IMPORTANCE OF SYSTEMATICS TO PUBLIC HEALTH: TICKS, MICROBES, AND DISEASE[1]

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ABSTRACT

Ticks are vectors of nematodes, protozoa, rickettsiae, spirochetes, other bacteria, and viruses that cause disease in humans and other animals. Complex relationships have evolved between particular tick species, certain organisms that they harbor and transmit, and susceptible vertebrate host species. Effects of tick-borne organisms on host species vary from asymptomatic to fatal depending on the species involved and their interactions. It is critical that arthropod vectors and the organisms they transmit be identified accurately. Unfortunately, there is a crisis in biosystematics of arthropods due to several factors noted in the introduction. Approximately 80 of the estimated 850 described tick species occur in the United States; although all feed on vertebrate blood, only a relatively small number impact people and livestock directly. These few species, however, are responsible for considerable illness and economic loss. Tick-borne Lyme borreliosis is prevalent in North America, Europe, and Asia. It accounts for more than 90% of all reported vector-borne disease in the United States. Totals of 9,677, 8,185, and 11,424 cases were reported for 1992, 1993, and 1994, respectively, by the Centers for Disease Control and Prevention. An overview of interactions among tick species, tick-borne microorganisms, and hosts is provided, with major emphasis devoted to ticks of the *Ixodes ricinus* species complex and the Lyme disease spirochete *Borrelia burgdorferi* sensu lato. Systematics play a crucial role in understanding these interactions.

Complex and fascinating relationships have evolved between particular tick species, certain organisms that they harbor and may transmit, and susceptible vertebrate host species. The effects of tick-borne organisms on host species vary from asymptomatic to fatal depending on the species involved.

For obvious reasons, it is necessary to recognize tick species and the organisms they harbor before a rational plan can be developed for tick control or prevention of disease. Likewise, if a tick bite has occurred, the clinician needs to know whether and how to treat the patient. Identification of tick species is crucial to both decisions. Identification of the transmitted organism is also desirable prior to attempts at intervention, and this may involve complicated taxonomic considerations. The science of systematics, therefore, forms one of the foundations of public health, veterinary medicine, and agriculture. Regrettably, there is a crisis in biosystematics of arthropods, especially those of medical and veterinary importance (Oliver, 1988).

The deterioration of biosystematics capacity is due to several reasons, including decreasing numbers of specialists competent to carry out the needed tasks. Difficulties are exacerbated due to poor financial support. The advanced age of many scientists involved in biosystematic research and lack of new specialists being trained in this area suggest that the condition will worsen unless attention is focused on this problem. A recent report titled, "Endangered Species: Doctoral Students in Systematic Entomology" (Daly, 1995) indicates there were 111 such students in 1992 in the United States and Canada, down from 155 in 1982. Forty percent of the departments surveyed that have insect systematists on their faculties have no doctoral students in insect systematics. If the 28% drop recorded between 1982 and 1992 is extrapolated, the number of such students might reach zero by 2017. These facts do not bode well for a world experiencing new and reemerging arthropod-transmitted and other diseases. If the trend of neglecting systematics research and training continues, it will cripple the Consortium Systematics Agenda 2000 goal to discover, describe, and classify the world's species. It

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will also devastate the newly created United States National Biological Service. Clearly, there is a practical and immediate need for expertise in systematics.

Ticks are obligate blood feeders in one or more active stages of their development. They serve as vectors (transmitters) of nematodes, protozoa, rickettsiae, spirochetes, other bacteria, and viruses that may cause disease in humans and other animals. In addition to serving as vectors of the above-mentioned organisms, they may also cause severe problems to hosts simply by feeding on them. Feeding results in blood loss and produces a puncture wound that can itself become secondarily infected. Injections of tick saliva from some species cause an immediate and/or delayed hypersensitivity. Strains of some tick species secrete a toxin that causes an ascending paralysis (tick paralysis) in their hosts that previously was confused with symptoms due to polio. Clearly, ticks are a global medical and veterinary problem causing severe host reactions and large economic losses under certain circumstances. However, only about 10% of the approximately 850 described species impact humans and livestock directly. Approximately 80 species occur in the United States. Some species are host specific, with all developmental stages (larvae, nymphs, adults) feeding primarily on one host species (e.g., *Boophilus microplus* (Canestrini) feeds on cattle), whereas other species (e.g., *Ixodes scapularis* (Say)) may feed on at least 119 different species of reptiles, birds, and mammals (Anderson & Magnarelli, 1994).

