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Trematode–gastropod associations in nine non-lacustrine habitats in the Mwanza region of Tanzania

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SUMMARY

Between August 1978 and July 1979, freshwater gastropods were collected at monthly intervals from 9 different non-lacustrine habitats in the Mwanza region of Tanzania. Of a total of 11708 gastropods representing 14 species, 1748 (14·9 %) were infected with trematode sporocysts and/or rediae. Altogether 38 morphologically distinguishable 'species' of cercariae were recovered (13 furcocercous, 10 xiphidiocercaria, 6 echinostome, 4 cystophorous, 3 gymnocephalous and 2 amphistome species), 22 of which did not conform to previously described African species. The majority (63·8 %) of all mature infections were xiphidiocercariae. *Biomphalaria pfeifferi*, *B. sudanica* and *Ceratophallus natalensis* each yielded 11 species of cercariae. *Lymnaea natalensis* had the highest overall prevalence of infection (36·9 %). *Cercaria guttera* from *L. natalensis* accounted for 20·4 % of all recovered trematode infections and *C. blukwa* from *Biomphalaria* accounted for 18·4 % of all infections; the high prevalence of these two xiphidiocercariae may alter the transmission patterns of *Fasciola gigantica* and *Schistosoma mansoni*, respectively. *S. mansoni* was recovered from both *B. sudanica* (22 of 2393 infected) and *B. pfeifferi* (79 of 1913 infected); *S. haematobium* (or related species) was recovered from *Bulinus* (*Physopsis*) *nasutus* (50 of 1503 infected) and to a lesser extent from *B.* (*P.*) *africanus* (6 of 186 infected). The findings are discussed in relation to the biological control of trematode diseases in Tanzania.

INTRODUCTION

Numerous surveys to ascertain the prevalence of *Schistosoma mansoni* (Webbe, 1962*a*; Teesdale, 1962; Prentice, Panesar & Coles, 1970; Magendantz, 1972) and *Schistosoma haematobium* (Webbe & Msangi, 1958; Maclean, Webbe & Msangi, 1958; Webbe, 1962*b*; Kinoti, 1964*a*; McCullough, Eyakuze, Msinde & Nditi, 1968; Baalawy & Moyo, 1970) in populations of their snail intermediate hosts have been undertaken in East Africa. Likewise, some attention has been given to the prevalence of bovine schistosomes in *Bulinus* (*Physopsis*) *ugandae* (Berrie, 1964) and of *Fasciola gigantica* in populations of *Lymnaea natalensis* (Ogambo-Ongoma, 1971) from Uganda, but relatively little information on the abundance, morphology and host relationships of other East African trematode species not of medical or veterinary importance has accumulated.

Further documentation of the larval trematode fauna is important not only for its own sake, but also to provide a more realistic understanding of the ecological setting in which schistosomiasis, fascioliasis and other snail-borne diseases occur. For instance, as reported by Chu, Dawood & Nabi (1972), under certain circumstances the prevalence of *S. haematobium* infections in *Bulinus truncatus* in the Nile Delta may be reduced by antagonistic larval echinostomes naturally present in this endemic area. In the Gezira irrigation system of Sudan, larval echinostomes have also been noted to be abundant in local *B. truncatus* populations, a factor which may to some extent be responsible for the uneven distribution and low prevalence of *S. haematobium* in this region (Amin, personal communication cited by McCullough, 1981).

Also, study of the trematode fauna in endemic areas may reveal the existence of certain species that could be manipulated to achieve biological control of snail-transmitted diseases. Field experiments in Thailand by Lie, Kwo & Owyang (1971) and Lie, Schneider, Sornmani, Lanza & Impand (1974) have shown that in some cases *Schistosoma spindale* infections in *Indoplanorbis exustus* can be reduced or eliminated in natural ponds by introduction of large numbers of eggs of carefully selected antagonistic species originating from the same geographic area.

Finally, knowledge of the trematode fauna present is important because high levels of trematode infections may in some cases be responsible for eliminating certain snail populations. In an extensive study of the biology of cercariae from Danish freshwaters, Wesenberg-Lund (1934) frequently observed that if a snail population had been highly infected with trematodes, the population often totally disappeared by the following year. In a variety of Ugandan freshwater habitats, Cridland (1957*a*, *b*, 1958) often noted an intriguing correlation between the prevalence of larval trematode infections and the reduction in size of snail populations, and he postulated that parasitism was responsible for the observed declines. Morris (1970) has concluded that the irregular distribution of the planorbid snail *Helisoma trivolvis* in ponds of central Alberta may be a consequence of the repeated introduction of the trematode *Echinoparyphium recurvatum* into these habitats; such introductions eventually resulted in excessive juvenile snail mortality and castration of adult snails which in turn led to snail population crashes and in some cases, extinction. Lie *et al.* (1971, 1974) have reported that after artificially inducing very high echinostome infection rates in a natural population of *I. exustus*, the host population declined significantly due to the adverse effects on host reproduction and survivorship of the trematodes. In Guadeloupe, eggs of *Ribeiroia marini guadeloupensis*, a cathaemasiid trematode capable of parasitically castrating *Biomphalaria glabrata*, were introduced over a 15-month period into a pond containing a population of this snail host; almost all the snails had disappeared by the end of the trial (Nassi, Pointier & Golvan, 1979).

This study was undertaken as a preliminary step to define the digenetic trematode fauna in a geographic area in which a number of snail-borne diseases are endemic. It is hoped that this investigation will provide useful background information on future studies of the biological control of these diseases.

DESCRIPTION OF THE MWANZA REGION

Five of the 9 habitats sampled at monthly intervals were located in Mwanza, a rapidly expanding city situated on the south shore of Lake Victoria. Two habitats were located between Mwanza and Misungwi, the latter a village situated 46 km south of Mwanza on the road to Tabora. The remaining two habitats were located near Misungwi. The geology and climate of this portion of Tanzania are described by Webbe (1962*b*) and McCullough, Webbe, Baalawy & Maselle (1972). Briefly, the area lies at an altitude of 1020–1220 m above sea level and consists of rolling plains interspersed with low rugged granite outcrops and hills. Rainfall is usually 700–1000 mm per year, most of which falls from mid-November to May, often with a brief intermission in January or February. March and April are frequently the wettest months and are followed by a long dry season which extends from May to October. In general, the rainfall for Mwanza and Misungwi during the present study conformed to the expected seasonal patterns (Table 3). Aquatic snail habitats abound in this area, particularly during the rainy season, and include Lake Victoria and its backwaters, streams, large and small impoundments, seepage areas, temporary pools, rice paddies and irrigation ditches in small gardens.

