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BORRELLIA

STRAINS, VECTORS, HUMAN AND
ANIMAL BORRELIOSES

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By

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DEDICATION

TO: Dr. M. Baltazard, Director
Institute, Teheran; Professor
rector Emeritus, Hessara
Professor A. Geigy, Swiss
ical Medicine, Basel; Dr. C
er, Research Entomologist
and the Memory of the late Pr
Parasitology Institute, Pari
whose patient instructions, frien
encouragement, competent sup
standing criticism have made n
relia possible and pleasurable c
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using chloroform, washed the brains with saline, emulsified them, and then injected the emulsion into fresh animals. The incubation period was 6 to 12 days.

Weyer (725) studied different methods of preserving *B. duttonii*, *B. turicatae*, and *B. crocidurae*. They remained alive when quick frozen at -76°C . *B. recurrentis* in lice, and tick-borne in *Ornithodoros*, remained alive in the deep freeze for years. Even more effective was the propagation of *B. recurrentis* by inoculation into the hemolymph of lice. When borreliae were numerous, they could be frozen in rat blood. Weyer's method can be recommended provided the arthropods are not thawed and refrozen.

BORRELIAE AND THEIR VECTORS

It will be seen on subsequent pages that it is difficult, perhaps even impossible, to speak about species of *Borrelia*. All of these so-called species may well be the variants of one single organism adapted to different environments programmed by vectors, hosts, and their mutual relationship. However, following the present custom of classifying borreliae according to their vectors (which is of considerable epidemiologic interest), the vectors will be discussed together with the "strains" they usually carry, or are said to harbor. Experiments with cross-infections of vectors will be listed, as well as strains that have been described but either were lost or were found to be mere variants of established *Borrelia* types. It is necessary to present separate discussions of the louse with *B. recurrentis* and ticks with their borreliae for reasons which are evident.

The Human Louse and *Borrelia Recurrentis*

As mentioned before, Mackie was the first to incriminate the human body louse as the vector of epidemic relapsing fever. Nicolle and his co-workers (531, 532, 537, 538) worked out many details of the louse-*Borrelia* relationship. Nicolle and Anderson (521) believed that the contemporary strains of *B. recurrentis* were derived from tick-borne strains. Adler and Ashbel (4) agreed with this concept.

Lice

General accounts of the life cycle of the louse and of the mode of transmission of borreliae by this insect have been given by

TABLE 2
SIZE OF SOME ARTHROPODS CARRYING BORRELIAE
AND THEIR NICKNAMES*

Scientific Name	Male*	Female	Nickname
<i>Pediculus humanus corporis</i>	2.5-3.3 x 0.8-1.1	3.2-3.6 x 1.1-1.4	
<i>Pediculus humanus capitis</i>	1.6-2.1 x 0.6-0.8	2.4-2.8 x 0.9-1.1	
<i>Ornithodoros moubata</i>	4.2-5.8 x 3.7-4.2	7.8-12.8 x 6.9-10.2	Ochiopo, Tampan, Garrapato (Angola) Kufu, Bu (Zambezia) Kibu, Bibo (Uganda) Papasi (Zanzibar) Kimputu (Congoes) Curdud (Somaliiland)
<i>Ornithodoros erraticus</i>	2.8-4.2 x 1.8-2.5	4.2-6.8 x 2.4-4.1	
<i>Ornithodoros tholozani</i>	3.5-6.2 x 2.8-5.2	7.6-9.1 6.8-7.4	
<i>Ornithodoros rudis</i>	3.3-4.2	4.8-6.4	Cuescas, Mordjini (Venezuela)
<i>Ornithodoros talaje</i>	x 2.4-3.3	x 2.8-4.2	Talajas (Colombia)
<i>Ornithodoros turicata</i>	4.8-6.2 x 3.4-5.2	5.3-7.4 x 4.7-6.2	
<i>Argas persicus</i>	2.7-4.4 x 2.3-2.9	4.6-6.9 x 3.3-4.3	Pajaroello (Mexico)
	4.0-5.5 x 2.6-3.3	5.0-10.1 2.4-7.5	

* In mm, length x width.