The eight major tick-borne diseases that infect humans in the United States today are Lyme disease, relapsing fever, tularemia, Rocky Mountain spotted fever, ehrlichiosis, babesiosis, Colorado tick fever, and tick paralysis (Spach et al., 1993). Of these, Lyme disease (Lyme borreliosis) is most prevalent in North America, accounting for more than 90% of all reported vector-borne diseases, including those vectored by mosquitoes, fleas, etc. Totals of 9,677, 8,185, and 11,424 cases were reported for 1992, 1993, and 1994, respectively, by the Centers for Disease Control and Prevention (CDC) (1994, 1995). Because of the impact of Lyme disease (LD) in North America, Europe, and Asia, this disease has been chosen as an example to illustrate the importance of systematics to public health. Emphasis will focus on the fascinating interactions among vector tick species, the etiologic agent (spirochete) causing LD, and reservoir hosts of the etiologic agent. Inter- and intraspecific differences among tick vectors, among the causative spirochete species, and among vertebrates serving as tick and spirochete hosts are presented in relation to enzootic cycles in nature and human LD. Prior to discussing these relationships, however, it is necessary to provide a brief background on LD to allow a better understanding of variations and interactions that will be emphasized.

Lyme Disease

Lyme disease is maintained in an enzootic cycle in nature. The cycle involves spirochetes as the etiologic or causative agent, rodents as the most common, but not exclusive, reservoir hosts for the spirochetes, and ticks as the vectors of the spirochetes among the rodents or other animals. Humans are incidental to the natural cycle and are not involved in its maintenance.

Symptoms

Lyme disease (LD) is a multi-systemic illness in humans. Early symptoms include an annular erythematous expanding skin lesion called erythema migrans (EM). It generally clears in the center and is often called a "bull's-eye" rash. Approximately 60% of patients present an EM rash, which occurs days to weeks after infection. Other early symptoms may occur with or without EM and include severe headache, extreme fatigue, joint pains, muscle pain, low-grade fever, swollen lymph glands, stiff neck, keratitis of the eyes, and a general feeling of body discomfort. These symptoms may or may not be followed by neurologic or cardiac symptoms and migrating attacks of arthritis (including pain and swelling) especially in the large joints. The neurologic complications include facial palsy, headaches, difficulty concentrating or sleeping, irritability, and poor motor coordination. Cardiac problems often include irregular heartbeat and varying degrees of heart block that may cause dizziness. Late or chronic stage LD often occurs months to years after infection and usually involves chronic arthritis and/or chronic neurologic effects. Clinical symptoms vary from patient to patient. Arthritis caused by Lyme disease is less common in Europe than the United States, but neurologic complications are more prevalent in Europe as is another LD skin manifestation, acrodermatitis chronica atrophicans.

Etiologic Agents

Lyme disease is caused by the spirochete *Borrelia burgdorferi* sensu lato. Spirochetes are a group of motile gram negative spiral-shaped bacteria in the order Spirochaetales, which includes two families: Spirochaetaceae and Leptospiraceae. The

Table 1. Several examples of spirochetal infections.[a]