S. mansoni is particularly widespread in urban Mwanza and is transmitted in Lake Victoria by *Biomphalaria choanomphala*, around the lake margins and in streams by *Biomphalaria sudanica*, and elsewhere in the region by *Biomphalaria pfeifferi* (Webbe, 1962*a*; Magendantz, 1972; McCullough *et al.* 1972). *S. haematobium* is also endemic and is transmitted primarily in rural areas, in temporary pools and manmade habitats where *Bulinus* (*Physopsis*) *nasutus* is the principal intermediate host (Webbe, 1962*b*; McCullough *et al.* 1968). *Bulinus* (*Physopsis*) *africanus* is also known to transmit urinary schistosomiasis in streams (Kinoti, 1964*a*). Trematodes of domestic ruminants include *Schistosoma mattheei* and *Schistosoma bovis* (Dinnik & Dinnik, 1965), *F. gigantica* and paramphistomes.

Habitats sampled

Snails were collected with dip nets at monthly intervals (August 1978 to July 1979) from the 9 habitats indicated below. Although sampling was usually restricted to 1·5 man-hours/habitat/month, the snail collections should not be regarded as quantitative monthly determinations of relative snail population density. Attempts were made to ensure that the relative abundance of different species and size categories of snails in our collections accurately reflected the situation in the habitat, that is, we did not preferentially collect particular size classes of snails. Usually 100–200 snails were collected from each habitat each month. A description of the 9 habitats is given below.

(A) Small shallow pool located in the Bwiru section of Mwanza, separated from Pasiansi Bay of Lake Victoria by a narrow strip of sandy beach. Human activity along this sandy beach was extensive although little direct use of the water in the pool by either humans or domestic animals was observed.

(B) Series of parallel irrigation ditches located in the Kigoto section of Mwanza. These ditches were orientated perpendicular to the shore of North Mwanza Bay of Lake Victoria and the water in this habitat was confluent with that of the lake.

A portion of this habitat flooded when the lake level rose in February 1979. Women and children made extensive use of the lakeshore adjacent to this habitat.

(C) Kirumba Stream, adjacent to Airport Road in Mwanza. The course of this small, intermittent stream was frequently altered by human activity. Heavy rainfall occasionally made collection at this habitat difficult. Many houses were located around this stream.

(D) Kitangiri Stream, adjacent to the new football stadium in Mwanza. This 'stream' actually consisted of shallow, interconnected grass-choked pools; water flow through this habitat was minimal. This habitat was immediately surrounded by rice fields and children were often seen playing near the stream.

(E) Nyakabungo Stream, adjacent to Mirongo School in Mwanza. This gentle-flowing stream consisted of several shallow, interconnected pools containing dense emergent vegetation. Children from the school were frequently observed playing in and around this stream.

(F) Spring-fed seepage area situated 21·6 km south of Mwanza on the road to Misungwi, in an area known as Nyahomongo. This series of small pools contained very little water and few snails during the first 4 months of this study, but they later expanded as the rainy season commenced and snails became abundant.

(G) Temporary, rain-fed pool situated 33·9 km south of Mwanza along the road leading to Misungwi, in an area known as Ngombe. This turbid pool contained little water during August and September and was completely dry in October and November. By January it had filled with rain and supported dense snail populations. Little emergent vegetation was evident in this habitat.

(H) Misungwi Stream, 0·5 km east of Misungwi. This intermittent stream consisted of a series of deep interconnected pools. It was not observed to be flowing during the first 5 months of this study, but by April it was flowing at such a high level that collection became difficult.

(I) Spring-fed seepage area 6·4 km east of Misungwi in an area known as Itale. The pools comprising this habitat retained water until February when they were drained by local rice farmers. Otherwise, little human contact with this habitat was noted.

Unless otherwise indicated, the habitats retained water throughout the 12-month study period.

METHODS

Once collected, snails were brought to the laboratory as soon as possible and were isolated in 10 ml beakers which were placed in darkness until the following day; the beakers were then inspected at least twice for the presence of cercariae. Snails were measured to the nearest half millimetre and were eventually crushed and examined under a stereoscopic dissecting microscope for evidence of trematode infections. Snails harbouring sporocysts or rediae containing cercariae insufficiently developed to permit identification were classified as 'infected' when calculating prevalence rates. Fully developed cercariae were vital stained with nile blue sulphate and examined under the compound microscope. Additional morphological observations and measurements were made using cercariae that had been fixed in hot 10% (v/v) formalin, subsequently stained in Mayer's paracarmine and fast

green and mounted on microslides. Cercariae were compared with existing descriptions of African cercariae, and were classified as 'undescribed' if not closely corresponding to described species. Sufficient information on size, flame cell patterns, stylet shapes, head spine counts etc. was collected in most cases to unambiguously recognize the cercariae, but time did not permit exhaustive description of all the morphological features of each species of cercaria recovered. Slides, drawings and descriptions of the cercariae recovered in this study are available from the Experimental Taxonomy Unit, Department of Zoology, British Museum (Natural History), London.

Comments on identification of the molluscan hosts

Dr David S. Brown of the British Museum (Natural History) has examined specimens from most of the taxonomically perplexing populations of snails discussed in this paper and he has confirmed or corrected the original identifications of the authors. Correspondence with Dr Brown has raised the following points.

(1) The *Biomphalaria* snails recovered from habitats D and H were originally identified as *B. pfeifferi* by the authors but their shells show some resemblance to *B. sudanica* and conceivably, the snails from these 2 populations may be the products of hybridization. A thorough study of the morphology, biochemical properties and genetics of these and other populations would be necessary to answer satisfactorily this question. For the present, the snails from habitats D and H are considered to be *B. pfeifferi?* and they are referred to as *B. pfeifferi* throughout this paper. Of a total of 1913 *B. pfeifferi* examined for trematode infection, 1150 were from habitat D and 85 were from habitat H.

