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Review

Ticks feeding on humans: a review of records on human-biting Ixodoidea with special reference to pathogen transmission

AGUSTIN ESTRADA-PEÑA[1]* and FRANS JONGEJAN[2]

[1] *Departamento de Parasitología, Facultad de Veterinaria, C/. Miguel Servet, 177, 50013-Zaragoza, Spain;* [2] *Department of Parasitology and Tropical Veterinary Medicine, Utrecht University, PO Box 80165, 3508 TD Utrecht, The Netherlands*

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Abstract. In this article, literature records of argasid and ixodid ticks feeding on humans worldwide are provided in view of increased awareness of risks associated with tick bites. Ticks can cause paralyses, toxicoses, allergic reactions and are vectors of a broad range of viral, rickettsial, bacterial and protozoan pathogens. Approximately 12 argasid species (*Argas* and *Ornithodos*) are frequently found attached to humans who intrude into tick-infested caves and burrows. Over 20 ixodid tick species are often found on humans exposed to infested vegetation: four of these are *Amblyomma* species, 7 *Dermacentor* spp., 3 *Haemaphysalis* spp., 2 *Hyalomma* spp. and 6 *Ixodes* species. Personal protection methods, such as repellents and acaricide-impregnated clothing are advised to minimize contact with infected ticks. Acaricidal control of ixodid ticks is impractical because of their wide distribution in forested areas, but houses infested with soft ticks can be sprayed with acaricidal formulations. Attached ticks should be removed without delay. The best way is to grasp the tick as close to the skin as possible with fine tweezers and pull firmly and steadily without twisting. Finally, despite the fact that most people who are bitten destroy the offending tick in disgust, it is recommended that they preserve specimens in ethanol for taxonomic identification and detection of pathogens by molecular methods.

Key words: ticks, Ixodidae, Argasidae, vectorial capacity, global distribution, tick-borne diseases, removal

Introduction

Ticks (Acari: Ixodoidea) are among the most important vectors of diseases affecting both humans and animals (Sonenshine, 1991). Diseases transmitted by ticks to livestock constitute a major factor which limits animal production in many tropical and sub-tropical areas of the world and have been reviewed elswhere (Jongejan and Uilenberg, 1994). In humans, ticks can cause severe toxic conditions such as paralyses and toxicoses, irritation and allergy, and their ability to transmit a great variety of infectious diseases is a major public health concern. In this article a

* To whom correspondence should be addressed at: Fax: +34–76–761612; e-mail: aestrada@posta.unizar.es

distinction is made between tick species which are frequently encountered, and those that are found occasionally on humans. Species commonly found on man are also important vectors of viral, rickettsial, bacterial and protozoan diseases.

The bites of soft ticks, notably *Argas* and *Ornithodoros* species, usually inhabitants of nests and burrows of birds and rodents and human dwellings in rural areas, cause irritation, blisters, bruising and a more or less severe pruritus. Typical outbreaks of argasids tick bites occur when people intrude into tick-infested caves, nests and burrows. *Argas monolakensis*, *Ornithodoros coriaceus*, *Ornithodoros erraticus* and *Ornithodoros moubata* are some of the major argasids reported to feed on humans. Ixodid ticks are encountered by humans while exposed to infested vegetation, usually in forested areas. Ticks frequently found on humans are *Amblyomma americanum* and *A.hebraeum*, *Dermacentor andersoni* and *D. variabilis*, *Hyalomma anatolicum* and *H.marginatum*, *Haemaphysalis spinigera*, and *Ixodes scapularis*, *I. ricinus*, *I. persulcatus* and *I. holocyclus*.

Ticks transmit a greater variety of pathogenic micro-organisms than any other arthropod vector group. Some of the major diseases transmitted by argasids (mainly *Ornithodoros*) are caused by *Borrelia* species, which induce relapsing fevers. Man-biting *Ixodes* ticks transmit viral infections causing European Tick-borne Encephalitis and the more severe Russian Spring Summer Encephalitis. Other viral infections, such as Crimean-Congo Hemorrhagic Fever transmitted by *Hyalomma* spp, occur sporadically throughout vast areas of Africa, Asia and Europe, but can cause mortality. Another potentially deadly flavivirus is transmitted by *Haemaphysalis* ticks which causes Kyasanur Forest Disease in India, claiming many victims annually. Bacterial diseases, such as Lyme disease caused by *Borrelia burgdorferi* sensu lato, occur in the United States, Europe and Asia and are transmitted by *Ixodes* ticks. The tick-borne rickettsiosis, Rocky Mountain spotted fever, a life-threatening but treatable rickettsial disease widespread throughout the eastern United States, is transmitted by *Dermacentor* ticks. Another rickettsial infection, fièvre boutonneuse, occurs mainly in Europe, caused by *Rickettsia conorii*. In southern Africa, *Amblyomma* ticks transmit *Rickettsia africae*, whereas *Dermacentor reticulatus* transmits Omsk Hemorrhagic Fever, caused by *Rickettsia sibirica*, in the former Soviet Union. Two other rickettsioses, monocytic and granulocytic ehrlichiosis, caused by *Ehrlichia chaffeensis* and *Ehrlichia phagocytophila* group, respectively, were discovered relatively recently. *E. chaffeensis* is transmitted by *Amblyomma americanum*, whereas *E. phagocytophila* is transmitted by *Ixodes scapularis* in the USA, and *Ixodes ricinus* in Europe. Protozoan diseases play a relatively minor role; *Babesia divergens* and *B. microti* are both transmitted by *Ixodes* ticks in the USA and Europe, and there are possibly other species. In this article we bring together literature records of human biting ixodoidea worldwide, with emphasis on ticks of medical and veterinary importance, geographical distribution, vectorial capacity, preventive measures and removal of attached ticks.

Argasidae: the genus *Argas*

Argas monolakensis is an important argasid tick feeding on humans. It is the vector of Mono Lake virus and occurs in California, USA (Schwan *et al.*, 1992a). *Argas moreli* and *Argas neghmei* have been implicated in human parasitism in Peru and Chile, respectively, where humans and chickens cohabit (Kohls and Hoogstraal, 1961; Keirans *et al.*, 1979). Pruritus lasting for several weeks has been described following bites by *A. cucumerinus* (Clifford *et al.*, 1978).

Authentic records of *Argas persicus* parasitizing man are rare. Among almost 300 records of tick bites of humans in western Siberia, only two (in Omsk) were attributed to *A. persicus* (Fedorov, 1968). The extensive review of argasids in the former Soviet Union by Filippova (1966) does not mention *A. persicus* feeding on man. However, records of human dwellings infested with this species are quite numerous. Although viral and rickettsial pathogens have been found in *A. persicus* collected in nature, this does not mean that *A. persicus* is a competent vector.

Argas reflexus is another argasid tick found on humans, especially following pigeon eradication from European buildings. When pigeons are removed from the attics of old houses, ticks appear seeking new hosts on curtains and windows (Roman *et al*., 1960). Furthermore, anaphylactic shock, caused by an unidentified toxin of *A. reflexus*, has been reported in Italy (Miadonna *et al*., 1982) and Poland (Grzywacz and Kuzmicki, 1975). When pigeons were driven from resting places infested by *Argas polonicus* in Krakow, Poland, frequent tick bites in humans resulted, with symptoms such as erythema, fever, weakness and diarrhoea (Siuda *et al*., 1982). *Argas vulgaris*, a species closely related to *A. polonicus*, has been reported from humans in the former Soviet Union (Filippova, 1966).

