

FIGURE 14. *Ornithodoros tartakovskyi*, male, ventral view. Photograph by Dr. T. C. Orihel.

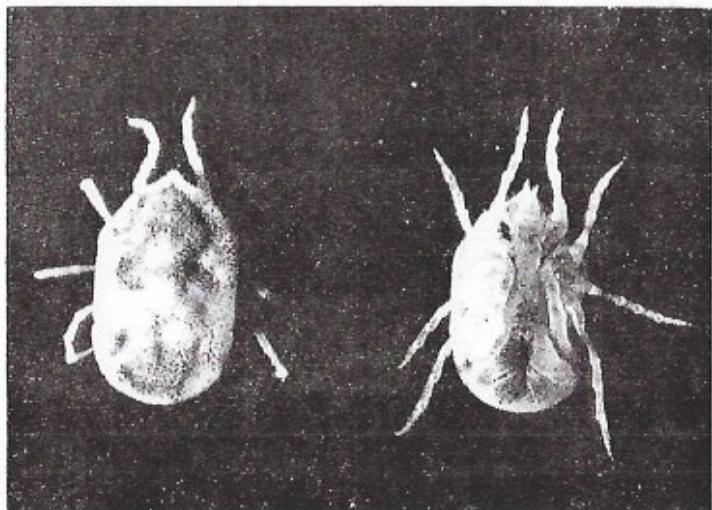


FIGURE 15. Dorsal (left) and ventral (right) view of *Ornithodoros tartakovskyi*, male.

spect to American ticks. *O. rufus* is synonymous with *O. venezuelensis* (*O. venezuelensis*) and is the vector of *B. venezolensis* Brumpt 1921 and *B. neotropicalis* Bates and Saint-John 1922. *B. neotropicalis* has been reported also from Panama where it is transmitted by *O. rufus*. *O. talaje* bites animals but not man. Clark (182) believed that it transfers the infection only from animals to animals, whereas *O. rufus* takes part in the animal-vector-man-animal cycle. Davis also discussed the role of coxal fluid in the transmission of borreliae. Coxal fluid is expelled by the feeding tick as it becomes engorged with blood. It contains and transmits borreliae to the wound caused by the bite of the tick. Many ticks, like *O. turicata*, and particularly nymphs, do not expel coxal fluid but infect through their bite. This will be discussed in detail later.

Horsfall (374) added to the list of ticks carrying relapsing fever *O. brasiliensis* that harbors *B. brasiliensis*, *O. tholozani* as a carrier of *B. babylonensis*, *O. normandi* as a vector of *B. normandii*, and *O. dugesii* as a carrier of *B. dugesii*. It is doubtful, however, that *B. babylonensis* and *B. normandii* represent independent species. Horsfall emphasized that *O. erraticus* has two subspecies, namely, *O. erraticus erraticus*, the large form, the vector of *B. hispanica*; and *O. erraticus sonrai*, the small form, carrying members of the crocidurae subgroup. *O. e. erraticus* likes some moisture, *O. e. sonrai* dry burrows.

Nicolle and Anderson (524) stated that *Ornithodoros* have to be infected in the nymphal stage to become effective vectors.

Ornithodoros, therefore, may propagate borreliae from one generation to another. The borreliae may be transmitted to man and animals through the coxal fluid which contaminates the site of the insect bite, or, principally by young nymphs and in North American species also by adult ticks, through the salivary glands. The tick does not have to be injured, as does the louse, to transfer *Borrelia* to man or animals.

Observations on individual *Ornithodoros* and *Borrelia* species that are important from the medical point of view follow.

Specific Ticks and Borreliae

Ornithodoros moubata and *Borrelia duttonii*

Ornithodoros moubata, the eyeless tampan, has four subspecies, *O. compactus*, *O. apertus*, *O. porcinus*, and *O. porcinus domesticus*.

cus (714, 715). It carries *B. duttonii*. Its principal homes are West and East Africa. Manson and Thornton (467) stated that the infection is severe, with many complications, in Europeans; severe but with few complications in the indigenous population. Moreover, these authors believed that several strains of *B. duttonii* may be carried by *O. moubata*. The organisms were described as 20 to 35 μ long, about 0.25 μ wide, with 5 to 9 spirals. Short and longer forms were common. Of 600 *O. moubata* ticks, 29% harbored borreliae. Dubois (247) also found different serotypes of *B. duttonii* in this tick.