(2) It must be acknowledged that at present it is very difficult to separate accurately *Bulinus* (*Physopsis*) *globosus* and *B.* (*P.*) *ugandae* originating from the Lake Victoria region. Bulinid snails from habitat D are considered to be *B.* (*P.*) *globosus* because their shells possess a strong columellar ridge and at least some microsculpture, and progeny of snails collected from this habitat were successfully infected with *Schistosoma haematobium*; of 42 snails exposed to 5 miracidia each, 9 eventually shed cercaria (Loker, unpublished observations). The bulinid snails collected from habitats B and E were designated as *B.* (*P.*) *ugandae* because their shells possessed a weak columellar ridge and poorly developed microsculpture. Much additional study of the *africanus* group of the genus *Bulinus*, including further analyses of isoelectric focusing of digestive gland enzymes (for example, Rollinson & Southgate, 1979), is required before specific identities can be confidently assigned.

(3) The viviparid snail of the genus *Bellamya* which was collected from habitat H is considered to be *Bellamya capillata* on the basis of shell morphology, but examination of additional material is required before this identification can be solidly reconfirmed.

RESULTS

From the 9 habitats sampled, a total of 11 708 snails representing 5 families, 9 genera and 14 species were collected, of which 1748 (14·9 %) were infected with trematode sporocysts and/or rediae (Table 1). A total of 38 morphologically distinguishable 'species' of cercariae were recovered from these snails (13 furcocercous, 10 xiphidiocercariae, 6 echinostome, 4 cystophorous, 3 gymnocephalous and 2 amphistome species). The great majority (63·8 %) of all mature infections were xiphidiocercariae. Twenty-two of the cercarial species recovered did not conform to previous descriptions (Table 2).

B. sudanica, *B. pfeifferi* and *Ceratophallus* (= *Anisus*) *natalensis* each yielded a diverse cercarial fauna (11 species); the host species with the highest overall prevalence of infection was *L. natalensis* (36·9 %). Of all trematode infections recovered in this study, 36·9 % were found in *L. natalensis*.

The most common species of cercaria recovered was *Cercaria guttera* Fain (no. 17 of this study) from *L. natalensis* which accounted for 20·4 % of all trematode infections recorded. *C. blukwa* Fain (no. 16) was also abundant and represented 18·4 % of all recovered infections. Snails infected with sporocysts and/or rediae which contained incompletely developed cercariae were found 388 times and accounted for 22·2 % of all infections. Many of these unrecognizable infections were probably either *C. guttera* or *C. blukwa*.

Overall prevalence in 7 of the 9 habitats ranged between 10 and 20 % but was particularly high in habitat E (27·2 %) due to a large population of heavily infected *L. natalensis*, and very low at habitat G (1·0 %) which supported a large population of *B.* (*P.*) *nasutus* with low infection rates. The number of cercarial species recovered from each of the 9 habitats ranged from 9 to 17, except for habitat G which yielded only 2 species. The much lower prevalence rate and diversity of cercarial species observed in habitat G were undoubtedly consequences of the ephemeral nature of this habitat and the presence of a snail population composed almost entirely of a single species, *B.* (*P.*) *nasutus*.

Although considerable variation existed between snail species and habitats, the combined prevalence of infection in all habitats for all species was highest at the beginning of this study (Aug–Oct) which represented the end of the 1978 dry season (Table 3). By November, the overall prevalence rate had dropped and fluctuated throughout the rainy season and early 1979 dry season. It reached its lowest point during June but showed a sharp increase during July, the final collection month. The seasonal changes in the overall infection rate to a large extent reflect fluctuations in the relative numbers of *B. pfeifferi* and *L. natalensis* collected. These 2 snail species were relatively abundant and were considerably more likely to be infected than other species. The particularly high overall infection rate noted for the month of September was in part a consequence of the relatively large number of *B. pfeifferi* collected but nonetheless, most populations of this and other species did reveal comparatively high infection rates during this month. Of the 9 snail species for which over 500 specimens were collected, peak trematode infection rates were observed in the late dry–early rainy season for 6 of them (*B. pfeifferi*, *B. sudanica*, *B.* (*B.*) *forskali*, *B.* (*P.*) *globosus*, *B.* (*P.*) *ugandae* and *Pila ovata*). *C. natalensis* infection rates were highest from January to March, and *B.* (*P.*) *nasutus*

Table 1. *Habitats, number collected, number infected and infection rates for the* 14 *snail species collected*

(Each of the 38 cercarial species found was assigned a number (see Table 2). The cercarial species represented by these numbers are listed according to the host species from which they were recovered and their morphological category (i.e. furcocercous). The total number of different cercarial species found in each snail species is indicated as is the total number of species in each morphological category.)

Snail species	Habitats recovered from	No. infected / No. collected	(%)	Furcocerous	Xiphidiocercaria	Echinostome	Cystophorous	Gymnocephalous	Amphistome	No. of cercarial species /snail species
Prosobranchia										
Viviparidae										
Bellamya capillata	H	6/80	(7·5)	—	18	—	—	—	—	1
Pilidae										
Pila ovata	All except E	22/587	(3·7)	—	—	26, 27	—	—	—	2
Thiaridae										
Melanoides tuberculata	E	0/12	(0·0)	—	—	—	—	—	—	0
Pulmonata										
Planorbidae, Planorbinae										
Biomphalaria pfeifferi	C, D, E, H, I	427/1913	(22·3)	1, 5, 7, 9	14, 16	25, 28	38	30	33	11
Biomphalaria sudanica	A, B	338/2393	(14·1)	1, 8, 10	14, 16	24, 25, 28	38	30	33	11
Ceratophallus natalensis	All except E	113/907	(12·5)	3, 4, 7, 9, 13	15, 16, 19	29	37	—	34	11
Lentorbis junodi	A	2/112	(1·8)	—	—	28	—	—	34	2
Segmentorbis kanisaensis	C	10/209	(4·8)	—	19	28	—	—	34	3
Planorbidae, Bulininae										
Bulinus (B.) forskali	All nine	49/700	(7·0)	6, 12	—	25, 28	35	—	33, 34	7
Bulinus (P.) africanus	H, I	7/186	(3·8)	2	—	25	—	—	—	2
Bulinus (P.) globosus	D	51/525	(9·7)	6	—	—	35	32	—	3
Bulinus (P.) nasutus	F, G, H, I	57/1503	(3·8)	2	—	28	—	—	—	2
Bulinus (P.) ugandae	A, B, E	21/832	(2·5)	12	21, 23	25	35	—	—	5
Lymnaeidae										
Lymnaea natalensis	All except I	645/1749	(36·9)	11	17, 20, 22	—	36	31	—	6
Totals	—	1748/11708	(14·9)	13	10	6	4	3	2	—

