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REVIEW ARTICLE

Schistosomes causing cercarial dermatitis: a mini-review of current trends in systematics and of host specificity and pathogenicity

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Abstract. The human infection known under the names cercarial dermatitis or swimmers' itch is generally associated with swimming in lakes all over the world, however, a number of outbreaks of cercarial dermatitis developing in salt or brackish waters are also reported. The disease presents as allergic reaction which is able to trap and eliminate the parasites in the skin. However, the infection can be linked to more than skin symptoms under certain circumstances. Recent studies on bird schistosomes have shown that during primary infections of noncompatible hosts (mice) the parasites may migrate through visceral and nervous tissues of mammals. Up to date, cercarial dermatitis has been mostly associated with the cercariae of bird schistosomes of the genus *Trichobilharzia*. Recent findings of new genera and species indicate, however, broader spectrum of causative agents of the disease with different life cycles, host specificity and pathogenicity.

Cercarial dermatitis is a common non-communicable water-borne disease which has been recently regarded as an emerging infection (de Gentile et al. 1996). Clinical symptoms of cercarial dermatitis were firstly reported by Fujii in 1887 (cited by Oda 1973) and the causative agents, schistosome larvae (cercariae), were identified by Cort in 1928 in the USA. Shortly thereafter, the agents of the disease were reported from the United Kingdom (Matheson 1930) and France (Brumpt 1931). Since then the infection has been described in many countries under different names, the most common of which is swimmers' itch, used for the first time by Christensen and Green (1928).

The disease presents as a strong maculo-papulovesicular skin eruption accompanied by intensive itching which develops as a consequence of repeated infections by the parasites in natural waters (for review see Horák et al. 2002). Usually, cercarial dermatitis is related to human infections; however, the skin syndromes also develop in various animals, including rabbits and dogs (Herber 1938, Augustine and Weller 1949, Olivier 1953).

Initially, the disease was associated with infection by cercariae of bird schistosomes (Cort 1928). However, as recognized later, larval stages of other genera and species of the family Schistosomatidae are also able to invoke cercarial dermatitis. Nevertheless, to date, the most frequently reported causative agents of the infection are cercariae of bird schistosomes, larval development of which takes place in freshwater bodies (Horák et al. 2002).

OCCURRENCE OF CERCARIAL DERMATITIS

The occurrence of the disease depends on conditions that favour parasite transmission; i.e., a complex of interactions among the parasites and their specific intermediate (water snails) and definitive hosts (birds and mammals, including man) is required at the same place. The intermediate hosts of various animal and human schistosomes may co-occur in a particular water body, and some data suggest that larval stages of different genera can also develop in the same snail species (Nassi 1987). Under certain circumstances, therefore, man can be infected simultaneously by schistosome cercariae of different genera and species by swimming in a particular water body.

Larval development of the majority of schistosome species takes place in freshwater snails (Table 1) and this is why cercarial dermatitis is generally associated with swimming in lakes or ponds all over the world where cercariae of bird schistosomes are usually reported as the causative agent of the disease (Horák et al. 2002). Nevertheless, a number of outbreaks of the disease developing after swimming in salt or brackish waters have also been reported. To date, cercariae of the avian genera *Austrobilharzia* Johnston, 1917 and *Gigantobilharzia* Odhner, 1910 have been identified as the causative agents of the disease in New England, California, British Columbia, Australia, Germany, Japan (Komiya and Ito 1952, Grodhaus and Keh 1958, Dönges

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Table 1. Overview of schistosome genera the larval stages of which are able to cause cercarial dermatitis in fresh, salt or brackish waters.

