

Observations on the compatibility between *Bulinus* spp. and *Schistosoma haematobium* in the Senegal River basin

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Snail-infection experiments were carried out with a number of different species and populations of *Bulinus* and isolates of *Schistosoma haematobium*. The parasites came from six localities in the Senegal River basin (SRB), in the Lower Valley (Mbodiène); Middle Valley (Podor, Diatar and Nguidjilone), and Upper Valley (Aroundou and Galladé). Isolates of *S. haematobium* from the Middle and Upper Valleys all showed some compatibility with laboratory-bred *B. truncatus* from Mali, but none of these isolates was compatible with laboratory-bred *B. truncatus* originating from Senegal. *Schistosoma haematobium* from Diatar (Middle Valley) was compatible with *B. senegalensis*, whereas *S. haematobium* from Mbodiène (Lower Valley), which is naturally transmitted by *B. globosus*, was incompatible with *B. senegalensis* and *B. truncatus*. These data demonstrate that different isolates of *S. haematobium* from different regions of the SRB exhibit distinct intermediate-host specificities, which in turn will have an effect on the epidemiology of the disease, including the periods of transmission. It is apparent that, in addition to *B. senegalensis* and *B. globosus*, *B. truncatus*, the most widespread bulinid snail in the SRB, may be playing a role in the epidemiology of urinary schistosomiasis. This conclusion has obvious implications for the future spread of urinary schistosomiasis in the SRB.

Chemical and physical measurements from assorted habitats along the SRB, including pH, temperature, salinity, conductivity, and resistivity, are also reported.

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Recently, there have been massive increases in the prevalence and intensity of human infections with *Schistosoma mansoni* and, to a lesser extent, *S. haematobium*, in the Lower Valley of the Senegal River basin (SRB). These increases followed the construction of two dams, one on the Senegal River at Diama, in Senegal, built to prevent the intrusion of sea water, and the other on the Bafing River (a tributary of the Senegal River) at Manantali, in Mali, built to control the flow of the river and eventually to produce hydro-electricity (Southgate, 1997). It is known that in the Lower and Middle Valleys, *S. haematobium* is transmitted primarily by *Bulinus globosus* and by *B. senegalensis*, respectively (Vercruyse et al., 1994), and that, in the Upper Valley in Mali (in the area of the Manantali dam), this parasite is transmitted by *B. truncatus* (Rollinson et al., 1997). The Middle Valley of the SRB, in Senegal, is of particular interest because there is little known about the biology and transmission of *S. haematobium* in this area. There is no doubt that it represents a transition zone between the different types of transmission of urinary schistosomiasis in the Lower Valley (in Senegal) and the Upper Valley (in Mali). Strains of *S. haematobium* that are compatible with *B. globosus* are generally incompatible with *B. truncatus* and vice versa. In areas where two or more strains of the parasite are sympatric, however, gene flow between the strains may produce exceptions to this rule, as seems to occur, for example, in some areas around Lake Volta (Chu et al., 1978). One of the enigmas of the intermediate hosts responsible for the transmission of the parasites causing urinary schistosomiasis in the SRB is the identification of the area of transition between that of *B. globosus* and *B. truncatus*.

The main aim of the present study was to find out whether *S. haematobium* from the environs of Podor, Matam and Bakel showed any compatibility with *B. truncatus*. *Bulinus globosus* is scarce in this area (Malek and Chaine, 1981), but another species belonging to the *Bulinus africanus* group, *B. umbilicatus*, is more commonly found, as indeed is *B. senegalensis*. Clearly, it is of the utmost im-

portance to understand the basic epidemiology of transmission of urinary schistosomiasis throughout the SRB (i.e. the species of snail responsible for transmission in each area and the period of active transmission), if control measures are going to be successfully implemented in the future.

A secondary aim was to provide experimental data to support the epidemiological evidence indicating that *B. senegalensis* is compatible with some isolates of *S. haematobium* from the SRB.