Table 2. *Morphological category, habitats, intermediate hosts, abundance and identification of each of the* 38 *recognizable 'species' of cercariae recovered*

(Each species was assigned a number which is referred to in Table 1 and elsewhere.)

Cercaria number	Morphological category	Localities recovered from	Intermediate hosts (No. infected/No. examined, percentage infected)	Identification
1	Mammalian schistosome	A, B,	*Biomphalaria sudanica* (22/2393, 1·0%)	*Schistosoma mansoni*
		C, D, E	*Biomphalaria pfeifferi* (79/1913, 4·1%)	
2	Mammalian schistosome	H	*Bulinus* (*Physopsis*) *africanus* (6/186, 3·2%)	*Schistosoma haematobium* or related species
		F, G, H, I	*Bulinus* (*Physopsis*) *nasutus* (50/1503, 3·3%)	
3	Sanguinicolid	H	*Ceratophallus natalensis* (7/907, 0·8%)	Undescribed
4	Apharyngeate, brevifurcate, monostome	B	*C. natalensis* (1/907, 0·1%)	*Cercaria congolensis* Fain 1953
5	Clinostomatid	D, I	*B. pfeifferi* (3/1913, 0·2%)	Undescribed
6	Strigea	D	*Bulinus* (*Physopsis*) *globosus* (2/525, 0·4%)	
		B, D	*Bulinus* (*Bulinus*) *forskali* (3/700, 0·4%)	Undescribed
7	Strigea	D	*B. pfeifferi* (3/1913, 0·2%)	
		A	*C. natalensis* (1/907, 0·1%)	Undescribed
8	Strigea	B	*B. sudanica* (2/2393, 0·1%)	Undescribed
9	Strigea	D	*B. pfeifferi* (1/1913, 0·1%)	
		F	*C. natalensis* (3/907, 0·3%)	Undescribed
10	Strigea	B	*B. sudanica* (1/2393, 0·04%)	*C. berghei* Fain 1953
11	Strigea	C	*Lymnaea natalensis* (3/1749, 0·2%)	Undescribed
12	Strigea	E	*Bulinus* (*Physopsis*) *ugandae* (1/832, 0·1%)	*C. gilleti* Vercammen-Grandjean 1960
		A	*B.* (*B.*) *forskali* (3/700, 0·4%)	
13	Strigea	A	*C. natalensis* (2/907, 0·2%)	Undescribed
14	Ornatae xiphidiocercaria	B	*B. sudanica* (34/2393, 1·4%)	
		E, H, I	*B. pfeifferi* (31/1913, 1·6%)	*C. porteri* Fain 1953
15	Ornatae xiphidiocercaria	F, I	*C. natalensis* (14/907, 1·5%)	Undescribed
16	Armatae xiphidiocercaria	A, B	*B. sudanica* (132/2393, 5·5%)	
		D, E, I	*B. pfeifferi* (174/1913, 9·1%)	*C. blukwa* Fain 1953
		A, B, F, I	*C. natalensis* (15/907, 1·7%)	
17	Armatae xiphidiocercaria	B, C, D, E, H	*L. natalensis* (357/1749), 20·4%)	*C. guttera* Fain 1953
18	Armatae xiphidiocercaria	H	*Bellamya capillata* (3/80, 3·8%)	Undescribed
19	Armatae xiphidiocercaria	A, F, H, I	*C. natalensis* (34/907, 3·7%)	Undescribed
		C	*Segmentorbis kanisaensis* (6/209, 2·9%)	
20	Armatae xiphidiocercaria	B, C, H	*L. natalensis* (55/1749, 3·1%)	Undescribed
21	Armatae xiphidiocercaria	B	*B.* (*P.*) *ugandae* (3/832, 0·4%)	*C. dartevellei* Fain 1953

Table 2 (*cont.*)

