

Zeitschrift: Acta Tropica
Herausgeber: Schweizerisches Tropeninstitut (Basel)
Band: 37 (1980)
Heft: 2

Artikel: Demonstration of several sporocysts generations as a normal pattern of reproduction of "Schistosoma mansoni"
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DOI: <https://doi.org/10.5169/seals-312647>

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Demonstration of several sporocysts generations as a normal pattern of reproduction of *Schistosoma mansoni*

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Summary

A thorough study of the development of *Schistosoma mansoni* demonstrates that asexual reproduction within the vector-mollusc does not proceed according to the usually accepted process. Under natural conditions, daughter sporocysts are capable of stopping production of cercariae and orienting production towards an additional generation of sporocysts, which themselves will be able to evolve in the same manner. This process intervenes without exception provided that the duration of parasitosis exceeds 40 days (at 26° C). It is observed in three different american strains of *S. mansoni*. We believe that this is the first demonstration of the existence of several sporocysts generations as an habitual mode of reproduction in the life cycle of *Digenea*.

Key words: *Digenea*; *Schistosoma mansoni*; *Biomphalaria glabrata*; intra-molluscal larval demography; cercariae producing sporocyst; primordial gland cells; metasporocyst; secondary daughter sporocyst; small motile sporocyst; sporocyst replication, morphogenetic bipotentiality of germinal cells; microsurgical transplantation.

Introduction

At the level of larval demography the *Digenea* are traditionally separated into two groups considered to be fundamentally different: *Digenea* reproducing asexually by rediae and *Digenea* reproducing asexually by sporocysts. In the first group, the number of larval generations is potentially infinite (Dönges, 1971). On the other hand, in the second group, it is considered that only two generations are possible. This ontogenic divergence, for which no rational explanation is apparent, prevents in many ways the construction of a coherent phylogenic model of the *Digenea* (Pearson, 1972).

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Lie (1969) was the first to mention, in a work on larval interactions between two *Digenea* in the mollusc, the appearance, in degenerating secondary sporocysts of *S. mansoni*, of larval forms which he considered to be tertiary sporocysts. Since this work several authors have pointed out, in the framework of general studies and always with considerable reserve, the possibility of replication of second generation sporocysts.

Having recently brought to light in *S. mansoni* (Jourdane and Theron, 1980), in the course of transplantation experiments, the effective existence of additional generations of sporocysts, we were naturally led to look for this mode of reproduction in the natural cycle of this *Digenea*.

Materials and methods

Our study material was represented firstly by a Caribbean strain (Guadeloupe) of *Biomphalaria glabrata* and a strain of *Schistosoma mansoni* of the same geographical origin. We infected 60 planorbs from 5 to 6 mm in diameter, each with 1 miracidium. From the 45th day infection onwards 1 or 2 planorbs per fortnight throughout the parasitosis were sacrificed for histological study. The last planorb to be studied had been parasitised for 8 and a half months. The planorbs, once their shells have been removed, are fixed in Halmi, completely cut into serial sections of 6 μm and stained with Heidenhain's azan. The same work was then carried out with a Brazilian and another Caribbean strains (from Martinique) of *B. glabrata* and *S. mansoni*.

Results

Detailed microscopic examination permitted the discovery in all the molluscs (at all ages of infection including at 8½ months) of sporocysts within which larval morphogenesis is no longer directed towards cercarial differentiation. These sporocysts (Fig. 1A, 1B) numbering from 10 to 20 per mollusc, become localised in the digestive and genital glands among the cercariae producing metasporecysts. Their cavity is occupied by embryonic forms resembling in every way daughter sporocysts formed in the primary sporocysts during the prepatent period. They possess the essential distinguishing characters: vermiform appearance, well-differentiated tegument, distribution of germinal cells in a central cluster, absence of primordial gland cells. In the context of our knowledge of the cycle of *S. mansoni*, the discovery of this phase of reproduction, until now barely suspected under natural conditions and always with a great deal of reserve, poses ipso facto the problem of the origin of these new mother sporocysts. The monomiracidial nature of our infection precludes all assimilation with randomly localised primary sporocysts, since we have always counted at least ten per mollusc. On the other hand, the observation in several planorbs of sporocysts containing at the same time some cercariae and daughter sporocysts reveals that we are dealing with genuine metasporecysts in which there has occurred a reconversion of organogenesis. In the latter we witness, at the end of the period of cercarial emission, an orientation of differentiation towards the