Size often depends on time since last feeding.

+ Nicknames according to Brumpt, E.: *Précis de Parasitologie*, 6th ed. Mason & Cie., Paris, 1963.

numerous authors. Nicolle *et al.* (534) found that the organisms are not transmitted to the progeny of lice. Chapcheff (155) and Chiao (163) emphasized that only *Pediculus humanus corporis* (*vestimentii*) and *Pediculus humanus capitis*, i.e., the clothes or body louse, and the head louse, respectively, but not the pubic or crab louse, *Phthirus pubis*, transfer relapsing fever organisms. This was confirmed by data in the monograph on lice by Buxton (135) and in the textbook of Horsfall (374). Thus we are concerned only with the human body louse and the closely related head louse.

The genus *Pediculus* is a member of the family Pediculidae that

belongs to the order Anoplura (Siphunculata) or sucking lice. The body louse, *P. h. corporis* is also called *P. humanus humanus*. The head louse is about 2.5 mm long and slightly smaller than the body louse but they can interbreed. Lice are strictly host-specific. Geigy (303) stated that head lice must have preceded body lice and adjusted themselves to man before he started to wear clothing. Lice cling to hair. The body louse does not invade the head hair and beard but *P. h. corporis* may migrate to the body. *P. h. corporis* lives also in the folds of clothing, principally in the underwear. The fertilized female lays about 300 eggs which adhere to hair or cloth-



FIGURE 5. Head of louse, *Pediculus humanus*.

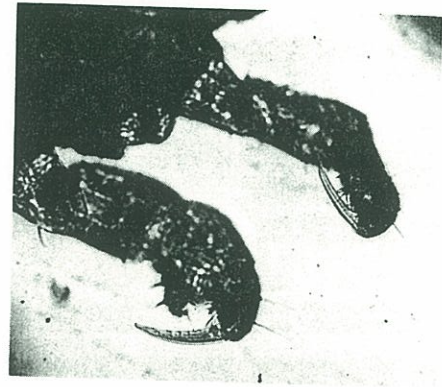


FIGURE 6. Claws of human louse, *Pediculus humanus*.



FIGURE 7. Male louse, *Pediculus humanus (corporis)*.

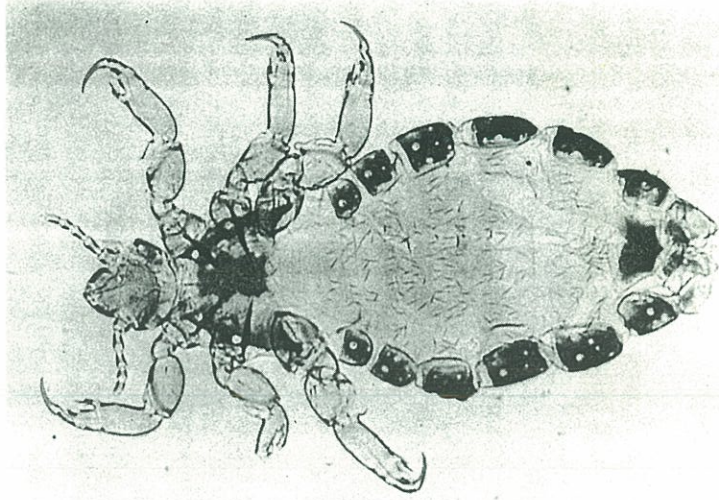


FIGURE 8. Human louse, *Pediculus humanus (corporis)*, female. Slide preparation.

ing and hatch at 28° to 32° C in 8 to 9 days. Three larval stages develop within 9 to 10 days. The larvae and nymphs descend to the skin and feed. One adult louse takes up about 1 mg blood at one meal but it is possible that smaller amounts are consumed and then the lice feed more often. Feeding is rapid and followed by a quick evacuation of feces. If the louse has a meal on a patient with *B. recurrentis* in his blood, the organisms reach the stomach of the louse but many are destroyed. Heisch *et al.* (355) found that the density of the borreliae in the blood consumed by the louse must be at least one or two per oil immersion field to make the meal infective.

