyl blue. (Dorsal view).
7. The epidermal plate pattern of the miracidium of *S. mansoni.*

NOTE.—Figures 1, 9, 10, 14 *a–e,* 15, 19 *a–b,* 21, 22 *a,* 23, 24, 25 *a–b,* 26, 26 *a* and 28 have been reproduced to a magnification of about 80 diameters: figures 2, 3, 4, 5, 7, 11, 12, 13, 16, 17, 18, 20, 27, 27 *a* and 28 *a,* to a magnification of about 280; figure 6, × 800; figure 8, × 8; figure 17 *a,* × 1200, and figure 22 *b,* × 120. Figure 23 *a* is not drawn to scale.



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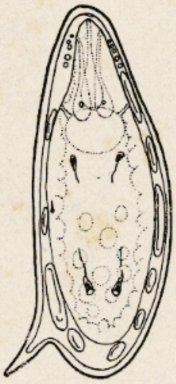

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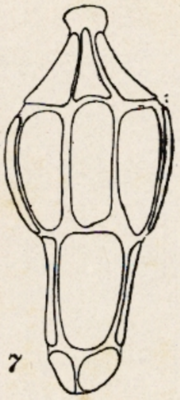

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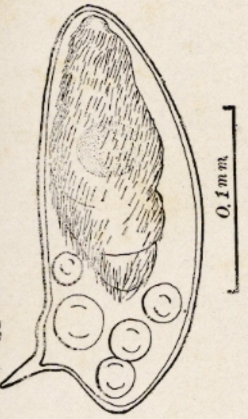

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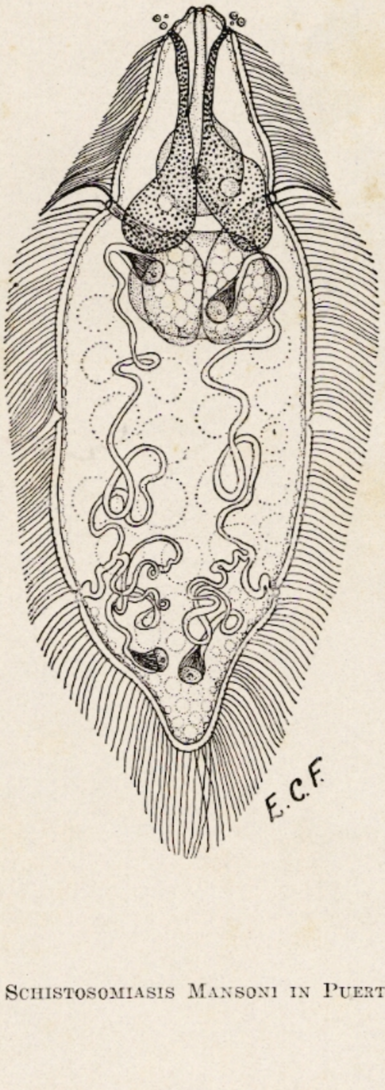


5

Plate II

Figure 8

8. *Australorbis glabratus* dissected out of shell and opened to show (1) important landmarks, (2) migration route of miracidia and (3) progressive development of *Schistosoma mansoni* within the mollusc.

An — anus
Aur — auricle
Buc C — buccal cavity
Buc Gl — buccal gland
Cb Ga — cerebral ganglia
Ce — cecum
Es — esophagus
F — flagellum
G Op — genital opening
Int — intestine
L — liver
L D Gl — lumen of digestive gland
Lung — respiratory organ
Lung Op — external opening of respiratory organ
M — mouth
♂ *G Or* — male genital orifice
O T — ovotestis
R — renal gland
R D — renal duct
Re — rectum
Sept — transverse septum
Sp D — spermatic duct
St — stomach
Vd — vas deferens
Vent — ventricle
Vs — vesicula seminalis

The arrows show the progressive stages in the migration of the miracidia and sporocysts into the digestive gland; the numerals indicate the progressive steps in the development of the intra-molluscan phase of the life cycle.