Feng and Chung (270) could observe borreliae for a long time (11 days) in the stomach of *O. moubata* after a blood meal, but the borreliae appeared in the celomic fluid and in the salivary glands, neural ganglion, and coxal glands of the tick as early as within 6 hours. Multiplication of the borreliae took place in the organs and celomic cavity, by transverse division. No borreliae were seen by these authors in the Malpighian tubules or in the feces. The same writers stated later (271) that the central neural ganglion is the predilection site of *B. duttonii*. After long starvation, the borreliae may disappear from the coxal fluid and ovaries (428). The tick can fast long, even a year or more, and remain



FIGURE 16. Holes in fallen trees, where *Ornithodoros turicata* were found.

alive. Adults usually feed every 6 weeks, nymphs every 2 to 3 weeks.

The subspecies of *O. moubata* usually prefer a single animal



FIGURE 17. Rodent burrows harboring *Ornithodoros turicata*.



FIGURE 18. Semidesert in Asia, harboring *Ornithodoros erraticus* with small rodents.

host for their blood meal (309, 709). The blood meal lasts 20 to 30 minutes but the blood is digested very slowly. Precipitin tests showed its presence 7 months after feeding (721). The blood passes through the esophagus into the midgut and its diverticula which are relatively spacious and have quite elastic walls.

Molting takes place between meals. The life-span of *O. moubata* is 2 years, on the average. They withstand severe dehydration (110, 134).

Transovarian transmission of borreliae is the rule in *O. moubata*. Males may harbor *B. duttonii* in the genital organs but do not transfer them by the sexual act (313). Freshly fed females



FIGURE 19. African forest with rodent burrows. Photograph by Dr. Clyde Jones.

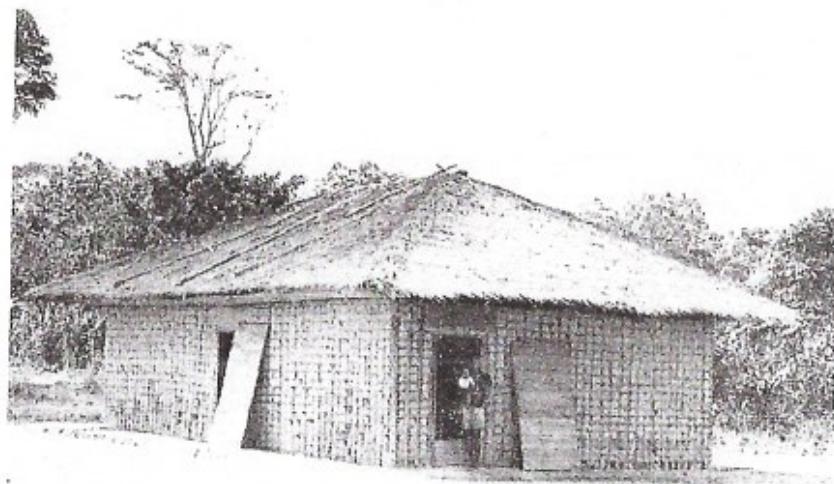


FIGURE 20. African hut in which *Ornithodoros moubata* thrives. Photograph by Dr. Clyde Jones.

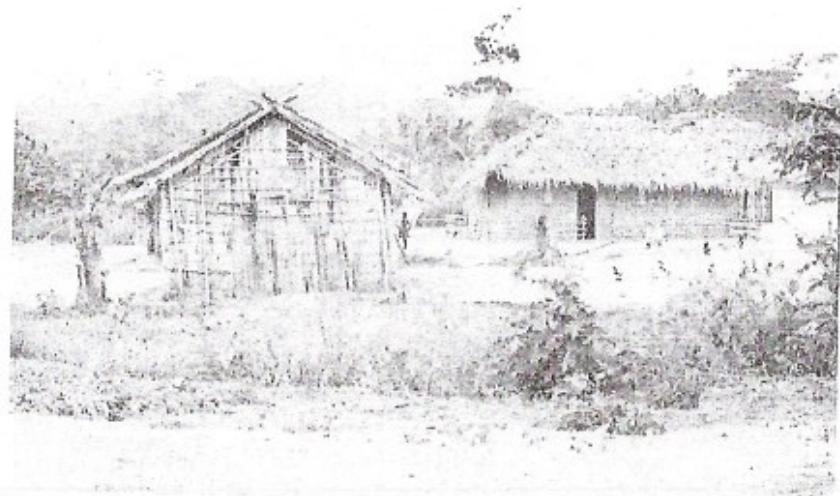


FIGURE 21. Huts with wooden walls (foreground) and clay walls (back) in Africa, where *Ornithodoros moubata* has been found. Photograph by Dr. Clyde Jones.

mate, burrow into the sand, and lay 30 to 80 eggs of about 0.6 mm diameter (303). The six-legged larvae hatch best at about 25° C. Six 8-legged nymphal stages follow, then the adult stage, within about 8 months. About 40 to 60% of the offspring are infected with *B. duttonii* (313). This proportion may vary, however, from one village to another, with an average of 15% (303). The salivary glands are irregularly infested in adults but contain many borreliae in the nymphs (699). Therefore, young adults and nymphs propagate the infection principally through their saliva, whereas adults spread it through the coxal fluid (302). The tick becomes infective 5 to 6 days after feeding on blood that contains *B. duttonii*. The first nymphal instar is the most effective transmitter also because of its rapid mobility. Geigy and Burgdorfer (129, 300, 301, 302, 306) demonstrated the efficiency of *O. moubata* in maintaining the infection without a vertebrate host.

