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A Protandrous Haploporid Cercaria, Probably the Larva of *Saccocoelioides sogandaresi* Lumsden, 1963

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During the summer of 1967, an unusual cercaria was found among larval trematodes developing in *Amnicola comalensis* collected from a drainage canal near Galveston Bay, Texas. It not only is the first freshwater cercaria reported for the Haploporidae, a predominantly marine family of trematodes, but also is sexually precocious with a degree of protandry apparently unique among larval trematodes. Many cercariae have well developed genital primordia and a few azygiid larvae even contain eggs on escape from the mollusk. The Texas species lacks eggs but the body is otherwise equivalent to an adult trematode. It has a large seminal vesicle filled with sperms but the testis consists of a largely empty sac when the larva is shed by the snail. That gonad becomes conspicuously developed in the cercarial embryo, produces sperms, and retrogresses before development in the snail is complete. In respects other than sexual development, the cercaria agrees with the only other reported haploporid larva, a marine species (Cable, 1962). Given a testis like that of the cercarial embryo, the body would have features of the genus *Saccocoelioides* which Szidat (1954) erected for freshwater species in Argentina.

Infected snails were collected near the brackish ponds where Lumsden (1963) found sailfin mollies, *Mollienesia latipinna,* infected with a new species of *Saccocoelioides,* S. *sogandaresi.* Several dimensions of the haploporid larva fall within the ranges Lumsden gave for his species. Although the two differ in some other respects, they probably are stages of the same species as Sogandares has suggested in a personal communication. Evidence to that effect will be presented after describing the stages provided by infected snails.

The entire cercaria was drawn to scale from measurements of a representative specimen among spontaneously emerging larvae killed in near-boiling 2% formalin and measured immediately under a freely floating coverglass. Details were added freehand from the study of living specimens and wholemounts stained with Semichon's carmine and counterstained with indulin. The metacercaria was drawn from a living specimen in the same manner, and the cercarial embryo by microprojection of a wholemount. All measurements are given in microns; lengths and widths of certain cercarial structures were measured parallel to those dimensions of the entire larva.

Description of Stages

Cercaria (Figs. 2–4)

Biocellate, distomate; tail slender, unadorned, attached subventrally. Larva strongly photopositive, swimming smoothly and almost continuously before encysting in the open. Body linguiform to pyriform, 410–436 long; maximum width 175–190, at or somewhat posterior to midlevel. Tail 485–510 long, 41–45 wide at slight swelling near base. Tegument of body thick, colorless, uneven; with fine spines from anterior end almost to eyespot level; parenchyma yellowish, with much brown pigment posterior to eyespots, first clumped, then dispersed except for concentration near caudal attachment; eyespots 23 by 20. Oral sucker 61–67 long, 70–76 wide; ventral sucker equatorial, 69–76 in diameter. Mouth subterminal; pharynx about midway between suckers, 41–58 long, 53–62 wide. Prepharynx almost as long as pharynx, esophagus longer; bifurcation near posterior edge of ventral sucker; ceca short, divergent, inflated. Testis in emerging larva an elongate, largely empty sac superimposed on excretory bladder; well developed in embryo, smooth at first but becoming slightly indented as sperms form. External seminal vesicle filled with sperms, most conspicuous feature of hindbody; beginning as a wide sac near midlevel of that region, then tapering as it extends anterolaterally and loops dorsomedially at right of ventral sucker to turn anteriorly and enter hermaphroditic sac. That sac spherical, overlapping ventral sucker anterolaterally; containing internal seminal vesicle, prostatic complex and metraterm. Ovary small, ovoid, with few cells; slightly to left, overlapping external seminal vesicle posterolaterally. From ovary, oviduct extends anterolaterally to left, joined first by Laurer's canal, then by common vitelline duct before bending medially to join oötype posterolateral to ventral sucker. Uterus short, curving to right from oötype, around ventral sucker to cross neck of external seminal vesicle, enter hermaphroditic sac and join male duct anterior to pars prostatica. Common gonoduct short; genital pore median, near anterior edge of ventral sucker. Seminal receptacle absent, amphitypy not observed. Vitelline cells large, in massive follicles not in two lateral fields but filling parenchyma of hindbody not otherwise occupied and compressing inconspicuous cystogenous glands against subtegumental muscles. Excretory system stenostomate; primary pores at sides of tail, near base. Bladder elongate sacciform, extending almost to ovary; with distinctly thickened wall containing nuclei. From bladder, main tubules extend to sides of oral sucker, then posteriorly to ventral sucker where each receives an anterior and posterior secondary tubule. Flame cells numerous, apparently three groups served by each secondary tubule; five or six flame cells per group posterior to ventral sucker. Development