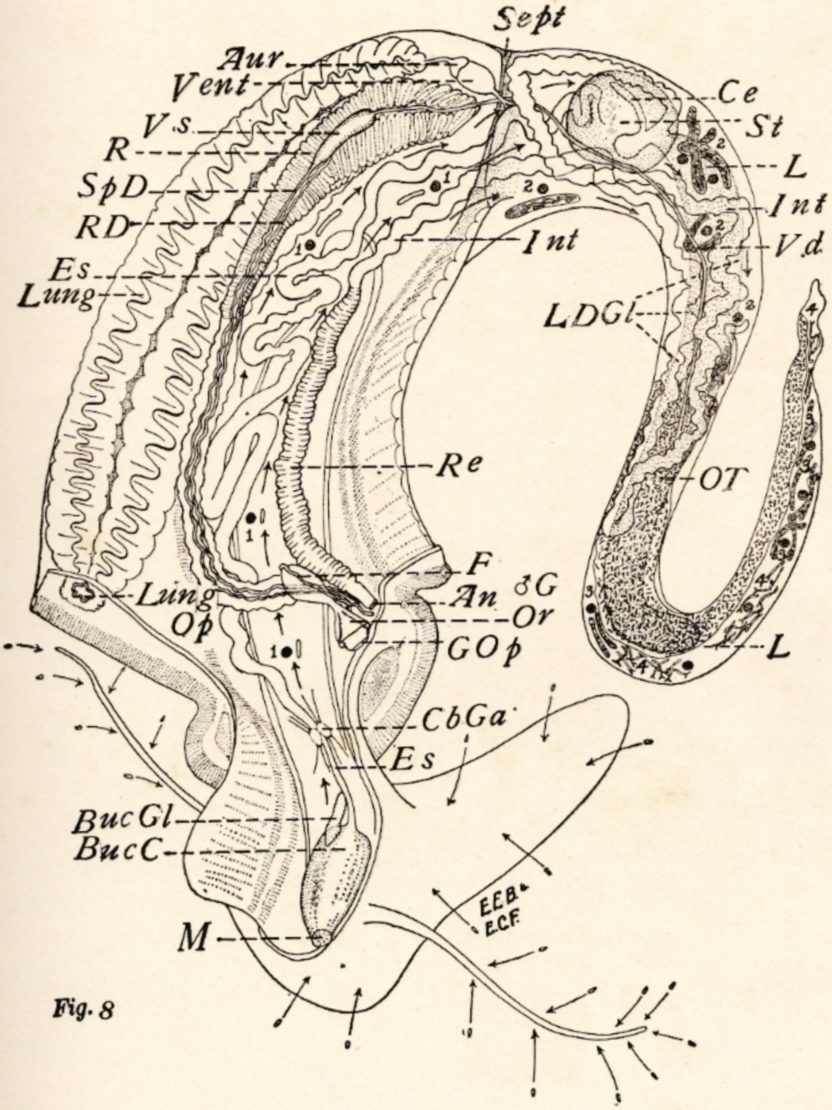
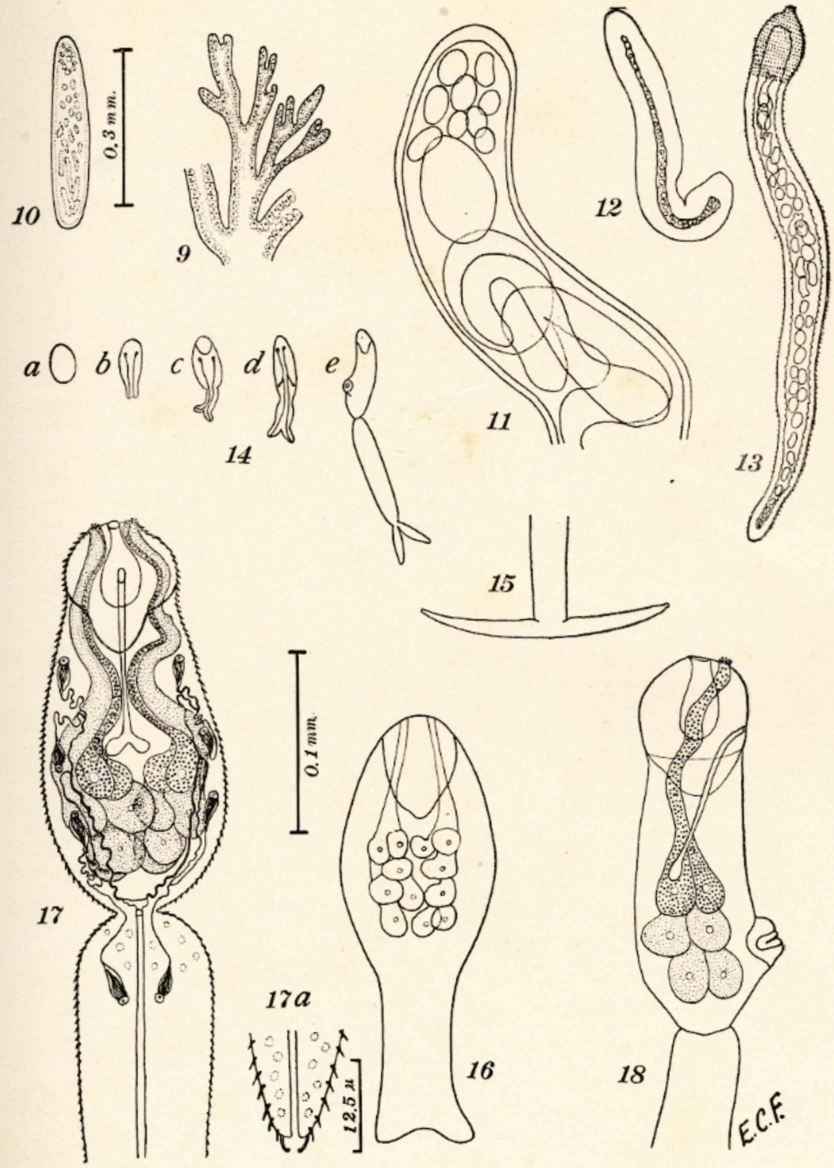