Genus	Distribution	Intermediate host	Definitive host
FRESH WATERS			
Bivitellobilharzia Vogel et Minning, 1940	India, Africa?	Unknown	Elephants
Heterobilharzia Price, 1929	North America	Pulmonata	Carnivores, rodents
Macrobilharzia Travassos, 1922	Cosmopolitan	Unknown	Birds
Orientobilharzia * Dutt et Srivastava, 1955	Asia	Pulmonata	Subungulates, carnivores
Schistosoma * Weinland,1858	Cosmopolitan	Pulmonata, Prosobranchia	Mammals, including man
Schistosomatium Tanabe, 1923	North America	Pulmonata	Rodents
Bilharziella * Looss, 1899	Northern Hemisphere	Pulmonata	Birds
Trichobilharzia * Skrjabin et Zakharow, 1920	Cosmopolitan	Pulmonata	Birds
Jilinobilharzia Liu et Bai, 1976	Asia	Pulmonata	Birds
Dendritobilharzia Skrjabin et Zakharow, 1920	Cosmopolitan	Unknown	Birds
SALT OR BRAKISH WATERS			
Austrobilharzia * Johnston, 1917	Cosmopolitan	Prosobranchia	Birds
Ornithobilharzia Odhner, 1912	Northern Hemisphere	Prosobranchia	Birds
Gigantobilharzia * Odhner, 1910	Cosmopolitan	Pulmonata, Opisthobranchia	Birds
UNKNOWN			
Allobilharzia Kolářová, Rudolfová, Hampl et Skírnisson, 2006	Northern Hemisphere	Unknown	Birds

*Literary confirmed causative agents of human infections.

1964, Appleton and Lethbridge 1979, Matsumara et al. 1984, Barber and Caira 1995, Leighton et al. 2000), and also in Italy where *G. acotylea* Odhner, 1910 was, probably, a source of human dermatitis in the Venice Lagoon (Nobile et al. 1996). Despite the fact that bird schistosomes are the most frequently reported causative agents of swimmers' itch, cercariae of the mammalian genera (Table 1) are of similar importance. However, except for *Schistosoma* Weinland, 1858 (e.g., Davis 2003) and *Orientobilharzia* Dutt et Srivastava, 1955 (Sabha and Malek 1979), there are no data available to confirm this assumption.

In a temperate climate, cercarial dermatitis occurs seasonally, mainly during warmer months when both the release of cercariae from snail intermediate hosts and the number of people swimming in natural waters reach peak levels (Appleton and Lethbridge 1979). However, under certain circumstances, the infection can be acquired in a particular water body during the whole year. Skírnisson and Kolářová (2005) reported human cases of swimmers' itch during August and December 2003 as well as in late winter 2004 in a slowly streaming brook with geothermally heated groundwater in Landmannalaugar, the most frequently visited area in the interior of Iceland.

The identification of potential transmission sites for cercarial dermatitis is commonly based on the detection of schistosome cercariae in water snails collected in a particular water body. However, search for the parasites is complicated by the low infection rate, which usually does not exceed 5% (Loy and Haas 2001). As the cercariae are able to actively find and penetrate quickly into the skin of various vertebrates (Haas and Haberl 1997), even a low number of the infected snails present in a lake can lead to a relatively high risk of infection (Loy and Haas 2001). Due to low prevalence rates in snails, various methods of cercariometry (filtration, the use of phototactic response equipment and continuous flow centrifugation) have been developed to detect schistosomes in natural waters (Théron 1986). To monitor schistosome-infested waters, traps containing a matrix with unsaturated fatty acids, which stimulates the attachment and penetration of the cercariae, were also used for collecting and subsequent visualisation of cercariae of human as well as avian schistosomes (Schiff et al. 1993, Graczyk and Schiff 2000). Molecular methods can further increase the sensitivity of detection; for example, Hertel et al. (2002) were able to detect 100 fg of DNA of *Trichobilharzia ocellata* (La Valette, 1855), 1 cercaria in 0.5 g of plankton using PCR.

