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SCHISTOSOMA WEINLAND, 1858 FROM *HIPPOPOTAMUS AMPHIBIUS* LINNAEUS, 1758 IN THE KRUGER NATIONAL PARK

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ABSTRACT

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Adults of *Schistosoma edwardiense* Thurston, 1964, were recovered from *Hippopotamus amphibius* in the Kruger National Park. Small round to oval *Schistosoma margrebowiei*-like eggs, presumed to be those of *S. edwardiense*, were found fairly frequently in the faeces of infected hippopotami together with a few *Schistosoma haematobium*-like eggs the identity of which remains uncertain.

Biomphalaria sp., exposed to the droppings of infected hippopotami, shed cercariae thought to be those of *S. edwardiense*. No evidence of shistosoma adults was found at necropsy in rodents exposed to these cercariae. The parasite appears to be host specific to the hippopotamus.

Arguments, based on biological and anatomical characteristics are put forward regarding *Schistosoma hippopotami* Thurston, 1963 as synonymous with *Schistosoma mansoni*.

Résumé

LE SCHISTOSOMA *WEINLAND*, 1858 *DE L'*HIPPOPOTAMUS AMPHIBIUS *LINNAEUS*, 1758 *AU PARC NATIONAL KRUGER*

Des adultes de Schistosoma edwardiense *Thurston*, 1964 *ont été recouvrés de l'*Hippopotamus amphibius *au Parc National Kruger. De petits oeufs ronds à ovals semblables à ceux du* Schistosoma margrebowiei, *présumés être ceux du* S. edwardiense, *furent trouvés assez fréquemment dans les faeces d'hippopotames infectés avec un petit nombre d'oeufs semblables à ceux de* Schistosoma haematobium *et dont l'identité demeure incertaine.*

Biomphalaria *sp. exposés aux déjections d'hippopotames infectés, rejetaient des cercaires qu'on pense être ceux du* S. edwardiense. *Aucune évidence de schistosomes adultes n'a été trouvée à la nécropsie de rongeurs exposés à ces cercaires. L'hippopotame apparaît être l'hôte spécifique de ce parasite.*

Des arguments basés sur les caractéristiques biologiques et anatomiques, pour considérer Schistosoma hippopotami *Thurston*, 1963 *comme synonyme de* Schistosoma mansoni, *sont avancés.*

INTRODUCTION

Two species of *Schistosoma*, *Schistosoma hippopotami* Thurston, 1963 and *Schistosoma edwardiense* Thurston, 1964, were recovered from hippopotami in Uganda. In both instances no extra-uterine eggs were seen, the number of mature female worms available was small and the uterus of both species contained one egg or none. It was clearly indicated that *S. hippopotami* had a sub-terminal spined egg. Subsequently, Thurston (1971) stated that *S. hippopotami* were recovered from the hepatic veins and *S. edwardiense* from the mesenteric veins. She also recovered *S. hippopotami* from the pulmonary arteries and venae cavae of a further 5 out of 17 hippopotami, and *S. edwardiense* from the mesenteric veins of a further 20 out of 31 hippopotami. She was unable, however to recover schistosome miracidia or eggs from the liver, gut scrapings, faeces and other organs of these animals. On several occasions, she obtained long shafted, brevifurcous cercariae from wild snails caught in hippopotami habitats in Uganda, but was unable to passage these through 4 species of laboratory animals. She considered the huge suckers of *S. hippopotami* a valid distinction between these 2 schistosomes.

McCully, Van Niekerk & Kruger (1965) reported a prevalence of 100% *S. hippopotami* amongst 100 *Hippopotamus amphibius* culled in the Letaba River in the Kruger National Park during the winter of 1964. *S. edwardiense* was also tentatively identified. The majority of worms were found in sites such as the posterior venae cavae, hepatic veins, aorta, heart, etc. In 1967 they described the pathology resulting from these infections, and stated that *S. edwardiense* was not found, that the ages of the animals ranged from 6 months to old adults, that worm burdens were heavy and that the culling operation followed a prolonged 3 year drought. Evidence of viable ova was only found in the suprarenals and the numbers of ova in the gastrointestinal and urinary tract were insufficient for the natural infestation of snails. They suggested that this might be due to seasonal periodicity of ovigenesis but found little histological evidence such as dead encapsulated eggs to support this. They considered the huge suckers of the male schistosomes an adaptive characteristic.

