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NON-HUMAN VERTEBRATE HOSTS OF *SCHISTOSOMA HAEMATOBIUM* AND *SCHISTOSOMA MANSONI*

A. VIANNA MARTINS

Ministerio da Saude, Departamento Nacional de Endemias Rurais, Brazil

SYNOPSIS

The author reviews the results of experimental infections of various species of mammals, other than man, with *S. haematobium* and *S. mansoni*, and discusses investigations in Africa and Brazil into the possibility of the natural infection of non-human vertebrates with these two parasites. Only a few species, besides monkeys, could be easily infected with *S. haematobium* in the laboratory, while—outside man—natural infection with this parasite appears to be practically non-existent. On the other hand, many animals are good experimental hosts for *S. mansoni*, and at least 21 species of mammals have been found infected with this parasite in Africa and America. It is thus possible to state, provisionally, that man is the only reservoir of *S. haematobium*, but the question still remains open where *S. mansoni* is concerned. Further research is suggested in order to assess the importance of non-human reservoirs in the epidemiology of bilharziasis.

Introduction

Not only domestic animals—oxen, pigs, dogs, cats, sheep, goats, horses, carabaos (water buffaloes)—but also various species of rodents (*Microtus montebelloi*, *Apodemus speciosus*, *Mus molisimus*, etc.) have long been known as reservoirs of great epidemiological importance for *Schistosoma japonicum*, one of the three principal species of the schistosome parasites of man.

As for the other two species, *S. haematobium* and *S. mansoni*, it was believed until recently that man was their only definitive epidemiologically important host.

In 1868, Cobbold apparently found, in Africa, the mangabey " *Cercopithecus fuliginosus* " spontaneously infected with *S. haematobium*; and Cameron, in 1928, proved the existence, in the island of St Kitts, British West Indies, of specimens of the imported African monkey " *Cercopithecus sabaeus* " naturally harbouring *S. mansoni*.

These observations, however, did not arouse great interest and, in 1949, Mackie, Hunter & Worth could still affirm: " Man serves as the principal host for both *S. haematobium* and *S. mansoni.* Although monkeys have been found to be naturally infected with both species, it is believed that they do not play an important role as reservoir hosts."

Recent works, however, show that some non-human hosts may play an important role in the dissemination of these two parasites, and especially of *S. mansoni.*

It is the aim of the present report: firstly, to study the results of experimental infection in various species of mammals; secondly, to review the reports from Africa and America which indicate that numerous species —chiefly rodents—are naturally infected with *S. mansoni*; and, thirdly, to discuss the importance of these findings and stimulate further investigations which seem to be indispensable for the elucidation of this important aspect of bilharziasis epidemiology. We shall consider exclusively the species *haematobium* and *mansoni*, leaving aside the other species of the so-called *haematobium* complex: *S. bovis*, *S. intercalatum*, *S. mattheei*, *S. capense*, whose infectivity for man is doubtful or whose taxonomic status is questionable, as well as *S. rhodaini*, undoubtedly closely related to *S. mansoni*, but still considered as a parasite only of rodents (Schwetz & Stijns, 1951; Schwetz, 1954) and dogs (Deramee et al., 1953).

Laboratory Infection

Certain species of mammals are easily infected, in the laboratory, with *S. haematobium* and *S. mansoni*; others are less susceptible to the infection, while a few are resistant to it.

The verification of the susceptibility of different mammals to schistosomes is desirable for two reasons: to permit an evaluation of their utility as experimental hosts in the laboratory, and above all, to determine the possibility of their becoming important factors in the dissemination of the parasites, particularly if they are common species in the different endemic areas. It must be borne in mind, however, that a species that readily acquires an experimental infection does not always possess the natural, ecological, ethological or other factors which would make it an efficient reservoir in nature.

A good example of this was given by Kuntz & Malakatis (1955b) who, having demonstrated that the Nile rat (*Arvicanthis niloticus*) was an entirely satisfactory experimental host, were not able to find a single infected specimen in a total of about 100 captured on the banks of canals, in places where the prevalence of *S. mansoni* in the human population was very high.

