

Distribution and habitats of the *Bulinus africanus* species group, snail intermediate hosts of *Schistosoma haematobium* and *S. mattheei* in South Africa

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Abstract

As intermediate host of *Schistosoma haematobium* and *S. mattheei*, the *Bulinus africanus* group plays a major role in the transmission of urinary and bovine schistosomiasis, diseases that negatively affect the health status of millions of people and their livestock in South Africa. *Bulinus* spp. can also play a role in the transmission of cercarial dermatitis (swimmer's itch) caused by the immune reaction of incompatible hosts to the penetration of cercariae of non-human schistosomes. This can cause considerable discomfort to humans bathing in infested waters. This article focuses on the geographical distribution and habitats of this group as reflected by the samples taken from 2 930 collection sites on record in the database of the National Freshwater Snail Collection (NFSC) at the Potchefstroom Campus of the North-West University. The 414 different loci ($1/16$ -degree squares) on record, reflect an extensive distribution from the western parts of the North-West to Gauteng, Mpumalanga, Limpopo and KwaZulu-Natal Provinces and the coastal areas of the Eastern Cape Province. Details of each habitat as described by collectors during surveys, as well as altitude and mean annual temperature and rainfall of each locality, were processed and chi-square and effect size values were calculated. A decision tree constructed from all the available data indicated that temperature and altitude, followed by the type of water-body, seemed to be the more important factors that had a significant influence on the distribution of this group in South Africa. The role of the *B. africanus* group in the transmission of schistosome species is briefly discussed and the urgent need for co-ordinated surveys to update the geographical distribution of host snails, as well as the schistosome parasites in South Africa, is stressed.

Keywords: geographical distribution, habitat preferences, epidemiology of schistosomiasis, *Bulinus africanus*, *Bulinus globosus*

Introduction

As intermediate hosts of both *Schistosoma haematobium* (human urinary schistosomiasis) and *S. mattheei* (bovine schistosomiasis) freshwater snails belonging to the *Bulinus africanus* group play a major economic role in South African rural communities in the endemic areas of South Africa. When he revised the *B. africanus* group (= subgenus *Physopsis*, Krauss, 1848) Mandahl-Barth (1957) recognised only the two species, *B. (P.) africanus* (Krauss) and *B. (P.) globosus* (Morelet) in Southern Africa. This author considered the copulatory organ to provide the most reliable taxonomic character. After a study of the inter- and intra-population variation in this organ, Brown (1966) came to the conclusion that the penis sheath of *B. africanus* was considerably longer and thicker than the preputium while in *B. globosus* it was just the opposite in the majority of specimens. However, intermediate individuals were reported for Angola (Wright, 1963) and Zambia (Hira, 1974) and many intermediate individuals, especially from areas in the former Transvaal Province are on record in the database of the National Freshwater Snail Collection (NFSC) of South Africa. Of the 2 930 samples on record for this group 508 could be identified as *B. africanus* and 800 as *B. globosus* while the remainder was considered to be from intermediate populations. This report there-

fore focuses on the geographical distribution and habitats of this group as such, as reflected by the 2 930 samples in the database of the NFSC. Details of each habitat, as well as mean altitude and mean annual temperature and rainfall for each locality, were processed to determine chi-square and effect size values. An integrated decision tree that could make a selection of those variables that could maximally discriminate between this group and all the other species in the database was also constructed. The results indicated that temperature and type of water-body seemed to be some of the major factors determining the distribution of this group in South Africa. The ecological implications of the range of values reported by several authors for the demographic parameter r (intrinsic rate of natural increase) are also discussed. The possibility of a hybrid schistosome that could become more widespread and the fact that schistosomiasis is considered as one of South Africa's most neglected health hazards are briefly discussed. The urgent need for co-ordinated surveys to update the geographical distribution of freshwater snails in general and of intermediate host in particular, as well as of the schistosome parasites, is brought to attention.

Methods

Data pertaining to the habitats and geographical distribution of the *B. africanus* group were extracted from the database of the NFSC, which dates from 1956 up to the present. Only those samples for which the collection sites could be pinpointed on the 1:250 000 topo-cadastral map series of South Africa, were included in the analysis. The majority of these samples were collected during

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Received 12 August 2004; accepted in revised form 14 September 2004.