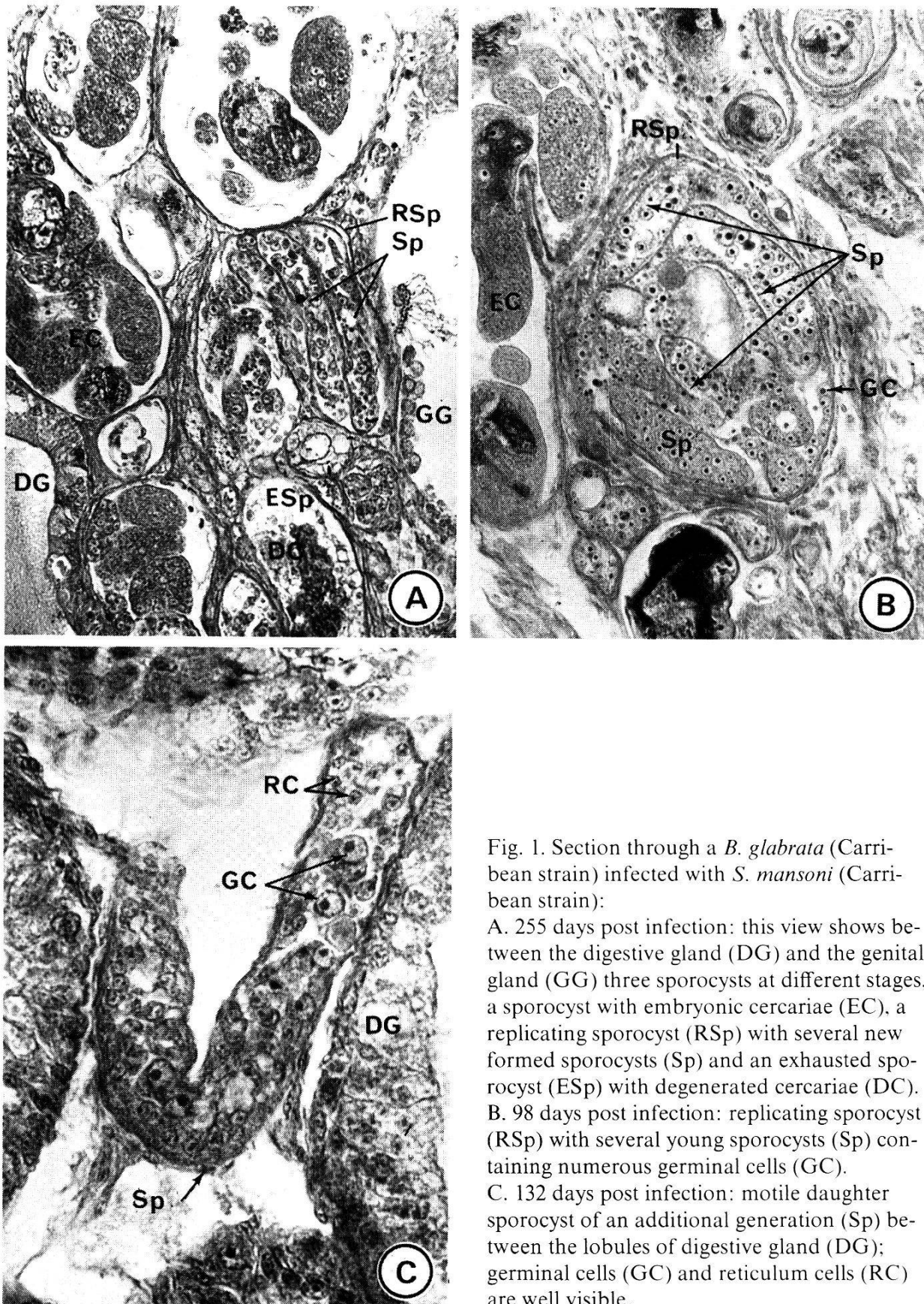


Fig. 1. Section through a *B. glabrata* (Carribean strain) infected with *S. mansoni* (Carribean strain):
 A. 255 days post infection: this view shows between the digestive gland (DG) and the genital gland (GG) three sporocysts at different stages, a sporocyst with embryonic cercariae (EC), a replicating sporocyst (RSp) with several new formed sporocysts (Sp) and an exhausted sporocyst (ESp) with degenerated cercariae (DC).
 B. 98 days post infection: replicating sporocyst (RSp) with several young sporocysts (Sp) containing numerous germinal cells (GC).
 C. 132 days post infection: motile daughter sporocyst of an additional generation (Sp) between the lobules of digestive gland (DG); germinal cells (GC) and reticulum cells (RC) are well visible.