Susceptibility to infection with S. haematobium

Only a few species of mammals, besides man, are really sensitive to *S. haematobium.*

This problem has not received much attention from research workers, perhaps because of the little success achieved " in previous incidental researches " (Kuntz, 1955). We shall now examine the results obtained to date, according to the orders of mammals investigated.

Primates. Some African primates are good experimental hosts for *S. haematobium.* Archibald & Marshall (1932a) were able to infect two monkeys (*Cercopithecus sabaeus*), obtaining adult worms in the mesenteric and portal veins and eggs with terminal spine in the intestinal mucosa. Stunkard (1946) infected the baboon (*Papio* sp.). Kuntz & Malakatis (1955a) obtained good results with five monkeys (*Cercopithecus* sp.) and seven baboons (*Papio hamadryas*), although the majority of the adult worms were lodged in the mesenteric veins and only a few of them (3-4%) attained the vesical plexus. Newsome (1956), working on *Papio hamadryas*, also obtained infections, which did not, however, last for more than six months.

The rhesus monkey (*Macaca mulatta*) of Asiatic origin was used by Meleney & Moore (1954), who obtained infections that lasted for a few months. The same monkey was employed by Standen (1949), who obtained one positive result in three, all the worms being localized in the mesenteric veins or in the intra-hepatic portal system. One related species, *Macaca irus* (= *Cynomolgus*) was infected by Brumpt in 1928.

Insectivora. In 1928 Brumpt was able to infect the hedgehog *Erinaceus europaeus*, which he considered extremely receptive, although he obtained only intestinal lesions. One African insectivore (*Hemiechinus auritus aegyptius*) was used, with positive results, by Abdel Azim & Cowper (1950), who obtained eggs in the faeces, and by Kuntz & Malakatis (see Kuntz, 1955).

Rodentia. Many rodents have been successfully infected with *S. haematobium.* Amongst the species generally used in laboratories, the most sensitive are the albino mouse and the golden hamster. The albino mouse (*Mus musculus domesticus*) was used with success by Leiper (1915), Bettencourt & Borges (1922), Brumpt (1928a), Brumpt & Chevalier (1931), Standen (1949), Gillet (1949), and chiefly by Moore & Meleney (1954) and Kuntz & Malakatis (1955a), who obtained 100% positive results, with viable eggs in the faeces. Amberson & Schwarz (1953), however, did not obtain viable eggs in the faeces and Abdel Azim & Cowper (1950), working with an Egyptian stock of *S. haematobium*, failed to get positive results.

The golden Syrian hamster (*Mesocricetus auratus auratus*), used with good results by Standen (1949) and Amberson & Schwarz (1953), is consi-

dered by Moore & Meleney (1954) and Kuntz & Malakatis (1955a) as " the best all around host ". These authors observed the presence of adult worms not only in the veins of the portal system, but also in those of the vesical plexus—a finding not reported in the case of the mouse.

The guinea-pig (*Cavia porcellus*) shows little susceptibility to infection with *S. haematobium*; Brumpt (1928a), Blackie (1932), Gillet (1949), Amberson & Schwarz (1953) were unable to infect it. Becker (1916), Cawston (1921), Blacklock & Thompson (1924), Kuntz & Malakatis (1955a) met with only relative success, and Moore & Meleney (1954) were able to infect only 2 out of 14 guinea-pigs.

The albino rat (*Rattus norvegicus*), whose susceptibility is as low as that of the guinea-pig, was infected by Leiper (1918) and Brumpt (1928a), who obtained one positive result in 8 animals. Moore & Meleney (1954) and Kuntz & Malakatis (1955a) also got results that were scarcely encouraging.

