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## Precociously Developed Brachylaimid Metacercariae within Sporocysts

By MARTIN J. ULMER

The occurrence of precociously developed metacercariae among digenetic trematodes has been noted by numerous investigators both here and abroad. Included in the literature are references to species representing more than a dozen families which have been recorded as exhibiting this phenomenon. Among many groups it manifests itself in progenetic development, i. e., the attainment of sexual maturity by metacercariae (or cercariae occasionally) while still within the first intermediate host, with resultant egg production, and at times the appearance of viable miracidia within such metacercariae. Buttner (1950, 1951) in an intensive study of progenesis among digenetic trematodes provides experimental evidence indicating that some life cycles may be considerably shortened through such progenetic development of metacercariae. Other families of digenetic trematodes, among them the Echinostomatidae, include species in which encystment of metacercariae within rediae is of common occurrence, even though such metacercariae do not exhibit sexual maturity.

In the family Brachylaimatidae, species of the genus *Leucochloridium* and *Neoleucochloridium* (subfamily Leucochloridiinae) normally undergo unique development in which branching sporocysts give rise to cercariae which move to specialized branches of the sporocyst known as broodsacs. Here they develop into encysted infective metacercariae. The three-host life cycle is thus reduced to a two-host cycle by the elimination of a free-living cercarial generation. Among members of the subfamily Brachylaimatinae, on the other hand, two intermediate hosts are usually required for the development of infective metacercariae. Krull (1935) has reported, however, that in *Glaphyrostomum mcintoshi* the branching sporocysts produce cercariae which become infective larvae without encysting and without leaving the sporocyst.

The present report deals with instances of precocious development in a species of the subfamily Brachylaimatinae, whose members generally require a second molluscan host for the development of metacercariae. A preliminary report has been published elsewhere by the author (1950).

During the course of investigations dealing with the life cycle of *Postharmostomum helicis* (a brachylaimid trematode employing the land snail *Anguispira alternata* as its intermediate host), several snails of this species were collected near Ann Arbor, Michigan, which harbored branching sporocysts, cercariae and metacercariae of a closely related species, differing from *Postharmostomum helicis* in the following respects: cercariae possessing ciliated patches in the ascending collecting tubules of the excretory system, metacercariae with straight intestinal crura, and metacercariae normally localized within the renal chamber of the snail intermediate host. Reference to these findings appear in the writer's published account (1951) of the life cycle of *Postharmostomum helicis*.

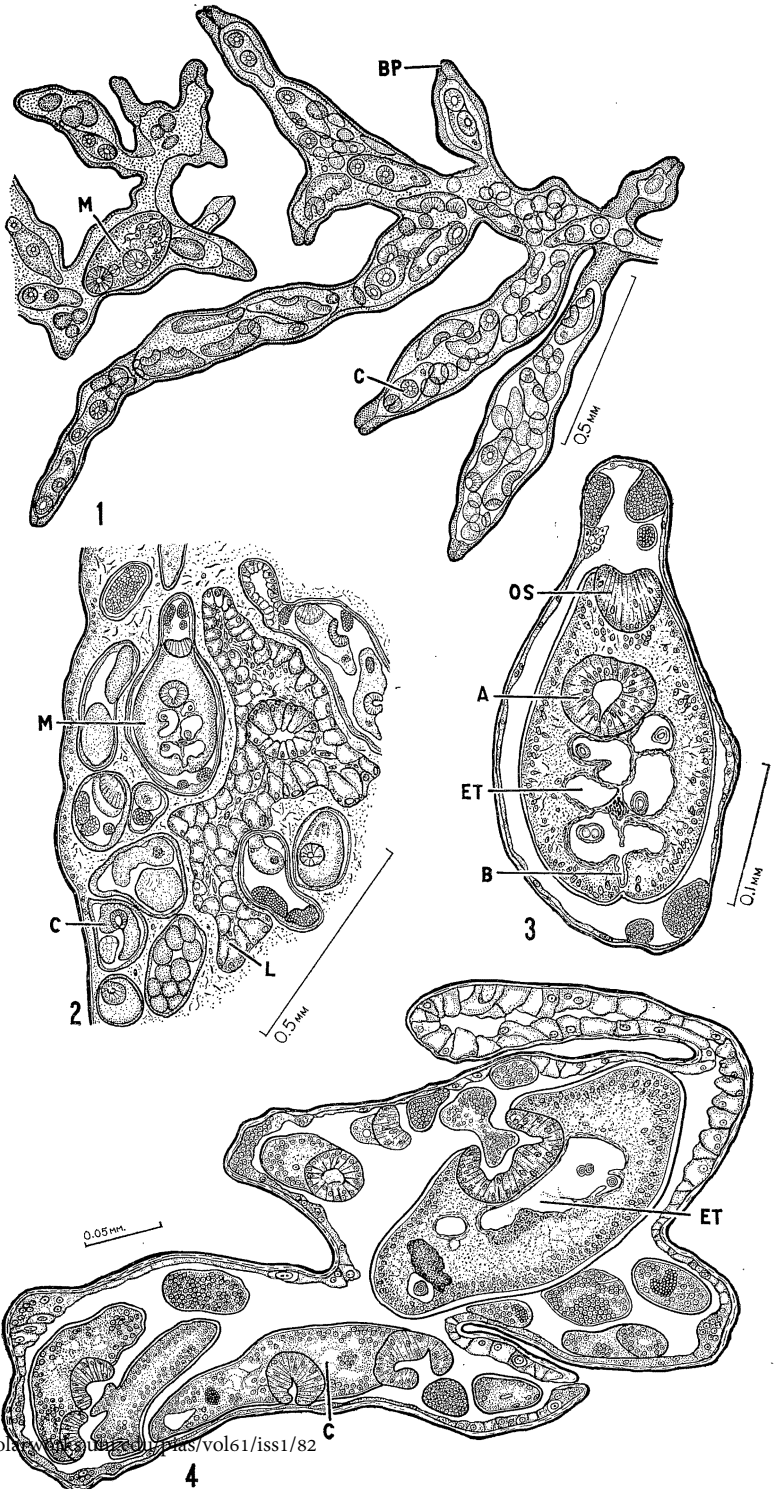
Collections of *Anguispira alternata* from the same area at subsequence intervals provided several snails containing a number of large well-developed metacercariae within the branches of the sporocyst. Of a total of more than 6000 *Anguispira alternata* examined, 10 contained sporocysts and cercariae of this related and as yet unidentified brachylaimid, and three snails contained precociously developed metacercariae. Collections of snails from this area in recent years have yielded no additional snails harboring such metacercariae within the sporocysts.