production of sporocysts. The systematic exploration of the histological material as a whole has also shown the presence, within parasitised tissues, of small motile daughter sporocysts having as their obvious origin the newly formed sporocysts (Fig. 1C). The small motile sporocysts cannot be descended from the mother sporocyst, the latter ceasing all multiplication and degenerating after the 30th day of infection (Schutte, 1974; Hansen, 1975). It is worth noting that such larval forms had already been observed either at the end of very long patent periods (Maldonado and Acosta, 1947) or in the framework of infection by transplantation (Chernin, 1964). Nevertheless, the precise origin of these larvae could not be determined by these authors.

Discussion

The appearance of sporocysts of a higher order than secondary has until now been interpreted in the following ways:

Lie (1969) considered the replication of secondary sporocysts to be a degenerative phenomenon leading to the differentiation of abnormal and non-productive tertiary sporocysts.

Diconza and Hansen (1972) were the first to demonstrate that the larval population responsible for the invasion of the host mollusc after the transplantation of secondary sporocysts consists of an additional generation of tertiary sporocysts arising from the differentiation of secondary sporocysts. Nevertheless, this replication is presented by the authors as an exceptional mechanism (4 successes from 49 planorbs transplanted) and its participation in the natural cycle of *S. mansoni* is not suggested.

Hansen et al. (1973, 1974) pointed out the appearance, under specific conditions of in vitro culture, of a second generation of sporocysts which does not develop beyond the embryonic stage.

Hansen (1973) refers briefly to the observation of progeny daughter sporocysts in molluscs 14 days after infection. It is difficult to reconcile this observation with the chronology of the sequence of multiplication which has been demonstrated, notably in our laboratory, as the liberation of secondary sporocysts, still in the embryonic stage, is considered to begin on the 14th day.

Finally, Hansen (1975) analysed all preceding studies and pointed out the observation in molluscs harvested in the field of an additional sporocyst generation in sporocysts which are most likely of secondary order. However, no indication is given of the frequency of this observation, the approximate age of the molluscs or of the histological characteristics of the observed specimens.

To sum up the above data it can be noted that:

- sporocysts of a higher order than secondary are either mentioned in passing or considered as part of a sequence of the type Sp I–Sp II–Sp III ... cercariae;
- it has not been demonstrated that these sporocysts intervene in the normal process of intramolluscal multiplication.

According to our observations, the intra-molluscal development of *S. mansoni* brings into play a succession of generations of sporocysts of limited life expectancy. At the end of every cercarial production period, the morphogenesis of certain sporocysts enters into the production of an additional generation of daughter sporocysts. The latter gather in the digestive gland in replacement of those sporocysts having ceased all cercarial production. Given the perenniality of sporocyst replication in the transplantation sequence (Jourdan and Theron, 1980), the small motile daughter sporocysts observed successively throughout the duration (8½ months) of our experiment correspond to larval generations of increasing order (tertiary, quaternary sporocysts, etc.). The new generation thus installed progressively ensures the relaying of the production of metasporecysts in the process of involution. The succession of generations is thus not of the type Sp I – Sp II – Sp III ... cercariae, but of the type Sp I – Sp II (→ cercariae) – Sp III (→ cercariae) – Sp IV (→ cercariae) ...

The morphogenetic bipotentiality of the germinal elements appears henceforth to be a fundamental character of the cycle of *S. mansoni* from which probably derive the characters proper of its larval demography (such a patent production periods of very long duration: Pan, 1965; Schutte, 1974) and perhaps even the existence of cercarial production rhythm (Pitchford et al., 1969). The importance of this process in the dynamics of production is paramount, since it ensures, by regular renewal of the germinal material, the maintenance of phases of high cercarial productivity throughout the whole life of the mollusc. Its impact on the ecology of the transmission of schistosomiasis is obvious, the cercarial density representing a primary component of the risk of human contamination.

On a fundamental level, our work shows that the two main types of asexual reproduction observed in *Digenea* (reproduction by sporocysts and reproduction by rediae), classically recognized as being fundamentally different, in actual fact obey the same demographic process. The bringing to light in *S. mansoni*, a sporocyst Digenean, of a bipotentiality of the germinal cells, unknown until now in this group, constitutes a consequent factor bringing the two groups of *Digenea* closer together.

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