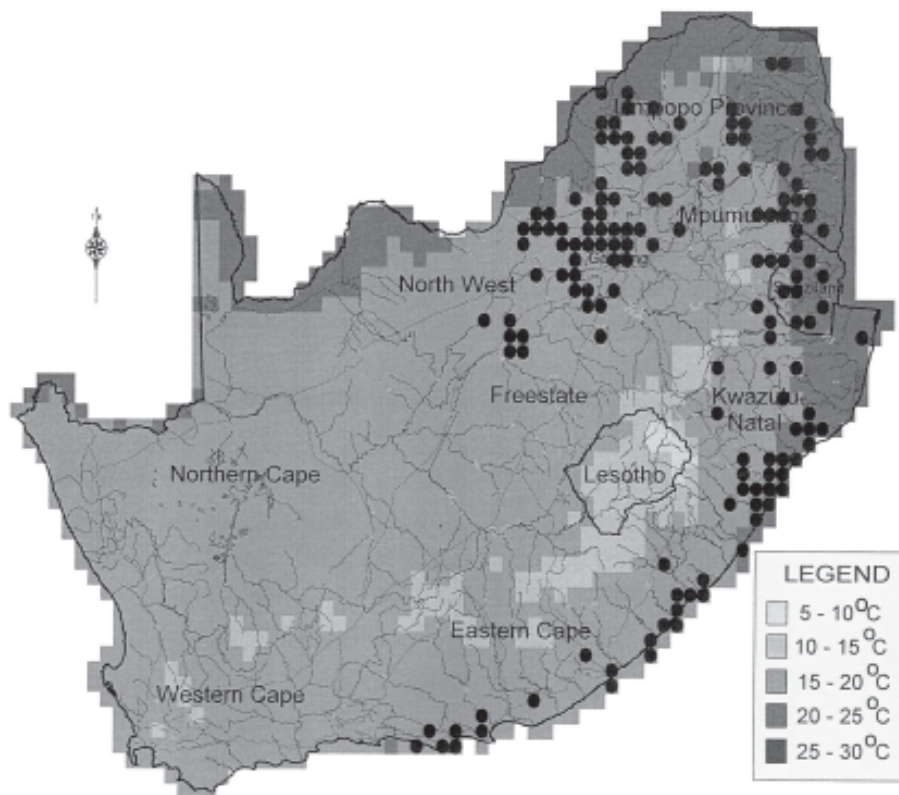


Figure 1
The geographical distribution of *Bulinus africanus* in $1/16$ square degree loci and mean annual air temperature in South Africa

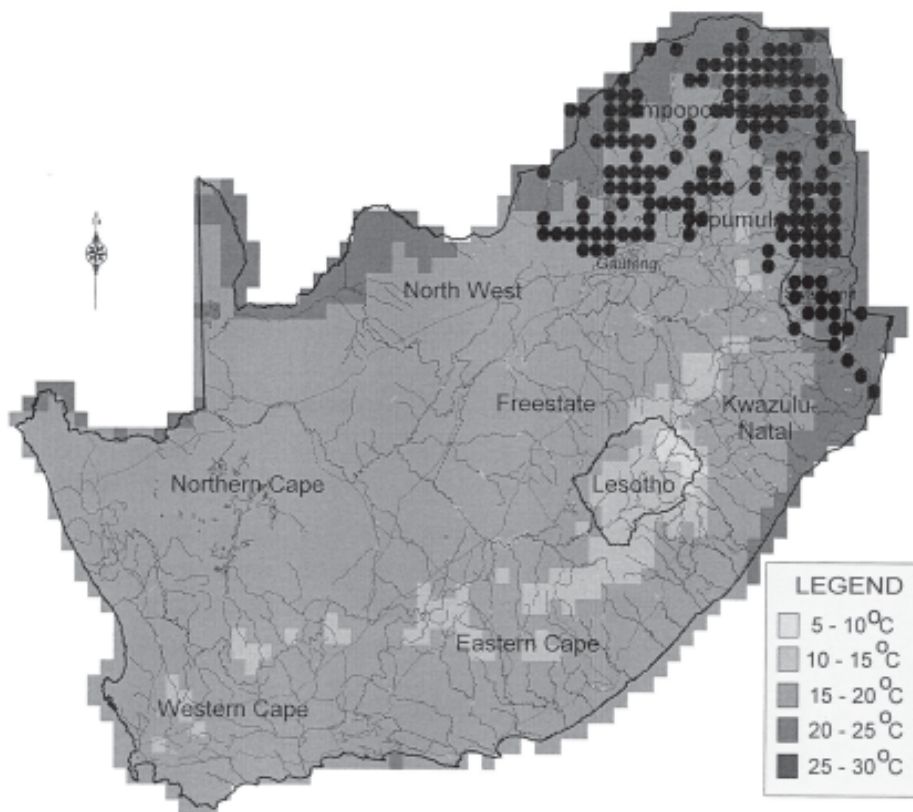


Figure 2
The geographical distribution of *Bulinus globosus* in $1/16$ square degree loci and mean annual air temperature in South Africa

surveys conducted by staff of government and local health authorities and then sent to the former Snail Research Unit at the Potchefstroom University for identification to be added to the NFSC. The geographical distribution of those samples that could be identified as *B. africanus* and *B. globosus* with reference to the criteria discussed by Brown (1966), are plotted in Figs. 1 and 2, respectively. However, as many of the 2 390 samples on record for this group in the NFSC could not be identified conclusively as either one of the two species on the strength of these criteria, the geographical distribution of the group as such, is given in Fig. 3.

Details of the habitats were recorded by collectors during surveys by selecting the relevant options on forms compiled by the staff of the Snail Research Unit. The number of loci in which the collection sites were located was distributed in intervals of mean annual rainfall and air temperature, as well as intervals of mean altitude to illustrate the frequency of occurrence within specific intervals. Rainfall, temperature and altitude data were obtained from the Computing Centre for Water Research (CCWR), University of Natal. A temperature index was calculated for all mollusc species in the database from their frequencies of occurrence within the selected temperature intervals and the results used to rank them in order of association with low to high climatic temperatures. This was done by allocating numeric values, ranging from one for the coolest to five for the warmest, to the five selected temperature intervals. The proportion of the total number of loci of each species falling within a particular temperature interval was then multiplied by the value allocated to that specific temperature interval. This was done for each temperature interval in which the species was recorded, the sum of these scores was then taken as the temperature index for that particular species, and the results presented in Table 5. Brown (2002) recommended this analysis. Chi-square values were calculated to determine the significance in difference between the frequency of occurrence in, on, or at the different options for each variable, such as type of water-body, type of substratum and temperature interval. Furthermore, an effect size (Cohen, 1977) was calculated for all the different variables discussed in this paper. The effect size is an index that measures the degree of discrepancy

between the frequency distribution of a given species in the set of alternatives of a given variable such as water-bodies, as compared to the frequency distribution of all other mollusc species in the database in the set of alternatives of the same variable (Cohen, 1977). Values for this effect size index of the order of 0.1 and 0.3 indicate small and moderate effects respectively, while values of 0.5 and higher indicate significantly large effects. A value for this index in the order of 0.5, calculated for the frequency distribution of a given mollusc species in the different types of water-body, for instance, would indicate that this factor played an important role in determining the geographical distribution of this particular species as reflected by the data in the database.