On the other hand, the transmission site can also be identified by examination of birds. Adult schistosomes are detected mostly in waterfowl and, therefore, it is suggested the disease is most often found along the major avian migratory flyways. The distribution of cercarial dermatitis in Europe and Africa is probably influenced by the Palaearctic-African bird migration (Horák et al. 2002). In North America, the dermatitis seems to be distributed along the Mississippi flyway and the Pacific distribution may follow the Nearctic-Hawaiian, Asiatic-Palauan and Japanese-Marian flyways (Jarcho and Burkalow 1952, Chu 1958).

Various studies showed that the prevalence in birds can be quite high compared with that in snails and often exceeds 50% (Horák et al. 2002, Kolářová et al. 2005). Most commonly, infections of birds by schistosomes are diagnosed through faecal examination which is, however, suitable for detection of visceral schistosomes only and fails to show the presence of nasal flukes, which are also common in waterfowl. Both visceral and nasal schistosomes can develop concurrently in a bird host (Kolářová et al. 2005).

Factors explaining the emergence of human infections by bird schistosomes are not fully understood. Allgöwer and Effelsberg (1991) suggest that high eutrophication of water reservoirs, colonisation of ponds by susceptible snails and by nesting ducks, combined with long periods of sunshine in the summer, are the most important factors that led to a recent increase in the number of outbreaks of cercarial dermatitis all around the world.

IDENTIFICATION OF THE CAUSATIVE AGENT OF THE DISEASE

The causative agent of cercarial dermatitis is usually determined by microscopical observation of larval stages isolated from water snails. Despite the fact that larval stages of various genera have been described as the causative agent of swimmers' itch (Table 1), the infection is mostly associated with cercariae of the genus *Trichobilharzia* Skrjabin et Zakharow, 1920, the life cycles of which include freshwater snails (families Lymnaeidae and Physidae) and birds (mainly waterfowl of the order Anseriformes) as intermediate and definitive hosts, respectively. According to the literature, the most common name used for the description of ocellate furcocercariae in Europe is *T. ocellata*, which was also reported from North America and Japan (Horák et al. 2002). However, the molecular studies of Rudolfová et al. (2005) showed that the identity of various *T. ocellata* isolates is questionable. Comparing the literary data, the authors found differences among various *T. ocellata* isolates that led them to the conclusion that North American and Japanese findings are not identical with the European *T. ocellata*. Moreover, the authors showed that the frequently reported *T. ocellata* isolates from Europe correspond to *Trichobilharzia szidati* Neuhaus, 1952.

The results of Rudolfová et al. (2005) demonstrated clearly that microscopical determination of material collected from naturally infected snails brings difficulties due to the fact that cercariae of different species closely resemble each other and cannot be identified to the species level. Identification of a particular genus/species of the cercariae, therefore, requires other data such as the isolation and characterisation of adult flukes from experimentally infected host, life-cycle data and DNA analysis of the samples (Horák et al. 2002).

Contrary to the cercariae, the morphology of adult stages is considered to be the most valuable characteristic for taxonomical determination of schistosomes (Horák et al. 2002). Recent data of Kolářová et al. (2006), however, suggest that problems with taxonomical determination of schistosomes may also arise from studies on adult worm morphology. During investigation of Icelandic whooper swans *Cygnus cygnus* (L.), the isolated schistosomes showed certain similarities with the flukes of *Trichobilharzia*, but detailed morphological and DNA studies revealed that Icelandic isolates belonged to a new genus and species of schistosome flukes, *Allobilharzia visceralis* Kolářová, Rudolfová, Hampl et Skírnisson, 2006. Moreover, recent molecular studies (Loker and Brant 2006) on different isolates, which were originally described as various schistosome species, revealed that also adult worms of different families may exhibit similar morphological features. In 1991, Platt et al. found a new schistosome species in crocodiles and erected *Griphobilharzia amoena* Platt, Blair, Purdie et Melville, 1991 for this blood fluke and placed it in a separate subfamily Griphobilharziinae of the family Schistosomatidae. Although not all characters of the species were originally observed, because of its small size, the opinion that it belongs to this family and has characters of taxonomic significance to justify the recognition of the new genus and the subfamily prevailed (Khalil 2002). Thus, *G. amoena* was considered to represent a bizarre schistosome maturing in cold-blooded vertebrates. However, molecular studies of Brant and Loker (2005) indicated that the crocodile fluke is likely to be an aberrant member of the family Spirorchiidae, species of which are known as parasites of turtles.