The overall objective of the present work was to add to current knowledge of the role of different *Bulinus* species in the transmission of *S. haematobium* in the SRB.

MATERIALS AND METHODS

In order to investigate the intermediate-host-parasite relationships with different isolates of *S. haematobium*, two visits were made to the Lower and Middle Valleys of the SRB to collect freshwater snails and test them for infection, and to collect eggs of *S. haematobium* to facilitate snail-infection experiments. The snails were identified under a binocular microscope using morphological criteria (shell structure), and maintained as live collections. The first visit was made (by V.R.S. and Drs D. S. Brown and M. Picquet) in September-October 1995 and the second (by V.R.S., D.d.C. and M.S.) in 1997. (A snail survey was also carried out, by D.d.C. and M.S., during May 1997.). The positions of the localities surveyed (see Fig.) were determined using a global positioning system (GPS 12XL; Garmin International, Olathe, KS).

Snail-infection Experiments

In the first visit, uninfected, wild-caught *B. senegalensis* were used for snail-infection experiments. These snails were collected from numerous (non-transmission) habitats near Podor, including a temporary pool at Guia (16°35.815' N, 14°55.527' W), a flooded rice field near Dianga, and temporary laterite pools at Boube, Dimar Dier and Thianguaye (all situated on the Matam road).

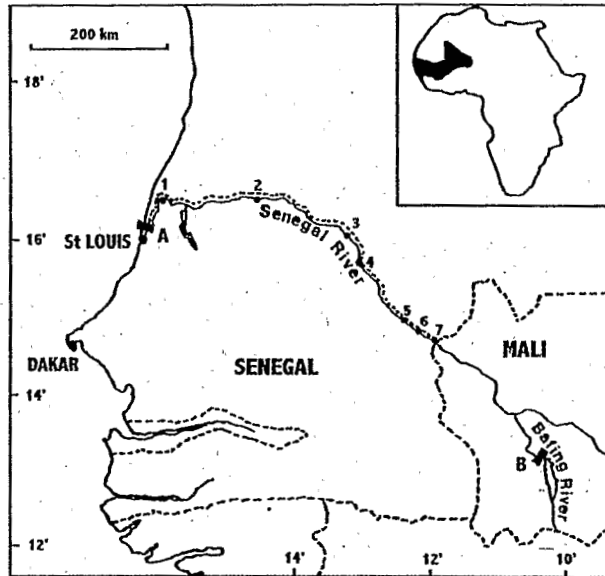


Fig. Sketch map of the Senegal River basin, indicating the positions of the Diama (A) and Mananatali (B) dams and of Mbodiene (1), Podor (2), Nguidjilone (3), Matam (4), Galladé (5), Bakel (6) and Aroundou (7).

In the second visit, uninfected, laboratory-bred *B. truncatus* were carried to the field, together with laboratory-bred *B. wrighti*, which acted as controls for the infection experiments (as *B. wrighti* is compatible with all species of schistosome belonging to the *S. haematobium* group). All of these snails came from populations maintained in the Biomedical Parasitology Division, The Natural History Museum, London, each of which is identified by a four-figure code. The laboratory-bred *B. truncatus* used were derived from snails collected in Zone Malado, Mali (1721), Boutou Batt, Senegal (1785), Firia, Lake Manatali, Mali (1797), or Ndiayenne, near Podor, Senegal (1893), and the *B. wrighti* (1697) were the descendants of snails collected in Oman. Wild-caught *B. umblicatus*, from a temporary pool under the first bridge on the Ourosogui-Matam road (15°38.070' N, 13°16.387' W), were also used during this second visit.