Argas boueti is usually associated with bats, although Hoogstraal (1956) found it on humans in Egypt. *Argas vespertilionis*, another parasite of bats, can be highly aggressive towards man (Hoogstraal, 1985). This species has been removed from humans in Iraq (Keirans, 1984), the former Soviet Union (Galuzo, 1957) and Africa (Hoogstraal, 1956). In Spain, two adult *A. vespertilionis* ticks were found feeding on the arm of a man inhabiting a country house in Huesca province, where many bats (*Eptesicus serotinus* and *Pipistrellus pipistrellus*) lived under the roof of the house (A. Estrada-Peña, unpublished observations). Several people experienced extensive bruising from the bites of *A. brumpti* after spending the night in a cave in Zimbabwe (Condy *et al.*, 1980; see Fig. 1).

Argasidae: the genus *Ornithodorus*

The widely distributed argasid genus *Ornithodoros* has several representatives involved in the parasitism of humans. In summary, a total of 22 species of

Figure 1. Extensive bruises on the back of a man from bites of the argasid tick *Argas brumpti* after spending the night in a cave in Zimbabwe. Reproduced with permission from The Central African Journal of Medicine, Vol. 26, 1980, p. 212. (Article by J.B. Condy, R.A.I. Norval, N.K. Blackburn and P. Clemence)

Ornithodoros species have been reported on humans, and 12 species are found frequently (Table 1).

O. boliviensis and *O. kelleyi* are usually parasites of bats, and bite humans only when they enter caves or bat-infested houses (Hoogstraal, 1985). New World representatives of the genus are well known ectoparasites of man, and act as vectors

Table 1. Summary of some of the most important soft tick species found attached to human victims, with data on their vectorial capacity and geographical distribution

Species	Pathogen	Distribution
Argas monolakensis	Mono Lake virus	Western USA
A. reflexus	–	Southeastern Europe
Ornithodoros asperus	*Borrelia caucasica*	Caucasus, Iraq
O. capensis	Soldado virus	Cosmopolitan
O. coriaceus	*Borrelia coraciae*	Pacific coast of USA into Mexico
O. erraticus	*Borrelia crocidurae*	North and East Africa, Near East, Southeastern Europe
O. erraticus	*Borrelia hispanica*	Spain, Portugal
O. hermsi	*Borrelia hermsi*	Western USA
O. maritimus	Soldado virus	France
O. moubata	*Borrelia duttoni*	East Africa and Southern Africa
O. tartakovskyi	*Borrelia latyschevi*	Central Asia
O. turicata	*Borrelia turicatae*	Southwestern USA, Central America
O. savignyi	–	Africa and parts of Asia

of diseases, such as relapsing fever caused by spirochetes of the genus *Borrelia*. Relapsing fever is a zoonotic disease with a variety of nest- or burrow-inhabiting mammals, especially rodents, acting as reservoir (Sonenshine, 1993). Since most *Ornithodoros* ticks are nidicolous parasites, humans are particularly involved in the cycle of transmission when they intrude into the nest environment. The epidemiology is therefore characterized by isolated outbreaks in scattered localities inside endemic areas (Burgdorfer, 1986). *Borrelia* spirochetes persist in the argasid vectors for many years, probably for their entire life. Thus, the remarkable longevity and cryptic habits of the *Ornithodoros* ticks perpetuate this zoonosis in endemic areas.

Ornithodoros coriaceus is distributed along the Pacific coast of the USA into Mexico. The tick is feared because of its very painful bites, *O. coriaceus* transmits *Borrelia coriaciae*, the cause of bovine epizootic abortion (Furman and Loomis, 1984). *Ornithodoros hermsi* occurs in the American states of California, Nevada, Idaho, Oregon, Utah, Arizona, Washington and Colorado, as well as in Canada, and is the primary vector of *Borrelia hermsi* (Schwan *et al.*, 1992b). *O. hermsi* is found in cavities of dead trees, log cabins and human dwellings, and usually feeds on tree squirrels. People become infected with *B. hermsi* when rodents are driven out during rodent-trapping activities (Sonenshine, 1993).

Borrelia parkeri, transmitted by the bite of *Ornithodoros parkeri* (western United States, California), seldom if ever infests man, although the tick vector feeds on the same hosts and occurs in the same geographical area as *O. hermsi*.

Ornithodoros talaje is distributed throughout the western states of the USA, Mexico, Venezuela, Uruguay, Brazil, Panama, Ecuador, Chile and Argentina. *O. talaje* can transmit *Borrelia talaje* in some parts of central and south America, although adults of this tick are seldom observed in dwellings and are not avid parasites of man.

Ornithodoros turicata inhabits the south-western part of the USA and Central America, and is a vector for *Borrelia turicatae*. This borrelia species is transmitted mainly via salivary fluids and not via coxal fluids, as is common in the *Ornithodoros*-*Borrelia* relationship. Few human infestations have been recognized in the USA, but in Oklahoma, where *O. turicata* infests homesteads and sheds, entire families have developed relapsing fever (Burgdorfer, 1980). The bite of *O. turicata* is painless, but is usually followed by intense local irritation and swelling several hours later and subcutaneous nodules may persist for months (Cooley and Kohls, 1944).

Ornithodoros amblus has been occasionally reported on humans in Peru (Clifford *et al*., 1980). *Ornithodoros rudis* is distributed throughout Panama, Paraguay, Colombia, Venezuela, Peru and Ecuador and is the primary vector of *Borrelia venezuelensis*, although clinical and epidemiological details are poorly documented (Hoogstraal, 1985). *O. rudis* is apparently well adapted as a parasite of humans, but feeds on other mammals as well. *Ornithodoros rostratus* has been implicated in human parasitism in South America, where it is well-known for its painful bite, which becomes pruritic and often secondarily infected. *O. rostratus* is able to transmit *R. rickettsii* (Hoogstraal, 1985).

In the Caucasus and Iraq, *Ornithodoros asperus* which inhabits rodent burrows, transmits *Borrelia caucasica*, which can cause severe disease in humans with numerous rapidly recurring relapses. *Ornithodoros coniceps* has been reported on humans in France and Spain (Gil Collado, 1947; Keirans, 1984), usually as the result of sleeping in caves where rock pigeons nest. Human hosts developed local oedema and pain with chills lasting from a few hours up to three days (Hoogstraal *et al.*, 1979).

Ornithodoros erraticus occurs on humans in Spain and parts of Africa. The bite of larvae of this species may result in allergic reactions, as observed in one patient in Spain (A. Estrada-Peña, unpublished data). This species transmits *Borrelia crocidurae* (North and East Africa, the Near East, including Southeastern Europe) and *Borrelia hispanica* (Tunisia, Algeria, Morocco, Spain and Portugal). Reports of human cases of relapsing fever due to *B. crocidurae* have become rare in North-east Africa, where the disease has declined since the 1940s. However, Trape *et al.* (1991) reported a wide distribution for *B. crocidurae* in Senegal, where relapsing fever appears to be a major cause of morbidity in rural areas. Epidemiological relationships of *B. hispanica* and the tick vector(s) remain obscure. Anda *et al.* (1996) reported the isolation of a new *Borrelia* species from patients with relapsing fever and from *Ornithodoros spp*. in southern Spain. This pathogen is closely related to other tick-borne relapsing fever spirochetes in Europe and Africa, and causes a disease with serological similarities to Lyme disease.

Ornithodoros maritimus is commonly found on sea birds, but has also been reported on humans in France (Chastel *et al.*, 1984). It transmits Soldado virus, a public health problem in urban environments where sea gulls feed. *Ornithodoros lahorensis* is a common ectoparasite of man found in most parts of the former Soviet Union and can be infected experimentally with *Rickettsia sibirica* (Sidorov and Kokorin, 1980). *Ornithodoros tartakovskyi*, distributed throughout most of Central Asia, may be infected with *Borrelia latyschevi* the agent of Central Asia relapsing fever, which can cause a mild human illness.