VERTEBRATE INFECTIONS

Free-living cercariae are released from snails in high quantities especially on sunny days and, during their short life span (1–1.5 day at 24°C according to Neuhaus 1952), they need to infect a definitive host quickly. Studies on the host-finding behaviour revealed that cercariae of *T. ocellata* exhibit a positive phototactic and negative geotactic orientation, response to shadow, water turbulence and temperature. Prior to an initial contact, they are able to recognize some compounds (ceramicides and cholesterol) released by the vertebrate skin (Haas 2001). After contact with a host, cercariae of

T. ocellata and *Schistosoma mansoni* Sambon, 1907 attach and find a suitable entry point where they penetrate into the skin (Haas and Haberl 1997). The penetration is stimulated by chemical stimuli; *T. ocellata* and *Austrobilharzia variglandis* (Miller et Northup, 1926) initiate the process in response to free fatty acids and free sterols, respectively (Clegg 1969, Haas and van den Roemer 1998).

The attachment and penetration processes are accompanied by morphological and physiological changes associated with the parasite transformation from a free-living to a paratrophic organism. Morphological changes start with the loss of tail, shedding of the thick glycocalyx and releasing of the penetration gland contents. The loss of glycocalyx leads to considerable changes in the antigenic properties of the parasites and may represent a way to escape recognition by the host immune system (Horák et al. 1998, Blažová and Horák 2005). The studies on *T. szidati* and *T. regenti* Horák, Kolářová et Dvořák, 1998 showed that the contents of both postacetabular and circumacetabular glands are released *in vitro*; the soluble secretions containing proteolytic enzymes were identified as cysteine proteases (Mikeš et al. 2005).

In vitro studies revealed that further migration into deeper skin layers of the epidermis is also accompanied by changes in parasite behaviour: after the penetration and transformation of *S. mansoni* and *T. ocellata* to schistosomula, the parasites shifted to negative photo-orientation in agar substrates (Grabe and Haas 2004a). In order to migrate normally, the parasites become chemotactically attracted by host components; in the case of visceral schistosomes, *in vitro* studies showed that both *S. mansoni* and *T. ocellata* were chemotactically attracted by a low molecular weight fraction of the serum of their hosts, human and duck, respectively (Grabe and Haas 2004b).

After entering blood vessels, the visceral species of *Trichobilharzia* leave the skin and migrate via the lungs to the portal or intestinal veins of a naturally infected host. The studies on migration routes of *T. szidati* (Chanová et al. 2007) and an investigation into the pathogenesis of infection caused by flukes of the species *A. variglandis* (see Wood and Bacha 1983) and *Ornithobilharzia* Odhner, 1912 (see Morales et al. 1971) suggest that non-human schistosomes which mature in the viscera of their definitive hosts follow the same migration route as *Schistosoma* Weinland, 1858 (see Basch 1991).

Only nine schistosome species were found in the nasal area of their definitive host. Except for one representative of *Schistosoma* (*S. nasale* Rao, 1933), the others belong to *Trichobilharzia*: *T. arcuata* Islam, 1986, *T. australis* Blair et Islam, 1983, *T. aurelanii* Fain, 1956, *T. duboisi* Fain, 1959, *T. nasicola* Fain, 1955, *T. regenti*, *T. rodhaini* Fain, 1955, and *T. spinulata* Fain, 1955. Unfortunately, with an exception of *T. regenti*, there are no details available regarding the migration route from the skin to the nasal tissues. In the case of *T. regenti*, prior to residence in the nasal cavity of the definitive avian host, the flukes migrate through the peripheral and central nervous system (Horák et al. 1999, Hrádková and Horák 2002).