The cotton rat (*Sigmodon hispidus hispidus*) is a poor host (Kuntz & Malakatis, 1955a). Some African wild rodents have already been experimentally infected. Stunkard (1946) makes reference to two " fat-tailed gerboas " (*Pachyuromys duprasi*) infected with *S. haematobium* in Africa by Dr Barlow, of which one at least " passed eggs in the faeces ", although the eggs were non-viable. Abdel Azim & Cowper (1950) got positive results with the " gerbil " (*Gerbillus* sp.), but with no eggs in the faeces. Finally Kuntz & Malakatis (see Kuntz, 1955) infected with *S. haematobium* the same species of African rodents they had infected with *S. mansoni*: the Nile rat (*Arvicanthis niloticus*), the spiny-backed mouse (*Acomys cahirinus*), the bandicoot (*Nesokia indica suilla*), several desert rodents (*Gerbillus pyramidum, Jaculus jaculus, Meriones shawi shawi*) and domestic murines (*Mus musculus praetextus* and *Rattus rattus*).

Lagomorpha. The rabbit (*Oryctolagus cuniculus*) seems to be totally resistant to *S. haematobium*. Brumpt (1928a), Amberson & Schwarz (1953), Moore & Meleney (1954) and Kuntz & Malakatis (1955a) failed in their efforts to infect this species, Blackie (1932) being the only author to mention positive results in this connexion.

Artiodactyla. Kuntz & Malakatis (1955a) exposed three goats (*Capra hircus*) to about 2000-5000 cercariae each, and succeeded in infecting two of them; however, the number of parasites recovered was extremely small. Leiper (1915), MacHattie & Chadwick (1932) and MacHattie, Mills & Chadwick (1933) were unable to infect sheep (*Ovies aries aries*).

Carnivora. Whilst Brumpt (1928a) was unable to infect five cats (*Felis cattus*), Kuntz & Malakatis (1955a) obtained two positive results in seven attempts to infect this species, all the worms being lodged in the liver.

According to Kuntz & Malakatis (1955a), seven dogs exposed to 4000-12 000 cercariae proved completely resistant.

Susceptibility to infection with S. mansoni

In general, much better results in the experimental infection of animals have been obtained with *S. mansoni* than with *S. haematobium*. In fact it may be said that relatively very few species are totally resistant to *S. mansoni*, whereas, with *S. haematobium*, the opposite is the case.

Primates. All species of primates—whether African, Asiatic or American—on which experimental infection has been attempted have been easily infected with *S. mansoni*. Archibald & Marshall (1932b) in Sudan, and Blackie (1932) in Southern Rhodesia, succeeded in infecting the monkeys *Cercopithecus aethiops sabaeus* and *Cercopithecus aethiops cynosurus* (=*pygerythrus*) respectively. Kuntz, Malakatis & Wells (1953), using several monkeys (*Cercopithecus* sp.), which were exposed to 1000-3000 cercariae, obtained large numbers (800 to 2100) of adult schistosomes.

The baboon, *Papio ursinus griseipes*, was infected by Le Roux (1939) and a related species, *Papio hamadryas*, retained an infection with *S. mansoni* for years (Newsome, 1956).

Stunkard (1946) and Standen (1949) infected rhesus monkeys (*Macaca mulatta*), obtaining viable eggs in the faeces over several months, and similar results were obtained with another species, *Macaca mordax*, by Stunkard (1946) and Meleney & Moore (1954). Amberson & Schwarz, in Venezuela, infected both the local capuchin monkey (*Cebus capucinus apella*) and the Amazonian subspecies (*C. capucinus albifrons*). Coelho & Magalhães (1953), in Pernambuco, Brazil, obtained very strong infections in monkeys (*Cebus* sp.).

Insectivora. Kuntz & Malakatis (1955b) obtained slight infections in the Egyptian hedgehog (*Hemiechinus auritus aegyptius*), with only limited quantities of eggs, mainly non-viable, in the liver and intestines.

Rodentia. The albino mouse (*Mus musculus domesticus*) is extremely susceptible to *S. mansoni* (Brumpt & Chevalier, 1931; Stunkard, 1946; Abdel Azim & Watson, 1948; Standen, 1949; Moore, Yolles & Meleney, 1949; Stirewalt, Kuntz & Evans, 1951; Kuntz, Malakatis & Wells, 1953). In general, 100% infection is obtained with an over-all return of worms of about 20%. Viable ova are always present in large numbers in the walls of the small intestine.