The borreliae pass from the gut into the hemocele (celomic cavity) where they multiply. In the louse, organs like the salivary glands, the ovaries, or the Malpighian bodies are not invaded. This precludes hereditary transmission. Only about 12% of the lice fed on relapsing fever patients became infected in the experiments of Nicolle *et al.* (534). In one instance 4,407 lice were fed on a patient, and none acquired borreliae. On the other hand, Riding and MacDowell (603) found that one-half of the lice that were collected from persons who were ill with relapsing fever for 1 to 10 days were infected with borreliae. The organisms become visible in the celomic fluid (hemolymph) about 5 to 8 days after the blood meal. The borreliae remain in the louse until its death. Since borreliae are not present in the gut and salivary glands, they cannot be transmitted by the bite of the louse. Neither can they be propagated by fecal material. Borreliae may escape from the celomic cavity only when the louse is crushed (179).

Heisch and Harvey (353) described several basic data on the relationship of lice and borreliae. They showed that the hemocytes of the louse may act as phagocytes and destroy some borreliae. These authors found borreliae also in the neural ganglion and nucleus but never in the salivary gland of the louse. The penetration of the borreliae into the hemocele took place from the anterior part of the midgut.

After a blood meal containing borreliae, the organisms disappear from the midgut of the louse within a few hours, to reappear in the hemocele after 5 to 8 days. This has been called the "negative phase." It has given rise to speculations about a filtrable phase of borreliae. The appearance of granules, short and cork-screw-like

forms of borreliae, in the beginning of their sojourn in the celomic cavity has stimulated speculation and research also about metacyclic forms (54, 63, 296, 348, 353, 355). These investigations showed that a metacyclic development does not exist in the louse. The organisms become slender and small when penetrating the midgut but they can be found by diligent search. The "granula" theory is difficult to prove or disprove except with the aid of fluorescent microscopy, as our group did (264), because "granules" occur naturally in the celomic cavity of lice.

The number of surviving borreliae is determined by the temperature and the hitherto not fully explored qualitative and quantitative changes of the gut juices of the louse. Wolman and Wolman (736) found, for instance, that lice kept at 37° C were unable to infect man 1 to 18 days after a meal on a patient with relapsing fever.

The borreliae are tightly enclosed by the limiting membranes of the celomic cavity. Lice are delicate, however, and easily damaged. Their limbs and antennae are easily broken off. This permits the celomic fluid to flow out and to infect the site of the bite. This usually happens when a bitten person scratches himself. Scratching will also rub the borreliae into the skin (179, 537, 538). Small children develop relapsing fever less often than adults. This may be because they seldom crush lice. In Europe, lice are crushed between thumbnails. In China and South America, lice are often popped between the teeth. A few authors (177) believe that putting lice into the mouth does not convey the infection but it has been shown (59, 365) that borreliae may enter the human body through uninjured mucosae, including that of the gastrointestinal tract. The last practice may therefore lead to an increased number of relapsing fever infections.

After acquiring *B. recurrentis*, the louse remains infectious for its entire life, which is about 3 weeks, sometimes longer (63, 134, 453).

Experiments with louse-borne relapsing fever are hampered by the unwillingness of the human louse to bite other animals, except monkeys (59, 95, 532). It has also been reported that it is possible to feed human lice on newborn rabbits and other newborn rodents (208, 209, 219).

Human lice have a narrow temperature tolerance and die when

it becomes too hot (207). This has epidemiologic significance, which will be discussed later.

"Strains" of *B. recurrentis*

Coleman (194) emphasized strain specificity but pointed out pitfalls encountered in cross-protection tests. Chen *et al.* (160) used hamsters and monkeys to ascertain whether the Chinese and the American strains are identical with the aid of such tests.

Without the benefit of strain comparison, a *Borrelia* was isolated from a patient with relapsing fever at Bellevue Hospital in New York in 1907. This strain has been kept in numerous laboratories and used in animal and biochemical experiments. It is not known whether it was louse- or tick-borne. After literally thousands of rodent passages, this strain is widely used as a model for laboratory experimentation with borreliae under the designation *B. novyi*. It is not certain whether conclusions reached from experiments with this "strain" are valid for other borreliae.