The factors which determine the life span of the majority of schistosome species remain unclear. According to the literature, marked differences in the life span have been observed among schistosomes of various species within the genus; whereas flukes of *T. szidati* and *T. regenti* die approximately about 3 weeks post infection (p.i.) in ducklings (Horák et al. 2002), mature *T. ocellata* was observed in the duck liver 248 and 370 days p.i. (Bourns et al. 1973). Nevertheless, the patent period of non-human schistosomes and potentially also the life span of adult schistosomes are shorter than those of human schistosomes (Basch 1991).

Schistosomes are considered to be highly pathogenic for migratory waterfowl (Graczyk et al. 1993), but there are relatively few reports on the clinico-pathological aspects of the infections (Horák et al. 2002, van Bolhuis 2004). The general paucity of this information can be explained in part by the ease with which the parasites can be overlooked during gross necropsy due to their small size and occurrence within blood vessels (Wojcinski et al. 1987). The available data on pathology of the infection focus mostly on symptoms of patent infections, however, recent investigations have elucidated that immature flukes may also cause severe tissue injuries (Kolářová et al. 2001, Chanová et al. 2007). In general, it is suggested that pathogenesis of the infection with visceral schistosomes in birds is comparable to those caused by *Schistosoma* flukes in mammals (Horák et al. 2002). In the case of nasal *T. regenti*, the pathogenesis reflects the parasite pathway and, therefore, tissue injuries develop in the host central nervous system (CNS) and nasal area (Kolářová et al. 2001). Whereas mild infections with visceral schistosomes are often asymptomatic (Basch 1966), even a small number of nasal schistosomes in the CNS may cause severe syndromes (Kolářová et al. 2001).

It is of interest that schistosomes migrate along similar routes in both compatible and noncompatible hosts. However, in a noncompatible host, the parasites do not start reproduction and die at various intervals p.i. The initial contact of mammals with cercariae leads to dermatitis, an allergic response to the infection by the parasites (Olivier 1949). Immunohistochemical studies showed that the disease caused by bird schistosomes in mammals comprised both immediate and late phases of a cutaneous hypersensitivity reaction (Kouřilová et al. 2004a).

It seems that cercariae of all genera of the family Schistosomatidae are able to produce similar symptoms when infecting humans (Brackett 1940, Cort 1950, Batten 1956, Malek and Armstrong 1967, Appleton and Lethbridge 1979, Wiley et al. 1992, Kouřilová et al.

2004b). According to the literary data (Basch 1991), human schistosomes usually induce a milder skin reaction. However, our observations of patients with cercarial dermatitis acquired in European waters (i.e., those infected by bird schistosomes only) and individuals infected with cercariae of the genus *Schistosoma* in African lakes showed that there are no differences in the intensity of skin reaction caused by bird and human schistosome cercariae (L. Kolářová, unpublished).

For a long time it was generally assumed that the strong skin reaction is responsible for a quick death of bird schistosome cercariae soon after the infection of noncompatible host (mammals, including man). However, studies on various species of the genera *Trichobilharzia*, *Gigantobilharzia*, *Bilharziella* Looss, 1899 and *Ornithobilharzia* revealed that the parasites can escape from the skin and subsequently migrate in experimentally infected mammals under certain circumstances (Olivier 1953, Appleton and Brock 1986, Haas and Pietsch 1991, Horák and Kolářová 2000, Bayssade-Dufour et al. 2001, Hrádková and Horák 2002, Kouřilová et al. 2004b, Chanová et al. 2007). Depending on the species, particular schistosomes were found either in the lungs and other visceral organs of various mammals or in the CNS of mice (Haas and Pietsch 1991, Horák et al. 1999, Horák and Kolářová 2000). The migrating juvenile flukes can survive for several days and even weeks, causing severe tissue injuries in mammals (Bayssade-Dufour et al. 2001, Kolářová et al. 2001, Kouřilová et al. 2004b, Blažová and Horák 2005, Chanová et al. 2007). Experimental studies on various rodents and monkeys infected either with visceral or nasal schistosomes showed that the severity of pathologies depends on the host immune status. Contrary to the repeated infections leading to the development of severe skin inflammatory reaction, the most severe tissue injuries in the mammalian lungs and central nervous system develop during primary infections by the schistosome cercariae (Batten 1956, Bayssade-Dufour et al. 2001, Kouřilová et al. 2004b). These findings suggest that cercarial dermatitis represents a protective reaction of a sensitized host against the parasites.