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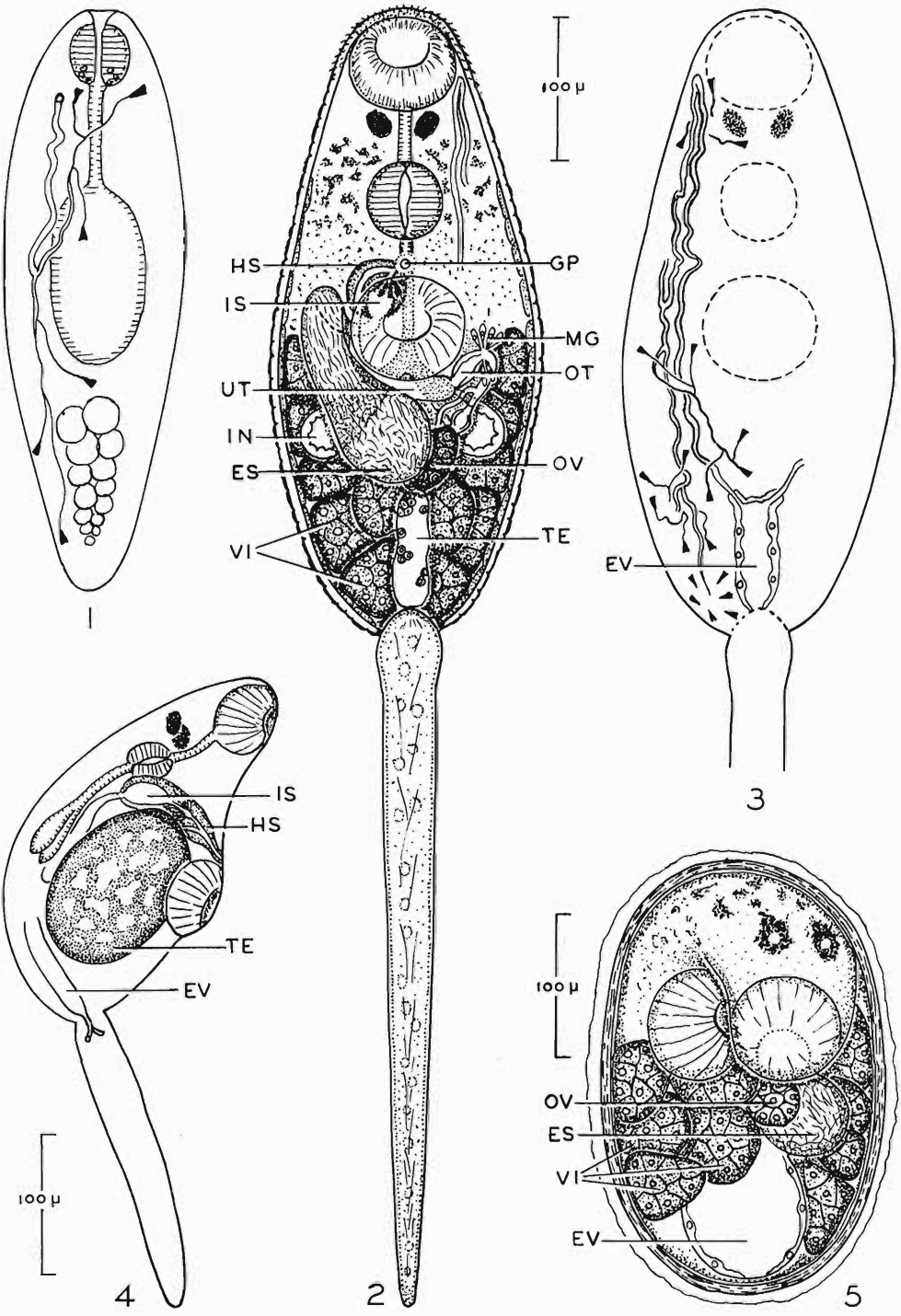
Figures 1–5. 1. Young redia drawn freehand to show excretory system of one side. 2. Cercaria, ventral view. 3. Same, showing excretory system on one side of body. 4. Lateral view of cercarial embryo showing precociously developed testis. 5. Metacercaria.

