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A study of the biological characteristics of a hybrid line between male *Schistosoma haematobium* (Dar es Salaam, Tanzania) and female *S. intercalatum* (Edea, Cameroun)

A. Mutani, N. Ø. Christensen, F. Frandsen

Summary

The viability of a hybrid between male *Schistosoma haematobium* (Dar es Salaam, Tanzania) and female *S. intercalatum* (Edea, Cameroun) was studied for up to the F_7 hybrid generation and the biological characteristics of the hybrid were compared with those of each of the parental species. Using the total cercarial production/100 exposed snails/5 weeks value (TCP) as an index the hybrid miracidial infectivity to *Bulinus forskalii* (Kinshasa, Zaire), the host snail for *S. intercalatum*, remained comparable to that of *S. intercalatum* for up to at least the F_5 generation and the TCP values for the hybrid/*B. wrighti* combination remained for up to the F_7 generation intermediate between those of the parental species in *B. wrighti*. The hybrid also retained the infectivity for up to at least the F_5 generation to *B. globosus* (Mazeras, Kenya), the host snail for *S. haematobium*, but the TCP values for the hybrid/*B. globosus* combination remained consistently lower than that of the *S. haematobium*/*B. globosus* combination. The hybrid cercarial infectivity to hamsters was for up to the F_7 generation comparable to that of both parental species and the egg production capacity/worm pair/day of production of the F_1 hybrid generation exceeded in both hamsters and mice that of both parental species. However, the egg production capacity subsequently decreased with that of the F_3 to F_6 generations in hamsters and with that of the F_2 and F_5 generations in mice being comparable to that of *S. intercalatum*. The pattern of distribution of eggs in tissue of hamsters of the F_1 and F_2 generations resembled that of *S. haematobium* and *S. intercalatum*, respectively, but the distributional pattern of the F_3 to F_6 generations deviated markedly from that of both the parental species and the preceding hybrid generations. The hybrid cercarial infectivity to mice and the pattern of

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egg distribution corresponded to that of *S. intercalatum*. The egg morphology of the P_1 generation corresponded to that of *S. intercalatum* while that of the F_1, F_2 and F_3 hybrid generations exhibited great polymorphism with a range of shapes through those of the parental species but with most eggs being intermediate in shape. However, the eggs of the F_4 to F_7 hybrid generations exhibited less polymorphism and resembled those of *S. bovis* in both size and shape.

Key words: hybridization; *S. intercalatum; S. haematobium;* experimental definitive hosts; intermediate snail hosts; host-parasite relationships.

Introduction

Natural hybridization between male *Schistosoma haematobium* and females of *S. intercalatum* and *S. mattheei* has been demonstrated in man (Pitchford, 1959, 1961; Wright and Ross, 1980; Wright et al., 1974; Southgate et al., 1976) and experimental hybridization studies involving the above mentioned (Wright and Southgate, 1976; Wright and Ross, 1980; Southgate et al., 1976) and also other schistosome species combinations (Wright, 1974; Taylor, 1970; Taylor and Andrews, 1973; Taylor et al., 1973) have provided much valuable information concerning the biological characteristics of especially the F_1 and F_2 hybrid generations. All interspecific pairings hitherto investigated between schistosomes belonging to the terminal-spined species complex appear to be at least partially successful and a common finding in the most successful interspecific pairings is a dual infectivity of the hybrid miracidium for each of the parental snail host species when these are mutually exclusive and an increase in the cercarial infectivity and in the egg production capacity per worm pair of the F_1 hybrid generations (see review by Wright and Southgate, 1976). However, further studies on the biological characteristics of the subsequent hybrid generations would be of value for a more complete understanding of important basic aspects of hybridization between schistosomes. The aim of the present study was on this background to elucidate the viability of a hybrid between male *S. haematobium* (Dar es Salaam, Tanzania) and female *S. intercalatum* (Edea, Cameroun) for up to the F_7 hybrid generation and to compare the biological characteristics of the hybrid with those of each of the parental schistosome species.