It was clear to Noguchi as early as 1912 that *B. kochi* Novy 1907 was closely related to *B. rossi* Nuttal 1908, and that both organisms, as well as *B. carteri* Mackie 1907 and *B. berbera* Sergeant and Foley 1910, were local strains of *B. recurrentis*. The author (O.F.) has been unable to find any laboratory that is still carrying either of these four strains. The description of *B. aegyptica* is not clear enough to warrant its acceptance as a "species."

It is possible that some or all of these strains were tick-borne rather than louse-borne. Nicolle and Anderson (520), working in Tunisia, believed that louse-borne borreliae can be transferred to ticks.

Baltazard and his co-workers (52) carried out extensive experiments by feeding lice and ticks on newborn rabbits artificially infested with borreliae. They found that lice could acquire infestation with *B. microti*, *B. turicatae*, and *B. hermsii* by sucking blood of infant rabbits infested with these tick-borne strains. Numerous metacyclic forms appeared in lice infested by this method. Heisch and Garnham (349) fed batches of lice from a relapsing fever-free area (Nairobi) on monkeys infected with a *B. duttonii* strain. The so-called negative phase (absence of visible forms in the insect) was shorter than in ticks; and the organisms appeared in

metacyclic, cork-screw forms. This observation is important in the study of transmission of borreliosis because Heisch and Garnham found persons infested with lice living in huts in which *O. moubata*, the carrier of *B. duttonii*, was a common inhabitant. Heisch (341) believed, therefore, that the human louse can transmit *B. duttonii* under natural conditions. Heisch (346, 347) also noted a definite multiplication of *B. duttonii* in the celomic cavity of lice 6 to 8 days after ingestion. The borreliae had a tendency to concentrate around the fat body in the head of the louse. Granular forms of the *Borrelia* also appeared. This may be a phenomenon related to life in an unusual vector, and perhaps it may also be a phenomenon of adaptation. Mooser and Weyer (502) could retransmit the borreliae to *O. moubata*. *B. duttonii* did not seem to be adversely affected during 21 louse passages. Boiron (97) succeeded in transmitting *B. crocidurae*, *B. duttonii*, and *B. hispanica* to lice from infected mice. Weyer and Mooser (726) used rectal or intracelomic inoculation of lice, with *B. duttonii*, *B. turicatae*, and a crocidurae-group strain. Sparrow (660) confirmed that *B. hispanica* can be adapted to the louse, and that small rodents may become reservoirs of louse-borne tick fever. Garnham (295) believed that lice may harbor *B. hispanica* and that a man-louse-man cycle is possible, thereby forming a reservoir without passage through *O. erraticus*, the tick-vector of *B. hispanica*, and also bypassing rodents that are frequent hosts of this strain. Baltazard *et al.* (54) experimented with *B. crocidurae* and an antigenically distinct *B. microti* strain. Lice were fed on patients, tritiated, and injected into human beings and animals. Of 62 individuals and rodents, 14 became infected. Talice (675), however, did not observe infestation of lice with *B. hispanica* when fed on infected man, mice, rats, and monkeys. Favrova *et al.* (261) fed 4,658 lice on patients with tick-borne relapsing fever. The borreliae penetrated into the hemolymph in 1.25% of the lice but multiplied only in one. This group of investigators did not believe, therefore, that tick-borne borreliae can be transmitted to lice.

There appears, however, to be satisfactory evidence that tick-borne borreliae can be transmitted to lice. The antigenic stability of borreliae in insects is much greater than in animals. Probably

repeated transmission cycles are required to establish variants and mutants with genetically modified characteristics that are relevant for such an adaptation. Baltazard (46) expressed this thought in considering *B. recurrentis* a transient, inconstant form of *Borrelia* that has been modified by passages in rodents and ticks. We would add to this as a governing factor the man-louse biotope.