Ornithodoros tholozani commonly lives in man-made shelters, caves, rocky overhangs and other localities where livestock is housed (Arthur, 1962). The species is distributed from China to eastern Libya, and transmits *Borrelia persica*, the agent that causes Persian relapsing fever, resulting in a severe and sometimes fatal human disease.

Ornithodoros capensis is a cosmopolitan tick of seabirds (Keirans *et al.*, 1992), which has also been reported on humans. The study by Chastel *et al*. (1981) on Soldado virus indicated that *O. capensis* is a potential public health problem where sea gulls feed in urban habitats. Visitors to penguin breeding sites in caves and on barren coasts were attacked by nymphs and adults of *Ornithodoros spheniscus* with subsequent pruritic, slowly-healing blisters (Hoogstraal *et al.*, 1985).

Ornithodoros moubata, a well-known African species distributed throughout East Africa, Madagascar and northern parts of southern Africa, transmits *Borrelia duttoni*, the agent of African relapsing fever. This borrelia apparently circulates only in man and in *O. moubata* inhabiting human dwellings (Felsenfeld, 1971). Coxal fluid of nymphs and adults and salivary fluids of nymphs are the main routes of *B. duttoni* transmission (Burgdorfer, 1951). In Kenya and adjacent countries of eastern Africa, spirochete-infected *O. moubata* survive in the cracks and crevices of huts of indigenous people, where optimal microclimatic conditions are maintained by cooking fires (Walton, 1962). Changes in home construction have greatly reduced the incidence of relapsing fever since Walton's report. Although hepatitis virus does not multiply in *O. moubata*, mechanical transmission from ticks to man may occur by crushing infected ticks, through a bite, or by contamination with coxal fluid when scratching tick bite lesions (Jupp *et al*., 1987). Joubert *et al*. (1985) detected this virus in *O. moubata* collected from the north-east strip of Namibia and suggested that mechanical transmission may be responsible for the high prevalence rate of hepatitis virus infection in humans in this area.

Ornithodoros muesebecki has been collected from humans in Arabia (Hoogstraal, 1982), the bite causing blisters, pruritus and fever. It has not been determined whether salivary toxins or pathogens are involved. *Ornithodoros savignyi* is found in human habitations in India, Africa and some parts of Asia (Keirans, 1984; Hoogstraal, 1985) and causes intense local irritation in man (Hoogstraal, 1956). Moreover, in dry areas of Africa and Asia *O. savignyi* commonly attacks humans resting under shady trees and around wells where animals gather, etc. The bite of this species can cause long-lasting intense pruritus (G. Uilenberg, unpublished experience in Somalia). The same effects are associated with the bite of the Australian *Ornithodoros gurneyi* (Roberts, 1970).

Argasidae: the genus *Otobius*

The spinose ear tick is found in the western part of the United States, Mexico and British Columbia, Canada. However, close association with livestock has resulted in its transportation to other areas of the world (Harrison *et al.*, 1997). Paralysis of a human patient was related to the bite of an *Otobius megnini* nymph in South Africa (Peacock, 1958). Painful ear infestations by this species have been reported in humans in India by Chellappa (1973) and although irritating, do not result in serious sequelae (Eads and Campos, 1984; Uilenberg *et al*., 1980).

Ixodidae: the genus *Amblyomma*

Amblyomma americanum is distributed throughout central and eastern parts of the USA as well as parts of central and south America. This tick is very aggressive and accounted for 34% of the ticks collected from US Air Force personnel across the USA (Campbell and Bowles, 1994). Also 83% of ticks feeding on humans from Georgia and South Carolina were *A. americanum* (Felz *et al*., 1996). *A. americanum* may be infected with *Francisella tularensis*, the agent of tularemia (Goddard, 1987) and *Rickettsia rickettsii*, the agent of Rocky Mountain spotted fever (Kardatzke *et al*., 1992). However, *A. americanum* does not appear to be a vector for either Lyme Disease (Piesman and Sinsky, 1988) or RMSF (Goddard and Norment, 1986). Spirochetes derived from *A. americanum* in Missouri appear to differ from *B. burgdorferi* in their antigenicity, growth characteristics in culture and the tick species they infect in the laboratory (Piesman and Gray, 1994). However, *A. americanum* does transmit *Ehrlichia chaffeensis*, the agent of human monocytic ehrlichiosis (Ewing *et al*., 1995). The ehrlichioses are emerging zoonotic infections, caused by obligate intracellular bacteria of the genus *Ehrlichia*. Human monocytic ehrlichiosis is caused by *E. chaffeensis* infecting mononuclear phagocytes in blood and tissues. *E. chaffeensis* infection has been documented in more then 400 patients in 30 states of the United States, as well as Europe and Africa (Walker and Dumler, 1996). Evidence that *A. americanum* is the vector of *E. chaffeensis* is based on its presence in areas where deer (*Odocoileus virginianus*) have high antibody titers against *E. chaffeensis*, and reactivity is lacking in areas where the tick is absent (Lockhart *et al*., 1996). Human infection by *E. chaffeensis* is suspected in both Portugal and Spain (Morais *et al.*, 1991; Guerrero, 1992; Saz *et al.*, 1994). However, since *Amblyomma* species are absent on the Iberian Peninsula, there may be another vector involved or these claims are invalid.

In the southern United States, transmission of *B. burgdorferi* to humans is still a controversial issue. Some investigators feel that *A. americanum* is the primary vector of human Lyme disease in the southern US (Masters *et al*., 1994) whereas others have expressed doubt that *B. burgdorferi* infects people in this region (Campbell *et al*., 1995). A new, uncultivable spirochete, *B. lonestari*, has been found infecting *A. americanum* (Barbour *et al.*, 1996) while it has been demonstrated that this tick is unable to transmit *B. burgdorferi* to mice (Piesman and Happ, 1997).

Amblyomma cajennense is distributed from southern Texas, throughout Mexico and Central America into parts of South America (Guglielmone *et al.*, 1991). All active stages of *A. cajennense* bite humans, leaving a painful lesion (Goddard, 1989). The tick may serve as a vector of RMSF in western and central Mexico and South America (McDade and Newhouse, 1986). *Amblyomma maculatum* has been recorded on humans in parts of the USA (Snoddy and Cooney, 1984; Harrison *et al*., 1987), and Argentina (Boero, 1945). It has been incriminated in the transmission of *Rickettsia conorii* to man in Uruguay (Conti *et al*., 1990) and of the RMSF in USA (Loving *et al*., 1978).

Amblyomma hebraeum is one of the most important African tick species on livestock and is widespread throughout Southern Africa. It is a vector of tick-bite fever (*Rickettsia africae* infection) (Kelly *et al*., 1994). Larval *A. hebraeum* (like

Table 2. Summary of *Amblyomma* tick species found feeding on humans, with data on their vectorial capacity and geographical distribution

Species	Pathogen	Distribution
A. americanum	*Ehrlichia chaffeensis*	USA, central and south America
A. hebraeum	*Rickettsia africae*	Southern Africa
A. maculatum	*Rickettsia conorii*	Uruguay
A. variegatum	Crimean-Congo Hemorrhagic Fever virus	Uganda, Senegal, Nigeria, Central African Republic

larval *A. americanum*) are aggressive and attack in large numbers on the legs and about the waist, causing intense irritation, rashes and occasionally pustules. Nymphs are also frequently encountered on humans, including tourists visiting selected parts of South Africa. Recently one person of such a group developed symptoms of tick-bite fever, caused by *Rickettsia africae*, two weeks after a nymphal *A. hebraeum* tick was removed from his body (F. Jongejan, unpublished observations, 1998).