Sept
Aur
Vent
V.s
R
SpD
RD
Es
Lung
Ce
St
L
Int
Int
V.d
LDGl
Re
OT
F
An
♂G
Or
GOp
Lung
Op
CbGa
Es
BucGl
BucC
M
L
E.E.B. & E.C.F.

Fig. 8


10
0,3 mm.
9
11
12
13
a
b
c
d
e
14
15
17
0,1 mm.
16
17a
12,5 µ
18
E.C.F.

COLORED PLATE

Section through the digestive gland of *Australorbis glabratus* infected with *Schistosoma mansoni.* The right side of the picture is filled with a portion of a sub-terminal branch of the gland, which shows evidences of marked necrosis of the epithelial cells bordering the lumen, extending well into the substance of the tubule. Cercariae in various stages of development are seen in the inter-glandular lymph spaces. Above and to the left is a mature cercaria in oblique section, showing one basophilic (red) and two oxyphilic (lavender) penetration glands. Below and to the right is a transverse section of a mature cercaria, with parts of three basophilic penetration glands. In the lower left hand quarter there is part of a longitudinal section of the anterior part of the cercaria's body. On the left margin are fragments of immature (undifferentiated) cercariae. Stained with Delafield's hematoxylin, counter-stained with Best's alum carmine. Camera lucida, × 420.