Materials and Methods

Parasite and snail material and snail infections

S. intercalatum (Edea, Cameroun) and *S. haematobium* (Dar es Salaam, Tanzania) routinely maintained in hamsters as the definitive host and in *Bulinus forskalii* (Kinshasa, Zaire) and *B. globosus* (Mazeras, Kenya), respectively, as the intermediate hosts were used. Repeatedly made experiments (Frandsen, unpublished) have shown that neither schistosome can develop in the snail

host used by the other. Following the initial cross-mating between male *S. haematobium* and female *S. intercalatum* (see below) the hybrid was passaged using cercariae obtained from *B. wrighti* (South Yemen) which may serve as the intermediate host for both the parental schistosome species. Miracidia for snail infections were hatched from eggs harvested from intestinal tissue of hamsters 14 days following start of excretion of eggs in faeces. The snail infection procedure, maintenance of infected snails, examination of snails for cercarial production, etc. were carried out as described by Frandsen (1979a) and examination of snails for cercarial shedding took place starting 30 days following miracidial exposure and thereafter once weekly for a period of 4 weeks.

Animal material

Female mice and male hamsters of outbred strains from the State Serum Institute, Copenhagen, Denmark were used. The weights of the mice and hamsters at the time of infection were 20–25 and 40–45 g, respectively.

Infection of rodents and recovery of schistosome eggs and worms

Infection of hamsters and mice with 200 and 150 cercariae per animal, respectively, was made using the ring method (Smithers and Terry, 1965) and the cercariae were obtained 1 to 2 weeks following patency of the infection. Worms were recovered by the perfusion technique described by Smithers and Terry (1965), counts of schistosome eggs in tissue were performed as described by Bjørneboe and Frandsen (1979) and the length of the prepatent period was determined by daily examinations for the presence of eggs in faeces using the miracidial hatching technique from day 50 following cercarial exposure. Recovery of worms and determination of schistosome tissue egg loads were made 14–15 days following first appearance of eggs in faeces. The number of eggs produced per worm pair per day of production was estimated using the following formula: total tissue egg counts/number of worm pairs $\times$ number of days between start of egg production and necropsy. Egg production was estimated to commence 8 days prior to first appearance of eggs in faeces. No account was thus taken to eggs excreted in faeces in that the size of the faecal egg output was negligible as compared with numbers of eggs deposited in tissue. The statistical evaluation of differences in egg production capacity was made using Student's t-test and a value of $p < 0.05$ was considered significant.

Observations on egg morphology

Eggs teased from the small intestines of hamsters were measured in 0.9% saline using an eyepiece micrometer and drawn using a camera lucida. All eggs drawn contained viable embryos.

Procedure for hybrid production

Hybridization was carried out by a simultaneous exposure of hamsters to 100 male cercariae of *S. haematobium* and 100 female cercariae of *S. intercalatum*. Production of cercariae of one sex was made by unimiracidial exposure of individual snails and the sex of the cercariae was determined prior to conducting the hybridization procedure by infection of mice with subsequent determination of the sex of the established worms.

Notation of generations

The notation in this publication is in agreement with that of Wright and Southgate (1976), i.e. the initial cross-mating results in production of P_1 generation eggs containing the F_1 miracidium. The F_1 miracidium gives rise to F_1 cercariae and F_1 adults and the F_1 adults produce F_1 generation eggs containing the F_2 miracidium which gives rise to F_2 cercariae and F_2 adults, etc.

Experimental plan

Following the initial cross-mating between male *S. haematobium* and female *S. intercalatum* in the hamster the hybrid was passaged for up to the F_7 generation using hamsters as the definitive host and *B. wrighti* as the intermediate host. Besides, the infectivity of the F_1, F_2, F_3 and F_5 hybrid

miracidial generations to *B. forskalii* (Kinshasa, Zaire) and to *B. globosus* (Mazeras, Kenya) was evaluated and the host-parasite relationship between the F_1, F_2 and F_5 hybrid generations and the mouse was also examined.

The host-parasite relationship between the rodent definitive hosts and the schistosomes (parental species and seven hybrid generations) was assessed using the following parameters: worm establishment, length of prepatent period, egg production capacity per worm pair per day of production and pattern of distribution of eggs in tissues. The snail/parasite compatibility level was evaluated using the size of the cercarial production per 100 exposed snails during an observation period of 5 weeks (TCP/100 snails/5 weeks) as the criterion. The TCP/100 snails/5 weeks value was estimated using the formula described by Frandsen (1979b) with the modification that snail death during the prepatent period, considered being primarily due to factors unrelated to the parasite infection, was not included in the calculation.