O. moubata is found only in Africa but not in the dry desert,



FIGURE 22. Huts in which man and fowl live together in Africa, where *Ornithodoros moubata* has been found. Photograph by Dr. Clyde Jones.

the rain forest, or above an altitude of 2,000 meters (6,600 ft.). *O. moubata* prefers fine loam on which African huts are built and in which man and fowl live together (712). *O. moubata* does not

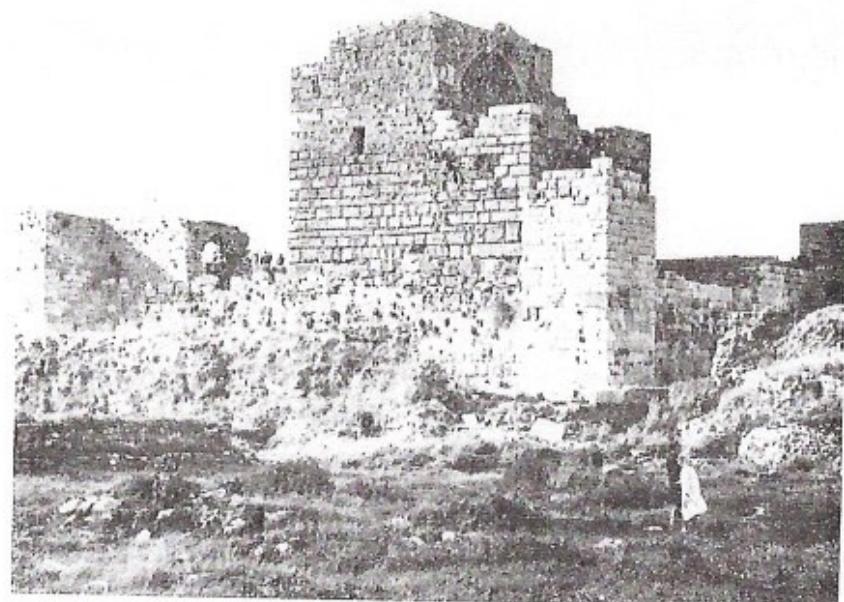


FIGURE 23. Ruins in the Mediterranean region where *Ornithodoros erraticus* was found.

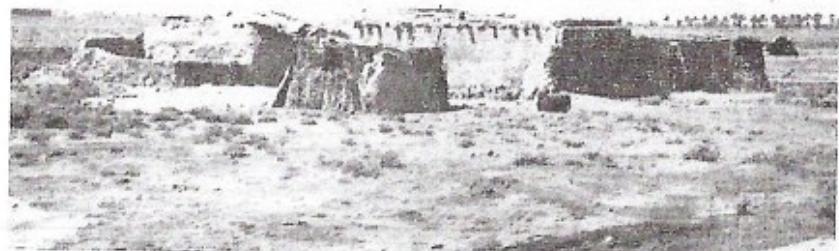


FIGURE 24. *Ornithodoros tholozani* was found in this building.

FIGURE 25. The home of *Ornithodoros tartakovskyi*.FIGURE 26. *Ornithodoros talaje*-infested building.

climb well, and likes to bury itself in the soil a few centimeters deep, particularly near dry places where people usually sit. It may be found in cracks, holes, and crevices of the mud floors and sometimes also in the grass walls. *O. moubata* appears to be domesticated but is still found in burrows of wart hogs, porcupines, hyenas, aardvarks (*Orycteropus*), and bats (344). Walton (711) believed that its original hosts were these animals, and that it came to human habitations with hunters. This tick adapts itself easily to other hosts and may learn to bite cats, dogs, and pigs which, however, are not susceptible to *O. duttonii* infections.

O. moubata emerges from its hiding places after sunset. It is attracted to the bodies of people sleeping on the floor, and to fire. All stages, except eggs and larvae, take blood meals.