Spirochete	Human disease	Vector or source of infection
Borrelia		
B. burgdorferi	Lyme disease	Ixodid ticks
B. recurrentis	Epidemic (louse-borne) relapsing fever	Body louse, *Pediculus humanus humanus*
B. hermsii	Endemic (tick-borne) relapsing fever	*Ornithodoros* spp. ticks
B. turicatae		
B. parkeri		
Leptospira		
Leptospira interogans	Leptospirosis (Weil's disease)	Exposure to contaminated animal urine
Treponema		
Treponema pallidum subspecies (subsp.) *pallidum*	Syphilis	Sexual contact, transplacental
T. pallidum subsp. *endemicum*	Bejel (endemic syphilis)	Direct contact with contaminated eating utensils
T. pallidum subsp. *pertenue*	Yaws	Direct contact with infected skin lesions
T. pallidum carateum	Pinta	Direct contact with infected skin lesions

[a] Slightly modified from Pavia (1994).

genera *Borrelia*, *Leptospira*, and *Treponema* are members of these families and contain species that cause several diseases of humans (Table 1) (Pavia, 1994). The pathogenic spirochetes are long, up to 50 μm, but very thin in diameter and exhibit a spiral, helical shape. They have a relatively slow rate of growth: 20- to 33-hour division time compared to *Escherichia coli*'s 20 minutes. Most pathogenic spirochetes (*Borrelia*, *Treponema*) are microaerophilic and were once thought to be anaerobes (Pavia, 1994). *Borrelia burgdorferi* has linear plasmids that code for outer-surface proteins. The spirochetes are extremely sensitive to elevated temperatures (≥38°C).

Originally, Lyme disease in the United States and Europe was thought to be caused by the same *Borrelia burgdorferi* strain that was isolated in New York by Burgdorfer et al. (1982) and described by Johnson et al. (1984). Data now indicate that the etiologic agent of human Lyme disease worldwide is best recognized as *B. burgdorferi* sensu lato, comprised of *B. burgdorferi* sensu stricto (Johnson et al., 1984; Baranton et al., 1992), *Borrelia garinii* (Baranton et al., 1992), and *Borrelia afzelii* (Canica et al., 1993). All three "genospecies" occur in Europe and cause human LD. Only *B. burgdorferi* sensu stricto has thus far been reported to cause LD in the United States. *Borrelia japonica* found in Japan is currently considered to be the fourth "genospecies" in the *B. burgdorferi* sensu lato complex, but its association with human disease is presently unknown (Kawabata et al., 1993).

TICK VECTORS

Borrelia burgdorferi is transmitted to humans by ticks in the *Ixodes ricinus* species complex. The main species responsible for infecting humans with LD in the United States are *I. pacificus* in the far west and *I. scapularis* in the central and eastern United States. In Europe, *I. ricinus* is the principal vector, as is *I. persulcatus* in parts of eastern Europe eastward to Japan. There are areas of geographic overlap of *I. ricinus* and *I. persulcatus* in eastern Europe and western Russia. The previously mentioned four most common vector species are opportunistic, feeding on various species of reptiles, birds, and mammals. Some of the most common hosts of larvae and nymphs, such as the mouse *Peromyscus leucopus* in the northeastern U.S., also serve as excellent reservoirs for *B. burgdorferi*; whereas others, such as deer, supply a blood meal to large numbers of adult ticks, but apparently may play only a minor role (Oliver et al., 1992) or no role as reservoirs for the spirochete (Telford et al., 1988).

There are ten other less common tick species worldwide assigned to the *I. ricinus* species com-

plex (Keirans et al., 1996a), and their vector status is unknown. *Borrelia burgdorferi* sensu lato also has been isolated from other *Ixodes* species not considered taxonomically to be part of the *I. ricinus* complex, and some of these ticks are involved in several different enzootic cycles of *B. burgdorferi* in nature. Some of these enzootic cycles may impact humans indirectly by providing a source of infective spirochetes. For example, in California *B. burgdorferi* is maintained in a natural enzootic cycle in the dusky-footed woodrat *Neotoma fuscipes* by the maintenance vector *I. neotomae*. *Ixodes neotomae* does not usually feed on humans, but *I. pacificus* feeds on humans and woodrats and thus serves as a bridge vector (Brown & Lane, 1992).