Results

Effects of hybridization on the schistosome-snail relationship

The length of the prepatent period was comparable among all snail-parasite combinations tested in never exceeding 30 days and the snail survival rates during the cercarial shedding period were relatively comparable in all series of exposures conducted being in the range of 50 to 100% (Table 1). Some intergeneration differences in the hybrid/snail compatibility level being unrelated to the hybrid miracidial infectivity as such may be expected, in that variable TCP values due to for example differences in the "quality" of the miracidia or to minor differences in the maintenance temperature are commonly experienced, even in different series of exposures involving the same schistosome/snail combination. However, the general trend as regards the effect of hybridization on the schistosome-snail relationship in the present study is in spite of this quite clear. The hybrid thus exhibited a dual infectivity for each of the parental snail host species for up to at least the F_5 generation and the TCP values of the hybrid/*B. forskalii* combinations being in the range of 110,426 to 284,365 remained in general comparable with that of the *S. intercalatum*/*B. forskalii* combination of 295,601. The TCP values of the hybrid/*B. wrighti* combinations, which were in the range of 149,135 to 393,384, were generally for up to the F_7 generation intermediate between that of 378,288 for the *S. haematobium*/*B. wrighti* combination and that of 136,465 for the *S. intercalatum*/*B. wrighti* combination. The TCP values for the hybrid/*B. globosus* combinations being in the range of 4,440 to 120,049 remained throughout lower than that of the *S. haematobium*/*B. globosus* combination of 189,696. These observations may together tentatively suggest that the hybrid exhibited a preference for the maternal host snail species *B. forskalii*.

Effect of hybridization on the host-parasite relationship between the schistosome and the hamster definitive host

The length of the prepatent period of *S. haematobium* and *S. intercalatum* in the hamster was 61–65 and 54–57 days, respectively. The length of the pre-

Table 1. Susceptibility of *Bulinus forskalii* (Kinshasa, Zaire), *B. globosus* (Mazeras, Kenya) and *B. wrighti* (South Yemen) to *Schistosoma intercalatum* (Edea, Cameroun), *S. haematobium* (Dar es Salaam, Tanzania) and their hybrid (male *S. haematobium* and female *S. intercalatum*)

Snail species	Schistosome	No. of snails exposed	No. infected/ No. surviving day 30	Infection rate day 30	Survival of infected snails 4 weeks post day 30	Total cercarial production/ 100 exposed snails/ 5 weeks
B. wrighti	*S. haematobium*	100	33/40	82.5%	100.0%	378.288
	S. intercalatum	31	19/30	63.3%	68.4%	136.465
	F_1 hybrid	39	25/29	86.2%	88.0%	327.875
	F_2 hybrid	30	12/29	41.4%	83.3%	150.600
	F_3 hybrid	53	14/38	36.8%	100.0%	183.355
	F_4 hybrid	15	8/15	53.3%	87.5%	N.R.
	F_5 hybrid	40	34/38	89.5%	91.2%	393.384
	F_6 hybrid	20	8/20	40.0%	62.5%	149.135
	F_7 hybrid	10	7/9	77.8%	66.6%	219.100
B. forskalii	*S. intercalatum*	80	60/70	85.7%	95.0%	295.601
	F_1 hybrid	55	30/52	57.7%	90.0%	284.365
	F_2 hybrid	30	10/29	34.5%	90.0%	110.426
	F_3 hybrid	50	12/40	60.0%	91.7%	157.330
	F_5 hybrid	22	10/11	90.9%	60.0%	283.912
B. globosus	*S. haematobium*	55	28/52	53.8%	78.6%	189.696
	F_1 hybrid	44	14/28	50.0%	71.4%	120.049
	F_2 hybrid	30	8/28	28.6%	87.5%	76.322
	F_3 hybrid	50	2/44	4.5%	50.0%	4.440
	F_5 hybrid	20	5/13	38.5%	80.0%	87.856

patent period of the F_1 hybrid generation corresponded to that of *S. haematobium* in being 62–65 days while that of the subsequent hybrid generations corresponded to that of *S. intercalatum* in being 52–57 days. From Table 2 it appears that the percentage worm establishment of *S. haematobium* and *S. intercalatum* in the hamster was comparable in being 20.2 ± 5.2 and $25.8 \pm 10.5\%$, respectively, and that the hybrid worm establishment was either comparable to, or as in the F_2 and F_7 generations, remarkably higher than that of the parental species.