The data were also adapted and processed to construct an integrated decision tree (Breiman et al., 1984). This is a statistical model that enables the selection and ranking of those variables that can maximally discriminate between the frequency of occurrence of a given species under specific conditions as compared to all other species in the database. This was accomplished by making use of the SAS Enterprise Miner for Windows NT Release 4.0, April 19, 2000 Programme and Decision Tree Modelling Course Notes (Potts, 1999).

Results

The 2 930 samples of the *B. africanus* group which could be pinpointed on our maps, were collected from 410 different loci (Fig. 3).

This group was present in a wide variety of water-bodies, but the highest percentages were recovered from rivers (28.2%) and streams (24.7%) which respectively represented 11.0% and 10.0% of the total number of samples of all mollusc species collected in these two water-bodies (Table 1). The frequency of occurrence of this group in rivers and streams did not differ significantly from each other ($\chi^2 = 3.8$, $df = 1$; $p > 0.05$) but in this respect both differed significantly from dams ($\chi^2 = 86.4$, $df = 1$; $p < 0.05$; $\chi^2 = 51.9$, $df = 1$; $p < 0.05$, respectively) from which the third highest percentage of samples (19.6%) was recorded. The majority of samples (70.8%) came from perennial habitats. Although habitats with standing water yielded more samples, the 147 samples collected in habitats with fast-running water represented 6.6% of the total number of recoveries of any mollusc species from fast-running water. This compared favourably with the 7.0% represented by the 1 131 samples for all collections made in standing water (Table 2), consequently there was no significant difference between the occurrence of this species group in standing or fast-running water ($\chi^2 = 35.9$, $df = 1$; $p < 0.05$). The 1 029 samples collected in habitats with slow-running water, however, represented the highest percentage of the total number of recoveries of any mollusc species from

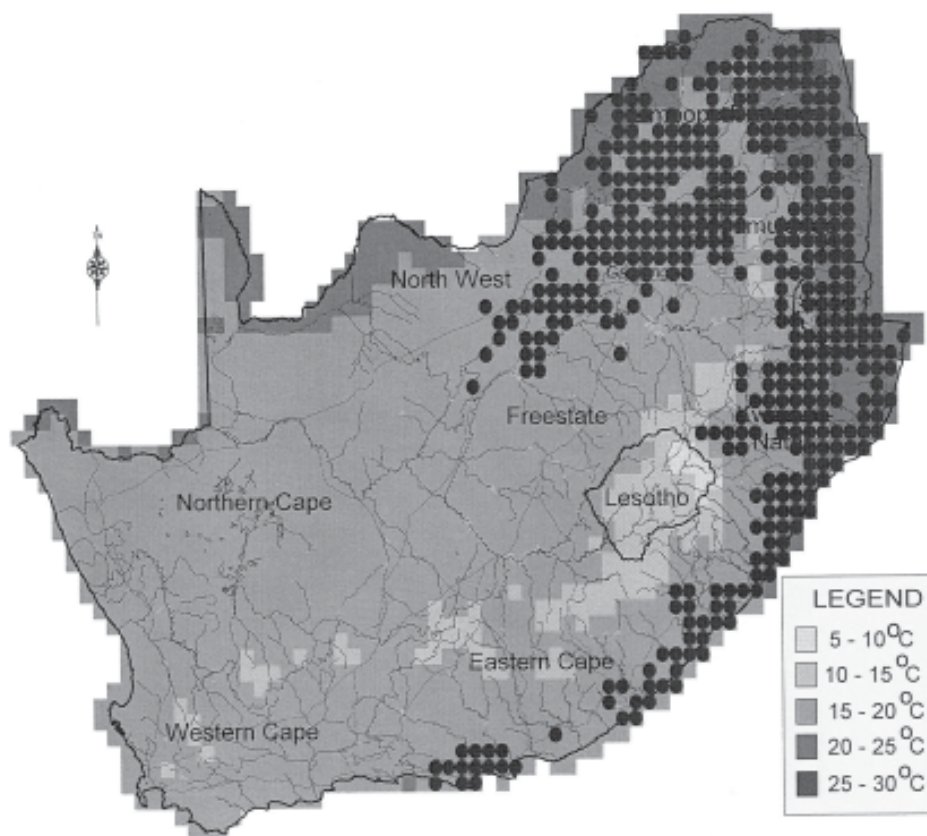


Figure 3
The geographical distribution of the *Bulinus africanus* group in $1/16$ square degree loci and mean annual air temperature in South Africa

TABLE 1 Types of water-body in which the <i>Bulinus africanus</i> group was found in 2 930 collection sites recorded during surveys				
Water-bodies	A	B	C	D
Channel	9	0.3%	169	5.3%
Concrete dam	19	0.6%	221	8.6%
Dam	574	19.6%	8400	6.8%
Ditch	34	1.2%	636	5.3%
Irrigation furrow	5	0.2%	113	4.4%
Pan	27	0.9%	306	8.8%
Pond	76	2.6%	1566	4.9%
Quarry	6	0.2%	122	4.9%
River	827	28.2%	7507	11.0%
Spring	20	0.7%	301	6.6%
Stream	723	24.7%	7211	10.0%
Swamp	64	2.2%	2076	3.1%
Vlei	1	0.03%	103	1.0%
Pool	9	0.31%	225	4.0%
Effect size $w = 0.31$ (moderate effect)				
A Number of times collected in a specific water-body				
B % of the total number of collections (2 930) on record for this group				
C Number of times any mollusc was collected in a specific water-body				
D % occurrence of this group in the total number of collections in a specific water-body				