Most of the data available on Lyme disease in the United States originate from research conducted in the hyperendemic northeastern region, where the white-footed mouse *Peromyscus leucopus* is the principal reservoir host for the spirochete and *Ixodes scapularis* is the main tick vector (see Lane et al., 1991, for review).

Variation and Heterogeneity of *I. scapularis*

Ixodes scapularis is extremely important from a public health and veterinary medicine perspective. It is the tick vector involved in most Lyme disease and human babesiosis cases in the United States. There has been controversy regarding its specificity for many years and this has intensified during the last decade. It provides a dramatic example of the importance of systematics to human welfare. When northern populations of *I. scapularis* were described as a separate species (*I. dammini*) and identified as the main vector of the Lyme disease spirochete (*B. burgdorferi*), there was a question as to the efficiency of *I. scapularis* (southern populations) to transmit the spirochete. The perceived absence of *I. dammini* (northern populations of *I. scapularis*) in the south was one of the reasons cited that Lyme disease occurred there rarely, if at all. Subsequently, laboratory experiments demonstrated that southern populations were also vector competent (Piesman & Sinsky, 1988; Mather & Mather, 1990). Later, when southern populations from nature were examined, specimens were found infected with *B. burgdorferi* (Oliver et al., 1993a). Because Lyme disease is so important, it justifies a fuller account and also serves as an example of the importance of systematics to public health.

A complete taxonomic history of *I. scapularis* is provided by Keirans et al. (1996b). Briefly, *Ixodes* (*Ixodes*) *scapularis* was described by Say (1821); however, subsequently several tick experts considered it a variety or a subspecies of *Ixodes ricinus* (Nuttall & Warburton, 1911; Schulze, 1939). Later authors accepted *I. scapularis* as a species and Cooley & Kohls (1945) redescribed it. Since that time it was accepted as a species (Keirans, 1982, 1985). There appeared to be general agreement about the taxonomic status of *I. scapularis* for more than three decades, until 1979. At that time, a new species (*I. dammini*) was described (Spielman et al., 1979) based on populations of *I. scapularis* from the northeastern United States.

Since the description of *I. dammini*, there has been disagreement regarding its status as a separate species distinct from *I. scapularis*. Recently, it was determined to be conspecific with *I. scapularis* (Oliver et al., 1993b); and, since the name *Ixodes scapularis* (Say), 1821, had priority over the name *Ixodes dammini* Spielman, Clifford, Piesman & Corwin, 1979, *I. dammini* was relegated to a junior subjective synonym of *I. scapularis* (based on Article 23 of the *International Code of Zoological Nomenclature*, Ride et al., 1985). Data supporting conspecificity of *I. dammini* and *I. scapularis* include hybridization and assortative mating experiments, morphometric comparisons, chromosome and isozyme analyses, and laboratory life cycles (Oliver et al., 1993b). Earlier data indicated similar laboratory vector competency of *B. burgdorferi* (Burgdorfer & Gage, 1986; Piesman & Sinsky, 1988) and similar host preference and feeding success in the laboratory (James & Oliver, 1990).

Additional support for conspecificity includes confirmatory chromosomal analysis (Chen et al., 1994) and comparison of sequence variation in the internal spacer regions of the ribosomal DNA genes among and within populations of *I. scapularis* and the former *I. dammini* (Wesson et al., 1993). These rDNA comparisons indicate that the geographic populations continually overlap and suggest that there is a continual gene flow (Wesson et al., 1993). Subsequent analysis of the variation in rDNA ITS1 among eastern U.S. populations of *I. scapularis* indicates only 23% sequence variation occurs between regions (Georgia, Florida vs. North Carolina, Maryland vs. Massachusetts, New Jersey, New York), but 77% variation occurs within regions. This further supports the concept that all of the *I. scapularis* populations constitute a single species (McLain et al., 1995). Moreover, lack of evidence of clear differentiation between northern and southern populations was shown in a study on the phylogeny of ticks based on mitochondrial 16S ribosomal DNA sequences (Black & Piesman, 1994). While the latter work is not focused on the question