The albino mouse is probably the animal of choice for experimental work with *S. mansoni*. The Egyptian house-mouse (*Mus musculus praetextus*) was infected by Kuntz & Malakatis (1955b).

The Syrian hamster is also very susceptible to experimental infection by *S. mansoni*, passing mature eggs in the faeces (Stunkard, 1946; Moore, Yolles & Meleney, 1949; Yolles, Moore & Meleney, 1949; Buttner, 1953; Amberson & Schwarz, 1953) and showing a return of adult worms greater than that from any other experimental animal (Standen, 1949; Kuntz, Malakatis & Wells, 1953).

The guinea-pig (*Cavia porcellus*) is susceptible (Stunkard, 1946; Amberson & Schwarz, 1953; Buttner, 1953), but much less so than the albino mouse and the hamster. Very often no eggs are passed in the faeces (Standen, 1949; Moore, Yolles & Meleney, 1949), and the parasite return is usually low (Stirewalt, Kuntz & Evans, 1951; Kuntz, Malakatis & Wells, 1953).

The albino rat (*Rattus norvegicus*) is a poor host, no viable eggs being found in the faeces (Stunkard, 1946; Moore, Yolles & Meleney, 1949; Kuntz, Malakatis & Wells, 1953). Lagrange & Scheecqmans (1951) had no positive results among 100 rats exposed to 100 cercariae each. Buttner (1953) infected the brown rat (*Rattus norvegicus*), Amorim (1953) the white-bellied rat (*Rattus rattus frugivorus*), and Kuntz & Malakatis (1955b) and Schwetz (1955b) the house-rat (*Rattus rattus*).

The cotton rat (*Sigmodon hispidus hispidus*) is a good host, being able to withstand quite a heavy parasite load (Stirewalt, Kuntz & Evans, 1951; Lagrange & Scheecqmans, 1951; Kuntz, Malakatis & Wells, 1953).

Many species of wild rodents from Africa, America and Europe have been successfully infected with *S. mansoni*. Most of the species of rodents common to Lower Egypt are susceptible (Kuntz & Malakatis, 1955b): the Nile rat (*Arvicanthis niloticus*), the spiny-backed mouse (*Acomys cahirinus*), the common desert-mouse (*Gerbillus pyramidum*), the desert jumping-mouse (*Jaculus jaculus*), the jird (*Meriones shawi shawi*) and the Egyptian bandicoot (*Nesokia indica suilla*). The Nile rat (*Arvicanthis niloticus*) is considered one of the best hosts for *S. mansoni* infection, since it harbours a good number of well-developed parasites, which produce an abundance of eggs. Two-and-a-half years after the infection the hosts still maintain a fair proportion of their parasite load (8.8%) and viable eggs continue to be passed with the faeces until death.

Buttner (1953) infected *Meriones lybicus* and Schwetz (1955b) *Rattus* (*Mastomys*) *coucha*, both of African origin.

Tavares da Silva (1945) obtained positive results with *Cavia aperea*, a species closely related to the guinea-pig; Amorim (1953) with *Cercomys cunicularius inermis;* Ruiz (1953a) with *Cuniculus pacca pacca* and Price (1953) with *Dasyprocta aguti*, all of them South American species. Pinto & Almeida (1948), however, failed to infect the capybara (*Hydrochoerus hydrochoerus*), the largest of the rodents of Brazil.

Moore & Meleney (1952) demonstrated the susceptibility to *S. mansoni* of the North American rice-rats (*Oryzomys palustris palustris* and *O. p. natator*).

Buttner (1953) infected five species of European rodents (*Apodemus sylvaticus*, *Citellus citellus*, *Eliomys quercinus*, *Evotomys glareolus* and *Glis glis*) with one or more strains of *S. mansoni*.