In an attempt to establish the identity of the cercariae issuing from the branched sporocysts in *Anguispira alternata*, experiments were conducted in 1949 in which snails harboring active infections were placed in containers with laboratory-reared *Anguispira alternata*, *Mesodon thyroidus*, and *Triodopsis multilineata*. Fifteen *Anguispira alternata* and three polygyrid snails were used as hosts and these were checked periodically by crushing the animals and searching for the contained metacercariae. Examinations made between 10 days and 21 weeks showed metacercariae limited to the kidney chamber. None occurred within the adjacent pericardial cavity, the normal location of *Postharmostomum helicis* metacercariae. Lack of metacercariae in sufficient number prevented feeding them to susceptible definitive hosts in order to obtain sexually mature adult worms. Whole mounts of these experimentally-reared metacercariae, fixed in AFA and Bouin's, and stained in Mayer's HCl carmine and Harris' haematoxylin, show definitely that such metacercariae are not those of *P. helicis* nor of *Brachylaima virginianum* whose intermediate host, *Mesodon thyroidus*, is frequently found infected in this area. Further experimental data are needed to establish the precise identity of these metacercariae. Unfortunate-

ly, recent collections of *A. alternata* from the same vicinity have been consistently negative in regard to this infection.

Both whole mounts (Fig. 1) and sections (Figs. 2, 4) show precociously developed metacercariae within the confines of the walls of the branching sporocyst. Tissues for sections were fixed in Bouin's and stained in Heidenhain's iron haematoxylin and Delafield's haematoxylin. Terminal portions of some of the sporocyst branches, as in sporocysts of other species of the subfamily, are equipped with distinct birth pores (Fig. 1). Sporocyst infections are limited to the liver tissue of the snail host. Metacercariae within sporocysts were found in naturally-infected snails examined immediately after collection as well as in those maintained in the laboratory for weeks. They appeared to occur, however, only in well-established infections and were not found in the smaller infected *Anguispira alternata*. Metacercariae may lie free within the sporocyst (Fig. 3) or they may become attached to the sporocyst wall or to developing embryos by means of their suckers (Fig. 4). Such metacercariae are readily distinguishable from cercariae not only by their greater size and by the lack of rudimentary caudal appendage (characteristic of cercariae belonging to the subfamily), but also by the greatly distended excretory siphons of the metacercariae containing numerous rounded concretions (Fig. 3). Although such concretions are never seen within cercariae contained in the sporocyst, they are conspicuously present in both the precociously developed metacercariae and in those metacercariae recovered from the kidneys of experimentally infected snails. The reproductive fundament in precociously developed metacercariae, however, remains relatively undifferentiated as it does in normally-developed metacercariae up to 21 weeks of age, which was the maximum time the latter were maintained in the snails from feeding experiments noted above. In metacercariae of *Postharmostomum helicis*, the genital complex is well differentiated at 18 weeks, and in *Brachylaima virginianum* according to Krull (1935), metacercarial development is completed in as little as 14 days. These metacercariae differ too, from *B. virginianum* and *P. helicis* in possessing an acetabulum much larger than the oral sucker.

That the presence of precociously developed metacercariae as described above is not of normal occurrence seems to be indicated not only by its infrequency in nature but also by the small numbers of metacercariae found either in whole mounts or in sections. Its incidence, however, necessitates the inclusion of the family



Brachylaimatidae among those already cited as exhibiting precocious development in the larval generations.

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#### Explanation of Plate

- Fig. 1. Portions of branching sporocyst from *Anguipira alternata* containing cercariae and precociously developed metacercaria.
- Fig. 2. Section through liver of *A. alternata* showing metacercaria enclosed within sporocyst.
- Fig. 3. Enlargement of metacercaria shown in Fig. 2. Note enlarged excretory siphons and concretions.
- Fig. 4. Portion of sporocyst with enclosed metacercaria in parasagittal section, showing metacercaria attached to embryo by acetabulum.

#### Abbreviations used in Plate

(All drawings were made with the aid of the camera lucida.)

- A acetabulum  
 B bladder  
 BP birth pore  
 C cercaria  
 ET excretory tube  
 L liver  
 M metacercaria  
 OS oral sucker

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