Abbreviations: ES, external seminal vesicle; EV, excretory vesicle; GP, genital pore; HS, hermaphroditic sac; IN, intestine; IS, internal seminal vesicle; MG, Mehlis' gland; OT, ootype; OV, ovary; TE, testis; UT, uterus; VI, vitelline follicles.



completed in digestive gland of snail after escape from redia.

HOST: *Amnicola comalensis* Pilsbry and Ferriss, 1906.

HABITAT AND LOCALITY: Drainage canal near Galveston Bay, Texas.

DEPOSITED SPECIMENS: Nos. 71321–71323 USNM Helm. Coll.

Redia (Fig. 1)

Elongate, without collar or "feet"; gut short and wide in older rediae. Pharynx of young redia 32 in diameter. Excretory pores lateral, just posterior to pharyngeal level. Excretory formula 2[(3) + (3)] = 12 flame cells.

Metacercaria (Fig. 5)

Cyst symmetrically ovoid, not flattened on one side or adhering to surfaces; with indistinct outer layer and well defined inner one, fibrous, 8–11 thick when formed but becoming somewhat thicker with age and appearance of space between worm and cyst wall. Cavity of cyst 260–293 long, 200–230 wide. Eyespots begin to dissociate soon after encystment.

Discussion

Although the bladder wall of the cercaria is appreciably thickened and contains nuclei, it does not appear to be of the epithelial type. Instead, the nuclei seem to be those of the primary excretory tubules and retained after fusion of the tubules to form the bladder, giving it the appearance of being epithelial. A similar bladder has been seen in bucephalid cercariae (unpublished studies).

Features which at first made the cercaria seem unlikely to be the larva of *Saccocoelioides sogandaresi* were the limited body spination, long prepharynx, extent of the vitellaria, large external seminal vesicle, and reduction of the testis after its conspicuous development in the cercarial embryo. The last feature suggested that the adult would be short-lived, grow little if any in the vertebrate host, and have available only the sperms provided by the cercaria. In contrast, the adult of *S. sogandaresi* is described as having a large testis. However, examination of the paratype of that trematode and several additional specimens provided by Dr. R. D. Lumsden showed that worms comparable to the cercarial body in size contained eggs but not what could be recognized as a testis. That gonad was distinct only in larger and presumably older specimens; even then, it usually had the appearance of a young testis before the various stages of spermatogenesis are evident as cell clusters. The cercaria in question would account for that situation by providing sperms for early egg production before the testis redevelops and becomes functional. Larger adults are about one-fourth longer and considerably wider than the cercarial body but dimensions of the suckers and pharynx are essentially the same in both. During growth in the vertebrate, utilization of sperms and vitelline cells provided by the cercaria could account for the less extensive seminal vesicle and vitellaria in the adult. Meanwhile spination limited to the anterior end of the cercaria could develop over the entire body.