Amblyomma variegatum, another African tick species, is a vector of Crimean Congo Hemorrhagic Fever (CCHF) in Uganda, Senegal, Nigeria and Central African Republic (Linthicum and Bailey, 1994) and is sometimes found on man.

Amblyomma testudinarium has been recorded on humans in Japan (Suzuki *et al.*, 1990), Malaysia (Audy *et al*., 1960; Keirans, 1984), China (Kuo-Fan, 1991), and India (Dhanda and Rao, 1964). Its role in pathogen transmission to man is, however, unknown.

Amblyomma tholloni, commonly found on elephants in Africa, is known to parasitize man in Uganda, Mozambique and Tanzania (Matthysse and Colbo, 1989). It has not been implicated in the transmission of diseases to man. *Amblyomma* spp. commonly reported from humans are summarized in Table 2. Those species that occur occasionally on humans, or which lack adequate epidemiological data are included in Table 3.

Ixodidae: the genus *Boophilus*

Boophilus spp. ticks commonly parasitize bovines in temperate and tropical regions of the world, but very rarely attack man (Strickland *et al*., 1976). *Boophilus microplus*, however, has been rarely reported on humans in Cuba (de la Cruz *et al.*, 1991), Argentina (Guglielmone *et al*., 1991), and China (Kuo-Fan, 1991). There are no diseases known to be transmitted by *Boophilus* ticks to man.

Ixodidae: the genus *Dermacentor*

Several ticks of the genus *Dermacentor* are involved in parasitism and disease transmission to humans.

Table 3. Other *Amblyomma* species occasionally reported to feed on humans

Species	Distribution	Reference
A. coelebs	Paraguay	Keirans, 1984
A. cohaerens	Uganda	Matthysse and Colbo, 1987
A. cyprium	Papua New Guinea	Keirans, 1984
A. integrum	Sri Lanka	Keirans, 1984
A. loculosum	Australia	Keirans, 1984
A. neumanni	Argentina	Guglielmone *et al*., 1991
A. nuttalli	Ivory Coast	Aeschlimann, 1967
A. oblongoguttatum	Central and South America	Aragao and Fonseca, 1961
A. ovale	Panama	Obaldia, 1992
	Surinam	Keirans, 1984
A. parvum	Argentina	Guglielmone *et al*., 1991
	Brazil	Fonseca, 1959
	Panama and Guatemala	Fairchild *et al*., 1966
A. tholloni	Uganda, Mozambique and Tanzania	Matthysse and Colbo, 1987

A. cyprium, *A. dissimile*, *A. fossum*, *A. incisum*, *A. longirostre*, *A. marmoreum*, *A. tigrinum* and *A. triguttatum* are species reported in the Index Catalogue of Medical and Veterinary Zoology without further details (Doss *et al*., 1977).

Dermacentor andersoni has been recorded in the Nearctic region, from the USA (Nebraska to South Dakota and Sierra Nevada mountains) to Canada (British Columbia, Alberta, Saskatchewan). It is the primary vector of *Rickettsia rickettsii*, the agent of Rocky Mountain spotted fever (RMSF), in the Rocky Mountain States. This zoonosis involves circulation of rickettsiae between ticks and vertebrate hosts in an ecosystem independent of man, with the tick both acting as vector and reservoir of infection (Schriefer and Azad, 1994). Ticks develop systemic infection and rickettsiae invasion of the ovaries may result in 100% infection of oocytes. Transovarial transmission may thus represent a far more important mechanism for maintaining *R. rickettsii* in nature than infection of ticks by feeding on rickettsemic hosts (Burgdorfer and Brinton, 1975).

Dermacentor andersoni can also transmit the causative agent of Colorado Tick Fever (CTF) (Yunker and Cory, 1967). CTF is a zoonosis caused by an Orbivirus. Distribution of the disease coincides with the geographic range of the tick. It is maintained in natural, enzootic foci within its geographic range through the interaction of the vector ticks and susceptible hosts, mainly small mammals (Sonenshine, 1993). Transovarial transmission of CTF virus does not occur. Larval *D. andersoni* acquire the infection by feeding on viremic hosts. Trans-stadial transmission to nymphs occurs with moulting from infected larvae, and afterwards, to adults. Geographical foci with a high incidence of CTF virus in ticks and mammalian hosts are habitats that provide shelter for chipmunks, ground squirrels and other small mammals which serve as a blood source for immature ticks (Sonenshine *et al*., 1976). Although *D. andersoni* is an efficient experimental vector of the Powassan

Encephalitis virus, the agent has not been isolated from numerous field pools of ticks collected throughout its distribution range (Nuttall and Labuda, 1994).

Dermacentor variabilis occurs throughout the USA (except in parts of the Rocky Mountains) and also in Canada and Mexico. Felz *et al*. (1996) reported a frequency of 11.4% on humans in Georgia and South Carolina. Campbell and Bowles (1994) documented the presence of *D. variabilis* in 34% of ticks found on humans throughout the USA where most of the cases of the disease occur. In other reports, *D. variabilis* accounted for 94% in North Carolina (Slaff and Newton, 1993), 90% in South Carolina (Burgdorfer *et al*., 1975) and 34% in Ontario (Scholten, 1977). It is the primary vector of RMSF in the eastern parts of the USA, and has been incriminated as a vector of *Francisella tularensis* (Hopla and Hopla, 1994). A study of attachment site preferences of *D. variabilis* in humans showed that most ticks (50%) were taken from the head, while legs–feet and arms–axillae, accounted for 21.5% and 10.8% respectively (Slaff and Newton, 1993).

Dermacentor occidentalis occurs along the Pacific coast of the USA and inland for several hundred miles from Oregon to the southern tip of California and has been reported in Mexico (Hoffmann, 1962). It causes paralysis in livestock, but not in humans (Sonenshine, 1993), and it may transmit the agent of Tularemia, RMSF, and CTF (Goddard, 1987). Two other Nearctic species of this genus have been involved in a few cases of human parasitism: *D. parumapertus* and *D. albipictus* (Doss *et al.*, 1977).

Palearctic species of the genus *Dermacentor* have also been commonly involved in human parasitism. *Dermacentor marginatus* is one of the main Palearctic species reported on man. In Spain (A. Estrada-Peña, unpublished data) it accounts for approximately 10% of the total number of ticks collected from humans. It is the main vector of *Rickettsia slovaca* (Rehácek *et al*., 1990; Beati *et al.*, 1993) and plays a secondary role in the transmission of the Omsk Hemorrhagic Fever (OHF) virus (Nuttall and Labuda, 1994). Strains of *R. slovaca* isolated from Germany, Hungary and Armenia suggest a widespread distribution of this agent, and although few clinical cases have been reported, many individuals had antibodies against this rickettsia (Rehácek and Tarasevich, 1988). A survey of *D. marginatus* collected from sheep in Slovakia indicated a *R. slovaca* infection rate of 20%, without apparent change in prevalence over a 20-year period (Rehácek *et al*., 1990). The presence of CCHF virus has been demonstrated in field-collected *D. marginatus* ticks (Kondratenko, 1976).