	Type		Velocity			Colour		Salinity	
	Perennial	Seasonal	Fast	Slow	Standing	Clear	Muddy	Fresh	Brackish
A	2075	224	147	1029	1131	1657	504	1906	47
B	70.8%	7.6%	5.0%	35.1%	38.6%	56.6%	17.2%	65.1%	1.6%
C	22432	5350	2229	9501	16147	20408	6438	24089	657
D	9.3%	4.2%	6.6%	10.8%	7.0%	8.1%	7.8%	7.9%	7.2%
E	w = 0.24 (small to moderate effect)		w = 0.3.0 (moderate effect)			w = 0.02 (small effect)		w = 0.02 (small effect)	

A Number of times collected in a specific water condition
 B % of the total number of collections (2 930) on record for this group
 C Number of times any mollusc was collected in a specific water condition
 D % occurrence of this group in the total number of collections in a specific water condition

	Substratum types			
	Muddy	Stony	Sandy	Decomposing material
A	920	739	571	78
B	31.4%	25.2%	19.5%	2.7%
C	12835	7934	6523	632
D	7.2%	9.3%	8.8%	12.3%

Effect size w = 0.14 (small effect)

A Number of times collected in a waterbody with a specific substratum
 B % of the total number of collections (2 930) on record for this group
 C Number of times any mollusc was collected in a waterbody with a specific substratum
 D % occurrence of this group in the total number of collections in a water-body with a specific substratum

slow-running water (Table 2) and this differed significantly from recoveries from standing water ($\chi^2 = 113.5$, $df = 1$; $p < 0.05$) and fast-running water ($\chi^2 = 35.9$, $df = 1$; $p < 0.05$). More than 50% of the samples were collected in habitats with clear water (56.6%) and freshwater (65.1%) (Table 2) and the highest percentage of samples (31.4%) came from habitats with substrates described as predominantly muddy (Table 3). Aquatic plants were reported from 78.6% of the collections sites at the time of survey.

The majority of samples (73.5%) came from sites which fell within the 15 to 20°C interval; however, the number of samples recovered from sites which fell within the 20 to 25°C and the 25 to

30°C intervals both represented higher percentages of the total number of collections of all mollusc species from a site falling within a specific interval (Table 4). The frequency of occurrence in sites that fell within the 15 to 20°C interval differed significantly from all the other intervals (chi-square values ranging from $\chi^2 = 829.4$; $df = 1$; $p < 0.05$ to $\chi^2 = 279.5$, $df = 1$; $p < 0.05$).

Although 55.3% of the samples of this group came from sites that fell within the 600 to 900 mm rainfall interval, the 199 collections from sites that fell within the 900 to 1 200 mm interval represented 16.5% of the total number of collections of all molluscs from this specific interval (Table 4). The frequency of occurrence in sites that fell within the 600 to 900 mm rainfall interval differed significantly in this respect from all other rainfall intervals ($p < 0.05$) except from the 300 to 600 mm interval.

The majority of samples came from sites falling within the 1 000 to 1 500 mean altitude interval, however the interval ranging from 0 to 500 m, as well as the 500 to 1 000 m interval represented higher percentages of the total number of collections of all mollusc species within a specific interval (Table 4). The frequency of occurrence in sites that fell within the 1 000 to 1 500 m mean altitude interval differed significantly from all other intervals (chi-square values ranging from $\chi^2 = 50.9$ $df = 1$; $p < 0.05$ to $\chi^2 = 423.7$, $df = 1$; $p < 0.05$).

The effect size values calculated for all the factors investigated, are given in Tables 1 to 4 and the temperature indexes of all mollusc species in the database, as well as the effect sizes of their significance in difference as compared to the *B. africanus* group, are listed in Table 5. The decision tree analysis (Fig. 4) selected temperature and water-bodies as the most important factors of those investigated that determined the geographical distribution of this species group in South Africa.

Discussion

Bulinus africanus has a scattered distribution in Eastern and Southern Africa, unclear for many areas where critical comparison with *B. globosus* is needed (Brown, 1994). According to this author, *B. globosus* has the greatest range of any member of its species group, occupying much of Africa south of the Sahara. In Southern Africa *B. africanus* inhabits cooler climatic areas whereas *B. globosus* (Brown, 1994) occurs only in the warmer parts (Brown,

TABLE 4
Frequency distribution of the 2 930 collection sites of the *Bulinus africanus* group in selected intervals of mean annual air temperature and rainfall and mean altitude in South Africa

	Temperature intervals °C				Rainfall intervals (mm)					Altitude intervals (m)			
	10-15	15-20	20-25	25-30	0-300	300-600	600-900	900-1200	1200-1500	0-500	500-1000	1000-1500	1500-2000
A	9	2155	760	6	62	1053	1615	199	1	812	682	1329	107
B	0.3%	73.5%	25.9%	0.2%	2.1%	35.9%	55.3%	6.8%	0.03%	27.7%	23.3%	45.4	3.7%
C	4404	24928	4276	37	975	11994	19799	1203	28	6747	4491	14918	6998
D	0.2%	8.6%	17.8%	16.2%	6.4%	8.8%	8.2%	16.5%	3.6%	12.0%	15.2%	8.9%	1.5%
E	$w = 0.52$ (large effect)				$w = 0.19$ (small effect)					$w = 0.50$ (large effect)			