Morphological differences exclude as the adult of the present cercaria two other haploporids known to occur in the region. None was found in a variety of fishes which we seined from the canal where infected snails occurred, but *Mollienesia latipinna*, the definitive host of *Saccocoelioides sogandaresi* was not included. Lumsden (personal communication) found in a different snail species a haploporid cercaria which encysted in the open. He fed metacercariae to *M. latipinna* but with negative results which he considered inconclusive because he had found another haploporid adult, *Saccacoelium beauforti*, in mullet from the same region. It now seems that his cercaria may well be that species and the present one the larva of *S. sogandaresi*.

Although haploporids occur mostly in marine fishes, Szidat (1954) reported several species in Argentine freshwater hosts. He regarded the parasites as relicts of the ancient Tethys Sea which extended from the Mediterranean region to eastern South America and covered the lower watershed of rivers now in that area. In a similar manner, former inundations of central United States could account for the far inland occurrence of a few trematodes in such predominantly marine families as the Microphallidae, Lepocreadiidae, Microscaphiidae, Cryptogonimidae, and Didymozoidae. The life history has been elucidated for at least one freshwater species in each of those families except the Microscaphiidae and Didymozoidae, and recent unpublished studies have revealed the cercariae of *Microphallus opacus* and two

lepocreadiids, *Homalometron* sp. and *Microcreadium* sp., developing in *Amnicola limosa* Say in northwestern Indiana.

It seems significant to the zoogeography of digenetic trematodes that all known central and eastern North American freshwater cercariae in the above families as well as the Haploporidae develop in species of *Amnicola*, and brackish-water larvae in species of *Hydrobia*. The fact that malacologists disagree as to whether those genera and *Truncatella*, a genus of marine snails, belong in the same family indicates their close relationship. Formerly, all were placed in the Rissoidae which now also includes the marine host of the only other described haploporid cercaria (Cable, 1962). Knowledge of the life histories of Argentine freshwater haploporids might reveal such a close affinity of their molluscan hosts to marine gastropods. Manter (1957) pointed out that their vertebrate hosts are distantly related to those of Mediterranean haploporids, but he suggested that such euryhaline fishes as mugilids may have served as ecological "bridges" for trematodes between marine and freshwater environments.

Present knowledge of life histories strongly indicates that digenetic trematodes as a group are less specific for their vertebrate than molluscan hosts. Although both are essential to those parasites in extending their range, in doing so they would seem as a rule more adaptable in acquiring new vertebrate than molluscan hosts. Such adaptability within the marine environment is demonstrated by the cryptogonimid, *Siphodera vinaledwardsii*, which parasitizes shallow-water fishes from Cape Cod to South America. Throughout that range, the cercaria develops in snails of a single genus whereas the parasite changes its vertebrate host to fishes of different orders. Similarly, adults in the Bivesiculidae parasitize a variety of fishes in world-wide tropical and subtropical seas, but all of several known cercariae in that family develop in snails of the genus *Cerithium*. It thus is evident that discussions of host specificity and zoogeography of digenetic trematodes have unduly neglected molluscan hosts, and not entirely for lack of information concerning life histories.

Summary

A cercaria developing in *Amnicola comalensis* from a freshwater canal near Galveston Bay, Texas, is essentially an adult with a tail except for lacking eggs. A conspicuous testis develops in the embryo, fills a large seminal vesicle with sperms, and retrogresses to a largely empty sac before the cercaria emerges from the snail. Encystment is in the open. The morphology and ecology of the cercaria indicate it to be the larva of *Saccocoelioides sogandaresi*. The redia, cercaria and metacercaria are described. Representation of the Haploporidae and certain other predominantly marine families by freshwater species is discussed, suggesting that molluscan hosts have been neglected as factors in the spread of trematodes both within and between marine and freshwater environments.

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