Dermacentor nuttalli occurs throughout central and eastern Siberia, Asiatic Russia, northern Mongolia and China, with occasional records from western Russia. It is found in high grasslands, but is absent from dense forests, river lowlands and hilly wooded country. It is one of several vectors of *Rickettsia sibirica*, together with *D. marginatus*, *D. silvarum* and *D. reticulatus* (Pchelkin *et al*., 1989). This tick-borne rickettsiosis is widespread in far eastern Siberia and central Asia, Armenia, Azerbaijan, Mongolia and Afghanistan (Rehácek and Tarasevich, 1988). Commonly, larvae and nymphs feed on small mammals which amplify the infection, whereas humans are infected when bitten by infected adults. Both trans-stadial and transovarial transmission occur in the tick vectors. In the former Soviet Union it is considered an occupational disease, mainly in agricultural areas around pastures (Rehácek and Tarasevich, 1988). *D. nuttalli* is also a vector of tularemia in Russia (Olsufiev, 1984).

Dermacentor silvarum occurs primarily in eastern Russia and northern Mongolia and has also been reported from Romania and the former Yugoslavia. It is a vector of *Rickettsia sibirica* (Yastrebov and Reshetnikova, 1990) in Russia and Mongolia, as well as of viruses of the Tick Borne Encephalitis (TBE) complex (Muratkina and Leonova, 1992).

Dermacentor reticulatus, the main vector of Omsk Hemorrhagic Fever (OHF) (Lvov, 1988) has commonly been reported on humans in Russia, Austria, the United Kingdom, France and has also been found in Spain (A. Estrada-Peña, unpublished observations, 1990). OHF is caused by a Flavivirus which is a member of the TBE complex. It produces lethal encephalitis in many wild rodents, and casues a haemorrhagic disorder in humans. Adults of *D. reticulatus* feed on wild ungulates and humans, whereas immature forms feed mainly on water voles (*Microtus gregalis*) in forest-steppe habitats. Vole populations are cyclic, and expansion of the virus-infected tick population coincides with increases in vole populations (Hoogstraal, 1985). Humans may become infected when hunting or trapping musk-rats (*Ondatra zibethica*) (Kharitonova and Leonov, 1985). *D. reticulatus* may also acquire *Borrelia burgdorferi* (Kahl *et al*., 1992), but there are no reports of its ability to transmit, i.e., it is not vector competent. *D. reticulatus* is a vector of *R. sibirica* as well as of *C. burnetii* (Gosteva *et al.*, 1991; Sonenshine, 1993).

Finally, two further species of this genus have been recorded as ectoparasites of man: *D. auratus*, which occurs in India, Nepal, Thailand, China and Malaysia and *D. circumguttatus,* reported by Matthysse and Colbo (1987) on man in Uganda. Forested parts of the Himalayas are notorious for tick annoyance caused by nymphs of *Dermacentor auratus* (Hoogstraal, 1970). A summary of *Dermacentor* ticks frequently found on humans is given in Table 4.

Ixodidae: the genus *Haemaphysalis*

A large number of *Haemaphysalis* species are involved in human parasitism, however only the most important vectors are discussed (see Table 5). Others are listed in Table 6.

Haemaphysalis spinigera is common in India and Sri Lanka, nymphs of which avidly bite man. It is the main vector of the Kyasanur Forest Disease (KFD) virus. The original focus of KFD in man in the Kyasanur State Forest and surrounding villages has spread extensively within the state of Karnataka, in India (Banerjee,

Table 4. Summary of *Dermacentor* ticks commonly reported from humans, with data on their vectorial capacity and geographical distribution

Species	Pathogen	Distribution
D. andersoni	*Rickettsia rickettsii*	USA (Rocky Mountain states)
	Colorado tick fever virus	USA
D. marginatus	Omsk Hemorrhagic fever virus	Palearctic
	Rickettsia slovaca	
D. nuttalli	*Rickettsia sibirica*	Siberia, Russia, Mongolia, China
D. occidentalis	*R. rickettsii*	USA
	Colorado tick fever virus	USA
D. silvarum	*R. sibirica*	Eastern areas of Soviet Union, Northern Mongolia
D. reticulatus	Omsk Hemorrhagic fever virus	Former Soviet Union
	R. sibirica	
D. variabilis	*R. rickettsii*	USA
D. auratus	–	Parts of the Himalaya

Table 5. Summary of *Haemaphysalis* species commonly reported from humans

Species	Pathogen	Distribution
H. concinna	Tick Borne Encephalitis virus	Central Europe, Soviet Union
H. punctata	Tick Borne Encephalitis virus	Europe
	Crimean-Congo Hemorrhagic fever virus	
H. spinigera	Kyasanur forest disease virus	India, Sri Lanka

Table 6. Other *Haemaphysalis* species rarely reported on humans

Species	Distribution	Reference
H. aculeata	India, Sri Lanka	Keirans, 1984
H. anomala	Nepal	Hoogstraal, 1968
H. aponommoides	Nepal, India	Hoogstraal, 1968
H. bispinosa	Nepal, Vietnam, Malaya	Hoogstraal, 1968
H. darjeeling	Thailand	Keirans, 1984
H. flava	Japan, India	Hatsushika and Mimura, 1987
H. hystricis	Thailand, Burma, Laos, Vietnam	Keirans, 1984
	China	Kuo Fan, 1991
H. japonica	China	Kuo Fan, 1991
H. koningsbergeri	Thailand, Malaya	Keirans, 1984
H. leporispalustris	USA	Harrison *et al*., 1997
H. longicornis	Japan, Australia, China	Kuo Fan, 1991
H. mageshimaensis	China	Kuo Fan, 1991
H. montgomeryi	Nepal	Hoogstraal, 1968
	China	Kuo Fan, 1991
H. nepalensis	Nepal	Hoogstraal, 1968
	China	Kuo Fan, 1991
H. elongata	Madagascar	Uilenberg *et al*., 1980

1988). About 95% of the KFD virus isolates are from *H. spinigera*, the predominant tick species of the forest floor in the endemic regions. Larvae feed on small mammals and ground feeding birds, while nymphs infest larger animals including man and monkeys. The KFD virus is transmitted trans-stadially, but not transovarially. The virus also occurs in a number of other *Haemaphysalis* species that do not parasitize man, but infest small mammals (forest rats, shrews and porcupines). This secondary enzootic cycle helps maintain and spread the virus to other areas (Nuttall and Labuda, 1994). Furthermore, the modification of forest habitat by human intervention may have contributed to the epidemic spread of the disease (Bhat, 1990). Humans who visit forests to collect firewood or those working in adjacent fields are at higher risk of contracting KFD.

Haemaphysalis concinna is common in the forests of most of Central Europe, Russia, China, Korea, Vietnam and Japan. *Haemaphysalis punctata* is found on man in most parts of Europe. Both species are competent vectors of TBE virus, which has been isolated from field collected specimens (Gresiková, 1972). *H. punctata* is also involved in the transmission of CCHF virus to man (Linthicum and Bailey, 1994).

Ixodidae: the genus *Hyalomma*

Ticks of the genus *Hyalomma* are well-known vectors of viruses and avid parasites of man. Although many species are not involved in disease transmission, the considerable length of *Hyalomma* mouthparts provokes a painful bite. One of the most important diseases transmitted by *Hyalomma* ticks is Crimean-Congo Hemorrhagic Fever (CCHF), of which *Hyalomma marginatum* is one of the main vector ticks.