The available literature suggests the emergence of cercarial dermatitis in many countries and the important role of bird schistosomes in the spreading of the disease. Except for schistosomes of the genus *Schistosoma* (see Davis 2003) there are few data documenting that cercariae of other animal genera can infect man. Considering the fact that schistosomes of the genera *Heterobilharzia* Price, 1929, *Bivitellobilharzia* Vogel et Minning, 1940 and *Orientobilharzia* Dutt et Srivastava, 1955 are important parasites of various subungulates, rodents and carnivores (Khalil 2002), it cannot be excluded that human infections by the cercariae of mammalian species can lead to more severe pathologies in comparison with bird schistosomes.

To avoid the infection with schistosome cercariae, various preparations with different effects against the parasites were developed in the past (Horák et al. 2002). Recently, niclosamide in water-resistant sun-protecting cream, were found to have protective effects against infections caused by *T. szidati* and *S. mansoni* (Wulff et al. 2007).

CONCLUSIONS

The association between schistosomes and cercarial dermatitis was recognized many decades ago. However, the identification of particular species of schistosomes causing the disease remains difficult. Intermediate hosts as well as definitive hosts participating in the life cycle of many of bird and mammalian schistosomes are not known. It is often not possible to distinguish cercariae of different species within one genus and, thus, to be sure which parasite is responsible for the dermatitis. Therefore, laboratory maintenance of the life cycle with subsequent characterisation of all developmental stages of the parasites as well as application of molecular methods are absolutely necessary.

In comparison with snails, few data on the occurrence of schistosomes in naturally infected vertebrates are available. Nevertheless, schistosomes seem to be common parasites of waterfowl. From the veterinary viewpoint, schistosomes can cause severe tissue injuries; however, it seems that mild infections are well tolerated by animals. The pathogenesis of infections caused by visceral schistosomes is comparable to those caused by flukes of the genus *Schistosoma* in mammals. In the case of nasal schistosomes the infections are accompanied by tissue injuries due to parasites that migrate through the CNS. During the examination of definitive hosts it has to be taken account that naturally infected animals can be infected concurrently with different species of schistosomes.

The life span of most of the animal schistosomes has not been determined, however, some data suggest that the flukes can survive in definitive hosts for months. Considering waterfowl, therefore, the mature schistosomes (within the host), but also larvae (within snails transported on bird legs), can be transported to and from wintering locations. It can be, therefore, suggested that some schistosomes may be introduced to new geographical areas under certain circumstances. However, no data are available to support this view.

It has been documented that cercarial dermatitis develops as a consequence of repeated infections with the cercariae and represents an allergic response which is able to trap and eliminate the penetrating parasites. Thus, the disease represents a protective reaction of a sensitized organism against the parasite. However, the infections can be linked to more than skin symptoms under certain circumstances. Recent studies on bird schistosomes have shown that during primary infection of noncompatible hosts not all cercariae are necessarily

trapped in the skin and that some of the parasites may migrate through visceral and nervous tissues of mammals. To date there are, however, few data on the pathology of primary infections in mammals in general. As humans are more frequently exposed to these parasites, intensification of studies on clinical and immunopathological aspects of the infections caused by specific species of animal schistosomes is required.

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