A Number of times collected in a locality falling in a specific interval
 B % of the total number of collections (2 930) on record for this group
 C Number of times any mollusc was collected in a locality falling in a specific interval
 D % occurrence of this group in the total number of collections in a specific interval
 E Effect size values calculated for each factor

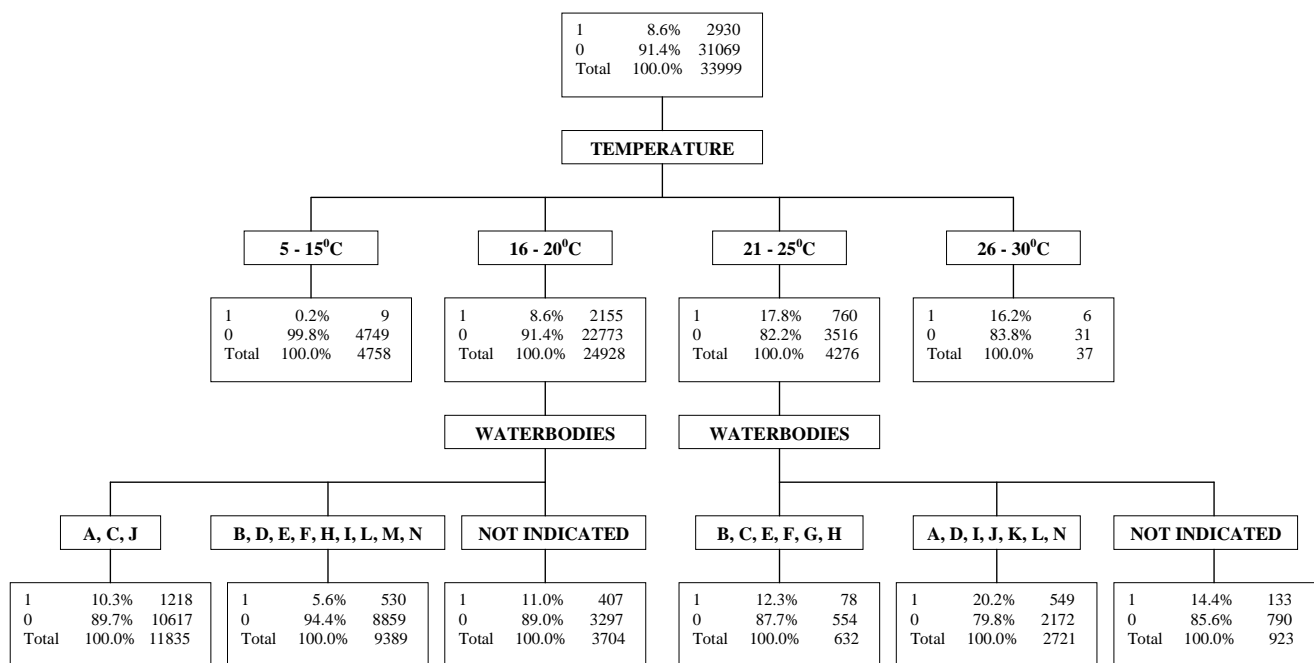


Figure 4
 Decision tree of the frequency of occurrence of the *Bulinus africanus* group for each variable as compared to the frequency of occurrence of all the other species in the database of the NFSC. 0 = percentages and frequencies of all other species, 1 = percentages and frequencies of the *B. africanus* group. Water-bodies: A = stream, B = channel, C = concrete dam, D = dam, E = ditch, F = irrigation furrow, G = pan, H = pond, I = quarry, J = river, K = spring, L = swamp, M = vlei, N = pool

1966; Appleton, 1980). This is supported by the geographical distribution of these two species plotted in Figs. 1 and 2 from the data in the database.

A review by Appleton (1978) of the literature on abiotic factors influencing the distribution and life cycles of bilharziasis intermediate host snails, led him to the conclusion that temperature emerges as the abiotic factor which, according to available evidence, is of greatest importance in determining the distribution of host snails in lentic environments and that current velocity is the most important factor in lotic environments. This conclusion is substantiated by the results of the present investigation. The decision tree analysis

(Fig. 2) singled out temperature as the most important factor in determining the geographical distribution of the *B. africanus* group in South Africa and more than 70% of the samples on record for this group were recovered from habitats with either standing or slow-flowing water (38.6% + 35.1%, Table 2). Appleton (1978) concludes that distribution is limited by temperature mainly where this becomes unfavourable for reproduction. Judging from earlier reports in literature intermediate host snails seem to have broad tolerance ranges to field water temperature (Gordon et al., 1934; Malek, 1958; Watson, 1958). Appleton (1978), however, is of opinion that these remarkably broad tolerance ranges may not be

TABLE 5
Frequency distribution in temperature intervals and temperature index of the *Bulinus africanus* group as compared to all mollusc species in the database of the National Freshwater Snail Collection