H. marginatum and its subspecies have been recorded from south-eastern Europe, southern Russia, the Near East and Africa (Goddard, 1987). It is the primary vector of CCHF virus where it occurs sporadically throughout Europe, Asia and Africa, ranging from Portugal eastwards to Crimea, and then further east into central Asia and China (Hoogstraal, 1979). It appears to be absent in African countries along the Mediterranean coast but it is present in most countries south of the Sahara. Ticks rather than their mammalian hosts are the natural reservoir of the CCHF virus, which is perpetuated in the ticks by feeding on viremic hosts and by trans-stadial and transovarial transmission (Linthicum and Bailey, 1994). The disease is most common in arid and semi-arid biotopes. Serious outbreaks have been reported along rivers and river floodplains, and in forest in steppes (Watts *et al*., 1988). Stable enzootic foci involve wild mammals, ground-feeding birds and ticks, although most birds are incompetent hosts for the infection (Hoogstraal, 1979). However, birds transport CCHF-infected ticks and serve as a bloodmeal source for tick populations (Watts *et al.*, 1988). Hares (*Lepus europaeus*) and hedgehogs (*Erinaceus europaeus*) are frequently infected and are important hosts of *Hyalomma marginatum*. Cattle may also be important in the epidemiology of CCHF, although evidence is based largely

Table 7. Summary of *Hyalomma* species commonly reported to feed on humans

Species	Pathogen	Distribution
Hyalomma. a. anatolicum	Crimean-Congo Hemorrhagic fever virus	Southern Europe, Russia, Near East
Hyalomma marginatum	Crimean-Congo Hemorrhagic fever virus	Southern Europe, Russia

on serology, with few isolates of the virus from cattle (Watts *et al.*, 1988). Other Hyalomma ticks involved in the transmission of CCHF virus include *H. truncatum*, *H. detritum* and *H. impeltatum*. The transmission of this virus by co-feeding to uninfected ticks has been also demonstrated (Gordon *et al*., 1993).

Hyalomma a. anatolicum, distributed in parts of the Near East, Asia Minor, southern Europe, southern Russia and India (Goddard, 1987), is a well-known vector of CCHF (Linthicum and Bailey, 1994). Other species of *Hyalomma* may also transmit CCHF virus. There are records that *Hyalomma asiaticum* from foothill semidesert regions of Russia, China, Afghanistan, Pakistan, Iran and Iraq may parasitize humans (Kuo-Fan, 1991). *Hyalomma* ticks frequently found parasitizing humans are given in Table 7.

Ixodidae: the genus *Ixodes*

Ixodes ricinus is common throughout most of Europe, including the British Isles. Stable populations are also scattered in northern Africa (Gray, 1991). The development and seasonal activity of *I. ricinus* vary considerably in different habitats, although activity in spring and early summer and again in late summer and early autumn is typical (Gray, 1991). *I. ricinus* is the primary European vector of the European TBE viral subtypes (Nuttall and Labuda, 1994). Disease occurs in most of Europe and in the eastern parts of Russia. The virus is maintained by trans-stadial transmission, with tick infection as the result of feeding upon viremic hosts. Although the virus has been isolated from other tick species, a strong correlation exists between human cases and the known distribution of *I. ricinus* (Sonenshine, 1993). Rodents are the main vertebrate hosts for the virus especially *Clethrionomys glareolus* and *Apodemus flavicollis*, as well as various insectivores (Nuttall and Labuda, 1994). Some wild carnivores and domestic ruminants are also susceptible to disease and may contribute to its spread to humans. Although TBE virus was detected in the faeces of *I. ricinus* (Benda, 1958), there is no evidence that transmission occurs via contact with contaminated tick faeces material.

I. ricinus is the most important European vector of Lyme disease spirochetes, including *B. afzelii*, *B. garinii*, *B. burgdorferi senso stricto*, *B.lusitaniae*, *B. valaisiana* and possibly others (Postic *et al.*, 1994; Le Fleche *et al.*, 1997; Wang *et al.*, 1997). The importance of *I. ricinus* in European Lyme Disease is due to its widespread distribution, feeding habits and its willingness to bite humans (Piesman and Gray, 1994). High risk of Lyme borreliosis occurs when habitats that are well utilized by the public harbour large numbers of infected ticks. Identification of high-risk locations may be possible if standard habitat characteristicis can be recognized. Gray *et al*. (1998) compiled data for 105 Lyme disease habitats in 16 European countries. The data showed that high-risk areas are heterogeneous deciduous woodland, generally with a recreational function and supporting a diverse fauna usually including deer. Large numbers of ticks occurred in some other habitats, but infection prevalence was low. Although there seemed to be good correlation between total numbers of ticks and numbers of *Borrelia*-infected ticks, this is not consistent enough for extrapolation from one to the other when diverse habitats are considered (Gray *et al.*, 1998). Locations cannot therefore be classified as posing a high risk for Lyme borreliosis simply on the basis of tick density. It is necessary to take other habitat characteristics into account, particularly the vegetation, which will have a strong influence on the variety and abundance of hosts present (Tälleklint and Jaenson, 1996). A study by Daniel *et al*. (1998) suggested the usefulness of LANDSAT satellite imagery to provide an estimation of *I. ricinus* risk habitats. Satellite imagery with higher temporal resolution and larger area coverage, as obtained from NOAA-AVHRR satellite series, can improve our knowledge of habitat seasonal variation, and hence the changes of *I. ricinus* activity within short time intervals.

I. ricinus may be an important vector and possible maintenance host of CCHF virus (Watts *et al.*, 1988) and also the vector of the protozoan parasite *Babesia divergens*, the causative agent of human babesiosis in Europe causing sporadic but usually fatal cases (Gray, 1991). A recent fatal case of a *B. divergens* infection was diagnosed in a splenectomized man in the Algarve, Portugal (V. doRosario and A.J. Maia, A.M. Freudenthal and F. Jongejan, unpublished, 1998).

Ixodes persulcatus, which aggressively attaches to humans, is found in Japan, Russia, Korea and China (Im *et al*., 1998). Populations from western Russia have moved into Europe, and it seems possible that migratory birds introduce *I. persulcatus* immatures into other areas (R. Mehl, pers. comm.). *I. persulcatus* inhabits small-leafed forests near primary coniferous forests, such as spruce-basswood combinations. It is a vector for the OHF virus (Hoogstraal, 1965), *Borrelia afzelii*, *B. garinii*, and *B. burgdorferi* (Korenberg *et al*., 1987). Foci of TBE virus infection (Far-eastern subtype) are found within the geographic distribution of *I. persulcatus*, mostly in the taiga containing mixed broad-leaved forests with high humidity. Sporadic foci of disease occur in river valleys covered by marshy meadows, and on undulating plains where suitable habitats overgrown with bushes are scattered among cultivated valleys (Nuttall and Labuda, 1994). Foci of the Far-eastern subtype of TBE virus, maintained by *I. persulcatus*, contain a comparatively high prevalence of infected ticks, and in such regions, seasonal tick activity occurs relatively briefly, approximately from April to June. The relative roles of both *I. ricinus* and *I. persulcatus* as vectors of the two TBE viral subtypes are undetermined for parts of Europe where the two species cohabit.

Ixodes hexagonus is a relatively common parasite of man in Germany and the United Kingdom (Liebisch and Walter, 1986). It is an experimental vector of *B. burgdorferi* (Toutoungi and Gern, 1993) and has been found infected under natural conditions. The vector competence of *I. hexagonus* for TBE virus has been also demonstrated although it lacks a prominent role in the epidemiology of the disease (van Tongeren, 1962).

Ixodes uriae is a circumpolar tick of marine birds in which an enzootic cycle of *B. burgdorferi* has been demonstrated (Olsen *et al.*, 1993). An ornithologist visiting marine birds colonies was bitten by an *I. uriae* tick and developed erythema migrans (R. Mehl, pers. comm.). *Ixodes ovatus* parasitizes humans in Tibet, Burma, Nepal, Japan and China (Keirans, 1984; Kuo-Fan, 1991). *Borrelia japonica* has been isolated from Japanese *I. ovatus* (Postic *et al*., 1994).