A survey of over 3 000 droppings from 27 animal species (excluding rodents) in the Kruger National Park produced evidence of *Schistosoma mattheei* in 16 species, *Schistosoma mansoni* in 2 species, and large *Schistosoma haematobium*-like eggs in 2 out of 153 hippopotami (Pitchford, Visser, Pienaar & Young, 1973, 1974).

Other reports of *Schistosoma* found in *H. amphibius* include the "*haematobium-bovis*" group from Ruanda (Dinnik, Walker, Barnett & Brocklesby, 1963) and one immature (sic) female with one *S. haematobium*-like egg in the uterus from the Kruger National Park (McCully, Van Niekerk & Kruger, 1967).

MATERIALS AND METHODS

The Olifants and Letaba Rivers run from west to east in the Kruger National Park, forming 2 sides of a rather narrow triangle before confluence near the Park's eastern boundary.

In 1977, a search for schistosomes in the heart and aorta of some 40 hippopotami in the Olifants River was unsuccessful (Pitchford & Visser, unpublished data). During August/September 1980 an opportunity was presented of examining a further 11 culled hippopotami from the Letaba River and 19 from the Olifants River. Search was made for worms in the heart, aorta, and mesenteric veins. Some worms were collected and preserved in the usual manner for

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TABL Mean measurements (µm) of eggs of various relevant *Schistosoma* spp.

Schistosome species	Author	Extra-uterine				Intra-uterine	
		Length	Width	Spine	Shape	Length	Width
S. edwardiense........	Thurston (1964)......	No eggs seen				47,7	28,7
Type 1..............	Present series.........	62,4	53,3	Minute on very few eggs	Round to oval	46,0	32,3
S. margrebowiei.......	Southgate & Knowles (1977)	$87,2\pm9,6$	$62,3\pm7,6$	0,25–0,6 Not always seen	Round to oval	—	—
S. margrebowiei.......	Pitchford (1974)......	71	63	—	Round to oval	—	—
Type 2..............	Present series.........	109,8	60,3	6,5	Oval	Not seen	
S. haematobium.......	Pitchford (1965)......	122–142*	—	6,3–7,3*	Oval	90*	—

* Range of means from 6 host species

anatomical studies and others were preserved for electrophoretic purposes. Faeces was collected from infected animals and 4 laboratory-bred species of snails were each exposed to about a handful of the fresh filtered material and maintained under outdoor laboratory conditions.

An initial intensive search for snails where the hippopotami were culled in the Olifants River produced only a few bivalves. Later 8 species of snails were collected in other sections of the Olifants River and its tributaries. None of these snails shed brevifurcous cercariae during the short time they remained alive.

Droppings from 141 animals, including 22 waterbuck (*Kobus ellipsiprymnus*), 12 kudu (*Tragelaphus strepsiceros*), 48 baboons (*Papio ursinus*), 4 elephant (*Loxodonta africana*), 17 buffalo (*Syncerus caffer*) and 38 hippopotami from the vicinity of the Olifants River, were collected and formalinised for subsequent examination.

Results

In direct contrast to previous findings no schistosomes were found in the animals from the Letaba River; from the Olifants River, 12 out of the 19 hippopotami were found harbouring schistosomes but only in the mesenteric veins.

On examination, the adult worms, after being cleared in glycerine and alcohol, were identical with *S. edwardiense* Thurston, 1964. (Ovary in anterior 1/6, no eggs or one oval to round spineless egg *in utero* in 25 females, 3–5 testes, ventral sucker 0,25 mm (0,21–0,28) in 44 males, females shorter than males, 4,7 mm and 7,2 mm respectively).

Two egg types were found in the faeces of the infected hippopotami after filtration and staining by a method previously described (Pitchford *et al.*, 1973).

Type 1

Round to oval shaped eggs resembling small *Schistosoma margrebowiei* eggs with a rudimentary lateral spine which was not visible on the majority of eggs (Table 1). They were readily confused with some round worm eggs and spores under the low magnification of the stereoscopic microscope and could easily have been missed on previous Kruger Park and other surveys. Again, in contrast to other observations on hippopotami, and considering the bulk of the droppings, numerous eggs were found which, with qualifications, were considered to be those of the only adults identified, i.e. *S. edwardiense*.

Type 2

A few (23) small *S. haematobium*-like eggs with a very distinct spine (Table 1). All contained a fully developed miracidium, but no adults to which these eggs could be related were found in the mesenteric veins.