Mollusc species	No. of samples	5 - 10°C	10 - 15°C	15 - 20°C	20 - 25°C	25 - 30°C	¹ Index	² SD	³ CV	Effect size
<i>Pisidium viridarium</i>	636	201	270	163	2		1.947	0.764	39.225	-1.720
<i>Lymnaea truncatula</i>	723	95	281	343	4		2.354	0.709	30.135	-1.277
<i>Pisidium castertanum</i>	5		2	3			2.600	0.548	21.066	-1.205
<i>Pisidium costulosum</i>	425	1	138	282	4		2.680	0.492	18.344	-1.180
<i>Pisidium langleyanum</i>	627	18	173	430	6		2.676	0.544	20.328	-1.073
<i>Bulinus tropicus</i>	8448	32	2326	5860	230		2.744	0.502	18.305	-1.027
<i>Gyraulus connollyi</i>	969		185	777	7		2.816	0.406	14.404	-0.986
<i>Ceratophallus natalensis</i>	1797		299	1430	68		2.871	0.433	15.092	-0.863
<i>Burnupia</i> (all species)	2778	7	287	2384	100		2.928	0.380	12.971	-0.739
<i>Ferrissia</i> (all species)	540		72	420	47	1	2.957	0.476	16.088	-0.636
<i>Bulinus reticulatus</i>	296		6	287	3		2.990	0.174	5.832	-0.600
<i>Assiminea umlaasiana</i>	2			2			3.000	0.000	0.000	-0.578
<i>Tomichia cawstoni</i>	4			4			3.000	0.000	0.000	-0.578
<i>Tomichia diferens</i>	10			10			3.000	0.000	0.000	-0.578
<i>Tomichia lirata</i>	2			2			3.000	0.000	0.000	-0.578
<i>Tomichia ventricosa</i>	89			89			3.000	0.000	0.000	-0.578
<i>Tomichia tristis</i>	81			79	2		3.025	0.156	5.162	-0.523
<i>Unio caffer</i>	76		6	63	6	1	3.026	0.461	15.237	-0.507
<i>Physa acuta</i>	755			719	36		3.048	0.213	6.997	-0.472
<i>Bulinus depressus</i>	552			519	33		3.060	0.237	7.755	-0.445
<i>Arcuatula capensis</i>	15			14	1		3.067	0.258	8.420	-0.430
<i>Lymnaea columella</i>	2302		81	1977	243	1	3.071	0.371	12.072	-0.419
<i>Lymnaea natalensis</i>	4721		205	3802	713	1	3.108	0.429	13.789	-0.338
<i>Assiminea bifasciata</i>	17			15	2		3.118	0.332	10.652	-0.316
<i>Bulinus africanus</i>	508			442	65	1	3.136	0.349	11.118	-0.276
<i>Gyraulus costulatus</i>	736		20	580	135	1	3.159	0.437	13.836	-0.225
<i>Bulinus forskalii</i>	1209		17	985	204	3	3.160	0.409	12.948	-0.223
<i>Pisidium ovampicum</i>	6			5	1		3.167	0.408	12.892	-0.207
<i>Sphaerium capense</i>	25		1	17	7		3.240	0.523	16.136	-0.038
<i>Bulinus africanus</i> group	2930		9	2155	760	6	3.260	0.450	13.816	0.000
<i>Corbicula fluminalis</i>	389		1	291	94	4	3.267	0.437	13.384	0.016
<i>Tomichia natalensis</i>	23			16	7		3.304	0.470	14.238	0.094
<i>Assiminea ovata</i>	5			3	2		3.400	0.548	16.109	0.256
<i>Thiara amarula</i>	10			6	4		3.400	0.516	15.188	0.271
<i>Melanoides victoricae</i>	49			29	19	1	3.429	0.540	15.752	0.312
<i>Bulinus globosus</i>	800			447	351	2	3.434	0.511	14.876	0.340
<i>Septaria tessellaria</i>	2			1	1		3.500	0.707	20.203	0.339
<i>Biomphalaria pfeifferi</i>	1639		5	880	751	3	3.459	0.508	14.692	0.391
<i>Coelatura framesi</i>	6			3	3		3.500	0.548	15.649	0.438
<i>Neritina natalensis</i>	16			8	8		3.500	0.516	14.754	0.465
<i>Bulinus natalensis</i>	245		2	97	146		3.588	0.510	14.204	0.643
<i>Segmentorbis planodiscus</i>	27			9	18		3.667	0.480	13.101	0.847
<i>Segmentorbis angustus</i>	32			7	25		3.781	0.420	11.108	1.158
<i>Melanoides tuberculata</i>	305			64	237	4	3.803	0.430	11.305	1.207
<i>Pisidium pirothi</i>	23			4	19		3.826	0.388	10.129	1.258
<i>Spathopsis petersi</i>	44			5	37	2	3.932	0.398	10.111	1.493
<i>Aplexa marmorata</i>	9				9		4.000	0.000	0.000	1.644
<i>Bellamya capillata</i>	31				31		4.000	0.000	0.000	1.644
<i>Eupera ferruginea</i>	169			6	157	6	4.000	0.258	6.455	1.644
<i>Lentorbis carringtoni</i>	8				8		4.000	0.000	0.000	1.644
<i>Lentorbis junodi</i>	12				12		4.000	0.000	0.000	1.644
<i>Segmentorbis kanisaensis</i>	9				9		4.000	0.000	0.000	1.644
<i>Spathopsis wahlbergi</i>	28			1	26	1	4.000	0.272	6.804	1.644
<i>Cleopatra ferruginea</i>	73				71	2	4.027	0.164	4.081	1.705
<i>Lanistes ovum</i>	41				38	3	4.073	0.264	6.473	1.807