Ixodes holocyclus causes tick paralysis in Australia. It occurs primarily in New Guinea and along the eastern coast of Australia, being active in the warmer months of the year. The bandicoot, the primary host for *I. holocyclus*, is increasing in numbers in urban areas as a result of control campaigns against dingoes and foxes (Bagnall and Doube, 1975). Clinical cases of tick are characterized by progressive paralysis up to 48 h, with a severe exacerbation of the symptoms after tick removal; recovery often takes several weeks (Stone *et al.*, 1989). In contrast with some paralytic conditions that resemble tick paralysis, it progresses rapidly and may be fatal within a few days after the onset of symptoms. *I. holocyclus* is the vector of *Rickettsia australis* (Sexton *et al*., 1991), and also able to transmit a Nearctic strain of *B. burgdorferi* from the larval to the nymphal stage (Piesman and Stone, 1991).

Several species of the genus *Ixodes* are well-known parasites of humans. *Ixodes scapularis* (formerly *Ixodes dammini*, according to Oliver *et al*., 1993) occurs along the Atlantic coast of Canada and the USA, and throughout the southern states, including Texas and Oklahoma. It is possible that its range is expanding towards the western states (Keirans *et al.*, 1996). *I. scapularis* ticks require moist microclimates for survival; habitats where leaf-litter is established and mixed deciduous forests with a high canopy provide the ideal environment. This species accounts for 76.2% of the ticks collected on humans in southern New York (Falco and Fish, 1988) but only for 3.9% in Georgia and South Carolina (Felz *et al*., 1996). Using a tick stage–specific regression equation for engorgement index in nymphs and adults of *I. scapularis*, Yeh *et al*. (1995) determined the duration of attachment for ticks removed by tick-bite victims. Most people (64%) found and removed adult *I. scapularis* before 36 h of attachment; by 48 h nearly all adult ticks were removed (79%). In contrast, few people found and removed nymphal ticks by 24 h of attachment (10%) or 36 h (41%).

I. scapularis is the main vector of *B. burgdorferi*, the causative agent of human Lyme disease in the eastern USA and Canada, with the white-footed mouse

(*Peromyscus leucopus*) acting as the primary reservoir of *B. burgdorferi* and immature *I. scapularis* ticks. In habitats were *P. leucopus* is absent, other rodents substitute as reservoirs, e.g., Norway rats (*Rattus norvegicus*) (Piesman and Gray, 1991). However, by itself, the Norway rat is relatively unimportant. An entomological index was proposed by Mather *et al*. (1996) to provide human health agencies with data on the density of permanent *I. scapularis* populations. This index has been revisited using daily satellite imagery over continental United States and Canada, obtaining a habitat suitability index from soil temperatures and standard vegetation index (Estrada-Peña, 1998). Variability in tick feeding rates in relation to spirochete transmission among different tick hosts has not been determined, making it impossible to know if findings from these animal studies are applicable to humans (Yeh *et al*., 1995). However, animal studies suggest that risk for *B. burgdorferi* transmission is low within the first 24 h of attachment but increases thereafter (Piesman, 1993).

Although RMSF rickettsiae has been isolated from *I. scapularis* (Burgdorfer, 1975) its role in the ecology of RMSF is not well understood. *I. scapularis* can also transmit *Babesia microti*, the protozoan responsible for human babesiosis in the Nearctic (Ristic and Lewis, 1977; Spielman, 1988). The most important reservoir host for *B. microti* is the white-footed mouse, *Peromyscus leucopus*, although meadow voles (*Microtus pennsylvanicus*) may also act as reservoirs, but are less frequently parasitized by *I. scapularis* (Spielman, 1988). Nymphs are primary vectors, although adults may transmit the infection. Human babesiosis caused by *B. microti* has remained a minor public health concern in the USA, with only about 200 cases since it was first recognized clinically (Sonenshine, 1993).

Human granulocytic ehrlichiosis (HGE) caused by *Ehrlichia phagocytophila* is an emerging disease, predominantly in the upper midwestern and northeastern US states, but also in northern California (Walker and Dumler, 1996; Dumler and Bakken, 1998). Pancholi *et al*. (1995) first implicated *I. scapularis* as a vector for HGE by association of an infected specimen with a human case report from Wisconsin. Madigan *et al*. (1996) confirmed that the DNA sequence of the 16S rRNA gene of the equine agent is identical to that of the human agent. Larval *I. scapularis* ticks acquired infection by feeding upon infected mice, and efficiently transmitted the ehrlichiae after moulting to nymphs, thereby demonstrating vector competence (Telford *et al*., 1996). The agent was also demonstrated in the salivary glands of field-collected adult *I. scapularis* ticks. Des Vignes and Fish (1997) demonstrated the infection of laboratory mice by *I. scapularis* nymphs collected from a natural focus of HGE. These mice were positive by PCR, microscopic examinations of blood smears and larval *I. scapularis* xenodiagnosis. Positive xenodiagnostic larvae maintained infection through moulting. Greig *et al*. (1996) studied dogs with natural granulocytic ehrlichiosis. No dogs seroreacted with *E. canis* or *E. chaffeensis* antigens, which are cross-reactive; however, 100% of the dogs tested during convalescence were seropositive for *E. equi* antigens. Granulocytic ehrlichial 16S rRNA gene DNAs from dogs were amplified and revealed as identical to the agent of human granulocytic ehrlichiosis, and very similar to *E. equi*. These findings suggest that granulocytic ehrlichiosis in dogs is a zoonotic disease and dogs possibly contribute to the enzootic cycle and human infection. In the Netherlands finally, granulocytic ehrlichiosis has been diagnosed in dogs (F. Jongejan, unpublished, 1998), and also in one human patient (van Dobbenburgh et al, 1999).

Ixodes pacificus occurs along the Pacific coastal margins of British Columbia, Canada and the USA, extending into California and parts of Mexico. The ecological conditions that permit *I. pacificus* to survive in western North America are even more variable than those supporting the survival of *I. scapularis*. Isolated populations have also been located in the non-coastal state of Arizona (Olse *et al.*, 1992). Recently, a zoonotic *Babesia*-like piroplasm (designated WA1) was identified in Washington State (Quick *et al*., 1993). Phylogenetic analysis of this new organism showed that it was most closely related to, but distinct from, the canine pathogen (*B. gibsoni*) rather than to other members of the genus *Babesia* (Persing *et al.*, 1995). *I. pacificus* may be the vector of this *Babesia*-like protozoan in California and Washington, although virtually nothing is known about the vector competence of the different tick stages nor the epidemiology of the disease. *I. pacificus* is a relatively inefficient vector of *B. burgdorferi*, probably because larvae and nymphs feed mostly on reservoir-incompetent lizards (Lane and Loye, 1989). It is also less efficient than *I. scapularis* in acquiring and maintaining *B. burgdorferi*. The second vector in the Pacific coast is *I. neotomae*, a non-man-biting species, which maintains a cryptic cycle among rodent and rabbits (Brown and Lane, 1992). In this particular case, both species contribute to the enzootic maintenance of *B. burgdorferi* among wildlife in nature, with *I. pacificus* also serving as the bridge vector for transmission of the spirochetes to man.

Ixodes cookei is found throughout Eastern and Midwestern states of the USA and Canada (Farkas and Surgeone, 1990), where it is the main vector of the Powassan Encephalitis (PE) virus (Nuttall and Labuda, 1994). *I. cookei* is opportunistic and readily attacks dogs, man and various wild mammals. The woodchuck (*Marmota monax*) is one of its most common hosts, in which PE virus is also found (Artsob *et al*., 1984). Spotted fever rickettsiae has also been identified in *I. cookei* (Burgdorfer, 1988) but little is known about its role as a vector of the disease. Lyme borreliosis may also infect *I. cookei* (Levine *et al*., 1991) but it is not considered a competent vector (Magnarelli and Swihart, 1991).