Details of the transmission of *B. duttonii* were worked out by Geigy and his co-workers (301, 302, 306, 311, 312) and others. Burgdorfer (129) observed that borreliae shorten from about 22μ to 10μ , gather at the stomach wall, and penetrate it. No borreliae are present in the stomach two weeks after the infective meal. The hemolymph of the tick sometimes harbors borreliae as early as the second day. Multiplication takes place in the celomic cavity. The coxal glands and the central ganglion may be invaded even on the third day, the Malpighian tubes somewhat later, but their lumina remain free from borreliae. There is a crossing of borreliae between the hemolymph and the organs for which it has predilection. The process of invasion of the *Ornithodoros* is slower at 20° than 30° C environmental temperature. Varma (699, 700) found the central ganglion infected in all instances, whereas the coxal glands harbored borreliae in 75%, and the Malpighian tubules in 25% of the examined ticks. Sarasin (622) believed that *B. duttonii* can enter any firm organ of *O. moubata* but that it lives always in intercellular spaces except in the oocysts. Aeschlimann (8) studied the transovarian transmission. *B. duttonii* enters oocysts early. The borreliae are located in the intercellular spaces but become intracellular after the tunica propria is formed.

Grün (327) observed that *O. moubata* did not acquire *B. duttonii* when this organism became nonpathogenic after numerous animal passages. The same strain of *O. moubata* could, however, transmit *B. hispanica*. Some loss of virulence of *B. duttonii* in the

5th generation of *O. moubata* was described by Aeschlimann (9). The transstadial and transovarian development, including the problem of filial variations in relation to the number of infective progenies, was summarized by Burgdorfer and Varma (130).

Colas-Belcour *et al.* (189) studied ticks from Madagascar which were not naturally infected and found that about 50% of these *O. moubata* will acquire *B. duttonii* if given a blood meal containing this *Borrelia*.

Further problems of the *O. moubata*-*B. duttonii*-animal-man relationship were investigated by several workers. Heisch and Grainer (350) found that *O. moubata* living in rodent burrows is not a reservoir for human infection because of the rarity of contact between man and tick in the areas inhabited by wild rodents. Arboni (23) stated that *O. moubata* may live with guinea pigs, rabbits, pigeons, other fowl, and horses, but not uniformly with pigs. Fresh cattle, goat, and sheep serum killed *B. duttonii* but this activity of the serum was destroyed by heating. The origin and quality of the antibodies in these sera are open to question. Geigy and Mooser (305) studied wart hogs, the natural host of a variant of *O. moubata*, without being able to find proof of infection.

Geigy and Herbig (308) stated that *O. moubata* does not have a known and useful natural host. On the other hand, Walton (712) observed *O. moubata* in the Digo district of Kenya near the border of Tanganyika but only in houses that also sheltered fowl. The ticks harbored *B. duttonii* but human cases of infections were rare. Walton considered this an example of an animal reservoir without overspill into the human population. It is possible, however, that the human inhabitants had acquired immunity during undiagnosed episodes of infection in their childhood, or that the ticks preferred to feed on chickens. Schwetz (633) also found infected *O. moubata* but no borreliemia in human beings who lived in the same huts in various localities between Lake Kivu and Lake Albert in the Congo. He explained this as a state of immunity following past infection in the local inhabitants.

O. moubata is an effective vector. It was shown to be able to carry *B. hispanica* for many months in laboratory experiments (296) but not the East African strain of *B. recurrentis*. Baltazard *et al.* (54) had moderate success in transmitting *B. crocidurae* to

it. *B. turicatae* lived in *O. moubata* in the laboratory for a long time but the tick did not transmit the *Borrelia*. Thus *O. moubata* appears to be carrying only *B. duttonii* in nature.

Ornithodoros erraticus erraticus and Borrelia hispanica

Ornithodoros erraticus erraticus or the "large" *O. erraticus* carries *Borrelia hispanica*.

Several strains of *B. hispanica* have been described. We believe, however, with Nicolle *et al.* (528), that both the so-called Moroccan and Mansourian (Bou Znika) strains are *B. hispanica*, as well as those labelled as Tripoli, Portuguese, Peloponese or Greek, and Normandian (South Tunisian) strain. Moreover, we include the atypical Syrian and Algerian strains (511, 625) also in this species.

The disease caused by *B. hispanica* is usually mild (230) whichever subtype is causing it. Exceptions are not rare, however.

According to Muñoz Cosin (510) *O. e. erraticus* is a nocturnal tick. It feeds for 15 to 20 minutes. It tolerates lack of food well even at 28° and 30° C if the humidity is high enough. *O. e. erraticus* apparently requires somewhat higher atmospheric moisture than does *O. moubata*. The borreliae are transmitted to the host after feeding, with the coxal fluid, but infection by the bite of the tick is also possible (277).