Lagomorpha. The rabbit (*Oryctolagus cuniculus*) is not a good host for *S. mansoni* (Stunkard 1946; Moore, Yolles & Meleney, 1949; Yolles, Moore & Meleney, 1949; Kuntz, Malakatis & Wells, 1953), since, although it can be infected, the worm return is low and ordinarily no viable eggs are found in the faeces. Abdel Azim & Cowper (1950) and Buttner (1953) failed in their attempts to infect rabbits.

Xenarthra. Pinto (1944) successfully infected a hairy armadillo (*Euphractus sexcinctus*), which passed eggs in the faeces for 41 days.

Artiodactyla. The cloven-hoofed mammals show very little susceptibility to *S. mansoni*. Pinto & Almeida (1948) failed to infect a calf (*Bostaurus*) and a Brazilian deer (*Mazama americana*). Although Pinto (1944) did not succeed in infecting it, the pig (*Sus scrofa*) is slightly susceptible (Riggin & Berrios, 1956). Goats (*Capra hircus*) are not satisfactory hosts, the yield of adult parasites being very small (Kuntz, Malakatis & Wells, 1953) and the susceptibility of sheep (*Ovis aries aries*) is individually very variable (A. V. Martins, unpublished data).

Carnivora. The dog (*Canis familiaris*) was considered resistant by Cram & Files (1947) and Stirewalt, Kuntz & Evans (1951), but was infected by Kuntz, Malakatis & Wells (1953) and Pinto & Almeida (1948), who state that puppies are easily infected, passing viable eggs with the faeces about 80 days after the penetration of cercariae.

The cat (*Felis cattus*) has been considered a fairly good host by Faust, Jones & Hoffman (1934) and Stirewalt, Kuntz & Evans (1951), but it seems actually to be a rather poor one, since the yield of adult worms is small and no eggs are recovered from the faeces (Stunkard, 1946; Le Roux, 1950; Kuntz, Malakatis & Wells, 1953).

A few wild carnivores (*Procyon cancrivorus*, *Nasua narica* and *Grison furax*) have been successfully infected in Brazil by Ruiz (1952, 1953a, 1953b), viable eggs being passed in the faeces. A "fox" (*Cerdocyon thous azarae*) was, however, resistant. In Egypt, Kuntz & Malakatis (1955b) showed that the weasel (*Mustela nivalis subpalmata*) and the mongoose (*Herpestes ichneumon ichneumon*) have only slight susceptibility, while the fox (*Vulpes vulpes aegyptiaca*) is totally non-susceptible.

Marsupialia. Two opossums, *Didelphis aurita* and *D. paraguayensis*, have been infected in Brazil with *S. mansoni* (Travassos, 1953; Ruiz, 1953b).

Natural Infection

The search for animals naturally infected with *S. haematobium* and *S. mansoni* is of the utmost importance, since such animals can represent reservoir hosts of great epidemiological significance. Our knowledge in this field of investigation has been greatly increased in the last few years as a result of researches in Africa and Brazil.

Natural infection with S. haematobium

The only record of a mammal, besides man, found naturally infected with *S. haematobium* is that of a mangabey "*Cercopithecus fuliginosus*" (*Cercocebus torquatus atys*), described by Cobbold in 1868. This case is, however, doubtful, since at that early date no other species of the *haematobium* complex were known, and so a misinterpretation was quite possible. It should be noted, however, that many African primates are susceptible to *S. haematobium*, as we have seen.

No rodents have ever been found to be naturally infected with *S. haematobium*, although Schwetz (1956) examined a total of 249 wild and domestic rats, representing eight species, in the *S. haematobium* focus of Kongolo, Belgian Congo. MacHattie & Chadwick (1932), examining sheep from a region in which the rate of urinary bilharziasis was over 80%, could not find typical specimens of *S. haematobium*.

Natural infection with S. mansoni

Many species of mammals, belonging to four different orders, are now recognised as natural hosts of *S. mansoni*.

Primates. Cameron (1928) found that, in the small island of St Kitts, British West Indies, the imported African green monkey, *Cercopithecus sabaeus*, was naturally infected with *S. mansoni*.