of conspecificity or on intensive examination of genetic structure, the sequence substitution rate between the individuals sampled from North Carolina and Massachusetts is equal to that found intraspecifically in the ticks *Amblyomma americanum* (L.) and *A. variegatum* (Fabricius). A more recent investigation dealing with molecular genetic variation of the 16S and 12S mitochondrial genes of *I. scapularis* from northern and southern populations indicates much more genetic variation within southern populations (Norris et al., 1996). Almost 200 specimens of *I. scapularis* from numerous populations in the Northeast, the Southeast, and the northern and southern Midwest were examined using single strand conformation polymorphism (SSCP) according to the methods of Hiss et al. (1994). Parts of the idiosoma from each specimen were used for PCR and the remaining parts (capitulum, coxae, and legs) were examined by J. E. Keirans (Curator, U.S. National Tick Collection) to confirm morphological identifications. Twelve to fourteen different presumptive haplotypes were examined among the different regions. Genetic variants were present among ticks from different populations even within the same states (for example, Georgia, North Carolina, and Oklahoma). Although the frequencies of haplotypes differed among the regions, there were no haplotypes that were unique to any one region. Moreover, morphological types were continuously distributed among the regions.

An expanded multivariate morphometric analysis of specimens from Minnesota, Massachusetts, Maryland, Missouri, North Carolina, Georgia, F_1 progeny from reciprocal crosses between specimens from Massachusetts and Georgia, and *I. pacificus* Cooley & Kohls from California for comparison, indicates that "*I. scapularis* appears to be a polytypic species with a widespread geographic distribution in eastern North America" (Hutcheson et al., 1995). The analysis indicates latitudinal (Massachusetts–Georgia) and longitudinal (Georgia–Missouri; Minnesota–Massachusetts) clines. Measurements of 28 morphological characters of nymphs are continuous in contrast to meristic, and the pattern of geographic variation is overlapping in contrast to disjunct. Hybrids resulting from MA × GA crosses appear morphologically intermediate between northern and southern morphotypes.

Heterogeneity of *Borrelia burgdorferi*

As noted in the section on etiologic agents, *Borrelia burgdorferi* sensu lato is currently considered to be composed of four "genospecies," including *B. burgdorferi* sensu stricto, which includes the type strain B-31 (Johnson et al., 1984; Baranton et al., 1992), *B. garinii* (Baranton et al., 1992), *B. afzelii* (Canica et al., 1993), and *B. japonica* (Kawabata et al., 1993). The first three "genospecies" occur in Europe; only *B. burgdorferi* sensu stricto is thus far reported from the United States. *Borrelia garinii, B. afzelii,* and *B. japonica* are known from Japan; it is unknown if *B. japonica* causes disease in humans. Prior to the recognition that *B. burgdorferi* consisted of four "genospecies," several investigators noted that European isolates of *B. burgdorferi* are more heterogeneous than those from the United States (Barbour et al., 1984; Anderson et al., 1989; LeFebvre et al., 1990; Anderson, 1991; Wilske et al., 1992). Although most *B. burgdorferi* strains from the northeastern United States appear to be rather similar, exceptions do occur.

Exceptions include the antigenically variable *Borrelia burgdorferi* isolated from cottontail rabbits (*Sylvilagus floridanus*) and *Ixodes dentatus* from New York (Anderson et al., 1989); an isolate from a veery songbird (Anderson et al., 1986; Barbour et al., 1985); a strain (25015) from *I. scapularis* from Millbrook, New York (Anderson et al., 1988; Fikrig et al., 1992); and perhaps others. *Borrelia burgdorferi* strains isolated from California appear to be antigenically quite variable (Brown & Lane, 1992) and more so than strains from the northeastern United States. Strain DN127 from *I. pacificus* (Bissett & Hill, 1987; Bissett et al., 1988) and strains from *I. neotomae* (Lane & Pascocello, 1989) and *I. spinipalpis* (Craven & Dennis, 1993) are especially unusual (David Persing, pers. comm.).