O. e. erraticus appears to have followed the route of the Moslem conquest, along the Mediterranean Littoral through North Africa to Spain. It established itself also in Portugal and Greece. The Moroccan strain was found in ticks in burrows of porcupines (230); others also in the dwellings of gerbils, hedgehogs, jackals, and wild rats (54); Muñoz Cosin (510) in addition to the foregoing observed the tick living with foxes, weasels (*Mustela vulgaris*), and pigs. It seems that pigs do not become infected with *B. hispanica* but may disseminate the tick. Neither is there an agreement that foxes are susceptible to *B. hispanica* infection. Baltazard (45) confirmed the findings of Nicolle and his co-workers in Tunisia, and isolated *B. hispanica* from wild rats, man, and *O. e. erraticus* in Casablanca. Delanoë (232) found hedgehogs infected, as well as young jackals. Older jackals appeared to have antibodies against *B. hispanica*. Young porcupines were also susceptible but grown animals had measurable antibodies (231). Similar results were observed in weasels (233). Wild rats were

found infected in Greece (141). Nicolle and Anderson (527) examined closely the relationship of hogs to relapsing fever in North Africa. *B. hispanica* did not circulate in their blood. Even though they may act as host to *O. e. erraticus*, they did not appear to be important as animal reservoirs of relapsing fever. A survey of cave-dwelling bats in Spain (515) showed 4 susceptible species (*Miniopterus schreibersii*, *Myotis myotis*, *Rhinolophus euryale*, and *R. hipposideros*).

Mathis *et al.* (480) commented on the observation that tick-borne relapsing fever in Tropical Africa is due to *O. moubata* with the exception of Dakar, where *O. erraticus* was also found. Boiron (95, 96, 97) investigated this problem and found that 18.5% of the blood and 40% of the brain or spleen specimens from 512 rodents belonging to 9 species were infected. *Cricetomys gambianus* and *Rattus rattus alexandrinus* were most frequently infected, and *O. e. erraticus* was found on them. More cases were in modern Dakar than in the adjacent township of Medina. The number of rat burrows in the hard soil of Dakar was higher than in the light sandy soil of Medina. Also, *O. e. erraticus* appeared to find more feasible moist shelter in Dakar. Boiron also stated that hedgehogs and some reptiles may serve as hosts but man encounters *O. e. erraticus* easily in Dakar.

Not only *R. r. alexandrinus* in Dakar has been found to be an important reservoir but also other rats have been implicated, as the gray rat (*Ratus norvegicus*) in Casablanca (85) and in Algeria (373, 465). The role of the porcupine in Africa was more closely investigated by Nicolle *et al.* (530). They concluded that porcupines may be reservoirs of *B. hispanica* but live away from human habitation and roads and are, therefore, not an important source of human infection.

O. erraticus was found feeding on crabs when mammalian blood was not available. The crabs were resistant to borreliae and their blood remained free of them (50).

Jahnel (382) studied the fate of *B. hispanica* in hibernating dormice. The borreliae disappeared faster in the cold than at room temperature. If the animals were infected during hibernation, *B. hispanica* was recovered over longer periods than when the infection took place before hibernation.

B. hispanica, Tripoli strain, was maintained by Nicolle and Blai-

zot (531) through 12 rabbit passages without loss of virulence. Chorine and Colas-Belcour (167), however, found gradual diminishing of virulence after human passages, at a slower pace also in rodents. The incubation period also becomes longer.

Brumpt (123) described *B. babylonensis* from *O. asperus* which, however, was easily transmitted by *O. persica*. It caused many relapses in guinea pigs and the organisms in the blood were as numerous as in *B. hispanica* infections. *O. tholozani* and *O. erraticus* could not be infected with this strain. *O. coriaceus* (which does not transmit any known *Borrelia*) could not transmit it. This strain, unfortunately lost by now, may be a variant or a transient organism, especially since *O. asperus* was shown to transmit *B. persica* in the laboratory. The geographical location of the finding of this *Borrelia* tips the balance in favor of *B. babylonensis* being a strain of *B. persica*.

Experimentally, *B. hispanica* has been transmitted to *Argas persicus*, *O. moubata*, *O. savignyi*, *O. tholozani*, *O. turicata*, *Haemaphysalis inermis*, *Pediculus humanus*, *Hemistomus suis*, and *Xenopsylla cheopis* by Muñoz Cosin (510) and to *O. moubata* by Kudicke *et al.* (428). It was isolated from the dog tick *Rhipicephalus sanguineus* in Greece (141). Davis and Mavros (227) observed its survival in *O. nicolai* for 5 years and noted that it was transmitted to the F₁ generation in this tick. Baltazard *et al.* (54) transmitted *B. hispanica* by *O. savignyi*, *O. moubata*, and *Rhipicephalus sanguineus* in the laboratory. It appears that this *Borrelia* can be transmitted in the laboratory by many genera and species of insects. It is questionable if the same holds true in nature.