Infection Experiments

Eggs of *S. haematobium* were collected from a

number of egg-positive children who had been found to have proteinuria when tested with dip-sticks (Hemastix®): five from the Ecole Sada Ndiaye, Nguidjilone, near Matam (15°56.575' N, 13°19.800' W); 22 from Aroundou, near Bakel (14°45.918' N, 12°14.977' W); adjacent to the Senegal River on the Mauritanian/Mali border; 11 from Galladé, near Bakel (15°5.348' N, 12°37.526' W); and 10 from Diatar, near Podor (16°37.812' N, 14°54.587' W). The urines from each locality were pooled, and the eggs allowed to sediment. The urine was pipetted off and water was added, after which the pot containing the eggs was subjected to either sunlight or artificial light, to induce hatching. The miracidia were then counted, drawn off using a pipette, with the aid of a binocular microscope, and then added, in varying numbers (see Table 1), to pots containing snails. Subsequent, patent infections in the snails were detected using standard methods: each day, the pots containing the snails were placed under a bright light for 2-3 h and then checked for cercariae.

TABLE 1
The results of snail-infection experiments with *Schistosoma haematobium* from various sites in Senegal, and laboratory-bred or wild-caught snails

Origin of parasite isolate	Snail:		No. of:				Pre-patent period (days)	
	Species	Origin and (laboratory population)	Snails exposed	Snails/group	Miracidia/snail in group	Snails surviving prepatent period		No. and (%) of survivors infected
Nguidjilone	<i>B. truncatus</i>	Mali (1797)	25	1 or 5	5 or ?*	9	2 (22.2)	54
	<i>B. truncatus</i>	Senegal (1893)	20	5	5	—	—	—
	<i>B. wrighti</i>	Oman (1697)	25	5	5	22	3 (13.6)	35
Aroundou	<i>B. truncatus</i>	Mali (1721)	25	2 or 3	5	13	3 (23.1)	46
	<i>B. truncatus</i>	Senegal (1893)	18	2	5	—	—	—
	<i>B. wrighti</i>	Oman (1697)	30	5	5	13	2 (15.4)	53
Galladé	<i>B. truncatus</i>	Mali (1721)	21	2 or 3	4	11	2 (18.2)	44
	<i>B. truncatus</i>	Mali (1797)	25	1 or 2	5	13	3 (23.1)	50
	<i>B. wrighti</i>	Oman (1697)	19	3 or 4	4	13	1 (7.7)	37
	<i>B. umbilicatus</i>	Ourosogui-Matam road, Senegal†	30	30	?‡	—	—	—
Diatar	<i>B. truncatus</i>	Mali (1797)	23	3 or 5	5	13	4 (30.8)	49
			10	10	?	3	2 (66.6)	49
	<i>B. truncatus</i>	Senegal (1785)	18	3 or 5	5	—	—	—
	<i>B. wrighti</i>	Oman (1697)	14	1	5	13	8 (61.5)	35
	<i>B. senegalensis</i>	Thiangaye, Senegal†	30	5	6	6	1 (16.7)	45
	<i>B. senegalensis</i>	Guia, Senegal†	50	10	4	31	4 (12.9)	30
Mbodiene	<i>B. senegalensis</i>	Dimar Dier, Senegal†	20	5	5	14	4 (28.6)	30
	<i>B. senegalensis</i>	Guia, Senegal†	48	1 or 5	3 or 5	—	—	—

* Seventeen of the snails were left overnight in the tray containing the hatching eggs.

† Wild-caught.

‡ The 30 snails were exposed to the miracidia remaining after the other infections.

Water Characteristics

The pH, temperature, conductivity, resistivity and salinity of the Senegal River at Nguidjilone and Galladé, and of water in rice fields and a temporary pool (*marigot*) at Nguuidjilone were measured, in November 1997, using electronic meters: a pH Boy 501 tester (Camlab, Cambridge, U.K.) for pH, and a Jenway water meter (Model 4200; Jenway, Felsted, U.K.) for the other measurements.

RESULTS

Snail-infection Experiments (Table 1)

NGUIDJILONE ISOLATE

The results indicate that *S. haematobium* from Nguidjilone had a poor compatibility, based on numbers of snails infected and cercarial productivity, with *B. truncatus* Mali (1797) and *B. wrighti* Oman (1697), and was incompatible with *B. truncatus* Senegal (1893).