¹Index = Temperature index; ²SD = Standard deviation; ³CV = Coefficient of variance

accurate since, as Shiff (1966) has demonstrated experimentally and in the field, *B. globosus* is sensitive to temperature gradients and will seek out parts of the habitat where temperatures are nearest its optimum. It was also demonstrated experimentally that there was a marked difference between the optimum temperature ranges for survival and the optimum range for reproduction for a particular species and that these ranges could differ even for the same species depending on their specific area of origin (De Kock (1973). The view that *B. africanus* is more capable of colonising habitats under cooler climatic conditions than *B. globosus* (Brown, 1994) is supported by the r values (intrinsic rate of natural increase) determined in life-table experiments by De Kock (1973) which indicated that the optimum value for reproduction was between 23° and 26°C for the former and 26° and 29°C for the latter species. In accordance with these results, *B. africanus* survived longest at constant low temperatures (Joubert et al., 1984), while *B. globosus* survived longest at constantly high temperatures (Joubert et al., 1986). This view is further supported by the lower temperature index (3.136) calculated for *B. africanus* in the present study compared to that of *B. globosus* (3.434) (Table 5). This also provides a logical explanation for the ability of the former species to colonise habitats on the highveld of the Free State, Gauteng and North-West Province of South Africa. The precarious existence of populations of *B. africanus* under cooler conditions on the fringe of its geographical distribution is attributed to the relatively low r values realised by cohorts of this species, even at optimal temperature regimes in life-table experiments (De Kock, 1973). Even though it is reported as a moderately good aestivator (Brown, 1994), the effects of the ephemeral nature of these habitats in general and its relatively low innate capacity of increase even at optimal temperatures, would result in great fluctuations in population numbers and survival would largely depend on the rainfall during a particular season and the length of the period without surface water. This was demonstrated in a study that spanned five summer seasons in such an area in the North-West Province (Pretorius et al., 1992). Even in a species that aestivates successfully, many individuals die as surface water disappears and there is further loss during dormancy (Brown, 1994). Recovery from such a population crash when water returns to the habitat would depend on the intrinsic rate of natural increase of a species (Brown, 1994). A species that aestivates successfully but has a low r is unlikely to become common under these circumstances (Brown, 1994). Apart from unfavourable climatic temperature, this is probably one of the main reasons for the sporadic occurrence and precarious existence of populations of *B. africanus* on the highveld of the North-West and Free State Province of South Africa.

Some of the other factors governing the distribution of this group, include type of water-body, stream geology, total dissolved chemical composition, or salinity and current velocity.

The *B. africanus* group was reported from all the types of water-body on record in the database (Table 1). The results in Fig. 4, however, show that rivers and streams were two of the three water-body types selected at the temperature category of 15 to 20°C and two of the seven selected at the temperature category of 20 to 25°C as most frequented by this group. This is in agreement with the water-body types reported in literature for this group (McCullough et al., 1968; Brown, 1975; Coulibaly and Madsen, 1990). The effect size of $w = 0.31$ indicates that type of water-body as such, had a moderate influence on the distribution of this group in South Africa as reflected by the records in the database.

During surveys in the Gladdespruit and Komati River (Mpumalanga Province) a potentially useful association was found between the occurrence of permanent lentic habitats produced by the weathering of bedrock with hardness above 5 in Moh's Scale of

Hardness and the longitudinal distribution of persistent populations of both the *B. africanus* group and *Biomphalaria pfeifferi* (Appleton, 1975). Appleton and Stiles (1976) came to the conclusion that practically the entire endemic area of the bilharzia intermediate host snails in South Africa is over rock formations which are resistant to erosion. While accepting that waters flowing over such rocks tend to provide permanent pools that serve as refuges for snails, Brown (1978) is of opinion that this effect is no more than locally significant and points to the fact that large parts of the area from which these snails are absent, contain apparently suitable habitats. It consequently seems that unfavourable climatic temperature is likely to be a factor of overriding influence in excluding these snails and a number of other freshwater molluscs (Brown, 1978). The nature of the substratum itself as a factor has not been emphasised as being of much importance (Appleton, 1978). This is supported by the small effect value ($w = 0.14$, Table 3) calculated for this factor in the present investigation. However, firm mud, usually rich in decaying organic matter, is usually associated with host snail habitats (Van Someren, 1946; Malek, 1958, Watson, 1958). This is also in accordance with the results of the present investigation where it was found that the majority of samples of this group was collected in habitats of which the substratum was described as predominantly muddy (Table 3).

Although the effect size ($w = 0.02$, Table 2) calculated for salinity of the water indicated that this factor should play a relatively unimportant role in the distribution of this group in South Africa, a natural population of *B. africanus* declined in relation to increasing salinity (Pretorius et al., 1982). It was also proved experimentally that mineral content of the water can be limiting, both when values are too high or too low (Williams, 1970; Jennings et al., 1973; Heeg, 1975; Jennings, 1976). This is supported by the results of an experimental investigation to determine the influence of salinity on certain aspects of the biology of *B. africanus* by Donnelly et al. (1983) who found a progressive and significant reduction in both the rate of hatching and the mean percentage egg hatch with increasing salinity. These authors also observed a difference between the salinity tolerance of adult snails and that of hatchlings and eggs which, in their opinion, could be attributed to differences in their tolerance to osmotic stress. They are further of opinion that the comparatively high sensitivity of eggs and hatchlings to osmotic stress could possibly be the limiting factor that determines the level of salinity in which this snail can establish breeding populations. This seems to provide a logical explanation for the observed decline in a natural population of *B. africanus* in relation to increasing salinity by Pretorius et al. (1982).