The egg production capacity per worm pair per day of production of the F_1 hybrid generation of 1280 ± 238 exceeded significantly that of *S. haematobium* and that of *S. intercalatum* being 569 ± 134 and 204 ± 13, respectively, and the figure for the F_2 hybrid generation of 518 ± 161 was significantly lower than that of the F_1 hybrid generation, markedly higher than that of *S. intercalatum* and comparable to that of *S. haematobium*. The egg production capacity of the F_3 to F_6 hybrid generations being in the range of 212 to 294 was comparable to that of *S. intercalatum* but significantly lower than that of *S. haematobium* and that of the preceding hybrid generations.

Only negligible numbers of eggs were found in the lungs, spleen, kidneys and heart and the pattern of distribution of eggs in other organs appears in Table 2. It appears that the overall pattern of distribution of eggs in tissue as expressed by the intestine/liver ratio of *S. haematobium* and *S. intercalatum* was comparable being 4.3:1 and 4.4:1, respectively, but that the large intestine/small intestine ratio differed markedly in being 11.5:1 for *S. haematobium* and 1.2:1 for *S. intercalatum*. The pattern of egg distribution of the F_1 generation corresponded to that of *S. haematobium* while that of the F_2 hybrid generation approached that of *S. intercalatum*. However, subsequent to the F_2 generation the pattern of egg distribution deviated markedly from that of both parental species and from that of the preceeding hybrid generations with a gradual relative shift of eggs from the intestines to the liver and from the large intestine to the small intestine (Table 2).

Effect of hybridization on the host-parasite relationship between the schistosome and the mouse definitive host

From Table 3 it appears that the percentage worm establishment of the F_1, F_2 and F_5 hybrid generations was comparable to that of *S. intercalatum* but markedly higher than that of *S. haematobium* of only $3.2 \pm 1.3\%$. The length of the prepatent period of all hybrid generations studied corresponded to that of *S. intercalatum* in being 54–58 days while the *S. haematobium* infections in the mouse never gave rise to egg production. The egg production capacity of the F_1 hybrid generation of 864 ± 18 exceeded significantly that of *S. intercalatum* while that of the F_2 and F_5 generations was significantly lower than that of the F_1 generation but comparable with that of *S. intercalatum*. Finally, the pattern of distribution of eggs in tissue of the different hybrid generations with an intes-

Table 2. Pathogenecity (worm establishment, egg production capacity and pattern of distribution of eggs) for the hamster of *Schistosoma intercalatum* (Edea, Cameroun), *S. haematobium* (Dar es Salaam, Tanzania) and their hybrid (male *S. haematobium* × female *S. intercalatum*)

Schistosome	No. of hamsters	Worm establishment ($\bar{x} \pm$ S.D.)				Egg production capacity/ worm pair/day ($\bar{x} \pm$ S.D.)	Pattern of distribution of eggs in tissue	
		♂	♀	♂+♀	♀/♂		Intestine/liver ratio	Large/small intestine ratio
S. haematobium	6	29.4 ± 11.6	11.0 ± 1.6	40.4 ± 10.4	20.2 ± 5.2	569 ± 134	4.3:1	11.5:1
S. intercalatum	6	40.5 ± 19.9	11.0 ± 3.6	51.5 ± 20.9	25.8 ± 10.5	204 ± 13	4.4:1	1.2:1
F_1 hybrid generation	6	36.8 ± 10.7	24.4 ± 10.8	61.2 ± 15.2	30.6 ± 7.6	1280 ± 238	5.3:1	11.2:1
F_2 hybrid generation	6	62.5 ± 17.8	22.4 ± 10.0	85.0 ± 21.6	42.5 ± 10.8	518 ± 161	4.0:1	2.7:1
F_3 hybrid generation	6	26.4 ± 13.6	17.8 ± 18.6	44.2 ± 13.3	22.1 ± 6.7	265 ± 65	0.9:1	1.0:1
F_4 hybrid generation	3	47.0 ± 21.2	23.5 ± 2.1	70.5 ± 23.3	35.3 ± 11.7	278 ± 48	1.0:1	0.5:1
F_5 hybrid generation	4	26.8 ± 5.1	17.2 ± 12.8	44.0 ± 27.4	22.0 ± 13.7	294 ± 125	0.5:1	0.4:1
F_6 hybrid generation	3	50.5 ± 6.3	21.5 ± 16.3	7.2 ± 22.6	36.0 ± 11.3	212 ± 22	0.2:1	0.4:1
F_7 hybrid generation	3	8.3 ± 2.5	93.0 ± 17.7	101.3 ± 20.3	50.6 ± 10.1	N.R.	N.R.	N.R.