Ornithodoros erraticus sonrai and the "Crocidurae" Subgroup

Ornithodoros erraticus sonrai or the "small" *O. erraticus* is the vector of a group of borreliae that are only moderately or not at all pathogenic for man, but may cause disease in rodents (60, 480). The first member of the group, *B. crocidurae*, shows some cross-immunity with *B. duttonii* (525). Some experts consider *B. crocidurae* identical to *B. merionesi* and *B. microti*, whereas *B. dipodilli* of Kenya is regarded as a distinct strain (303). Baltazard *et al.* (53, 60) reported this group in Senegal, from the countries along the Southern Mediterranean, Iran, and East Africa. There is consider-

able disagreement concerning the status of the individual strains of the crocidurae subgroup. One of the principal reasons for the separation of this group was the difference in the tick vector. *B. crocidurae* was isolated from the wild shrew (*Crocidura stämpfii*) in Dakar by Leger in 1917. *B. crocidurae* is more virulent than the other members of the subgroup and often fatal for rats (*Cricetomys gambianus*, *Rattus rattus alexandrinus*, *Ratus norvegicus*, and *Arvicantis sp.*), rarely for *Epimys*, *Rattus* and *Mus musculus* (478). Local people in Dakar appeared to be immune to *B. crocidurae* (481). Baltazard *et al.* (62) isolated it in Turkey, and found that this strain causes prolonged disease in guinea pigs but only weak or subclinical infections in man. Colas-Belcour (188) considered *B. crocidurae*, *B. microti*, and *B. merionesi* immunologically interrelated but different from *B. hispanica*. Dirk van Peenen (241) studied borreliae in *O. e. sonrai* that were found with Nile rats (*Arvicantis niloticus*) by Davis and Hoogstraal in Egypt. Newborn rats and mice seem to be susceptible to *B. crocidurae* but adult guinea pigs are not. Some investigators (195, 303) emphasized that *O. e. erraticus* is not hospitable to *B. crocidurae* but that this organism was transmitted by the ovum to the F₁ generation of that tick subspecies. Vertebrates were infected during feeding, through the saliva of the infected tick. *O. e. erraticus* did not carry other members of the crocidurae subgroup.

B. merionesi was isolated in South Morocco by Baltazard. It was studied by Baltazard's group (see above) and was found to be different from *B. duttonii* and *B. hispanica*. It frequently caused fatality in rats and hamsters. Blanc and Maurice (84) found it nonpathogenic to man.

B. microti was isolated from *Microtus mystacinus* and from *Tatera indica*, as well as from rats and *Cricetulus migratorius* in Hessarak and other localities in Iran by Rafyi (592). This strain did not infect guinea pigs but caused some disease in man. Delpy (234) studied this organism in Iran and found 35% of *Tatera*, 14.8% of *Cricetulus*, and less than 12% of other rodents, such as *Nesokia*, *Mus*, and *Microtus*, infected with it. *Meriones shawi* also carried this *Borrelia*.

B. dipodilli was described by Heisch (342, 343) from pygmy gerbils (*Dipodillus gerbillus*) in Kenya. It was mildly pathogenic

for rats, mice, monkeys, and young rabbits, but not for guinea pigs and man. Heisch believed that *B. dipodilli* is related to rodents in North Africa and the Middle East, and posed the question whether or not *B. duttonii* has evolved from it because of the belief that *B. duttonii* was originally a rodent-oriented *Borrelia*.

In laboratory experiments, *B. crocidurae* could be transmitted to the human louse but *P. humanus* did not transfer this organism to man (95, 98, 331). Monkeys have been found susceptible to *B. crocidurae* as well as to *B. merionesi* and *B. dipodilli*. The last (as well as *B. duttonii*) was able to infect the monkey louse, *Pedicinus longiceps*, and transmit the borreliae among nonhuman primates. The monkeys did not become seriously ill. This may point toward an additional life cycle of the members of the crocidurae subgroup. Ticks other than *O. e. sonrai* are not very hospitable to this group of borreliae (594). Therefore, adjustments, accommodation, and adaptation must have taken place before the present tick-reservoir of *B. duttonii* could develop, if the theory of Heisch is correct.

Ornithodoros tholozani (papillipes) and Borrelia persica

Ornithodoros tholozani (synonym: *Ornithodoros papillipes*) appears to be identical also to *O. crossi* which carries the Kashmir strain of *Borrelia*. It may have several subspecies. *O. tholozani* carries *B. persica*. *B. persica* was described by Dschunkowsky in 1913 (245). The domain of *O. tholozani* spreads from Lybia through Western Egypt, the Arab countries, Cyprus, and Turkey, to India and Central Asia. It is possible that *B. uzbekistanica* and *B. sogdiana* are variants of or identical to *B. persica* (444).