Fifty-two days after exposure 8 out of 16 *Biomphalaria salinarum* (58 exposed originally) shed long, tail shaft, brevifurcous cercariae. The mean length of the tail shaft was 397 µm or about twice the length recorded by Porter (1938) for *S. mansoni* and by Fripp (1967) for *Schistosoma rodhaini*. These cercariae were originally discharged between 09h00 and 12h00, but after about 2 days changed to a nocturnal rhythm (probably pre-sunrise). The last of these infected snails died after 88 days.

Of 17 *Saccostomus campestris* and 15 *Praomys* (*Mastomys*) *natalensis* exposed to large numbers of the pooled cercariae from these snails, none were found harbouring schistosomes at necropsy 56–126 days after exposure. A further 33 rodents still await examination, but the chances of recovering adults seem remote.

Examination of game droppings revealed *S. mattheei* eggs from the baboons and buffalo, *S. edwardiense* eggs from 6 hippopotami and *S. haematobium*-like eggs from one hippopotamus.

Discussion

(1) *Taxonomic features*

Original descriptions of *Schistosoma* have perforce often been based on examination of small numbers of adults and extra-uterine eggs or on material recovered from experimentally infected animals which are not necessarily the normal definitive hosts.

Various authors have commented on the unreliability of the anatomical features of schistosomes, but generally and within fairly wide limits certain adult characteristics and intra- and extra-uterine egg characteristics are together sufficient for differentiation of species. There may also be distinguishing biological differences.

Pitchford (1977) cast some doubt on the validity of *S. hippopotami* and *S. edwardiense* as distinct species, largely because mature eggs had not been seen and/or described, because of the seemingly "dead end" nature of the infections observed up to that time, and for other reasons relating to *S. hippopotami* that are here made apparent.

(a) *S. hippopotami*

Thurston (1963) differentiated *S. hippopotami* from *S. mansoni* by, amongst other variables, the sub-terminal spine of the former. However, it was shown by Teesdale & Nelson (1958) that in man the spine of *S. mansoni* may be distorted to sub-terminal as in *Schistosoma mansoni rodentorum* Schwetz, 1954 while Pitchford & Visser (1960) found that the distortion was dependent on the species and the diet of the definitive host. Thurston (1963) differentiated *S. hippopotami* from *S. rodhaini* by the numerous intra-uterine eggs of the latter and no eggs or a single intrauterine egg of *S. hippopotami* and by the number of testes (2–4) in *S. hippopotami*. Brumpt (1931) described *S. rodhaini* originally on very limited material as having several intra-uterine eggs. However, as McCully *et al.* (1967) pointed out, other workers have reported only one egg *in utero*, a feature supported by Fripp (1967) and by our own observations. The number of testes of *S. rodhaini* is variable: Brumpt (1931) gives 6–8, Saoud (1966) 6–11 (majority 7–9 and Fripp (1967) 4–8. These numbers are generally in excess of those given by Thurston (1964) for *S. hippopotami*, but Coles & Thurston (1970) have shown that in *S. mansoni* the number of testes is too variable to be of any diagnostic significance. The same would seem to be true for *S. rodhaini*.

If the shape of mature and *in utero* eggs is dependent on anatomical and functional characteristics of the female schistosome which are liable to change as in *S. mansoni rodentorum*, other changes, such as the number of testes (which within limits, is a variable characteristic), might occur in aberrant schistosomes. Since *S. hippopotami* is classified as a "sub-terminal spined egg" schistosome, it is possible that it may be aberrant *S. mansoni* or *S. rodhaini* harboured in the hippopotamus, with consequent anatomical distortions.

(b) *S. edwardiense*

The extreme anterior position of the ovary and the intra-uterine egg characteristics as described by Thurston (1964) and the present observations on extra-uterine eggs would seem to justify a distinct species.

(2) *Biological features*

(a) *S. hippopotami*

(i) *Relative to* S. mansoni

There is limited human faecal pollution within the Kruger National Park and a very low prevalence of *S. mansoni* along the Letaba River outside the Park. Under normal circumstances a high prevalence amongst hippopotami would be unlikely. On the other hand, several known schistosome (*S. mattheei*) epidemics (Le Roux, 1929; Strydom, 1963; Van Wyk, Bartsch, Van Rensburg, Heitman & Goosen, 1974) amongst stock in non-endemic or areas of low endemicity have occurred which probably originated from a single massive infection of snails. Look-out sites along the rivers in the Kruger National Park where tourists may leave their cars often have no latrine accommodation and this might account for *S. mansoni* found in waterbuck (Pitchford *et al.*, 1973). The hatching time for *S. mansoni* eggs in faeces may be protracted to 3 days or more (Pitchford & Visser, 1972), during which time they may travel long distances in flowing water. Under drought conditions, the ultimate effects of even a single stool could result in high snail infection rates followed by correspondingly high rates in definitive hosts.