Porter (1938), in South Africa, observed that in the faeces of the monkey *Cercopithecus aethiops cynosurus* (*Cercopithecus pygerithrus*) there were eggs which seemed to be from *S. mansoni*, and concluded: "Such possible sources of molluscan infection as naturally infected monkeys need to be borne in mind."

Insectivora. The insectivore, *Crocidura luna*, was found naturally infected in the Belgian Congo by Stijns (1952), and in Egypt examinations made by Kuntz & Wells (see Kuntz, 1955) revealed a number of infected shrews of the same genus from the banks of irrigation canals near Cairo.

Rodentia. Kuntz (1952) was the first to record the natural infection with *S. mansoni* of a rodent—the Egyptian gerbil or common desert-mouse, *Gerbillus pyramidum*. Schwetz (1953, 1954) discovered, in wild rodents

from the Albertville area of the Belgian Congo, a schistosome which he described as a new variety and named *Schistosoma mansoni* var. *rodentorum*. The infected rodents belonged to five different species: *Mastomys coucha*, *Pelomys fallax*, *Oenomys hypoxanthus*, *Dasymys bentleyae* and *Lophuromys aquila*. The same author (Schwetz, 1955a), examining 122 specimens of *Rattus rattus* caught at Albertville, found two (1.6%) infected with typical *S. mansoni*.

Amorim (1953) and Amorim, Rosa & Lucena (1954) reported the occurrence in the State of Alagoas, north-eastern Brazil, of five species of wild rodents naturally infected: *Nectomys squamipes* (45.31% infected), *Holochilus sciureus* (25.0%), *Oxymycterus angularis* (11.11%), *Zigodontomys pixuna* (1.78%) and *Oryzomys subflavus* (1.03%).

Barbosa, Dobbin & Coelho (1953), examining 27 specimens of the white-bellied rat (*Rattus rattus frugivorus*) in the State of Pernambuco, which is also in the north-eastern region of Brazil, found 16 (59%) infected with *S. mansoni*, with characteristic eggs in the faeces.

Martins, Martins & Brito (1955), searching for natural reservoirs of *S. mansoni* in two different areas of the State of Minas Gerais (eastern Brazil), including its capital (Belo Horizonte), found six different species of infected rodents: *Oryzomys mattogrossae* (100%), *Nectomys squamipes aquaticus* (57.5%), *Rattus norvegicus norvegicus* (46.8%), *Cavia aperea aperea* (33.3%), *Oryzomys subflavus* (12.0%) and *Zygodontomys lasiurus* (2.7%).

Marsupialia. Travassos (1953), in the State of Bahia, Brazil, found the opossum *Didelphis aurita* infected; Martins, Martins & Brito (1954, 1955) and Barbosa & Coelho (1954) found the related species *Didelphis paraguayensis* also infected, in the States of Minas Gerais and Pernambuco respectively.

Comments

Differences in susceptibility to S. haematobium *and* S. mansoni.

It seems quite clear that *S. haematobium* has a much more strict host specificity than *S. mansoni*. Only a few mammals, besides monkeys, can be easily infected with it and even in these the location of the adult worms is almost always abnormal, i.e., in the veins of the portal system and not in those of the vesical plexus, where they are found in the normal host, namely, man. The passing of viable eggs in the faeces occurs very seldom, and in urine the presence of viable eggs is of the utmost rarity. For this reason, the maintenance of the *haematobium* cycle in the laboratory is very difficult. If the infection of animals under ideal laboratory conditions is by no means easy, it is not surprising that natural infection is practically non-existent.

On the contrary, many animals are good experimental hosts for *S. mansoni*, so that the worms attain sexual maturity in normal locations, i.e., in the veins of the portal system, and an abundance of viable eggs pass in the faeces. At least 21 species of mammals, belonging to four different orders (Primates, Insectivora, Rodentia and Marsupialia) have been found infected in Africa and America, and this number tends to increase as the work progresses.