It should be mentioned that the monkey louse (*Pediculus longiceps*) is an excellent host of *B. duttonii* (342). In view of other extensive research on *O. moubata* (*vide infra*), it would be perhaps somewhat rash to conclude that monkeys or *P. longiceps* play an important role in the preservation of *B. duttonii*.

Tick-borne Relapsing Fever

General Tick-Borrelia Relationships

Geigy (303) pointed out that ticks are arthropods but not insects. Ticks carrying the agent of human relapsing fever are classified in the phylum Arthropoda, class Arachnoidea (Arachnida), order Acarina, suborder Ixodides. The order Acarina includes also spiders and scorpions. Ticks are wingless; their body lacks segmentation into head, thorax, and abdomen; and a capitulum with mouth parts and palps is on their ventral side. They have four pairs of legs (larvae only three pairs) which are articulated and equipped with terminal claws. They have many characteristics, however, of true insects, as the Malpighian (excretory) tubules, a tracheal breathing system, and a chitinous matrix of the hypodermis.

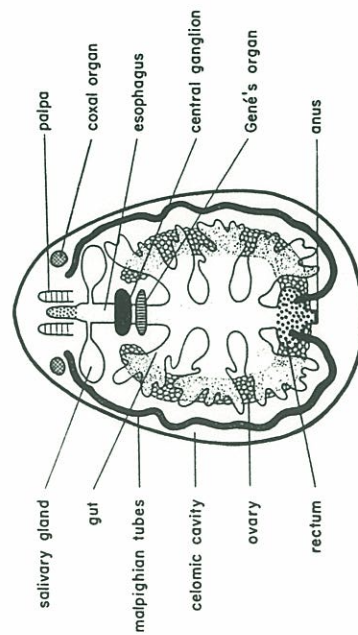


FIGURE 9. Schematic section through an *Ornithodoros*.

The suborder Ixodides consists of two main families: Ixodidae or hard ticks with 8 genera and about 400 species, and Argasidae or soft ticks, with 4 genera and about 120 species (543). Argasidae have a softer and more elastic surface than Ixodidae. They have usually only one or two principal hosts, whereas Ixodidae are willing to feed on several different animal species. Argasidae attach themselves to the host for the blood meal for only a short time and take up less blood at one feeding but their body expands considerably during the feeding. Then the females, if fertilized, lay 100 or more eggs. The number of eggs is limited (some other ticks lay them by the thousands) and the female does not die after oviposition. This fertilization and egg laying is repeated several times during life. The genus *Ornithodoros* of the family Argasidae has no scutum; the margin of the body is thick, rounded, without definite sutural line (as Argas); and the hypostome has well-developed teeth. The integument is mammillated (371, 543). *Ornithodoros* (formerly spelled *Ornithodoros*) ticks can survive for a long time without food and at a low humidity. A thin layer of wax-like substance in the epicuticle and the capability of absorbing moisture by closing the spiracles allows *Ornithodoros* to remain alive under unfavorable conditions. About 15 species of this tick have been proved to carry borreliae.

Ornithodoros feed exclusively on blood. They may ingest amounts equivalent to 2 to 6 times their own weight (438). Saliva reaches the capillaries in the skin of the bitten animal. Towards the end of the feeding the contents of the gut are evacuated through the mouth. There is no rectal outlet, only a urinary pore with a rectal bladder and two Malpighian tubes. The urinary pore is often called a rectal pore but feces are not discharged through it. Water is excreted through the coxal glands. The pressure of the engorged gut seems to aid in this process. There may be copious coxal fluid excretion (as in *O. moubata*) or only a drop which may not appear at all while the tick is in contact with its host during feeding. Normally, nymphs feed more often than adult ticks. After feeding, *Ornithodoros* leave their host.

Sautet (624) summarized the natural animal hosts of *Ornithodoros*. His studies and those of Mooser (501) and others show that *O. moubata* and the human body louse are primarily anthro-

pophilic, whereas other ticks are parasitic principally on other animals, mainly rodents and insectivores.