(ii) *Relative to* S. rodhaini

The only known definitive hosts of *S. rodhaini* in nature include the serval cat (*Felis serval*), domestic dogs (*Canis familiaris*) and 8 rodent genera (Pitchford, 1977). If domestic dogs are excluded, the normal hosts would therefore probably be indigenous to the Park. Of 69 faecal specimens from 6 feline and canine species examined during the Park survey, only 1 contained schistosome (*S. mattheei*) eggs and those had probably been ingested. Only *S. mansoni* and *S. mattheei* were found at necropsy from 3705 wild rodents caught in areas near or adjacent to the southern and mid-western Park (Pitchford & Visser, 1962). No cercariae from wild-caught *Biomphalaria* sp. in this area have proved to be *S. rodhaini* on passage through rodents (Pitchford, unpublished data, 1951–1965). It would appear therefore that *S. rodhaini* is not indigenous to the Eastern Transvaal Lowveld. Moreover, if a focus of *S. rodhaini* is assumed along the Letaba River, it would presumably give rise to repeated infections in the hippopotami, with consequent incriminating evidence, which has never been found.

Thurston's (1971) observations on wild snails, which may be irrelevant, are the only evidence that *S. hippopotami* is capable of perpetuating its life cycle: seasonal ovigenesis was not supported histologically; no additional definitive hosts have been found and death and disintegration of the hippopotamus and consequent release of miracidia seem unlikely.

Histological evidence in the form of dead encapsulated eggs (McCully *et al.*, 1967) did not support long-standing infections. Therefore it is suggested that the infections were of fairly recent origin and result from a "single" massive exposure during the summer of 1963/64, and that transmission of *S. hippopotami* in the Letaba River ceased sometime after 1964. This is supported by the negative observations since 1977, the dead-end nature of all the early findings and the lack of any additional definitive host species.

It is likely therefore that the *S. hippopotami* infections in the Kruger National Park were aberrant and acute.

McCully *et al.* (1967) attributed the dwarfed appearance of adult schistosomes in the old hippopotami to the suppressive action of immune bodies, presumably over the years. However, it has long been known that adult schistosome prosperity depends directly on the nutritional prosperity of the definitive host (De Witt, 1957a; De Meillon & Paterson, 1958). In addition, nutritionally deficient definitive hosts may be more susceptible to schistosomes and carry greater worm burdens, but at the same time the schistosomes lay fewer eggs, are severely stunted and many are sexually immature (De Witt, 1957b). The most prosperous members of a population under nutritional stress (drought) are those members which feed wholly or in part from "the backs of their mothers" and from these one would expect to recover the healthiest schistosomes. In fact, the whole bizarre presentation of so-called *S. hippopotami* in Uganda and South Africa might be explained by the effects of the diet and metabolism of *H. amphibius*. It is suggested, therefore, that *S. hippopotami* Thurston, 1963 be classified as synonymous with *S. mansoni* Sambon, 1907.*

* Since going to press, adults only of *S. hippopotami* have been recovered from hippopotami culled in the Engelhard Dam in the Kruger National Park. The results of electrophoretic analysis show isoenzyme patterns which closely resemble those of *S. mansoni* (Fripp, unpublished observations, 1981)

(b) *S. edwardiense*

The negative results from the waterbuck, kudu, buffalo and baboon and laboratory exposed rodents suggest that *S. edwardiense* is not a schistosome harboured by antelopes, bovines, primates and rodents. In support of this conclusion, no mention has ever been made of a schistosome adult remotely resembling *S. edwardiense* by Le Roux (1931, 1938, 1957), Dinnik & Dinnik (1965), Graber (1969, 1975) and Pitchford (1977) from material from antelopes and other game, cattle and other stock throughout Africa. Nocturnal shedding of cercariae might preclude infection in the baboons.

Since adjacent endemic and non-endemic schistosome areas are common amongst schistosome species, the absence of *S. edwardiense* from the Letaba River is not particularly surprising.

It appears from the present investigations that *S. edwardiense* is definitive host specific to *H. amphibius* and that the intermediate host is probably *Biomphalaria* species. The intermediate hosts of the schistosome with terminal spined eggs which were found in the hippopotamus faeces would be unlikely to be *Biomphalaria* species and the small numbers of these eggs suggest that the adults were not those identified as *S. edwardiense*.

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