Clinical symptoms of human Lyme disease patients in Europe and the United States are similar in several respects. However, as already stated, less arthritic but more neurologic symptoms are reported in European than American patients. Further, an acute dermatological condition known as acrodermatitis chronica atrophicans occurs in some European patients but is extremely rare in the United States. *Borrelia afzelii* appears to be associated with late cutaneous manifestations (Canica et al., 1993) in European patients, and as mentioned above, has not been reported from the United States. Although not thoroughly substantiated, it has been suggested that perhaps each "genospecies" might produce some common clinical symptoms in patients and yet may also be associated more often with particular symptoms not often produced by other "genospecies." For example, in a study of European Lyme disease patients, infections due to VS461 (= *B. afzelii*) were associated with cutaneous symptoms, whereas extracutaneous symptoms involved *B. garinii* (van Dam et al., 1993). More research is

needed before this observed correlation can be considered widespread.

In general, there does appear to be a great deal of consistency among the *B. burgdorferi* isolates from the northern United States and similar clinical symptoms in patients from these areas. In contrast, persons in the south that are diagnosed with Lyme disease rarely exhibit arthritis that unequivocally can be attributed to Lyme disease. The patients may present with classic erythema migrans (EM) dermatologic lesions, flu-like and/or neurologic symptoms, yet rarely with arthritis. Since it is accepted that patients in Europe have fewer occurrences of arthritic but more neurologic symptoms and acrodermatitis chronica atrophicans, it seems reasonable to suggest that perhaps patients in the southern United States might present with some but not all of the symptoms common in patients from the north. This suggestion might be more appealing if it were shown that *B. burgdorferi* is geographically widely distributed in the south, occurs commonly, and is maintained enzootically among wild animals; and if *B. burgdorferi* in the south were genetically heterogeneous, with some strains similar to those in the north and with others different. Currently, it appears that these requisites are being fulfilled.

Recently, isolates from Oklahoma (Kocan et al., 1992), Texas (Teltow et al., 1991), Missouri (Oliver et al., unpublished), Georgia (Oliver et al., 1993a), Florida (Oliver et al., 1995), North Carolina (Levine et al., 1993; Levin et al., 1995), and Virginia (Sonenshine et al., 1993) demonstrate that *Borrelia burgdorferi* is much more widely distributed than originally assumed. Most of these isolates have yet to be thoroughly analyzed; however, the few that have been characterized, especially from Missouri, Georgia, and Florida (Oliver et al., 1993a; Oliver et al., 1995; Oliver et al., unpublished), show more variability than most northern isolates thus far reported. Isolates of *B. burgdorferi* from cotton rats, cotton mice, woodrats, and the ticks *I. scapularis* and *I. dentatus* from Georgia, Florida, and Missouri show considerable heterogeneity among themselves and differences from most northeastern strains based on immunologic (monoclonal antibodies), protein (SDS-PAGE), and genetic (PCR) analyses (Oliver et al., 1993a; Oliver et al., 1995; Oliver et al., unpublished). Some strains also differ significantly in infectivity to mice (Sanders & Oliver, 1995; Oliver et al., unpublished). Pulsed-field gel electrophoresis (PFGE) analysis and DNA sequencing of a portion of the gene encoding the large ribosomal subunit 23S also support the hypothesis of greater genetic heterogeneity among spirochetes isolated from the southeastern United States than that found in isolates from the northeastern and Great Lakes regions (Persing & Oliver, unpublished data).