Table 3. Pathogenecity (worm establishment, egg production capacity, pattern of distribution of eggs in tissue) for the mouse of *Schistosoma haematobium* (Dar es Salaam, Tanzania), *S. intercalatum* (Edea, Cameroun) and their hybrid (male *S. haematobium* × female *S. intercalatum*)

Schistosome	No. of mice	Worm establishment ($\bar{x} \pm$ S.D.)				Egg production capacity/ worm pair/day ($\bar{x} \pm$ S.D.)	Pattern of distribution of eggs in tissue	
		♂	♀	♂ + ♀	♂♀		Intestine/liver ratio	Large/small intestine ratio
S. haematobium	6	3.8 ± 2.1	1.0 ± 0.9	4.8 ± 1.9	3.2 ± 1.3	0	–	–
S. intercalatum	6	16.9 ± 7.0	8.3 ± 5.0	25.2 ± 8.0	16.8 ± 5.4	109 ± 57	1.1:1	0.2:1
F_1 hybrid generation	5	16.8 ± 7.0	10.8 ± 4.1	27.6 ± 10.7	28.4 ± 7.1	864 ± 18	1.2:1	0.2:1
F_2 hybrid generation	6	17.5 ± 10.8	7.8 ± 4.4	25.3 ± 11.6	16.9 ± 7.7	312 ± 164	1.2:1	0.1:1
F_5 hybrid generation	4	15.0 ± 7.6	12.5 ± 4.1	27.5 ± 11.0	18.3 ± 7.3	173 ± 55	1.0:1	0.2:1

Table 4. Average dimensions of viable eggs harvested from the small intestines of hamsters of *Schistosoma haematobium* (Dar es Salaam, Tanzania), *S. intercalatum* (Edea, Cameroun) and their hybrid (male *S. haematobium* × female *S. intercalatum*)

Schistosome	Length (spine included) in microns ($\bar{x} \pm$ S.D. and range)	Maximum width in microns ($\bar{x} \pm$ S.D. and range)
S. haematobium	122 ± 7 (112–132)	48 ± 4 (44–60)
S. intercalatum	178 ± 22 (158–212)	56 ± 7 (45–68)
P_1	171 ± 18 (150–207)	57 ± 8 (44–68)
F_1	157 ± 10 (144–180)	46 ± 7 (36–56)
F_2	158 ± 12 (136–180)	53 ± 10 (38–74)
F_3	153 ± 11 (124–176)	45 ± 5 (36–54)
F_4	216 ± 21 (168–253)	43 ± 6 (35–53)
F_5	208 ± 15 (186–246)	49 ± 8 (38–58)
F_6	213 ± 35 (161–279)	46 ± 8 (35–58)
F_7	210 ± 8 (180–225)	45 ± 12 (35–56)

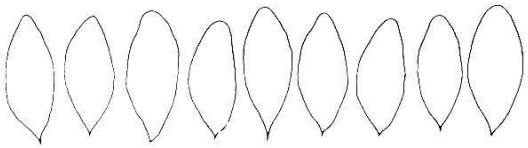
tine/liver ratio in the range of 1.0:1 to 1.2:1 and a large intestine/small intestine ratio in the range of 0.1:1 to 0.2:1 corresponded to that of *S. intercalatum*.