There are numerous animals on which certain species of *Ornithodoros* feed. The feeding usually takes 10 to 30 minutes, seldom 1 hour or longer, according to the species of tick. The bite of some species is painful, whereas others produce analgesia. *Borrelia*-transmitting ticks usually do not have a painful bite, and feed for a relatively short time, which affords them some safety from being scratched or shaken off by the host. Baltazard *et al.* (56), discussing host-vector relationship of ticks, stated that young animals are better hosts because they are unable to rid themselves of the tick with ease. Considering the greater susceptibility and higher mortality rate of young rodents when infected with borreliae, and the willingness of *Ornithodoros* to feed also on young dead animals, the tick-rodent relationship in a given ecosystem results in the survival of the tick but in a diminishing number of their young hosts. The time of the emergence of hungry nymphs often also coincides with that of new wild rodent litters, which further contributes to the effective survival of *Ornithodoros*.

As in the louse, the borreliae penetrate into the celomic cavity of the tick. First small, thick, and cork-screw-like forms are seen, as well as thin, elongated borreliae. They have a predilection for the central ganglion, the two coxal and salivary glands, and the genitals including the gonads. This results in transovarian transmission which does not take place, however, in all instances. Borreliae pass with the eggs but not all larvae become infested (7). Details were studied by Aeschlimann (8) and Wagner-Jevseenko (708). The borreliae appear to penetrate the follicular layer around the ovules, pass through the surface of the eggs, and reach the yolk through the protoplasmic cortex. The number of infested eggs varies according to the species: up to 100% *O. turicatae*, 80% *O. moubata*, but less than 2% *O. hermsi* eggs will become infested (222, 303). Borreliae multiply during larval development and reach the salivary glands, so that first-instar (F₁) nymphs are already infested.

The organotropism is probably of chemical nature. Bruen and Blatter (104) believed that it might be due to an oligosaccharide such as glucose.

Tick vectors and their life cycles have been discussed by Davis (219, 220) who listed in the Americas *O. hermsi* Wheeler, Herms, and Meyer 1935 and *O. parkeri* Colley 1936 from the Western United States; *O. rudis* Karsch 1880 from Colombia, Venezuela, and Panama; *O. talaje* Guérin-Ménéville 1849 from the same area and also Argentina; and *O. turicata* Duges 1876 from the United States and Mexico, among the *Borrelia*-carrying ticks in the Western Hemisphere. Desportes and Company (237) enumerated *O. tholozani* Laboulène and Méguin 1882 and other ticks of Asia Minor and Central Asia. Enigk and Grittner (257) presented a general survey of ticks and their biology.

Baker and Wharton (41) in their monograph suggested that borreliae evolved with Acarinae. This hypothesis implies that borreliae were primarily symbionts or parasites of ticks, specialized in *Ornithodoros* species by genetic evolution and adaptation, and invade mammals only by chance. This theory can be brought in accord with that of Nicolle and Anderson (520, 522) that ticks conserve and lice propagate borreliae, even though the latter authors believed that borreliae originated as parasites of small mammals, which does not seem plausible from today's vantage point.

The monographs of Baker and Wharton (41) and of Arthur (26) on ticks, that of Cooley and Kohls (200) on Argasidae in the Americas, the list by Hoogstraal of ticks in North Africa (371) and by Galouzo (290) in Central Asia, the review by Anastos (15) of Ixodides in the U.S.S.R., and numerous special communications of the group led by Geigy, Burgdorfer, and Aeschlimann on African ticks (*vide infra*), together with the reviews by Nicolle *et al.* (529) and by Heisch (343), should be consulted for details.

Other and equally important reviews of *Ornithodoros* and tick-*Borrelia* relationships include that of Bohls (89), who listed *O. venezolensis* among the tick vectors in the Americas, and described their habits and habitats as follows. In the Western United States and in Texas, *Ornithodoros* like to establish themselves firmly in caverns, in Southwest Kansas in burrows of prairie dogs, in the State of Washington in owl burrows, and in Southwest Texas in rodent burrows. Domestic animals do not appear to be hosts of these ticks in the United States but *O. venezolensis* and *O. talaje*

breaks have been recorded by several writers (156, 607, 608, 661, 664, 736), as well as the export of the disease to Kenya (296) and its movement from and to the Sudan (411). Sparrow (664) and Bryceson *et al.* (127) consider Ethiopia a highly important epidemic focus, with about 1,000 cases and 5% mortality per year in Addis Ababa. Relapsing fever in Ethiopia is at home also in the South-West Highlands especially among seasonal coffee bean pickers, along the railroad from the Red Sea Coast, and in the lowlands of Jijiga, where the tick-borne form is also present.