For example, a PFGE analysis of more than 200 *Borrelia burgdorferi* sensu lato isolates from throughout the United States, and including several from Europe, demonstrates a greater degree of genetic heterogeneity among southern isolates. *Borrelia hermsii,* a species causing relapsing fever and transmitted by the argasid tick *Ornithodoros hermsi* in the western United States, is used as an outgroup for comparison to the *B. burgdorferi* sensu lato isolates. *Borrelia hermsii* is different from all *B. burgdorferi* isolates. Among the latter, an isolate of *B. garinii* from Sweden (NBS16) and one from Russia (IP90) appear distinct from the others. The remainder form two major assemblages: one composed of type strain B31, many isolates from the northeastern and Great Lakes regions of the United States, and a few isolates from the southeastern U.S. and California. Within the B31 assemblage, three of the subdivision groups of isolates are similar to the N40 isolate from New York, whereas three other groups of isolates are more similar to the type strain B31. Five of the subdivisions contain isolates from human skin, cerebrospinal fluid, or blood. The largest number of isolates make up subdivision 5 and represent the widest geographic range as sites of origin. Sites include California, North Carolina, Florida, Wisconsin, Illinois, Massachusetts, and Connecticut. Most of the human isolates analyzed are in this group, which also includes isolates from rodents and ticks. Subdivision 6 is composed exclusively of isolates from California (human skin, woodrat, the ticks *I. pacificus* and *I. neotomae*), Georgia (cotton mouse), and two isolates from the Netherlands (human, *I. ricinus*).

The second major assemblage contains a more genetically heterogeneous group of isolates from generally more temperate climates, i.e., the southern United States and California. However, this major assemblage also contains isolates from Colorado and the 25015 strain from upstate New York. All of the isolates analyzed in this large assemblage were from non-human origin. They were isolated from rodents (cotton mice, cotton rats, woodrats, kangaroo rats) and ticks (*I. scapularis, I. dentatus, I. spinipalpis*).

Clearly, genetic analysis of *B. burgdorferi* sensu lato isolates by PFGE and DNA sequencing of a portion of the 23S gene support the contention that there is greater genetic diversity of strains in the southern and far western United States than present among strains from the northeastern and Great

Lakes regions. The trend could be even more significant than shown because relatively few southern isolates have been analyzed. It seems reasonable to consider the possibility that the heterogeneity of strains might produce variations in infectivity in humans as demonstrated in rodents (Sanders & Oliver, 1995). Perhaps different strains also produce variations in clinical symptoms and pathology as well (van Dam et al., 1993).

Distribution and Origins of *Ixodes scapularis*, *I. pacificus*, and *Borrelia burgdorferi*

The origins of *I. scapularis*, *I. pacificus*, and *B. burgdorferi* are unknown. *Ixodes scapularis* was described in 1821, but it must have been present in the United States much earlier. If it were present prior to the last Ice Age, it may well have been eliminated at that time except from the southern part of its distribution, which was not covered with glaciers. Another possible origin of *I. scapularis* might have been by the transport of *I. ricinus* from Europe to eastern North America by explorers and settlers and subsequent rapid speciation of *I. scapularis* from *I. ricinus*. As noted above, *I. scapularis* was considered a variety or subspecies of *I. ricinus* by tick experts (Nuttall & Warburton, 1911; Schulze, 1939) in the early part of the century. More recent studies (Cooley & Kohls, 1945; Keirans, 1982, 1985) list it as a separate species. We are currently investigating the species relationships among *I. scapularis*, *I. ricinus*, *I. pacificus*, and *I. persulcatus*. An hypothesis being tested is that at some point *I. scapularis* evolved from European *I. ricinus*, and *I. pacificus* evolved from Asian *I. persulcatus*. We are testing the hypothesis initially by attempting to evaluate genetic relatedness of the species. Hybridization attempts are under way between Georgia *I. scapularis* and Swiss *I. ricinus* and soon will begin between California *I. pacificus* and Russian *I. persulcatus*. The *I. scapularis* × *I. ricinus* cross has produced F_1 hybrids that have now been reared to the adult stage. Fertility of these F_1 adults is now being evaluated. Analyses of DNA sequences of various geographic populations of *I. scapularis*, *I. ricinus*, *I. pacificus*, and *I. persulcatus* are also in progress. Morphometric analyses of several southern and northern populations of *I. scapularis* indicate greater longitudinal variation among the southern (Georgia–Missouri) than among the northern (Massachusetts–Minnesota) populations (Hutcheson et al., 1995). Genetic sequence data of the mitochondrial 16S and 12S genes also indicate greater variability among southern populations (Norris et al., 1995). Shannon diversity indices of mitochondrial haplotypes calculated from haplotype frequencies among the southeastern, midwestern, and northeastern populations indicate greatest genetic diversity in the southeast, least diversity in the northeast, and intermediate diversity in the midwest (Norris et al., 1995). There was approximately three times more diversity in the southeastern than in the northeastern populations that were analyzed. Most phylogenetic analyses assume, and for some species it has been shown empirically (Baker & Stebbins, 1965), that genetic diversity is greatest in regions from which a species or population originates. The opposite view would be difficult to explain based on traditional models of migration and range expansion. This suggests that the *I. scapularis* tick populations in the northeastern areas may have been derived from those in the southeastern United States.