AROUNDOU ISOLATE

Both *B. truncatus* Mali (1721) and *B. wrighti* demonstrated some compatibility with *S. haematobium* from Aroundou, whereas *B. truncatus* Senegal (1893) was incompatible with this isolate.

GALLADÉ ISOLATE

Schistosoma haematobium Galladé showed some compatibility with two populations of *B. truncatus* from Mali. The level of compatibility was poor, however, since <25% of the snails surviving the pre-patent period became infected, and the pre-patent period in *B. truncatus* (44–50 days) was longer than that in *B.*

wrighti. None of the *B. umblicatus* (a member of the *B. africanus* group) exposed to miracidia from this isolate became infected.

DIATAR ISOLATE

Schistosoma haematobium from Diatar showed some compatibility with the control *B. wrighti* Oman (1697) and with populations of *B. truncatus* Mali (1797). The one population (1785) of *B. truncatus* Senegal that was exposed to miracidia of this isolate proved incompatible. The *S. haematobium* from Diatar clearly showed some compatibility with the wild-caught *B. senegalensis*.

MBODIENE ISOLATE

The *S. haematobium* from Mbodiene [which is naturally transmitted by *B. globosus* (Verlé *et al.*, 1994)] appeared to be refractory to the wild-caught *B. senegalensis*.

Water Characteristics

The characteristics of the habitats investigated in and around Nguidjilone and at Galladé are presented in Table 2.

DISCUSSION

Miller (1982) suggested that *Bulinus guernei* (= *B. truncatus*) was probably a poor intermediate host in the *diéré* of the SRB, because of the low levels of prevalence and intensity in the population and the correlation between the distribution of the disease and that of *B. guernei*. However, there was no experimental proof to support this suggestion: no experi-

TABLE 2
The characteristics of the water in four sites in the Senegal River basin, in November 1997

Site	pH	Temperature (°C)	Conductivity (µS)	Salinity (g/litre)	Resistivity (MΩ)
Senegal River at Nguidjilone	8.0	30.9	69	0.3	0.01
Rice fields at Nguidjilone	7.4	31.1	69	0.3	4.87
Temporary pool at Nguidjilone	8.1	32.8	103	0.3	1.00
Senegal River at Galladé	8.2	30.7	76.6	0.3	0.01

mental infection of laboratory mammals with cercariae from wild-caught snails, to produce the adult schistosomes that could be identified to species level, and no experimental infection of laboratory-bred snails. When Chaine and Malek (1983) exposed *B. truncatus*, *B. senegalensis* and *B. globosus* to miracidia of an isolate of *S. haematobium* from Ourosogui, Senegal (which was considered to be naturally transmitted by *B. senegalensis*), none of the snails became infected. Furthermore, exposure of the same three species of *Bulinus* to an isolate of *S. haematobium* from Ghana (which is naturally transmitted by *B. truncatus*) also failed to produce any positive infections. Later, the results of field and laboratory studies indicated that *B. truncatus* was not involved in the epidemiology of urinary schistosomiasis in the Lower and Middle Valleys of the SRB (Southgate et al., 1985; Vercruyse et al., 1985; Picquet et al., 1996). No *B. truncatus* from the Lower and Middle Valleys had been found to be naturally infected with *S. haematobium* and snail-infection experiments revealed total incompatibility between isolates of *S. haematobium* and laboratory-bred *B. truncatus*. More recently, Rollinson et al. (1997) showed that populations of *B. truncatus* from the Lower and Middle Valleys (in Senegal) and the Upper Valley (in Mali) were compatible with *S. haematobium* from Office du Niger (Mali), whereas *B. truncatus* from all over the SRB were not susceptible to infection with the *Bulinus-globosus*-borne isolate from Mbodiene, in the Lower Valley. The data presented by Rollinson et al. (1997) confirmed that differences in intermediate-host specificity influenced the distribution of schistosomiasis in the SRB, but also importantly demonstrated that *B. truncatus* from the Lower and Middle Valleys of the SRB were indeed compatible with some isolates of *S. haematobium*, albeit not those from Senegal. These authors predicted that urinary schistosomiasis would increase in the lower reaches of the SRB if a *Bulinus-truncatus*-compatible *S. haematobium* were to be introduced. The present snail-infection data indicate that isolates of *S. haematobium* ranging from Diatar to the environs of the Senegal-Mali-Mauritania border do in-