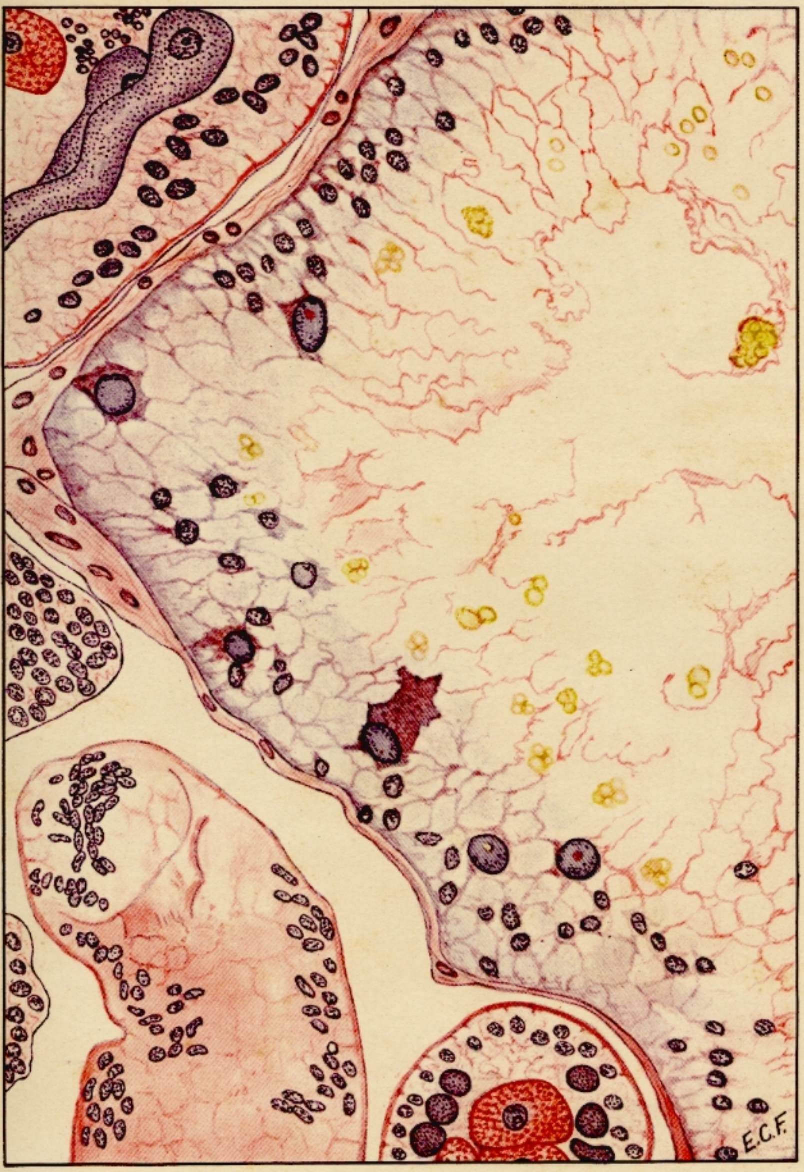


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PLATE IV

FIGURES 19 *a* – 22 *b*

19 *a*. Characteristic resting position of ***Cercaria neotropicalis***.

19 *b*. Cercaria of *C*. ***neotropicalis*** in active movement.

20. Body of *C*. ***neotropicalis*** (ventral view), showing digestive system, penetration glands, excretory system and eye-spots.

21. Second generation sporocyst of *C*. ***neotropicalis,*** with developing cercariae.

22 *a*. Slightly compressed tetracotyle of *C*. ***neotropicalis*** (?), within cyst capsule.

22 *b*. Somewhat compressed excysted tetracotyle of *C*. ***neotropicalis*** (?), showing digestive and excretory systems (ventral view).

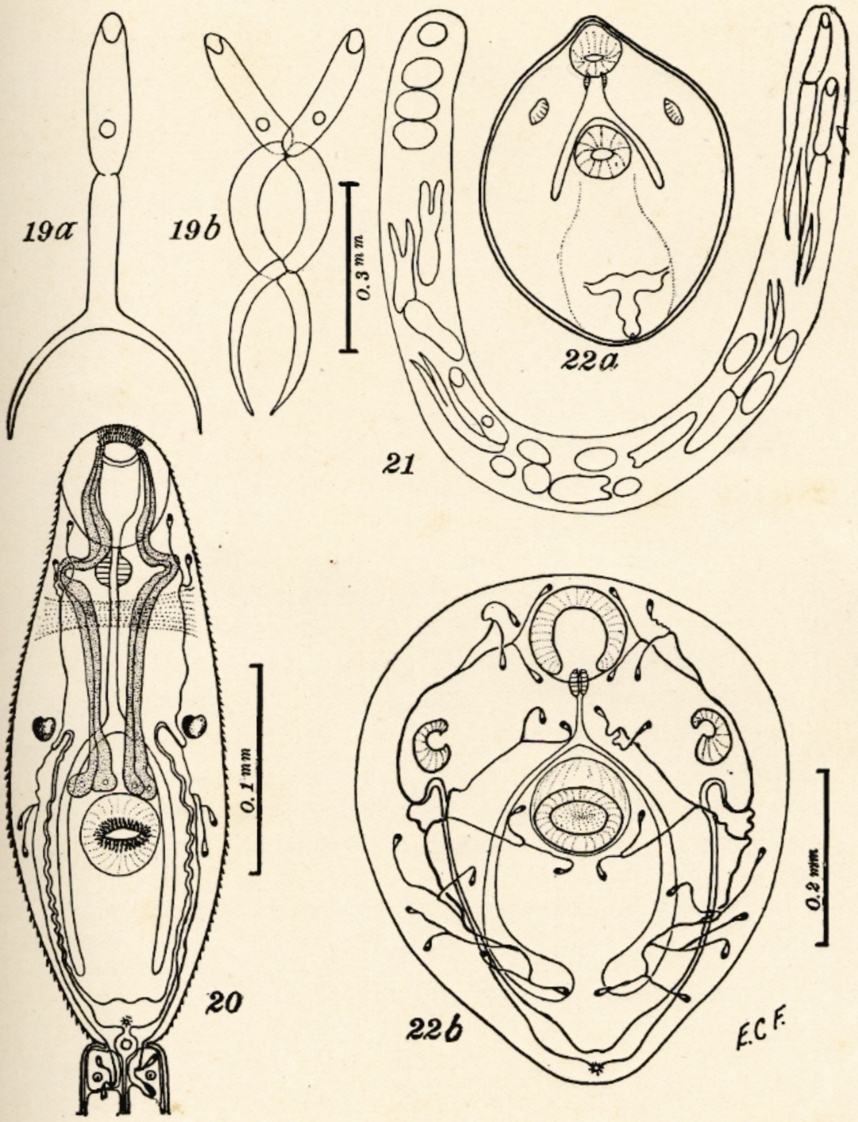

19a
19b
0.3 mm
22a
21
0.1 mm
20
0.2 mm
22b
E.C.F.