Effect of hybridization on schistosome egg morphology

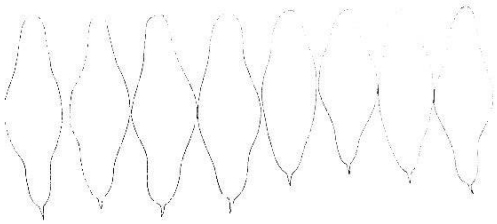
The average dimensions (mean length and width) of eggs of the parental schistosome species and of the hybrid generations are given in Table 4 and schematical illustrations of the eggs are presented in Figs. 1, 2 and 3. No overlap in length existed between the 2 parental species with the mean length of the eggs of *S. haematobium* and *S. intercalatum* being 122 ± 7 and 178 ± 22 μ, respectively, and the eggs of the P_1 generation resembled those of *S. intercalatum* in both size and shape. The mean length of the F_1, F_2 and F_3 hybrid generation eggs was intermediate between that of the parental species and the eggs showed a range of shapes through those of the parental species but with most eggs being intermediate in shape. However, a sudden and very dramatic change in both the size and shape of the eggs occurred in the F_4 hybrid generation with the mean length and the general shape resembling that of eggs of *S. bovis*. The size and the general shape of eggs of the F_5, F_6 and F_7 hybrid generations were comparable to that of the F_4 generation, i.e. being *S. bovis*-like in both size and shape.

Discussion

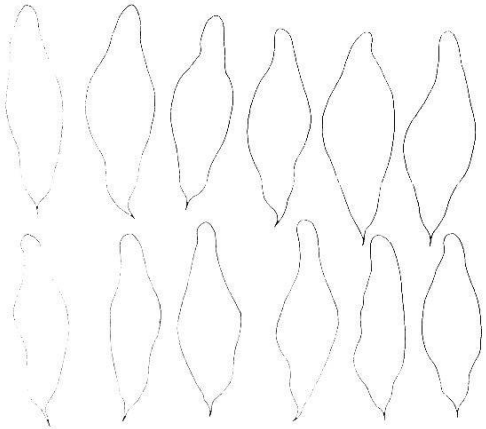
The demonstration in the present study of a dual infectivity for each of the parental snail host species for up to at least the F_5 generation of a hybrid between the male of the *B. africanus* snail group transmitted strain of *S. haematobium* from Dar es Salaam, Tanzania and female *S. intercalatum* (Edea,