The effect size value ($w = 0.30$, Table 2) calculated for current velocity suggests that this factor would have a moderate effect on the distribution of this group in South Africa. However, intermediate host snails of schistosomiasis in general have been found to have a remarkably low tolerance range to current velocity. The majority of habitats in which they occur, are lentic but established, persistent populations occur also in very slow-flowing water, up to a limit of approximately 0.3 m/s (Frank, 1964; Appleton, 1975). In accordance with this the majority of the samples of this group were collected in habitats with either standing or slow-flowing water (Table 2). The phenomenon that intermediate host snails are sometimes reported from habitats with fast-running water is explained by Brown (1994) in the following way: rivers contain many boulders and pools where the bedrock is hard, which provide refuges for snail populations where they are protected from current speeds above the tolerable maximum. This might account for the seemingly anomalous fact that 5.0% of the samples of the *B. africanus* group were reported from habitats with fast-flowing water (Table 2).

It is difficult to assess the importance of *B. africanus* as a host by itself for *S. haematobium*, because it is sometimes sympatric with other potential intermediate hosts (Brown, 1994), but it is undoubtedly responsible for some transmission in KwaZulu-Natal (Donnelly et al., 1984). We also demonstrated in the laboratory that snail stocks of *B. africanus* from three habitats in the North-West Province were highly compatible with a laboratory strain of *S. haematobium* originally obtained from the Research Institute for Diseases in a Tropical Environment (RIDTE), Nelspruit, Mpumalanga, South Africa. This parasite strain was successfully maintained by the senior author in offspring of these snails in our laboratory for several years. During extensive surveys in the North-West Province by the senior author, it was also established that *B. africanus* was responsible for the transmission of *S. mattheei* in two localities in the Mooi River and one locality in the Sterkstroom Spruit, a tributary of the Schoon Spruit, all of which form part of the Vaal River catchment area.

Bulinus globosus is an important intermediate host of *S. haematobium* in many areas, but the part played locally depends on the presence of a compatible parasite strain (Brown, 1994). In a study that spanned several years, *B. globosus* was found to be responsible for the transmission of *S. haematobium*, *S. mattheei* and what seemed to be a hybrid between these two species, to the local population in an informal settlement near Tzaneen in the Limpopo Province (Strauss, 2000). During this investigation a number of children passed three distinct types of terminal spined eggs that could be classified as typical *S. haematobium*, typical *S. mattheei* and an intermediate form.

After observations on a possible hybrid between the two schistosomes *S. haematobium* and *S. mattheei*, Pitchford (1961) came to the conclusion that the problem was still in its infancy but with the increased use of the same water supply by man and cattle in informal settlements in the endemic area, there was every likelihood that the incidence of *S. mattheei* in man might increase. The resulting hybrids would in time possibly supplant *S. mattheei* and *S. haematobium* with a schistosome infecting man and cattle with equal ease (Pitchford, 1961), a premise supported many years later by the large number of hybrid eggs passed by members of the community in the study area near Tzaneen, mentioned above.

The upgrading of existing and the construction of new water impoundments by government to supply freshwater to local communities country-wide, unfortunately also has the effect that existing habitats for freshwater snails become more permanent and stable and many more new habitats are also created in the process. It was already pointed out in 1995 by Schutte et al. that more land will have to be made available for agriculture, many more dams will have to be built and irrigation schemes established to provide for the basic needs of the expanding population. According to these authors the effect of this type of development on the endemicity of schistosomiasis can be expected to be profound as these water-bodies will often provide ideal habitats for intermediate host snails and there is bound to be close human contact with water, as happened elsewhere in Africa with dire consequences.

Unfortunately, co-ordinated extensive surveys to update the geographical distribution of intermediate host snails and the prevalence of schistosomiasis were discontinued in the early 1980s. Only occasional individual efforts have since been made, some of which are still in progress, to address this problem on a limited scale in certain rural communities. Unfortunately, large-scale co-ordinated surveys as launched in the past by government and local health authorities are currently non-existent. The need to update our knowledge of the current distribution of the freshwater snails in general in South Africa is emphasised by reports of the new invader

species *Aplexa marmorata* (Appleton et al., 1989) and *Tarebia granifera* (Appleton and Nadasan, 2002) from natural habitats in South Africa. From the results of a recent survey of the freshwater molluscs of the Kruger National Park, it seems justified to conclude that *A. marmorata* is in the process of invading suitable habitats in the Park and that it could even be a more aggressive and successful invader species than either *Physa acuta* or *Lymnaea columella* that has colonised large areas of our country (De Kock et al., 2002).

In an epidemiological study conducted in the Mamitwa Village, Limpopo Province an infection rate of more than 70% with *S. haematobium* was found in children under the age of 14 years (Wolmarans et al., 2001), while another recent epidemiological study conducted in 30 schools in the Mpumalanga Province revealed a prevalence of up to 35.1% and 6.3% for *S. haematobium* and *S. mansoni*, respectively, in primary-school children (Mngomezulu et al., 2002). Results of a study by the co-author to establish the prevalence of urinary schistosomiasis in children in selected schools in the Rustenburg district, not regarded as a highly endemic area, revealed an infection rate of between 6 and 9%. These findings emphasise the fact that bilharzia is still an important problem in this country and will not only remain so, but is bound to increase if government and local health authorities do not conduct co-ordinated epidemiological surveys to update the geographical distribution of both the snail intermediate hosts and the disease and to implement control measures. We would like to conclude with this quotation from Schutte et al. (1995) "South Africa has for many years been in the forefront of schistosomiasis research and we consider it unfortunate that the disease had to be relegated to a low priority issue".

Acknowledgements

We are indebted to Prof HS Steyn, head of the Statistical Consulting Service and Prof DA de Waal of the Centre for Business Mathematics and Informatics of the Potchefstroom Campus of the North-West University for their assistance in processing the data and to the National Research Foundation (NRF) and the Potchefstroom Campus of the North-West University for financial support and permission to publish.

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