PLATE V

FIGURES 23–28 *a*

23. *Cercaria marini* (ventral view), showing digestive and excretory systems and paraphyngeal (penetration?) glands.

23 *a*. Diagrammatic representation of the excretory pattern of *C. marini*.

24. Lateral view of *C. marini*, in characteristic position.

24 *a*. Laterial view of ventral sucker of *C. marini*, showing fluted membraneous rim.

25 *a*. Mother redia of *C. marini*.

25. *b*. Daughter redia of *C. marini*, developing in some mother rediae together with cercariae.

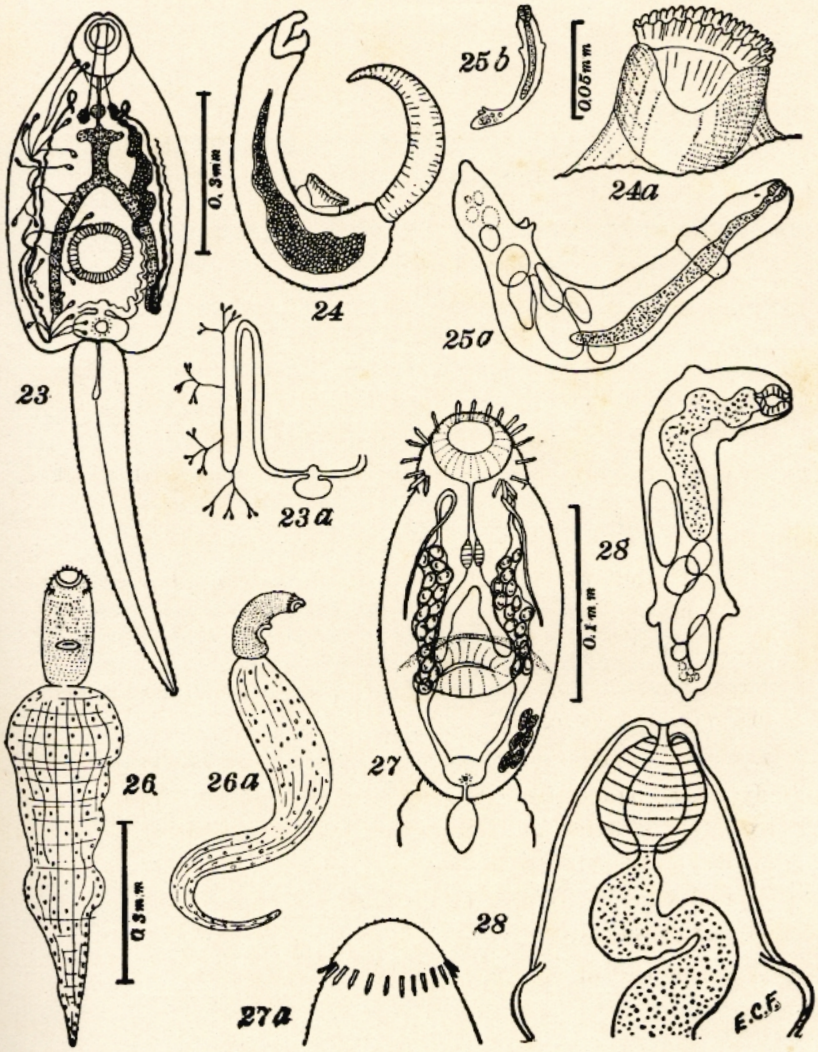
26, 26 *a*. Ventral and lateral views of *Cercaria paucispina*.

27. Body of *C. paucispina*, showing cephalic spines, digestive and excretory systems, and (in posterior lateral field) a few of the typical cystogenous glands.

27 *a*. Dorsal view of the cepholic spines of *C. paucispina*.

28. Redia of *C. paucispina*.

28 *a*. Anterior end of mature redia of *C. paucispina*.



23
0.3mm
23a
24
24a
0.05mm
25b
25a
26
0.5m.m
26a
27
27a
28
0.1m.m
28
E.C.F.