Thus, while it is possible, on the basis of the data now available, provisionally to accept as valid the statement that man is the only reservoir of *S. haematobium*, the question remains open with regard to *S. mansoni*.

Prevalence of S. mansoni *in African and Brazilian rodents*

Another point which needs further comment is the marked difference in the prevalence of *S. mansoni* infection in the rodent populations of Africa and Brazil.

Schwetz (1956) states that " it seems that natural infections of rodents with *S. mansoni* var. *rodentorum* are very rare, the existing cases being localized " and calls the attention to the strange fact that " in spite of the extreme receptibility of rats to experimental bilharziasis there are so few naturally infected rats... particularly in comparison with those infected with *S. rodhaini* ". In fact, Schwetz (1954) found only 18 specimens (3.7%) infected with the so-called *S. mansoni* var. *rodentorum* in 480 wild rats examined. It is easily seen that this infection rate is quite different from that of rodents in the *S. rodhaini* foci—namely, 23.6%. In house-rats (*Rattus rattus*), natural infection with *S. mansoni* is also rare; in 122 rats examined at Albertville, only two were infected (1.6%) (Schwetz, 1955a).

In Brazil, on the contrary, natural infection of rodents, wild or domestic, with *S. mansoni* seems rather common in all the foci of bilharziasis that have been studied. In north-eastern Brazil, Amorim, Rosa & Lucena (1953) found 8.54% of rodents infected in 674 examined, and Barbosa, Dobbin & Coelho (1953) found a 59% infection rate in *Rattus rattus frugivorus*. In eastern Brazil, Martins, Martins & Brito (1955) also observed a high rate (28.7%) in 160 rodents examined.

The reasons for this difference are not clear, but it seems that the problem of non-human reservoirs of *S. mansoni* will be much more important in America than in Africa.

Taxonomic status of S. mansoni *var.* rodentorum

The taxonomic status of the schistosome found in rodents is not completely settled. Although the adults of the schistosome found in wild rats in Albertville were identical with those of *S. mansoni*, Schwetz (1953) considered it as a new variety, *S. mansoni* var. *rodentorum*, in view of the

slight differences in the shape of the eggs. The eggs he found in domestic rats (*Rattus rattus*), were, however, typical of *S. mansoni* (Schwetz, 1955a).

All Brazilian workers agree that the schistosome found in Brazilian rodents (as well as in opossums) is typical *S. mansoni*, which is the only species of the genus *Schistosoma* found in the Western Hemisphere.

The microphotographs of eggs presented by Schwetz (1953, 1954) are far from convincing, since many of the eggs in question are quite similar to those of *S. mansoni*, which, we must remember, present some degree of variation.

Le Roux (1954), however, observed that the eggs of hybrids between *S. mansoni* and *S. rodhaini* bear a close resemblance to the eggs of *S. mansoni* var. *rodentorum*. Since Schwetz (1956) " could find rats infected with *S. mansoni* var. *rodentorum* only in the mixed foci of *S. mansoni* and *S. rodhaini* ", it seems possible that the schistosome from African rodents is actually a hybrid one.

Relationship between S. mansoni, S. mansoni *var.* rodentorum *and* S. rodhaini

Schwetz (1954) believes that rodents were the primitive hosts of a schistosome (*S. mansoni* var. *rodentorum*) which afterwards adapted itself to man and, " changing slowly morphologically, finally became *S. mansoni*, the typical schistosome of man". This would explain the difference between bilharziasis of rodents, which is chronic and seems to be of low virulence, and human bilharziasis, which is more acute and more virulent.

In Brazil, bilharziasis was undoubtedly imported with the African slaves and therefore man was the primitive host of *S. mansoni*, which afterwards adapted itself to rodents without morphological changes as yet.