O. tholozani has one larval and 3 to 4 nymph stages. Each one of these stages feeds on a vertebrate at least once but the adults take a blood meal more often (691). Hereditary transmission is the rule (6, 42, 506, 691) but Bourgain (108, 580) failed to prove it. He suggested that the nymphs become infected during their blood meals.

O. tholozani lives for a long time. Bourgain (107, 108) reported that nymphs may live 5 years, if no food is available that is a prerequisite for molting; adults live about 7 years.

Adler *et al.* (5) and others showed that *B. persica* is transmitted by the bite of *O. tholozani* and not by the coxal fluid. Slavina (651)

found 2% of ticks collected in their natural habitat infected with *B. persica*.

It appears that infected nymphs (108) and adult ticks (42) may lose borreliae during their lives, and the virulence of the strains may decrease in the ticks. Pirot and Bourgain (580) stated that infected ticks apparently die sooner than noninfected individuals. This problem should be further investigated since Balashov (42) saw an increased infection rate in successive tick generations, from 11 to 47%.

O. tholozani lives in caves and burrows of small animals in Central Asia in oases along the edges of the woodlands (563), and also with man. It was found in the huts of regimental followers in Qetta near the Afghan border (114), and collected in abandoned piggeries (691), often near fowl and camels.

Lice, especially those adapted to feeding on suckling rabbits, will take up *B. persica* (161).

O. tholozani has been infected artificially with *B. sogdiana* (21) but this experiment may have involved merely the transmission of the same strain or its variant. *B. recurrentis* can survive in *O. tholozani* (656) but lice fed on patients infected with *B. persica* do not transmit this organism. Rafyi and Maghami (594) were able to infect *O. tholozani* with *B. hispanica* and *B. microti*.

O. lahorensis has been thought of as a possible vector of *B. persica*. Pavlovskii (563) and others proved that this is not possible because *O. lahorensis* does not bite man and even though it acquires human-pathogenic borreliae by feeding on rodents in the laboratory, the borreliae die off in it rather quickly.

Babudieri (36) encountered two possibly distinct strains of *B. persica* in Jordan. One, the rural form, caused disease in sheep-herders, migrants, road builders, and other persons who rest in caves with dry and sandy floors harboring *O. coniceps*. The peak number of infections was in the winter. The other, the urban form, appeared in badly maintained and ventilated houses with earthen floors. The greatest number of infections was observed in the summer. Babudieri believed that *O. tholozani* is the vector in urban areas, where domestic rats could serve as a reservoir of the infection. It is still being debated, however, whether *O. coniceps* is a vector of borreliae (*vide infra*).

Ornithodoros tartakovskyi and *Borrelia latyschewii*

Sofiev (655) described *Borrelia latyschewii* from *Ornithodoros tartakovskyi*. This *Borrelia* was isolated from gerbils (*Rhombomys opimus* and *Gerbillus eversmanni*) as well as from *O. tartakovskyi* caught in burrows of rodents. It causes mild disease in man, often only a one-day fever, and one or two attacks in mice but not in rats, guinea pigs, and dogs. The number of borreliae is low in the blood even after successful infection. Sofiev and Leitman (656), analyzing tick- and louse-borne relapsing fever in Central Asia, pointed out that this *Borrelia* cannot be transmitted by lice to man in that region, nor can *O. tartakovskyi* propagate *B. recurrentis*. The latter *Borrelia* will, however, survive in *O. tartakovskyi* for 4 months.

Baltazard *et al.* (55) isolated *B. latyschewii* from *O. tartakovskyi* in Iran, near Meshed. This strain did not infect adult guinea pigs which is unusual in Old World tick-borne borreliae. The organism was slightly pathogenic for man but was not found in nature in rodents with which the tick lived. It appeared to prefer the burrows of merions and other wild rodents, tortoises, lizards, and toads. Wild rodents such as *Meriones*, *Microtus*, and *Rhombomys* could be infected in the laboratory.

O. tartakovskyi exudes coxal fluid some time after it has left the host on which it fed. This, perhaps, explains the small numbers of borreliae transmitted into the animal by the bite of the tick.