Cercaria number	Morphological category	Localities recovered from	Intermediate hosts (No. infected/No. examined, percentage infected)	Identification
22	Armatae xiphidiocercaria	B, E, F	*L. natalensis* (3/1749, 0·2 %)	*Oligolecithus elianae* Vercammen-Grandjean 1960
23	Armatae xiphidiocercaria	B	*B. (P.) ugandae* (6/832, 0·7 %)	Undescribed
24	Echinostome	A	*B. sudanica* (1/2393, 0·04 %)	Undescribed
25	Echinostome	A, B	*B. sudanica* (8/2393, 0·3 %)	
		C, D, I	*B. pfeifferi* (8/1913, 0·4 %)	Undescribed
		A	*B. (B.) forskali* (6/700, 0·9 %)	
		I	*B. (P.) africanus* (1/186, 0·5 %)	
		A	*B. (P.) ugandae* (1/832, 0·1 %)	
26	Echinostome	C, D	*Pila ovata* (15/587, 2·6 %)	Undescribed
27	Echinostome	D, F	*P. ovata* (5/587, 0·9 %)	Undescribed
28	Echinostome	A	*B. sudanica* (1/2393, 0·04 %)	
		I	*B. pfeifferi* (1/1913, 0·1 %)	
		I	*B. (B.) forskali* (1/700, 0·1 %)	Undescribed
		F	*B. (P.) nasutus* (2/1503, 0·1 %)	
		C	*S. kanisaensis* (1/209, 0·5 %)	
		A	*Lentorbis junodi* (1/112, 0·9 %)	
29	Echinostome	H	*C. natalensis* (1/907, 0·1 %)	Undescribed
30	Gymnocephalous	B	*B. sudanica* (57/2393, 2·4 %)	
		D	*B. pfeifferi* (3/1913, 0·2 %)	*C. lileta* Fain 1953
31	Gymnocephalous	C, D, F, H	*L. natalensis* (25/1749, 1·4 %)	*Fasciola gigantica*
32	Gymnocephalous	D	*B. (P.) globosus* (1/525, 0·2 %)	Undescribed
33	Amphistome	A	*B. sudanica* (3/2393, 0·1 %)	
		D, I	*B. pfeifferi* (5/1913, 0·3 %)	*C. obscurior* Fain 1953
		A, F	*B. (B.) forskali* (4/700, 0·6 %)	
34	Amphistome	A, B, F	*B. (B.) forskali* (8/700, 1·1 %)	
		F	*C. natalensis* (1/907, 0·1 %)	*C. nigrita* Fain 1953
		A	*L. junodi* (1/112, 0·9 %)	
		C	*S. kanisaensis* (3/209, 1·4 %)	
35	Cystophorus	B, E	*B. (P.) ugandae* (8/832, 1·0 %)	
		D	*B. (P.) globosus* (41/525, 7·8 %)	*C. aequatorialis* Fain 1953
		E	*B. (B.) forskalii* (1/700, 0·1 %)	
36	Cystophorus	E, F, G	*L. natalensis* (19/1749, 1·1 %)	Undescribed
37	Cystophorus	A, F, H	*C. natalensis* (4/907, 0·4 %)	Undescribed
38	Cystophorus	B	*B. sudanica* (9/2393, 0·4 %)	
		C, D, E	*B. pfeifferi* (54/1913, 2·8 %)	*C. bulla* Fain 1953

Table 3. *The number of specimens collected and the number which were infected with trematode sporocysts and/or rediae for each snail species for each of the* 12 *collection months*

(Overall totals for each month and for each species are also indicated. Rainfall figures for each month are also shown.)

Snail species	Aug 1978	Sept.	Oct.	Nov.	Dec.	Jan. 1979	Feb.	Mar.	April	May	June	July	Species totals
Prosobranchia													
Viviparidae													
Bellamya capillata	1/7	1/6	2/20	0/14	2/8	0/7	0/5	0/9	0/0	0/1	0/3	0/0	6/80
Pilidae													
Pila ovata	0/10	8/21	2/47	3/62	2/66	1/48	0/40	2/87	1/41	0/54	2/71	1/40	22/587
Thiaridae													
Melanoides tuberculata	0/0	0/0	0/2	0/5	0/0	0/1	0/2	0/0	0/0	0/1	0/1	0/0	0/12
Pulmonata													
Planorbidae, Planorbinae													
Biomphalaria pfeifferi	41/195	104/320	64/187	23/127	45/150	27/212	30/160	41/170	16/68	11/112	13/112	12/90	427/1913
Biomphalaria sudanica	57/175	23/102	11/156	28/221	30/158	19/196	24/184	58/242	41/166	34/234	6/282	7/277	338/2393
Ceratophallus natalensis	4/37	9/67	13/100	7/78	19/163	24/124	18/119	11/51	7/83	0/43	0/36	1/6	113/907
Lentorbis junodi	0/0	0/6	0/8	1/11	0/4	0/10	1/13	0/8	0/17	0/15	0/9	0/11	2/112
Segmentorbis kanisaensis	0/0	0/0	0/0	0/0	0/8	0/13	0/29	1/83	8/54	1/17	0/4	0/1	10/209
Planorbidae, Bulininae													
Bulinus (B.) forskali	1/7	16/95	1/29	1/30	7/67	5/113	12/119	2/87	1/100	3/44	0/4	0/5	49/700
Bulinus (P.) africanus	1/2	1/32	1/27	0/14	0/11	0/11	2/7	2/20	0/2	0/34	0/21	0/5	7/186
Bulinus (P.) globosus	0/18	18/55	4/90	8/45	9/59	2/31	4/62	2/38	0/11	0/28	4/55	0/33	51/525
Bulinus (P.) nasutus	1/56	0/9	1/6	0/15	1/30	8/32	7/168	17/227	9/154	14/277	4/283	0/196	57/1503
Bulinus (P.) ugandae	0/110	3/111	6/77	1/86	0/108	8/101	2/65	0/44	0/25	1/40	0/50	0/15	21/832
Lymnaeidae													
Lymnaea natalensis	29/162	68/161	42/77	31/61	30/75	36/65	45/103	37/70	44/100	63/276	87/256	133/343	645/1749
Monthly totals	135/779	251/985	147/826	103/769	145/907	125/1014	145/1076	173/1136	127/821	127/1186	116/1187	154/1022	1748/11708
Mwanza rainfall (mm)	46·5	60·8	72·3	150·3	197·7	79·5	194·9	97·9	69·4	62·6	21·0	0·0	—

Table 4. *Monthly prevalence of* Schistosoma mansoni *and* S. haematobium *(and related species) in their snail hosts*

(The numbers for all habitats have been combined. Percentages are in parentheses.)