deed show some compatibility with *B. truncatus*. It is interesting that those populations of *B. truncatus* that showed some compatibility were derived from snails collected in Mali and not from Senegalese snails. The results of a recent study indicate, however, that it is premature to determine whether there is any significance in this observation. When Sène and Southgate (1998) compared the ribosomal internal transcribed spacer (ITS) of two populations of *B. truncatus*—one from Boutou Batt (Lower Valley, Senegal), and the other from Firia (Lake Manantali, Mali)—using eight restriction enzymes, they failed to detect any differences between the two populations. An isolate of *S. haematobium* from Mbodiene (Lower Valley, Senegal) was shown to be incompatible with *B. truncatus* from various sites in Senegal, Mali and Malawi (Rollinson et al., 1997). Hence, different isolates of *S. haematobium* from various regions of the SRB clearly demonstrate distinct, intermediate-host specificities. Clearly, there is a genetic basis associated with this specificity. There is no doubt that the construction of dams has impinged upon the distribution of urinary schistosomiasis in the SRB; *S. haematobium* was first recorded in Galladé approximately 6 months after the construction of the dam at Manantali, Mali (M. Sène, unpubl. obs.). Furthermore, some of the *B. truncatus* collected from the water-contact sites in the Senegal River in May-June 1997 were naturally infected with schistosomes (D. de Clercq, unpubl. obs.). However, it was not possible to verify the species of schistosome involved because the infected snails died before mice could be exposed to the cercariae in St Louis (D. de Clercq, unpubl. obs.). Approximately 30% of the schoolchildren from Galladé are currently infected with *S. haematobium* (D. de Clercq, unpubl. obs.).

As *B. truncatus* is the most widespread bulinid in the SRB, the present data indicate that there will probably be further increases in the prevalence and intensity of urinary schistosomiasis in this area, a potentially disturbing scenario. It is puzzling that, for the first time in snail-infection experiments spanning a period of at least 15 years in The Natural

History Museum, London, isolates of *S. haematobium* from the Middle and Upper Valleys of the SRB have shown some compatibility with *B. truncatus*. The reason(s) for this change remains enigmatic, but may simply reflect the introduction of a compatible strain from neighbouring Mali or, indeed, from elsewhere in Africa. There is no doubt that human mobility is responsible for affecting the distribution of schistosomes. Nevertheless, the data from both laboratory and field indicate that *B. truncatus* is involved in the transmission of urinary schistosomiasis in some parts of the SRB.

The recordings of physical and chemical data from various habitats in the SRB, taken in November 1997, show the water to be consistently alkaline (pH 7.4–8.2), the temperature to be always > 30.0°C, and the salinity consistent at about 0.3 g/litre; the recordings of conductivity and resistivity showed much more variation, according to habitat. Although it is clear that such measurements will vary according to season and

time of day, it is apparent that the change from an acid pH to an alkaline pH and the reduction in salinity since the construction of the dam at Diama on the SRB have been pivotal in allowing populations of freshwater snails (and hence levels of transmission of *S. haematobium*) to increase, leading to high worm burdens in the human population (Picquet *et al.*, 1996).