The natural reservoirs of the Central Asian and the Caucasian parts of the U.S.S.R. were studied by Pavlovskii (565). *Dryomys nitedullus*, a small, widely distributed rodent, is readily infected with borreliae and carries them for a month or longer. The principal foci were not associated with forests but with oases along the base of the mountains. Petrishcheva (571) investigated the duration of natural foci in Turkmenia. Not only *O. tartakovskyi* but also *O. tholozani* and *O. neerensis* were found. Caves inhabited by *Hystrix hirsutirostris* were studied but a change of the inhabitants of the burrows did not reduce the danger of infection for man. Of 13 foci, 8 were active 16 to 19 years, 2 for 21 to 29 years, and 3 for 30 years. This bears witness to frequent and sustained transmission cycles. Chickens, pigeons, gold fish, and 19 bird and reptile species were found resistant to *B. latyschewii*.

and *B. persica* in the same area (496). No borreliae were found in 1,144 reptiles caught in homes. Thus, reptiles cannot be considered a reservoir of Central Asian tick-borne relapsing fever borreliae.

O. tartakovskyi intrudes into animal sheds, cattle serving as a source of its blood meals. It may also invade floors and the lower parts of walls, hiding in cracks, holes, and crevices. Moreover, when new lands are being opened for agriculture, people may come into contact with *Borrelia*-carrying ticks, and the cycle tick-rodent-tick may be extended to tick-rodent-tick-man-tick-man-(rodent)-tick.

Ornithodoros neerensis is also supposed to carry *B. latyschewii* (566, 587). It is not known if the two tick strains are identical or related.

Ornithodoros verrucosus and Borrelia caucasica

Ornithodoros verrucosus, the vector of *Borrelia caucasica*, lives in burrows of merions (*Meriones erythrourus caucasicus*), *Apodemus sylvaticus*, and *Mus musculus*. The disease in man may be severe and consist of 10 to 15 relapses within 3 months. Chubaryan (171) found jerboas (*Alactaga elater*, *A. williamsi*) susceptible to the infection. Laboratory rodents acquire mild disease or are only slightly susceptible to this *Borrelia*. Guinea pigs develop several attacks. To the knowledge of this author, *B. armenica* has not yet been studied outside the U.S.S.R.

Ornithodoros zumpti and Borrelia tillae

Geigy (303), when considering *Borrelia tillae*, regarded it as a phylogenetic problem. It may have evolved from human-borne *B. duttonii* by progressive specialization because *O. moubata* does not feed on domestic rodents, and wild rodents are resistant to *B. duttonii*.

Zumpt (748) described the tick vector in 1959. Zumpt and Organ (749) reported on *Borrelia tillae* isolated from *O. zumpti* Heisch and Guggisberg living in holes of the South African field vlei rat (*Otomys saundersiae*). White mice and the multimammalian rat (*Rattus natalensis*) are highly susceptible to the infection. Patas monkeys (*Erythrocebus patas*) and adult guinea pigs, as well as

some rabbits, were refractory to the infection. Geigy and Aeschlimann (305) succeeded in transmitting *B. tillae* to *O. moubata* but serologic tests and electron microscopic studies showed that *B. tillae* is not identical to *B. duttonii*. Moreover, *B. tillae* was not pathogenic for white rats, hamsters, and merions. On further investigation, *B. tillae* was isolated also from the brains of the four-striped rat (*Rhabdomys pumilio*) and *R. natalensis*. Heisch and Harvey (354) confirmed these findings. One may expect further developments in the study of this interesting *Borrelia*.

Relapsing Fever Vectors and Borreliae in the Americas

Calero (137) surmised that the American relapsing fever strains are tick-adapted *B. recurrentis*. Brumpt (118) believed, however, that American borreliae did not become tick-borne after the Spanish Conquest or after the settlement of the West commenced when louse-borne relapsing fever was introduced. Tick-borne borreliae were probably already present in the western mountain ranges and lands when the first immigrants arrived. Kemp et al. (407), Wynns and Beck (741), Beck (69), Wheeler (727), Davis (271, 218), and others gave detailed accounts of the borreliae and their vectors in the Americas.

Ornithodoros turicata and Borrelia turicatae

Ornithodoros turicata Dugés 1876 is the vector of *Borrelia turicatae* Brumpt 1933. Kemp et al. (406) observed that larvae and nymphs feed 10 to 30 minutes, adults for hours and even for two days. The borreliae are transferred by the bite of this tick. Coxal fluid is secreted after meals but does not contain borreliae. *O. turicata* is easily infected with *B. turicatae*. Practically all adults carry it and propagate the *Borrelia* at least to the F_3 generation (221). Francis (278, 279) observed that starving *O. turicata* may survive for 5 years.

O. turicata has been found in Canada, the Western United States as far east as Kansas, in Mexico, and in South America. Caves, especially those which are entered by goats and sheep, and burrows of redents, such as those of field mice in Central Mexico (483), and burrows of owls and snakes are the habitats of *O. turicata*. It is found under houses in Texas (89) and it is becoming domesticated in Mexican huts and animal barns.