It can perhaps be admitted that *S. rodhaini* is *S. mansoni* fully adapted to rodents—or, *vice versa*, that *S. mansoni* is *S. rodhaini* fully adapted to man—and that *S. mansoni* var. *rodentorum* is an occasional hybrid between the two species. This would explain why, in Africa, the prevalence of *S. mansoni* is very high in man and very low in rodents, while the prevalence of *S. rodhaini* is very high in rodents and almost non-existent in man, although in Brazil, where *S. rodhaini* is not found and *S. mansoni* was recently introduced, there is a marked parallelism between the prevalence of *S. mansoni* in human beings and rodents.

Suggestions

To ascertain the real importance of non-human reservoirs in the epidemiology of bilharziasis it seems to be necessary:

1. To determine the relative susceptibility of the most common mammals in the different endemic areas to the species of schistosomes prevalent in

these areas. For this it is advisable to expose the animals to counted numbers of cercariae and to sacrifice them at various intervals in order to estimate:

(*a*) the number of animals infected or non-infected;

(*b*) the number of worms recovered at autopsies, their sex, stage of sexual maturity, dimensions and location in the body of the host;

(*c*) the presence of viable and non-viable eggs in the organs, faeces and urine;

(*d*) the duration of infection.

2. To examine the greatest possible number of wild mammals, chiefly rodents, from the different endemic areas, determining, in the specimens found infected, the number of worms, their sex, location and presence of eggs in the organs, faeces and urine.

3. To infect snails with miracidia from eggs recovered from naturally infected animals, and to infect laboratory and wild animals with cercariae from these snails in order to study the biological characteristics of the animal strains.

4. To determine whether animal reservoirs alone are able to maintain the infection of snails in the absence of infected men. This can perhaps be done in small localities where there are fair numbers of naturally infected animals by treating all infected persons and providing for careful disposal of human excreta.

5. To determine whether man is susceptible to animal strains by using human volunteers. The ethical and practical problems involved in such an investigation should, however, be borne in mind.

RÉSUMÉ

On sait depuis longtemps que des animaux domestiques et diverses espèces de rongeurs constituent des réservoirs, épidémiologiquement très importants, de *Schistosoma japonicum*, une des trois principales espèces de schistosomes parasites de l'homme. En ce qui concerne les deux autres espèces, *S. haematobium* et *S. mansoni*, on pensait jusqu'à une date récente que l'homme était leur seul hôte important du point de vue épidémiologique. Or, il vient d'être établi que certains hôtes autres que l'homme peuvent jouer un rôle non négligeable dans la dissémination de ces deux parasites, en particulier de *S. mansoni*.

L'auteur de l'article passe en revue les résultats de l'infection expérimentale de diverses espèces de mammifères autres que l'homme par *S. haematobium* et *S. mansoni* et discute les recherches qui ont été faites en Afrique et au Brésil sur les possibilités d'infection naturelle de vertébrés non humains par les deux parasites. En dehors des singes, il n'y a qu'un petit nombre d'espèces qu'il est facile d'infecter par *S. haematobium* au laboratoire, et même alors la localisation des vers adultes est presque toujours anormale, puisqu'elle intéresse les veines du système porte et non celles du plexus vésical où on les trouve chez l'homme. Le passage d'œufs viables dans les fèces ne se produit que très peu souvent et la présence d'œufs viables dans l'urine est extrêmement rare. Mis à part l'homme, l'infection naturelle par ce parasite ne semble pratiquement jamais se produire.

En revanche, de nombreux animaux sont de bons hôtes expérimentaux de *S. mansoni*, car les vers y atteignent leur maturité sexuelle dans les localisations normales, c'est-à-dire dans les veines du système porte, et des œufs viables passent dans les fèces. De plus, l'infection naturelle par *S. mansoni* a été constatée en Afrique et en Amérique sur au moins 21 espèces de mammifères appartenant à quatre ordres différents (primates, insectivores, rongeurs et marsupiaux). On peut donc affirmer provisoirement que l'homme est le seul réservoir de *S. haematobium*, mais que le problème reste entier en ce qui concerne *S. mansoni*. De nouvelles recherches seront nécessaires pour qu'on puisse établir l'importance réelle des réservoirs non humains dans l'épidémiologie de la bilharziose.

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