Acta Tropica *36*, 133–136 (1979)

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Ticks and spirochetes

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In memoriam Oscar Felsenfeld

Summary

The concept is expressed that *Borrelia* developed as symbionts of ticks (especially Argasidae) but act as parasites in mammals and birds ... borrelial reservoirs and amplifiers following bites by infected ticks. Certain tick borreliae may multiply in lice but one *Borrelia* has evolved into an independent species *(B. recurrentis)* associated only with lice and humans. Seventeen argasid tick species are known as vectors of *Borrelia* species and 4 ixodid tick species are known as vectors of *B. theileri.*

Key words: ticks; spirochetes; concept; epidemiology.

Felsenfeld (1971) expertly reviewed the state of knowledge of associations between ticks and *Borrelia.* In this brief tribute to the memory of Felsenfeld and his outstanding scientific contributions, I suggest a refinement in the current concept regarding basic *Borrelia*-tick-vertebrate interrelationships, review some significant recent investigations into these phenomena, and mention recent reports of relapsing fever in humans following tickbite.

Most workers have agreed with the concept that the *Borrelia* developed primarily as parasites of ticks and evolved into different strains with the various tick species, and that mammals are merely accidental hosts of borreliae (Felsenfeld, 1971, p. 15). I venture to modify this definition as follows: "*Borrelia* developed as symbionts of ticks (chiefly Argasidae) but act as parasites in mammals and birds, which serve as borrelial reservoirs and amplifiers following bites by infected ticks." A biologically and epidemiologically important corollary would be: "Certain tick borreliae capable of multiplying in lice infesting infected vertebrates may undergo an occasional, enzootic, or epizootic louse-vertebrate-

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louse cycle, but one *Borrelia* has evolved into an independent species *(B. recurrentis)* associated only with lice and humans."

At least 17 argasid tick species [*Ornithodoros* (15), *Argas* (2)] are known to be reservoirs and vectors of *Borrelia* species and 4 ixodid tick species (*Rhipicephalus evertsi* and 3 *Boophlius* species) have been associated with *Borrelia theileri* (Felsenfeld, 1971; Burgdorfer, 1976). These ticks and spirochetes occur in each major Faunal Region (Palearctic, Nearctic, Neotropical, Oriental, Ethiopian, Australian). The relationships between spirochetes and ticks conform to those of symbionts, not parasites. The geographically and ecologically widespread, intimate tick-spirochete relationship, including transstadial survival and transovarial transmission, transmission to a vertebrate via infected salivary or coxal fluids, and/or spirochete amplification or invigoration in a cycle involving vertebrates parasitized simultaneously by infected and uninfected ticks, suggests a series of complex evolutionary interactions. These processes began with a symbiont in a tick to tick cycle and progressed to various patterns of a tick symbiont to vertebrate parasite to tick symbiont cycle. The *Ornithodoros-Borrelia*-mammal relationship has been especially successful; the *Argas* relationship is limited (so far as known) to *B. anserina* and birds (but is very successful in poultry yards); the ixodid-*B. theileri*-mammal relationship is poorly understood.

The notion, currently often expressed, that development of tickborne *Borrelia* species in experimentally infected human lice proves that all borreliae are derivatives of a single taxonomic entity, *B. recurrentis,* appears to be a biologically unsound anthropomorphic allusion reflecting intense interest in human relapsing fever resulting from contamination by *B. recurrentis*-infected human lice. After travel through biological history, Walton (1973) found other reasons to consider that all *Borrelia* are strains of *B. recurrentis.*

Weyer (1960) explained in detail the reasons for concluding that "lice must be considered recent hosts as compared to ticks", a concept originally proposed by Nicolle and Anderson (1927). The human louse may serve as a culture medium for spirochete development but the spirochetes can pass from louse to louse only when feeding on a human who has infected himself by crushing an infected louse on his broken skin. The louse-*Borrelia* model may thrive in a few environments where humans are especially heavily louse-infested or, occasionally and temporarily, among persons crowded by wars or other calamities. This pattern appears to be intimately associated with human civilization (!), not with primeval nature.

Felsenfeld's microbiological career coincided with the period of most active research on *Borrelia,* especially in the USA, the USSR, Switzerland, North and East Africa, and the Near East. However, Burgdorfer (1976) now states: "Unfortunately, the number of borreliologists throughout the world has decreased in spite of the great need for additional epidemiologic, ecologic, diagnostic, and taxonomic research on relapsing fevers. Unless interest and support are revived, competency to investigate these problems will soon be lost." Young scientists considering the borreliae as a field for research will find inspiration in the Rodhain (1976) review of the current epidemiological aspects of these organisms and relapsing fevers, which closes with the statement that the problems are as numerous as they are passionate.