	Schistosoma mansoni				*Schistosoma haematobium* (and related species)			
	Biomphalaria pfeifferi		*Biomphalaria sudanica*		*Bulinus (Physopsis) nasutus*		*Bulinus (Physopsis) africanus*	
August 1978	5/195	(2·6)	0/175	(0·0)	1/56	(1·8)	1/2	(50·0)
September	32/320	(10·0)	1/102	(1·0)	0/9	(0·0)	1/32	(3·1)
October	3/187	(1·6)	3/156	(1·9)	1/6	(16·7)	0/27	(0·0)
November	8/127	(6·3)	1/221	(0·5)	0/15	(0·0)	0/14	(0·0)
December	2/150	(1·3)	1/158	(0·6)	0/30	(0·0)	0/11	(0·0)
January 1979	6/212	(2·8)	2/196	(1·0)	3/82	(3·7)	0/11	(0·0)
February	8/160	(5·0)	0/184	(0·0)	6/168	(3·6)	2/7	(28·6)
March	13/170	(7·6)	14/242	(5·8)	14/227	(6·2)	2/20	(10·0)
April	0/68	(0·0)	0/166	(0·0)	8/154	(5·2)	0/2	(0·0)
May	1/122	(0·8)	0/234	(0·0)	13/277	(4·7)	0/34	(0·0)
June	1/112	(0·8)	0/282	(0·0)	4/283	(1·4)	0/21	(0·0)
July	0/90	(0·0)	0/277	(0·0)	0/196	(0·0)	0/5	(0·0)
Totals	79/1913	(4·1)	22/2393	(1·0)	50/1503	(3·3)	6/186	(3·2)

infection rates were highest from March to April. *L. natalensis* infection rates were consistently high throughout the 12-month observation period. One possible factor contributing to the high infection rates observed during the late dry–early rainy season is the reduced water volume observed in most habitats during this period; smaller water volumes accompanied by intensified use by definitive hosts would increase the probability of miracidium–snail contacts, other factors being equal.

The number of species of cercariae recovered was highest during September (22 species) and remained relatively high (between 15 and 20 species each month) through April, and began to decline sharply thereafter to a low of 10 species in July. This decline may be explained in part by a decrease in the relative proportion of *B. pfeifferi*, *C. natalensis* and *B. (B.) forskali* which were collected between May and July. These 3 host species all harboured a diverse trematode fauna; from January to March when diversity was high, these snails comprised 35·8 % of all snails collected, whereas from May until the end of July they accounted for only 13·5 % of the collected snails.

Cercariae identified as *S. mansoni* (Cercaria no. 1, Table 2) on the basis of general morphology and pattern of argentophilic papillae (Short & Kuntz, 1976) were recovered from both *B. sudanica* and *B. pfeifferi*, with the latter host more than 4 times as likely to be infected. *S. mansoni* was one of 14 species of cercariae recovered from these 2 hosts. Five of 9 habitats yielded *S. mansoni* infections, all of which were in Mwanza.

Of the 5 species of bulinid snails collected, only 2 were found to carry infections of mammalian schistosomes (Cercaria no. 2, Table 2), with the majority being recovered from *B. (P.) nasutus* (Table 4). The schistosome commonly recovered from *B. (P.) nasutus* was probably *S. haematobium* since Kinoti (1964*b*) has demonstrated that a Mwanza strain of this snail host is refractory to local *S. bovis* and a Nelspruit strain of *S. mattheei*; Webbe (1962*b*) has clearly implicated this snail species as a major intermediate host for *S. haematobium* in the Mwanza region. The specific identity of the schistosome infections noted in *B. (P.) africanus* is unclear; this snail species is known to be susceptible to all 3 of the above terminal-spined egg schistosome species (Kinoti, 1964*a*, *b*). Of 64 trematode infections observed in *B. (P.) nasutus* and *B. (P.) africanus*, 56 were mammalian schistosome infections. Four habitats were found to harbour schistosome-infected bulinid snails, none of which was located in Mwanza town.

F. gigantica (Cercaria no. 31) was found sporadically until March and was then found every month until the study was completed. Most of the infections were reported from habitat F (18 of 25). It was the third most common of 6 cercarial species recovered from *L. natalensis*.

Of 38 morphologically distinguishable types of cercariae, 22 were recovered from a single host species, 8 were obtained from 2 or more species of the same genus, 6 (nos, 7, 9, 16, 19, 25 and 33) were derived from snails of 2 different genera, and 2 (nos 28 and 34) were each recovered from 4 different genera of hosts. In the cases of Cercariae 7 and 9, the limited material available for study did not permit extensive observation of all morphological details; further study of this material may have revealed specific differences in similar cercariae from different hosts. With respect to Cercariae 33 and 34, due to the massive amounts of cystogenous material present in amphistome cercariae, much of the internal morphology was obscured and subtle differences could have easily been masked.

Table 5. *Recognizable double infections encountered in snails examined during this study*

Parasite combination observed	Host	No. of times observed
Sporocyst–sporocyst		
1 and 7*	*B. pfeifferi*	1
1 and 16	*B. pfeifferi*	4
14 and 16	*B. pfeifferi*	1
14 and 16	*B. sudanica*	2
Sporocyst–redia		
1 and 25	*B. pfeifferi*	1
14 and immature rediae	*B. pfeifferi*	1
14 and 38	*B. sudanica*	1
16 and immature rediae	*B. sudanica*	2
16 and 30	*B. sudanica*	1
16 and 38	*B. sudanica*	2
16 and 38	*B. pfeifferi*	4
36 and immature sporocysts	*L. natalensis*	1
Total		21

* Numbers in this column refer to the cercaria numbers listed in Table 2.

The remaining 4 species reported from hosts belonging to 2 or more genera may represent true examples of non-specificity of a single trematode species with respect to the first intermediate host. For each of these 4 cercariae, the reported host species were all members of the Planorbidae, suggesting that their host specificity may exist at the familial rather than the generic or specific level. Particularly intriguing was Cercaria No. 28, an echinostome which was found in 4 genera and 6 species of snail hosts only from February to April. Collar spine and flame cell counts appeared to be constant in the specimens of this cercaria recovered from different habitats and snail hosts, but other more subtle differences may have been overlooked and for this cercaria, as well as the others, the existence of sibling species may only be detected by the appropriate life-cycle experiments. It should also be noted that Cercariae 36, 37 and 38 all resembled *C. aequatorialis* Fain very closely but were considered as separate species on the basis of size differences, host species and habitat distributions.

Infections involving the sporocysts and/or rediae of 2 different trematode species in a single host were discovered 21 times (Table 5). Approximately 1·2% of all infected snails were found to contain such double infections, although the true prevalence of this condition was probably higher. No infections involving sporocysts and/or rediae of 3 different trematode species were noted.