Adults of *Ixodes dentatus* are host specific for rabbits, but immatures feed on a wide variety of birds and rarely on man. In nature, *Borrelia spp*. have been isolated from *I. dentatus* larvae (Anderson *et al.*, 1990) and, experimentally, *I. dentatus* larvae are able to acquire spirochetes from infected hosts and transmit them when feeding again as nymphs (Telford and Spielman, 1989). During the autumn, large numbers of *I. dentatus* are dispersed by migrating birds, providing opportunities for rapid spread of *B. burgdorferi* (Clifford *et al*., 1970; Levine *et al*., 1991). Species frequently encountered on humans are listed in Table 8. Other *Ixodes* species rarely

Table 8. Summary of *Ixodes* species commonly reported to feed on humans

Species	Pathogen	Distribution
I. holocyclus	*Rickettsia australis*	Australia
I. ovatus	*Borrelia japonica*	Japan
I. pacificus	*B. burgdorferi*	Western USA, Canada
I. persulcatus	Omsk Hemorrhagic fever virus	Japan, former USSR
	B. afzelii	
	B. garinii	
	B. burgdorferi	
	TBE virus	
I. ricinus	*B. afzelii*	Europe, western former USSR, northern Africa
	B. garinii	
	B. lusitaniae	
	B. valaisiana	
	B. burgdorferi s.s.	
	Ehrlichia phagocytophila group	
	TBE virus	
	Babesia divergens	
	Rickettsia helvetica	
I. scapularis	*B. burgdorferi s.s.*	USA (Atlantic coast), southeastern Canada
	Babesia microti	
	Ehrlichia phagocytophila group	

Table 9. Other *Ixodes* species rarely reported on humans

Species	Distribution	Reference
I. angustus	USA	Keirans and Clifford, 1978
I. cavipalpus	Angola	Keirans, 1984
	Zambia	F. Jongejan (unpublished)
I. nipponensis	Korea	Ruy *et al*., 1998
I. turdus	Japan	Woo *et al*., 1990

collected from humans, or which lack relevant epidemiological data, are summarized in Table 9.

Ixodidae: the genus *Rhipicephalus*

Rhipicephalus sanguineus group ticks are probably the most widely distributed of all ticks. Goddard (1989) reported 15 actively biting cases on humans from 756 *R. sanguineus* collected through USAF installations; this cluster was between Texas and Oklahoma. In another report about ticks on humans from USAF personnel, *R. sanguineus* accounted for 7% of the ticks collected (Campbell and Bowles, 1994). Felz *et al*. (1996) mentioned that *R. sanguineus* represents only 0.7% of ticks collected from humans in Georgia and South Carolina. However, Harrison *et al*. (1997)

Table 10. *Rhipicephalus* species occasionally reported on humans

Species	Distribution*	Reference
R. longus	Uganda, Tanzania	Matthysse and Colbo, 1987
R. muhsamae	Nigeria	Keirans, 1984
R. praetextatus	Uganda	Matthysee and Colbo, 1987
R. pulchellus	Kenya, Tanzania	Keirans, 1984
R. rhipicephali	Africa	Linthicum and Bailey, 1994
R. senegalensis	Sierra Leone	Keirans, 1984
R. haemaphysaloides	Nepal, Taiwan, Burma, Sri Lanka	Keirans, 1984
	China	Kuo-Fan, 1991

* The distribution refers to where the tick has been reported from humans.

reported a high incidence of immature *R. sanguineus* on humans in North Carolina. It can transmit the CCHF virus (Srivastava and Varma, 1964), and is the principal vector of *Rickettsia conorii*, the agent of Boutonneuse fever, in the countries around the Mediterranean littoral. *R. conorii* circulates in the natural environment between ticks and a wide spectrum of small and medium-sized mammals. Immature forms of *R. sanguineus* feed on rodents, hedgehogs and other small mammals, while adults parasitize larger animals, including dogs, wild carnivores, ungulates and man. Dogs may serve as reservoirs of the rickettsia (Arthur, 1962). Other rickettsial species have been isolated from *R. sanguineus*, including *Rickettsia massiliae* in France and Portugal, originally isolated and described from *Rhipicephalus turanicus* (Beati and Raoult, 1993), and a closely related strain was isolated in Greece (Babalis *et al.*, 1994). The role of *R. turanicus* as a human parasite is not clearly understood (Pegram *et al.*, 1989), but it was found infected with *Rickettsia massiliae* and a spotted group rickettsia (Mtu5) as reported by Beati *et al*. (1992).

Rhipicephalus bursa primarily parasitizes domestic and wild ungulates, but has been reported on humans in China, Yugoslavia, Bulgaria and Italy. It was found infected with the CCHF virus under natural conditions (Linthicum and Bailey, 1994). Other *Rhipicephalus* species occasionally collected from humans, or which lack relevant epidemiological data, are summarized in Table 10.

Discussion and conclusions

Tick-borne diseases of humans are a major public health concern. Notably, those of viral origin, characterized by encephalitis and hemorrhagic fevers, cause the highest morbidity and mortality. Lyme disease can be a debilitating disease if allowed to progress to the arthritic and neurologic stages, conditions that can be prevented by early diagnosis and appropriate treatment. Tick-borne rickettsioses (Rocky Mountain spotted fever, fievre boutonneuse, Omsk Hemorrhagic Fever and others) can develop serious infections when left untreated. Human ehrlichial diseases, which can occur simultaneously with protozoan infections (*Babesia* spp.), are gaining public health awareness. Several parasitological and epidemiological aspects of ticks involved in human parasitism remain poorly investigated.

Tick bites may also cause a severe allergic response, mediated by IgE specific for tick allergens (Gauci *et al*., 1989). Severe toxic reactions in man have been reported following the bites of *A. brumpti* and *O. moubata* (Sonenshine, 1993). One species that is widely feared because of the severe toxic reaction resulting from its bites is the pajaroello tick, *O. coriaceus*, in the western US and Mexico. In the Persian Gulf, visitors to islands serving as breeding sites of marine birds have developed intense pruritus and inflammation after being bitten by *O. muesebecki* (Hoogstraal, 1982).

Finally, acaricidal control of ixodid ticks is impractical because of their wide distribution in forested areas, whereas houses infested with soft ticks can be sprayed with acaricidal formulations. For further details see Rozendaal (1997). Consequently, personal protection methods, especially wearing of protective clothing and spraying with acaricides and the use of repellents, are advised to minimize contact with infected ticks. Attached ticks should be removed without delay. Considerable interest exists as to the correct way of removing an attached tick. Needham (1985) compared several methods of tick removal, including folk remedies such as vaseline, nail polish, alcohol and hot matches. He recommended grasping the tick as close as possible to the skin with blunt, curved forceps and pulling straight upward as the most effective method. Bowles et al. (1992) mentioned that the sharp tips of jeweller's forceps can puncture engorged ticks, increasing the risk of disease transmission. De Boer and Van den Bogaard (1993) reported that frequently advocated

Figure 2. Removal of a *Dermacentor marginatus* female tick by forceps from the leg of a man. (Photograph by A. Estrada-Peña)

chemical treatments (gasoline, nail polish, methylated spirit) failed to induce self-detachment of the tick within 30 minutes. Moreover, the success of the subsequent mechanical removal was not influenced by chemical treatment. The best way is to grasp the tick as close to the skin as possible with fine tweezers and pull firmly and steadily without twisting. This also depends on the length of the hypostome and the duration of attachment (before or after cement is formed around the hypostome). Finally, it is advisable to store removed ticks in ethanol to allow for taxonomic identification and, if needed, to PCR-amplify pathogen DNA from these ticks.

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