Whereas *B. hispanica*, an Eastasian tick, followed the route of the Moslem Conquest to the West, *B. recurrentis*, probably of African origin, spread by war and migration to all parts of the world except Australia, New Zealand, and Polynesia. Tick-borne borreliae have become louse-adapted in the laboratory but have not mutated into the epidemic strain. Lice do not transmit borreliae to their progeny by the transovarian (hereditary) route, which is contrary to most *Borrelia*-bearing ticks. Each vector-lice has to be infested individually, and less than 20% of the lice fed on patients are able to transmit the disease. The presence of infected man or some other, hitherto unknown reservoir appears to be a *condicio sine qua non* for the maintenance of relapsing fever caused by the epidemic strain, *B. recurrentis*, or else tick-borne borreliae mutate into a louse-borne type by a hitherto undiscovered mechanism. The continuity of louse-borne relapsing fever, demonstrated by Bryceson *et al.* (127), certainly speaks in favor of contiguous and continuous man-to-man transmission, while *O. moubata* and lice feeding on the same persons in Africa yet offer food for thought and consideration along another course.

Endemic Relapsing Fever

Endemic relapsing fever is tick-borne. Its ecology coincides with that of *Ornithodoros* species carrying human pathogenic borreliae. The occurrence of this type of relapsing fever also depends on the frequency of contact between man and arthropod. Man and *Ornithodoros* meet according to the life habits of the species involved. *O. moubata*, dwelling in huts inhabited by man, will have a greater and more frequent opportunity to feed on him and transfer bor-

reliae to man than will *O. parkeri*, which avoids human abodes. Man may, however, invade the habitats of the tick as a temporary visitor (hunter, vacationer, soldier, and so forth), or as a permanent resident when new lands are opened for cultivation and new roads are built.

Tick-borne relapsing fever is usually at home within the 24°C summer isotherm (471). *Ornithodoros* do not live in the monsoon and rain forests. They occur in semi-desert areas, but man seldom goes there. In colder climates these arthropods are active only during the warm season, but all year around in the tropics. The feeding time of the nymphs and adult ticks usually coincides with the period when relapsing fever is most frequent. In the Kashmir, however, ticks breed during the winter, but relapsing fever is most frequent in the summer (394) when man more often invades the habitats of ticks.

Lice have to be crushed to transfer *Borrelia*. They die as a result of such an injury and thus can infect only one person. However, ticks do not have to be damaged to transfer the borreliae they carry. A single *Ornithodoros* may infect a different person or animal at each feeding. Adult ticks usually transfer borreliae through their coxal fluid, which is excreted during or after feeding. Some ticks, especially young specimens and developmental forms, may transmit borreliae with their bite. Since ticks do not move far from their burrows, they infect only man and animals that enter their limited area. Some *Ornithodoros*, as *O. moubata*, seldom move farther than about 20 meters under their own power. However, they can be carried by man or animals to new locations and may originate new endemic foci but not epidemics.

At present, the best known foci of tick-borne relapsing fever are in Northwest and West Iran (591), in the desert-steppe regions of Central Asia (564), in Azerbaijan principally on the Aspheron Peninsula (39, 585), in Soviet Georgia (746), Southwest Turkestan (586), Turkmenia (566), Kazakhstan (651), Uzbekistan (657), along the Southwest Littoral of the Mediterranean (686), in the Arab countries (36), Israel (253), Kenya, Tanzania, and Uganda (303), South Africa (556), the Kashmir (600), in the Western part of the United States (69, 740), especially in Oklahoma (274), Kansas (183), Texas (195, 722), Oregon (218,

283, 356), and California (70, 652).^{*} Only scattered cases have been reported in the United States with the exception of an incident involving a small scout troop which visited a cave infested with *O. turicata* in Kansas (U.S. Communicable Diseases Center report). Several other occurrences of tick-borne relapsing fever were discussed in the chapter on *Ornithodoros* and the borreliae carried by them.