DISCUSSION

With the exception of *S. mansoni*, *F. gigantica* and the mammalian schistosome recovered from bulinid snails, there was little similarity between the cercariae observed in this study and those reported by Porter (1938) from South African freshwater snails. Selected results of the present study are compared with those of Fain (1953) and Vercammen-Grandjean (1960) in Table 6. Fain (1953) examined

Table 6. *Comparison of results of Fain* (1953) *and Vercammen-Grandjean* (1960) *with present study*

	Fain (1953)	Vercammen-Grandjean (1960)	Present study	Integrated totals
No. of snail species or varieties examined	25	10	14	31
No. of snails examined	27860	Approx. 15000	11708	54568
No. of snails infected (%)	1071* (3·8)	2188* (14·6)	1748 (14·9)	5007 (9·2)
No. of species of cercariae recovered	58	34	38	112
No. of species recovered for the first time	54	32	22	108
Bulinus				
No. examined	591	386	3746	4723
No. infected (%)	13* (2·2)	11* (2·8)	185 (4·9)	209 (4·4)
No. of species recovered	6	3	11	15
Biomphalaria				
No. examined	12917	5949	4306	23172
No. infected (%)	506* (3·9)	371* (6·2)	765 (17·8)	1642 (7·1)
No. of species recovered	16	8	14	31
Lymnaea				
No. examined	3371	5188	1749	10467
No. infected (%)	159* (4·7)	1655* (31·9)	645 (36·9)	2459 (23·5)
No. of species recovered	6	9	6	18

* These figures underestimate the true prevalence of infection because snails were only examined for shedding cercariae and were not dissected to reveal immature infections.

snails from in and around Lake Albert (with additional minor collections from Lake Kivu, Ruanda and Burundi), and 13 of the cercarial species reported by him were also noted in this study (Table 2). Many of the snails examined by Fain were prosobranchs from lacustrine habitats whereas few of the snails collected in the present study were prosobranchs and none was collected from lakes, otherwise the similarities in cercarial faunas of the two studies would have been even greater. For instance, one small collection made from Pasiansi Bay in Lake Victoria (Loker, unpublished observations) yielded 4 cercarial species from *Melanoides tuberculata* which closely corresponded to Fain's (1953) descriptions of *C. dimorpha*, *C. dissimilis*, *C. laticaeca* and *C. sigmoida*; also, one cercaria recovered from *Gabbiella humerosa* (= *Bithynia alberti*) closely resembled *C. schoutedeni* reported by Fain (1953) from *Melanoides*.

Of the 34 cercarial species recovered by Vercammen-Grandjean (1960) in snails from the Bukavu region of Lake Kivu, only 3 species were observed in the present study (Table 2). Thus, although Lake Kivu is closer to the Mwanza region than Lake Albert, the greater similarities observed in the cercarial fauna of the Mwanza region and Lake Albert may be a reflection of the fact that both locations are situated in the Nile drainage system, whereas Lake Kivu drains south into Lake Tanganyika.

The snail species in Fain's (1953) study which yielded the greatest number of cercarial species was *M. tuberculata* with 12, and the highest prevalence of infection was reported in *B. pfeifferi* (7·1 %). Vercammen-Grandjean (1960) found both the

maximum prevalence of infection (31·9 %) and number of cercarial species (9) in *L. natalensis*. The overall prevalence rates reported by these two authors apparently do not include immature sporocyst or redia infections, which leads to substantial underestimation of the true infection rate (22·2 % of all infections recorded in the present study fell into this category).

Of all trematode infections in *Biomphalaria* reported by Fain, 31·0 % were *S. mansoni* and 29·6 % were *C. blukwa*; the corresponding figures for the present study were 13·2 % and 40·0 % respectively.

Mammalian schistosome cercariae from bulinid snails were not reported by either Fain (1953) or Vercammen-Grandjean (1960); in the present study they comprised 30·2 % of all trematode infections from these hosts. Mammalian schistosomes were by far the most common type of cercaria recovered from *B.* (*P.*) *africanus* and *B.* (*P.*) *nasutus*.

F. gigantica accounted for 87 of 97 recognizable infections recovered from lymnaeid snails by Fain (1953), whereas in the present study only 3·9 % of 645 infections from *L. natalensis* were of this species. *C. guttera* infections were found in only 3 snails by Fain (1953) but in the present study this species was very common, accounting for 55·3 % of all infections from *L. natalensis*. The actual prevalence of this xiphidiocercaria in the present study was almost certainly higher, due to the large number of immature sporocyst infections that were recorded for *L. natalensis*.

The high infection rates of the xiphidiocercariae *C. guttera* in *L. natalensis* and *C. blukwa* in *Biomphalaria* here reported invite speculation that they may exert some influence on the prevalence of *F. gigantica* and *S. mansoni* infections respectively. *C. guttera* was 14 times more common than *F. gigantica* in *L. natalensis*, and *F. gigantica* was most commonly recovered from habitat F where *C. guttera* was absent. In the two habitats where *C. guttera* was most common (B and E), *F. gigantica* was absent. However, 4 of the 25 *F. gigantica* infections noted were reported from habitats where *C. guttera* was also found.

The ability of *C. guttera* (which is produced in sporocysts) to serve as an effective intramolluscan antagonist to prevent establishment of, or to displace *F. gigantica* rediae is not known. No double infections involving *C. guttera* were noted, which may imply that this species is an effective competitor. It was frequently observed that the largest specimens of *L. natalensis* collected were infected with this trematode, and that the survival of these snails in the laboratory was very poor. Although *C. guttera* is obviously not exerting an absolute suppressive effect and *F. gigantica* is widespread in the Mwanza region, interspecific trematode competition for intermediate hosts may be exerting some measure of 'natural biological control' similar to the postulated negative effects exerted by echinostomes on the infection rates of *Bulinus truncatus* with *S. haematobium* in Egypt (Chu *et al.* 1972).