S. haematobium

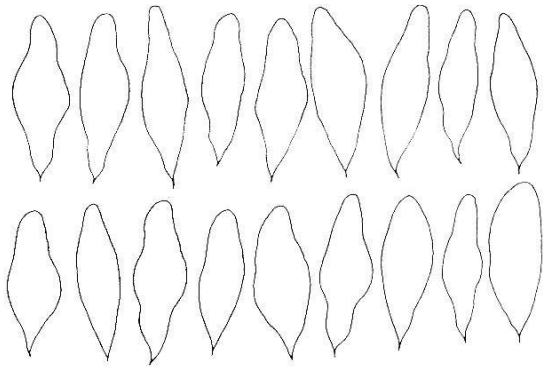


S. intercalatum

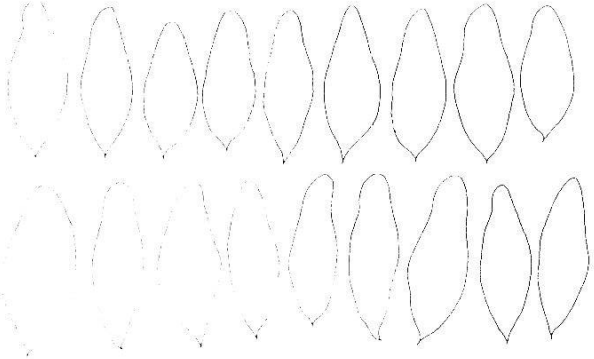


P_1 generation

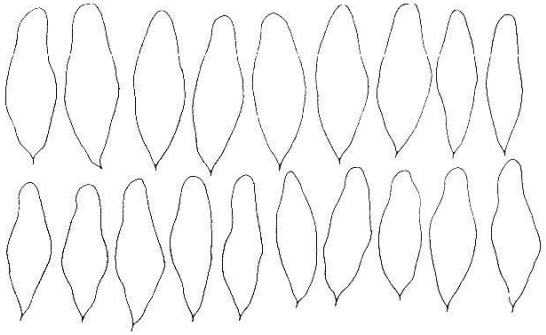
Fig. 1



F_1 generation

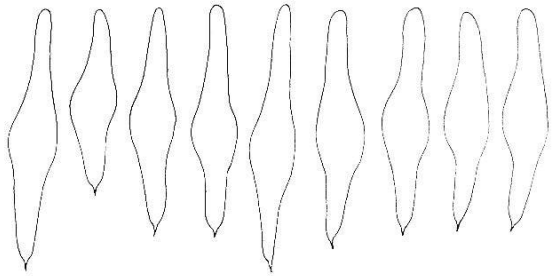


F_2 generation

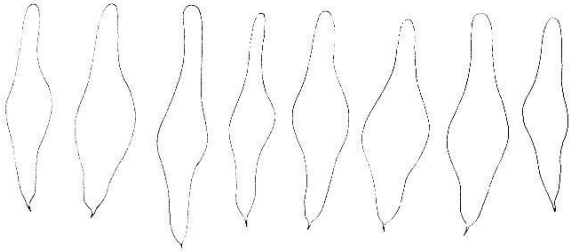


F_3 generation

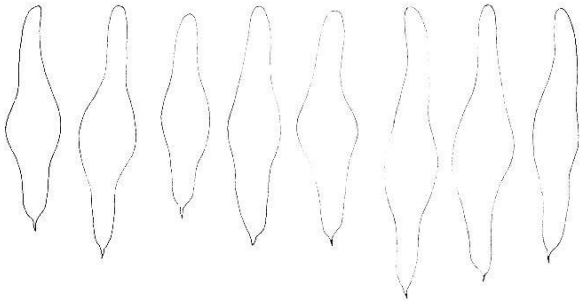
Fig. 2



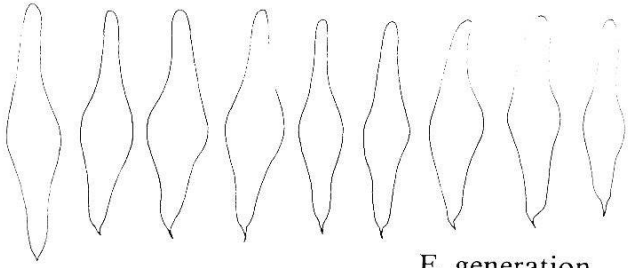
F_4 generation



F_5 generation



F_6 generation



F_7 generation

Fig. 3

Cameroun) confirms and extends earlier findings by Wright and Southgate (1976) on the F_1 and F_2 hybrid generations of several crosses involving females of the same *S. intercalatum* strain and males of several *B. truncatus* snail group transmitted strains of *S. haematobium*. The indication in the present study of a hybrid preference for the maternal host snail species *B. forskalii* contrasts interestingly the demonstration by Wright and Southgate (1976) of an apparent preference of the F_1 hybrid of a cross between female *S. intercalatum* (Edea, Cameroun) and male *S. haematobium* (Nyombe, Cameroun) for the paternal snail host. However, a direct comparison of these results is not possible due to the involvement of different strains of *S. haematobium* which are likely to be genetically different.

Previous studies in hamsters on the F_1 hybrid generations of crosses between the male of the *B. truncatus* snail group transmitted strain of *S. haematobium* from Nyombe, Cameroun and female *S. intercalatum* (Edea, Cameroun) (Wright and Southgate, 1976) and between male *S. haematobium* (Durban, South Africa) and female *S. mattheei* (Transvaal, South Africa) (Wright and Ross, 1980) have shown an apparent increase in the cercarial infectivity and an increase in the egg production capacity relative to that of the parental species, and some evidence for enhanced success of the F_1 and F_2 hybrid cercariae and adults was also obtained in some of the interspecific matings conducted by Taylor (1970). The hybrid worm return in hamsters in the present study was either comparable to, or as in the F_2 and F_7 generations, remarkably higher than that of the parental species. However, the marked variability in worm establishment commonly encountered during passage of terminal-spined schistosome species in hamsters due to factors unrelated to the innate cercarial infectivity as such prevents the conclusion that enhanced cercarial infectivity occurs in some of the hybrid generations. Even so, the data obtained at least show that the hybrid cercarial infectivity remained comparable to that of both the parental species for up to at least the F_7 hybrid generation. Although some intergeneration variability may occur in the reproductive potential during hamster passage of terminal-spined schistosomes (Mutani et al., in preparation) the demonstration of a marked increase in the egg production capacity relative to that of the parental species of the F_1 generation in both hamsters and mice strongly indicates an increased success of the F_1 generation as far as the reproductive potential is concerned. This finding thus confirms previous observations