A major post-1971 contribution to knowledge of interactions between *Borrelia* and ticks is an experimental study of the dynamics of *B. anserina* in 4 *Argas* species from Egypt (Diab and Soliman, 1977; Zaher et al., 1977). The ticks were *A. (Persicargas) persicus* from a domestic chicken house, *A. (P.) arboreus* from a heron *(Bubulcus ibis ibis)* rookery, *A. (P.) streptopelia* from a wild dove *(Streptopelia)* nest, and *A. (A.) hermanni* from a domestic pigeon house. After adults fed on infected chickens, spirochetes disappeared from the gut lumen of *streptopelia* rapidly (7–8 days) but in the other species they became immobile by day 15–20. The spirochetes penetrated the gut wall and were observed in the hemolymph of each species 2 hours after the infective feeding. Numbers in hemolymph increased for 7 days in *persicus* and *arboreus* but for only 2 days in *streptopelia* and *hermanni.* Numbers varied throughout the 60-day study period in *persicus* and *arboreus* but dropped to 0 on day 4 and afterward in *hermanni* and (with a single exception) *streptopelia.* Spirochetes were first seen in other tissues on day 7. The central nerve mass was the most heavily infected in *persicus* and *arboreus,* and remained infected throughout the 60-day period, but was only slightly infected in *streptopelia* and *hermanni.* Salivary gland infections were heavy to day 60 in *persicus* and *arboreus,* irregular (slight or nil) in *hermanni,* and nil in *streptopelia.* Infections in ovaries and testes were heavy to day 60 in *persicus* and *arboreus* but nil in *streptopelia* and *hermanni.*

There was transstadial survival to the adult stage in *persicus* and *arboreus* developing from experimentally infected larvae; each stage transmitted the borreliae when feeding on chickens. Borreliae survived only to first and second nymphal instars (N_1, N_2) in *hermanni* but not at all in *streptopelia.* In *persicus* and *arboreus* experimentally infected as N_2 and N_3, respectively, 84% of *persicus* females and 24% of *arboreus* females transmitted the infection transovarially to the F_1 generation. In *persicus* and *arboreus* filial infection rates were 80–83% for eggs deposited by originally infected females, 83% for N_2 of the F_2 generation, 100% for eggs deposited by F_1 females, and 100% for N_2 of the F_2 generations. There was no transovarial transmission in *streptopelia* and *hermanni.* Reasons for these striking similarities in 2 species and differences in 2 other species remain to be determined.

During the past decade, there have been 2 major outbreaks of human relapsing fever in the United States. In 1968, 11 of 42 members of a boy scout troop became ill after sleeping in rodent-infested cabins (1 in a nearby tent) on Browne Mountain near Spokane, Washington. Two of 14 *Ornithodoros hermsi* collected from a cabin were shown to be infected by *Borrelia hermsi.* Chipmunks *(Eutamias)* and pine squirrels *(Tamiasciurus)* appeared to be the vertebrate reservoirs for the disease (Thompson et al., 1969). In 1973, 62 visitors and employees sleeping in log cabins in North Rim Park of the Grand Canyon, Arizona, became ill with relapsing fever. The victims resided in 9 states of USA and in Germany. *O. hermsi* taken from 4 rodent nests in the cabins were pooled individually and fed on laboratory mice; one of the 4 pools transmitted *Borrelia hermsi.* The ticks in and near these cabins may have been more than usually aggressive toward humans because of a die-off of rodents, owing either to the exceptional severity of the previous winter (Boyer et al., 1977) or to an epizootic of plague the previous year (Burgdorfer, 1976). The origin of the first relapsing fever case seen in North Carolina (Lester et al., 1976) was traced retrospectively at the Communicable Disease Center (Atlanta) to probable exposure to tickbite while vacationing in a wooded resort in a high desert plateau on the eastern face of the Cascade Mountain range in Oregan; sporadic cases have been reported from Oregon mountains since 1940. California State Department of Public Health morbidity records for 1974 show 12 reports of tickborne relapsing fever; this disease is reported only on the option of physicians.

Acknowledgment. From Research Project MR041.09.01–0152, Naval Medical Research and Development Command, National Naval Medical Center, Bethesda, Maryland, USA. (The opinions and assertions contained herein are the private ones of the author and are not to be construed as official or as reflecting the views of the Department of the Navy or of the naval service at large.)

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