Using the same rationale applied above to the origin and distribution of the tick *Ixodes scapularis*, it is noted that there appears to be greater diversity of *Borrelia burgdorferi* sensu lato in Europe compared to the United States. If this concept does not change after additional isolates from southern and western U.S. locations are thoroughly analyzed, it would suggest that *B. burgdorferi* sensu lato may have been present longer in Europe. If the same rationale of greater genetic diversity is applied to origin and distribution of the spirochete in the United States, it appears that *B. burgdorferi* may have been present in the southern United States earlier than in the north. This notion is counter to the commonly held assumption that *B. burgdorferi* is currently extending its geographic range from the hyperendemic Lyme disease region of the northeast to other regions. Indeed, as already noted, until now many persons presumed, in the absence of data, that *B. burgdorferi* did not occur in the south. Data presented earlier in this paper and elsewhere disputes that presumption. Current data, much of which have yet to be published, indicate that *B. burgdorferi* is widely distributed in the southeastern states and is abundant in some locations along the south Atlantic coast.

Data on the antiquity of *Borrelia burgdorferi* in North America are limited to two reports. Persing et al. (1990) reported *B. burgdorferi* specific DNA (using polymerase chain reaction techniques) in museum tick specimens that were collected from Long Island, New York, in 1945 and in mouse specimens collected from Massachusetts in 1894 (Marshall et al., 1994). Similar analyses have yet to be reported using ticks and mammals from the southern United States. In any event, such analyses are likely to be based on relatively recent specimens

and it seems likely that the tick/*B. burgdorferi* cycle is one of great antiquity, dating back hundreds of years, perhaps to the last Ice Age.

Conclusions

The discipline of systematics is one of the foundations of science. Taxonomy of arthropod vectors and of the microorganisms harbored and transmitted by them has an enormous impact on public health globally. Taxonomic identification of arthropod vectors and pathogenic microorganisms is necessary if we are to make informed decisions about strategies to control existent and emerging diseases. Intervention in disease requires a knowledge of the identity of the causative organisms involved and their taxonomic relationships to related species. Society is best served when systematics and taxonomy utilize traditional and newer molecular techniques concurrently to focus on particular questions or problems. Science administrators, politicians, and the general public need to be informed of the importance of systematics to public health, agriculture, environmental issues, and other areas of immediate human welfare, as well as its pivotal role in inventories of biological diversity on planet Earth. Unfortunately, many taxonomic specialists are nearing retirement age and upon retirement are not being replaced. The alarming report, "Endangered Species: Doctoral Students in Systematic Entomology" (Daly, 1995), notes that such students in the United States and Canada have declined from 155 in 1982 to 111 in 1992 (28% drop) and that 40% of the departments surveyed that have insect systematists on their faculties have no doctoral students in this field.

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