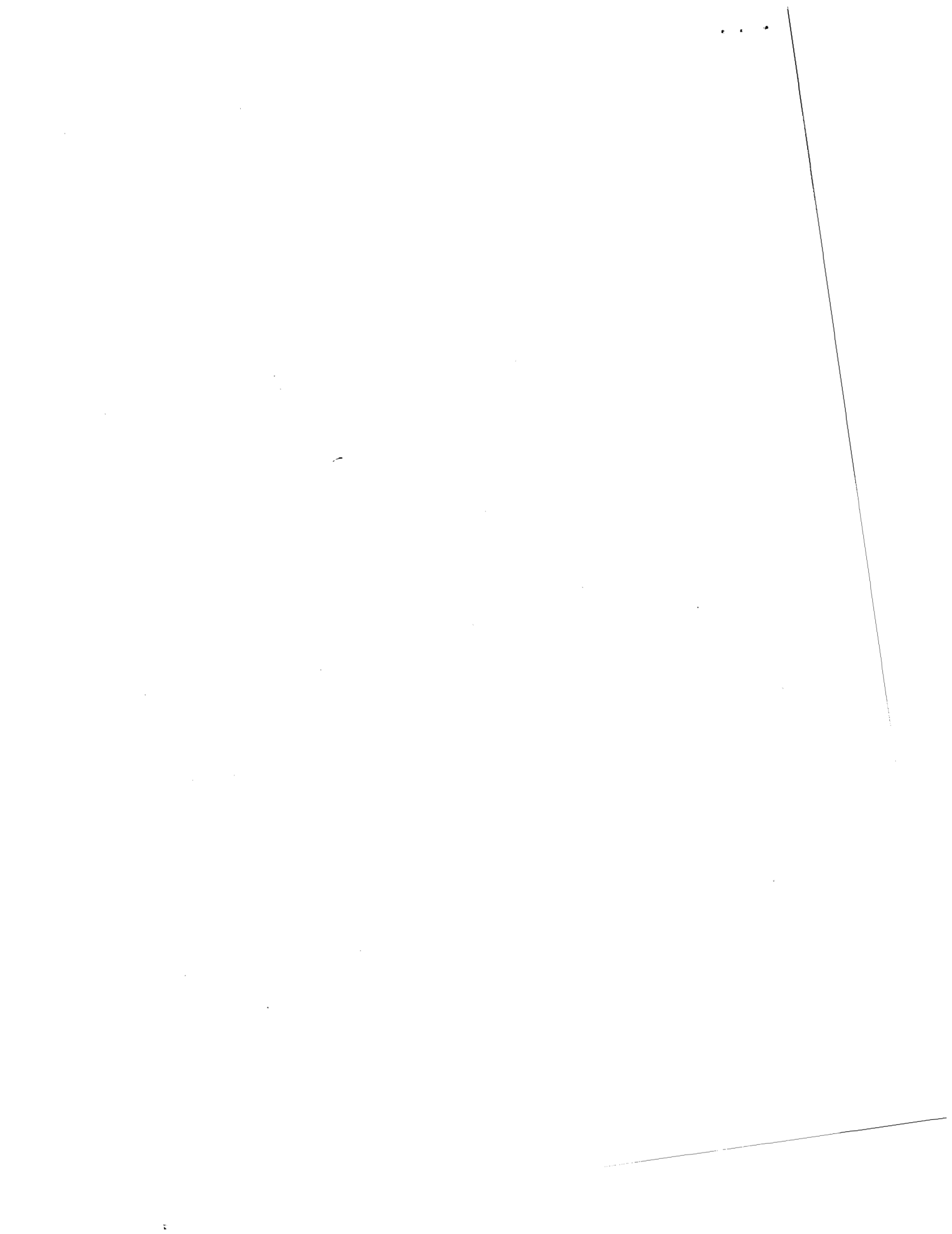
It will be important, timely and relevant to monitor (1) *B. truncatus* populations from the Lower and Middle Valleys for natural infections with *S. haematobium* and (2) any changes in the prevalence and intensity of infections in the human population in the foreseeable future.

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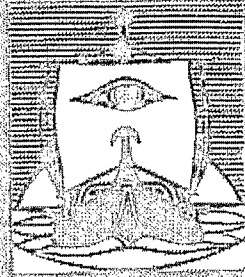
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