Reports from South America are meager. Marinkelle and Grose (474) isolated an unidentified *Borrelia* species from a bat (*Natalus tumidirostris*) in the large Macerogue cave near San Gil, in Colombia. This indicates that borreliosis is still present in that country. Vigers Earle (705) reported tick-borne relapsing fever in Ecuador, Colombia, and Venezuela.

An interesting summary of the relationship of the types of human habitations to the tick population was published by Walton (715). In regions where ticks are not infested in large numbers, the infection may be smoldering. An example is Madagascar, where *B. duttonii* is maintained by transovarian passage in relatively few individual *O. moubata* (189, 517). In Panama, the proportion of *Borrelia*-infested ticks may not have changed recently, but since canvas cots are replacing the old board or bamboo beds the ticks have been deprived of their hiding places, which has resulted in a lower infection rate in man (182).

As stated, soldiers, hunters, laborers, and tourists entering tick-infested areas are frequent victims of relapsing fever (137, 182). Local inhabitants of endemic areas may have acquired a certain degree of immunity during childhood (73). Therefore, it is principally the newcomer who becomes ill in such regions (705). This was the case in Cyprus during World War II where tick-borne *Borrelia* infestations were discovered also in local miners (291, 738). Tick-borne relapsing fever appeared in 41 soldiers entering native huts in Transvaal (492), in troops and travelers moving along tick-infested roads in Madagascar (189, 430), in the caravanserais of Iran (245, 739), and in the mountains of California where hunters and vacationers had used abandoned huts often infested with ticks (729). An episode of tick-borne relapsing fever

^{*}Thompson *et al.* (J.A.M.A., 210:1045, 1969) recently called attention to tick-borne relapsing fever also in the State of Washington.

in children who followed a porcupine into a cave was described in Palestine (6). Bates *et al.* (68) studied 6 cases in boys who went hunting in the Arriján area of Panama, were badly bitten by ticks, and developed relapsing fever. Konitzer (419) reported the occurrence of the disease in Arabs sleeping in a cave. Severe relapsing fever developed in soldiers visiting caves near Damascus (625). Cooper (201) found infected soldiers who had acquired the disease in caves, old dugouts, tank traps, and trenches infested with rodents in Tobruk. An identical situation developed in Cyprus (291, 738). Ashbel (29) compared the strains isolated from soldiers in Tobruk and Palestine, and found some differences. But soldiers off duty also may acquire tick-borne relapsing fever, such as one who chased a porcupine into a cave near Jerusalem (253).

Many infested ticks live in the desert areas of Africa (471), in the less inhabited regions of Central Asia (33, 398, 571), and in the Caspian area (39, 475, 746). Their contacts with man are few, and therefore the human infection rate is low. Sometimes the tick vector is associated with domestic animals, as with sheep in the Kashmir (394), and create a hazard to their tenders; or with fowl kept in living huts, as in East Africa (432). The huts in East Africa abound with tick vectors of *Borrelia* (338, 340).

It is said that indigenous people from East Africa carry *O. moubata* with them for good luck. This tick becomes easily domesticated. The relapsing fever in the Witwatersrand gold mines (742), and among other migrant Africans in South Africa (19), is a disease imported by man. Geigy (303) attempted to acquire "good-luck" ticks from these people for investigating the borreliae in them but did not succeed. *O. moubata* not dwelling with man is irregularly distributed in Africa but its ecology in the wild is the same as that of the warthog (303, 711). Geigy found it in the hair of warthogs which are hunted, and agrees with Walton (711) that the original habitat of *O. moubata*, the vector of *B. duttonii*, was probably with those animals but then the arthropod was transferred to huts by man carrying warthog pelts or carcasses.

Other *Ornithodoros* (principally *O. tholozani*) move with caravans, on sheep, camels, and other animals driven from one place to another, and may make their homes in used or abandoned stop-