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Fig. 1. The morphology of eggs of *Schistosoma haematobium* (Dar es Salaam, Tanzania) and *S. intercalatum* (Edea, Cameroun) and of the P_1 generation eggs of a cross between male *S. haematobium* (Dar es Salaam, Tanzania) and female *S. intercalatum* (Edea, Cameroun).

Fig. 2. The morphology of F_1, F_2 and F_3 hybrid generation eggs of a cross between male *Schistosoma haematobium* (Dar es Salaam, Tanzania) and female *S. intercalatum* (Edea, Cameroun).

Fig. 3. The morphology of F_4, F_5, F_6 and F_7 hybrid generation eggs of a cross between male *Schistosoma haematobium* (Dar es Salaam, Tanzania) and female *S. intercalatum* (Edea, Cameroun).

on F_1 hybrid generations by Wright and Southgate (1976) and Wright and Ross (1980) (see above), but the present study extends these previous findings by showing that the increase in the reproductive potential of the adult worms did not persist during subsequent hybrid generations and in fact declined to a level comparable to that of *S. intercalatum*.

The pattern of distribution of eggs in tissue of hamsters subsequent to the F_2 hybrid generation deviated markedly from that of the parental species and the tissue egg distributional pattern may thus be taken as a hybrid characteristic. The same is the case as far as the egg morphology is concerned with the eggs of the F_1, F_2 and F_3 generations exhibiting great polymorphism and with the eggs of the F_4 to F_7 generations being *S. bovis*-like in both size and shape. The finding that the hybrid egg becomes *S. bovis*-like following the F_3 generation appears especially relevant in the light of the finding by Southgate et al. (1976) of *S. bovis*-like eggs being a part of the hybrid egg series during natural hybridization between male *S. haematobium* and female *S. intercalatum* in man in Cameroun and of the finding of *S. bovis*-like eggs in the urine of man carrying mixed infections with *S. mattheei* and *S. haematobium* in South Africa (Pitchford, 1959). The development of an egg morphology resembling that of *S. bovis* might thus be a rather common phenomenon in hybridization between species of terminal-spined schistosomes.

The present study on hybridization between male *S. haematobium* (Dar es Salaam, Tanzania) and female *S. intercalatum* (Edea, Cameroun) thus shows that the pattern of distribution of eggs in tissue of hamsters following the F_2 generation and the egg morphology may be taken as hybrid characteristics; the hybrid stays viable for up to at least the F_7 generation with a dual infectivity for each of the parental snail host species for up to at least the F_5 generation and with an increase in the egg production capacity relative to that of the parental species in the F_1 hybrid generation. As judged upon the hybrid/snail and the hybrid/mouse relationships and on the egg production capacity in hamsters it appears that the biological characteristics with increasing hybrid generation number move towards that of *S. intercalatum*. This might, however, be due to segregation or to selection against *S. haematobium* genes in the hybrid line due to the hamster being a better host for *S. intercalatum* than for *S. haematobium* and the findings in the present study should therefore not provide the background for any conclusions concerning the natural hybrid/definitive host relationship. The hypothesis put foreward by Southgate (1978), mainly based on observations on the F_1 hybrid generation, that introgressive hybridization in man between male *S. haematobium* and female *S. intercalatum* should result in the creation of a new strain of *S. haematobium* and that this might be one of several possible factors responsible for the limited distribution of *S. intercalatum* in Africa may therefore still be valid.

The present study extends significantly the information available concerning important basic aspects of hybridization between male *S. haematobium* and

female *S. intercalatum* but the contribution to the understanding of important aspects of natural hybridization in man of the observations made on the inbred hybrid line is rather limited. Major attention in attempts to interprete events in natural hybridization should be given to the proporties of the F_1 generation and of the backcross between the F_1 hybrid generation and either of the parental species.

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