C. blukwa was 3 times more common in *Biomphalaria* than *S. mansoni*; of the 5 habitats in which *S. mansoni* was found, *C. blukwa* was present in 4 and abundant in 3. The 2 habitats most consistently yielding *S. mansoni* infections (B and D) yielded the greatest number of *C. blukwa* infections. *C. blukwa* was found in 16 of the 21 double infections reported in this study, including 4 with *S. mansoni*. Interestingly, of 42 double infections reported by Fain (1953), 34 apparently

involved *C. blukwa* and *S. mansoni*. The orange sporocysts of *C. blukwa* which were easily seen through the shell of infected *Biomphalaria* were typically located in the region occupied by the albumen gland, leaving the digestive gland largely unoccupied, a factor which may have contributed to the large number of double infections involving this species. Further study of the role these xiphidiocercariae play in modifying the prevalence of schistosomiasis and fascioliasis is needed, especially considering the observations of Bourns (1963) and Wright (1966) which suggested that infections with xiphidiocercariae may predispose snails to infections with other trematodes or *vice versa*.

In contrast, Paperna (1967) noted that *Bulinus truncatus rohlfsi* previously infected with xiphidiocercariae were considerably less likely to develop patent *S. haematobium* infections than were control snails not infected with xiphidiocercariae.

Of all trematode infections recovered in *Bulinus*, 40 % were redial infections and of these, the most common was *C. aequatorialis* (no. 35), a cystophorous cercaria which accounted for 27·0 % of all infections in this host genus. Approximately 20 % of all infected *Biomphalaria* contained redial infection. The cercarial species originating from rediae which were most commonly recovered from *Biomphalaria* were *C. lileta* (no. 20) and the cystophorous cercaria, *C. bulla* (no. 38). All 3 of these parasite species are apparently widespread as they were also recovered by Fain (1953). *C. lileta* closely resembles the cercariae of described species of the genus *Ribeiroia* (see Yamaguti, 1975). *R. marini guadeloupensis* has been shown to attain a very high prevalence in natural populations of *B. glabrata* in Guadeloupe (Pointier, Salvat, Deplanque & Golvan, 1977), and it is known to effectively castrate this snail host (Golvan, Combes, Bayssade-Dufour & Nassi, 1974). These attributes have led to field trials to investigate its efficacy as a biological control agent of *B. glabrata* in the Neotropics (Nassi *et al.* 1979).

Cercariae of *Echinoparyphium recurvatum* and *Echinostoma revolutum* which have been frequently reported from schistosome intermediate hosts in other parts of Africa (Bisseru, 1967; Moravec, Barus, Rysavy & Yousif, 1974; Wright, Rollinson & Goll, 1979) were not found in the 9 habitats studied.

Prevalence of infection and diversity of the trematode fauna were found to vary considerably between hosts and habitats and with season. As noted by Wright *et al.* (1979), such variability serves 'to emphasize the dangers of drawing conclusions concerning the host-capacity of a snail species from isolated samples'.

The highly seasonal nature of schistosome transmission in *B.* (*P.*) *nasutus* reported by Webbe (1962*b*) was noted in habitats F and G. Very few *B.* (*P.*) *nasutus* were collected from these 2 habitats during the late dry season of 1978, but when the rainy season began, these snails became more numerous and from February to the end of the study in July they were very abundant. Schistosome infections were recovered from these habitats from January to June (Table 4), with the highest monthly prevalence recorded in March (7·5 %), somewhat earlier than the peak infection rates in June, July and August (3–13 %) in the more extensive collections of this species reported by Webbe (1962*b*). Of 17293 *B.* (*P.*) *nasutus* collected by Webbe (1962*b*) in 20 temporary ponds south of Mwanza, 739 (4·3 %) were shedding *S. haematobium* cercariae. McCullough *et al.* (1968) recovered *B.* (*P.*) *nasutus* from 176 of 362 habitats in the Misungwi area but found schistosome-infected snails in

only 8 of the habitats; out of 6172 *B.* (*P.*) *nasutus* collected by these workers, only 23 (0·3%) shed mammalian schistosome cercariae.

In previous studies of *S. mansoni* transmission in urban Mwanza, Webbe (1962*a*) and McCullough *et al.* (1972) have observed that *S. mansoni* infections from *B. sudanica* and *B. pfeifferi* can be recovered throughout the year and that infection rates fluctuated considerably. In the present study, *S. mansoni* infection rates were observed to fluctuate, but a substantial overall decline in the infection rate was noted during the last 3 months of observation (Table 4).

The recovery of *S. mansoni*-infected *Biomphalaria* only from urban Mwanza, and of schistosome-infected bulinid snails only from rural areas conforms with earlier extensive observations on the transmission of schistosomiasis in the Mwanza region (summarized by McCullough & Eyakuze (1973)). This distinction is certainly not absolute, and although no *S. mansoni* infections were found in *Biomphalaria* examined from rural areas, low-level *S. mansoni* transmission is known to occur in the Misungwi area (McCullough & Eyakuze 1973). Likewise, in Mwanza no natural schistosome infections were found in several bulinid snails of the sub-genus *Physopsis* (including several collected in habitats frequented by children), but *B.* (*P.*) *globosus* from Kirumba Stream has on one occasion been previously found to shed *S. haematobium* cercariae (McCullough *et al.* 1972). It is perhaps noteworthy that laboratory-reared progeny of bulinid snails originating from Kitangiri Stream (habitat D) and tentatively identified as *B.* (*P.*) *globosus* were found to be susceptible to the local strain of *S. haematobium*.

Much additional study is needed to elucidate the biocontrol potential of many of the trematode species here reported, and of other as yet undiscovered species, in their African snail hosts. The magnitude of the competitive effects exerted by these species against trematodes of medical or veterinary significance may be greater than realized if, as suggested by Basch (1975), snail populations are heterogeneous with respect to their susceptibility to trematode infection. Thus, although at any given time the proportion of hosts infected within a particular population is low, the proportion of susceptible snails that is infected may be quite high. If the determinants of susceptibility are the same or similar for two species of trematode species utilizing the same host population, interspecific competitive interactions may be much more intense than the overall infection rates for the entire host population might suggest. The admirable theoretical approach taken by Anderson & May (1979) to predict the prevalence of schistosome infection within molluscan populations can perhaps be modified to include consideration of other trematodes utilizing the same host population. An understanding of the magnitude of these potential competitive effects would be relevant to future control programs.

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